Topics in Biodiversity and Conservation

Indraneil Das
Andrew Alek Tuen *Editors*

Naturalists, Explorers and Field Scientists in South-East Asia and Australasia

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Preface

A century after the death of the naturalist and co-founder of the theory of evolution through natural selection, Alfred Russel Wallace continues to inspire. Indeed the relevance of Wallace for fields of study as disparate as ecology, systematics, evolution, ethnobiology, biodiversity, and conservation, has never been greater.

The Institute of Biodiversity and Environmental Conservation, within Universiti Malaysia Sarawak (UNIMAS), has been in the forefront of Wallace studies in Southeast Asia, through research and its application, in addition to the organisation of meetings of minds in the field of biodiversity. We organised, between 13 and 15 July 2005, an international conference entitled "Wallace in Sarawak – 150 years later" here in Kuching, Sarawak, which was attended by natural historians, biologists, and other scholars of Wallace studies. The proceedings of the same were published by the Institute in 2005. A second conference on the same broad theme, "Wallace 2013. 2nd International Conference on Alfred Russel Wallace – His Predecessors and Successors. Naturalists, Explorers and Field Scientists in Southeast Asia and Australasia" was also organised by our Institute on 7–8 November 2013. The present volume comprises selected papers presented at this most recent effort to honour Wallace and to remember his legacy, a century after his passing.

We have organised the papers into three broad themes: *Wallace and His Period* presents papers on the life and contributions of Wallace, and those of some of his contemporaries, from museum builders to evolutionary theorists. *Natural History and Systematics* gathers together papers as diverse as the contribution of systematics to understanding the zoological sciences, as well as autecological and community level studies. Finally, *Biodiversity and Conservation* brings together studies on biodiversity and conservation of the Wallace area, from trees to butterflies, frogs to birds and dolphins. It concludes with the all important paper that challenges the conventional views on economic growth, and how sustainable development and conservation need to be incorporated into the rapid economic development now taking place in the region where Alfred Russel Wallace spent his defining years.

We are grateful to a number of individuals and agencies for supporting the conference on which this volume is based: to the State Government of Sarawak for sponsoring the Conference, and to Tan Sri Datuk Patinggi Haji Adenan Satem, then

Minister of Special Functions, Sarawak, and currently, Chief Minister of Sarawak, for delivering the inaugural speech. Our partners, the Sarawak Forestry Corporation and the Sarawak Museum, including Oswald Braken Tisen and Charles Leh, formed the backbone of the organising committee. Within UNIMAS, we are grateful to the staff of the Institute of Biodiversity and Environmental Conservation, and our graduate students helped with all stages of organising the meeting and presenting papers. Individual manuscripts were reviewed by Aaron M. Bauer, C. Kenneth Dodd, Michael Flannery, Gathorne, Earl of Cranbrook, Ulmar Grafe, Stefan Hertwig, Robert F. Inger, Elena M. Panova, and Mustafa Abdul Rahman. Finally, we are thankful to David L. Hawksworth, for initiating the idea of this volume, and Nel van der Werf of Springer for seeing the volume through press.

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Part I
Wallace and His Period

Wallace and Incipient Structures: A World of 'More Recondite' Influences

Charles H. Smith

Abstract Alfred Russel Wallace is well-known for his co-discovery of the principle of natural selection. Natural selection is usually considered a process, but it is not clear that Wallace regarded it in exactly these terms. In fact he more likely thought of the relationships involved as representing what we would now term a "state space," a negative feedback loop wherein populations are maintained at healthy levels through elimination of the unfit. Both before and after the advent of natural selection, Wallace clung to the idea that "more recondite forces" were shaping the nature and direction of evolution; this is especially evident in his treatment of incipient structures, and continuing allusions to the probable existence of extenuating local influences on process. In this work, the history of these leanings is detailed, in the hope that Wallace's overall position on evolution may be better understood.

1 Introduction

In February of 1858, Alfred Russel Wallace, weak with fever, had a now-famous epiphany. Recalling his field experiences of the past several years and adding to them the logic of Malthus, he came up with a principle, natural selection, which seemed to explain how populations might indefinitely move away from "original types." Pleased with his thinking, he decided to write up the idea as an essay and send it to Charles Darwin, who he knew through earlier correspondence, was interested in the subject. But his real target was Charles Lyell, whose theories on biogeography he had just challenged in a paper published in late 1857 (Wallace 1857), and to whom Wallace was asking Darwin to relay the manuscript if he thought it worthy. Wallace now had a theory that backed his criticisms, and he must have been very eager to receive some feedback. Fate intervened, however, and Lyell never

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responded: instead the essay was read before the Linnean Society 2 weeks later and published immediately, without Wallace's permission.

Although initially Wallace was overjoyed to receive this attention from two of the world's top naturalists, as time wore on he seems to have become less pleased about this treatment. Although too polite to be outwardly derogatory, he nevertheless drew attention no fewer than five times over the next 40-odd years, in print, to how he had never been given the option of going over proofs before the essay was published. Was there something more – or less – that he had wanted to say? Had he been prematurely cut off, and then unfairly cast as a "Darwinist," as opposed to just an "evolutionist"?

The ramifications of this question will never be thoughtfully explored if we continue to pay most of our attention to the Ternate essay in terms of sensationalist accusations of intellectual theft on the part of Darwin. Frankly, of what importance is this matter to Wallace studies? Does it help us better understand Wallace's intellectual path to that point? I think not.

In this paper, I will examine some threads of that journey that I feel go a long way toward explaining Wallace's words in the Ternate essay, and many of his subsequent directions. Let us begin by noting that Wallace himself regarded his principle not as a theory, but as a law (see Wallace 1870a: 302, and many other such referrals); accordingly, in Wallace's eyes natural selection was not so much the "survival of the fittest" as it was the "elimination of the unfit." Lest there be any doubt on this score, note the following Wallace words, three from published articles of his:

> Natural selection . . . does not so much select special variations as exterminate the most unfavourable ones (from an 1866 letter to Darwin printed in Marchant 1916).
>
> The survival of the fittest is really the extinction of the unfit. In nature this occurs perpetually on an enormous scale, because, owing to the rapid increase of most organisms, the unfit which are yearly destroyed form a large proportion of those that are born (Wallace 1890: 337)
>
> The survival of the fittest is really the extinction of the unfit . . . (Anonymous 1893: 3)
>
> It is undoubtedly this survival, by extermination of the unfit, combined with universally present variation, which brings about that marvellous *adaptation to the ever-varying environment* . . . (Wallace 1908a: 424)
>
> The survival of the fittest is really the extinction of the unfit . . . (Wallace 1913: 152)

Wallace's view of the matter is also evident in famous words he included in the Ternate essay itself:

> . . . The action of this principle is exactly like that of the centrifugal governor of the steam engine, which checks and corrects any irregularities almost before they become evident; and in like manner no unbalanced deficiency in the animal kingdom can ever reach any conspicuous magnitude, because it would make itself felt at the very first step, by rendering existence difficult and extinction almost sure soon to follow (Wallace 1858: 62).

In 1972 the anthropologist Gregory Bateson made a related observation:

> . . . The steam engine with a governor is simply a circular train of causal events, with somewhere a link in that chain such that the more of something, the less of the next thing in the circuit . . . If causal chains with that general characteristic are provided with energy, the result will be . . . a self-corrective system. Wallace, in fact, proposed the first cybernetic model . . . Basically these systems are always *conservative* . . . in such systems changes occur to conserve the truth of some descriptive statement, some component of the *status quo*. Wallace saw the matter correctly, and natural selection acts primarily to keep the species unvarying . . . (Bateson 1972: 435)

If Bateson is correct in this assessment (and I believe he is), Wallace's "negative feedback loop" view of the way natural selection operates must be connected to a complementary positive feedback process that pushes systems away from stability and incrementally toward higher levels of order (and probably, at some times, lower levels). I have argued elsewhere (Smith 1986) that this process is geographically nonrandom range change connected with the integration of populations into community structures, as influenced by varying-efficiency biogeochemical and hydroclimatological cycling processes inherent in the surrounding environment. I doubt that Wallace had any of these details worked out, but it is evident in his later writings that he felt that, somehow, the results that natural selection produced were relatable to causes found in characteristics of the environment, as broadly defined (i.e., including its biotic elements).

From what source did Wallace pick up this kind of thinking? Certainly not from any of the usual suspects: Charles Lyell, Robert Chambers (author of *Vestiges of the Natural History of Creation*), Thomas Malthus, or even Darwin. Lyell's uniformitarian views helped steer Wallace away from creationist, Lamarckian, and catastrophist thoughts, but Lyell was a geologist primarily interested in historical records, not ecological interactions leading to biological transformations. Malthus certainly provided some of the demographic pieces, but his writings were rather remote from any considerations of the natural environment. Who, then?

The answer is: Alexander von Humboldt.

2 Wallace and Alexander von Humboldt

Humboldt (1769–1859) was the most famous scientist of his time, and perhaps the most influential one as well. His method, "Humboldtian science," is succinctly described at the head of a *Wikipedia* entry:

> Humboldtian science incorporates many ideals and concepts, though it roughly encapsulates a shift toward an understanding of the interconnectedness of nature through accurate measurement. One central concept was what Humboldt called "terrestrial physics," which encompassed an extensive and pervasive study of the earth's many features and forces with accurate scientific instrumentation. Humboldtian science is founded on a principle of "general equilibrium of forces." General equilibrium was the idea that there are infinite forces in nature that are in constant conflict, yet all forces balance each other out.

It has been appreciated for many years that Humboldt was a major influence on Wallace's decision to become a traveling naturalist, especially as a result of Humboldt's *Personal Narrative of Travels*, dedicated to his expedition to South America, 1799–1804 (von Humboldt and Bonpland 1814). Wallace apparently became aware of this work (and possibly others of his such as *Aspects of Nature*) in the early 1840s. But he also became aware of another, Humboldt's crowning achievement, *Cosmos*, as its first volumes came off the press in the mid-1840s. Whereas *Personal Narrative* stuck more to the details of Humboldt's trip, *Cosmos* included a good deal on Humboldt's philosophy of nature, including remarks on the abovementioned "interconnectedness of nature" and "general equilibrium of forces." In a 28 December 1845 letter to Bates, Wallace wrote: "As a further support to the 'Vestiges' I have heard that 'Cosmos' the celebrated work by the venerable Humboldt supports in almost every particular its theories not excepting those relating to Animal and Vegetable life – This work I have a great desire to read" (Wallace 1845). That he did read it is supported by several lines of evidence (Smith 2013), probably before he left for the Amazon in 1848, and likely no later than during his first months in the Malay Archipelago.

On opening Volume 1 of *Cosmos*, Wallace would have noted a good number of passages in its Introduction alone that would influence him for the rest of his life. For example, in a writing on spiritualism in 1871, he quotes from it, how "a presumptuous skepticism, which rejects facts without examination of their truth, is, in some respects, more injurious than an unquestioning incredulity" (Wallace 1871: 30). He featured this same basic admonition some 10 years earlier in a famous 1861 letter from the field on religious belief to his brother-in-law (Marchant 1916: 65–67), and other instances of the same thinking are sprinkled throughout Wallace's literary career.

A few more passages from the Introduction to *Cosmos* may be considered:

General views lead us habitually to regard each organic form as a definite part of the entire creation, and to recognise, in the particular plant or animal, not an isolated species, but a form linked in the chain of being to other forms living or extinct. They assist us in comprehending the relations, which exist between the most recent discoveries, and those which have prepared the way for them (Humboldt 1846: 23). These sympathies re-emerge in the celebrated closing passage on biodiversity in Wallace's "The Physical Geography of the Malay Archipelago" (1863).

> Who will venture to affirm, that we yet know with precision that part of the atmosphere which is not oxygen, or that thousands of gaseous substances affecting our organs may not be mixed with the nitrogen? or who will say that we already know even the whole number of the forces which pervade the universe? (*ibid.*, p. 32: This previews Wallace's continuing allusion to "more recondite forces.")
>
> . . . those who are able to escape occasionally from the restricted circle of the ordinary duties of civil life, and regret to find that they have so long remained strangers to nature, may thus have opened to them access to one of the noblest enjoyments which the activity of the rational faculties can afford to man. The study of general natural knowledge awakens in us as it were new perceptions which had long lain dormant (*ibid.*, pp. 35–36: Wallace's two earliest known writings, *circa* 1841–1843, dwell on this very idea).
>
> . . . the final aim of physical geography is to recognise unity in the vast variety of phenomena, and by the exercise of thought and the combination of observations, to discern that which is constant through apparent change. In the exposition of the terrestrial portion of the Cosmos, we may sometimes find occasion to descend to very special facts, but it will only be for the purpose of recalling the connection existing between the laws of the actual distribution of organic beings over the surface of the globe, and the laws of the ideal classification by natural families, analogy of internal organisation, and progressive evolution (*ibid.*, p. 48).

It is not surprising to find that Wallace cites Humboldt 19 times (in five works) in his pre-1857 writings (and Lyell only twice). Nevertheless, Wallace was probably a bit disappointed on reading *Cosmos* to find that Humboldt was not a transmutationist. He would be left to find his own way in that direction.

Humboldt’s influence on Wallace extended beyond direct connections. At least three of Humboldt’s staunchest followers also had demonstrable impact on him: Lyell, Franz J. F. Meyen, and Justus von Liebig. Lyell’s allegiance to Humboldt’s method is evidenced by the several dozen mentions he makes of Humboldt in his most famous works, and Lyell’s own attention to detail and measurement. Meyen and Liebig were outright protégés of Humboldt. Meyen (1846) refers to Humboldt some 75 times in his important 1846 book *Outlines of the Geography of Plants*. Liebig, famous among other contributions for his development of the limiting factor concept, dedicated his most influential work, *Organic Chemistry in Its Application to Agriculture and Physiology*, from 1840, to him (Liebig 1840). All three provided Wallace with ideas that undoubtedly influenced his thought during his Amazonian and Indonesian travels (Smith 2013).

Humboldtian science’s effect on Wallace’s thinking was a two-edged sword. While helping him evade dead ends such as catastrophism, creationism, and Lamarckism, it also moved him away from a useful understanding of the role of adaptation in evolution. Refusing to accept any connection between characters and specially created functions, for many years, right through to the Ternate essay, Wallace treated adaptations as secondary features that while somehow “correlated” with evolutionary advance had no causal role in the process. This is evident from lines in an article on the natural history of the orangutan he published in 1856:

> Do you mean to assert, then, some of my readers will indignantly ask, that this animal, or any animal, is provided with organs which are of no use to it? Yes, we reply, we do mean to assert that many animals are provided with organs and appendages which serve no material or physical purpose. The extraordinary excrescences of many insects, the fantastic and many-coloured plumes which adorn certain birds, the excessively developed horns in some of the antelopes, the colours and infinitely modified forms of many flower-petals, are all cases, for an explanation of which we must look to some general principle far more recondite than a simple relation to the necessities of the individual. We conceive it to be a most erroneous, a most contracted view of the organic world, to believe that every part of an animal or of a plant exists solely for some material and physical use to the individual, – to believe that all the beauty, all the infinite combinations and changes of form and structure should have the sole purpose and end of enabling each animal to support its existence, – to believe, in fact, that we know the one sole end and purpose of every modification that exists in organic beings, and to refuse to recognize the possibility of there being any other (Wallace 1856: 30).

Meanwhile, however, he was taking to heart other elements of the program inherited from Humboldt, Lyell, Meyen, and Liebig. He kept careful records of – everything – whether geographical distribution data, or catches for the day, or measurements of physical characteristics of the environment, or the vocabularies of the peoples he encountered. He was also embracing the philosophy; the last quotation given above alone contains multiple nods to Humboldtian thinking. A close examination of all of Wallace’s writings through 1857 will doubtlessly turn up many more. As early as 1852 he had written:

> On this accurate determination of an animal’s range many interesting questions depend. Are very closely allied species ever separated by a wide interval of country? What physical features determine the boundaries of species and of genera? Do the isothermal lines ever

> accurately bound the range of species, or are they altogether independent of them? What are the circumstances which render certain rivers and certain mountain ranges the limits of numerous species, while others are not? None of these questions can be satisfactorily answered till we have the range of numerous species accurately determined (Wallace 1852: 110–111).

Attention to measurement, as in all good Humboldtian science, is the central theme in this passage – and, it should not be ignored, Humboldt was the inventor of the isothermal line concept mentioned in it.

Eventually, of course, with the aid of Malthus and a creative approach to the concept of variation, Wallace was able to get past his hang-up over adaptations. Simply, and because of variation, characters could change in *whatever* way that might accrue competitive advantage. It should be noted, however, that Wallace's new appreciation of the function of adaptations in no way reduced his feeling that "the environment" was holding final causes to which the "elimination of the unfit" was still somehow subservient. The evidence for this comes in three forms: Wallace's interest in incipient structures, his continuing allegiance to the influence of "local causes," and his ongoing nod to "more recondite" forces and the Humboldt-related idea (earlier quoted) that a theory shouldn't be expected to explain everything.

3 Incipient Structures

In Wallace's time character variation was a commonly witnessed phenomenon, but just about nothing was known about the *origins* of that variation. Did a character come into being spontaneously, only to change over time in response to yet unknown forces? Wallace apparently thought so; at the least this model shielded him from thoughts of creationism or catastrophism. But as the years passed the "unknown forces" did not reveal themselves. This did not stop Wallace from continuing to theorize that particular characters of individual species suggested the influence of a "great natural law" in operation. For example, there were instances of what he termed "rudimentary organs," incipient structures on their way to recapitulating the plan of nature. In the Sarawak law essay he writes:

> Another important series of facts quite in accordance with, and even necessary deductions from, the law now developed, are those of *rudimentary organs*. That these really do exist, and in most cases have no special function in the animal œconomy, is admitted by the first authorities in comparative anatomy. The minute limbs hidden beneath the skin in many of the snake-like lizards, the anal hooks of the boa constrictor, the complete series of jointed finger-bones in the paddle of the Manatus and whale, are a few of the most familiar instances. In botany a similar class of facts has been long recognized . . . To every thoughtful naturalist the question must arise, What are these for? What have they to do with the great laws of creation? . . . If each species has been created independently, and without any necessary relations with pre-existing species, what do these rudiments, these apparent imperfections mean? There must be a cause for them; they must be the necessary results of some great natural law. Now, if, as it has been endeavoured to be shown, the great law which has regulated the peopling of the earth with animal and vegetable life is, that every change shall be gradual; that no new creature shall be formed widely differing from

> anything before existing; that in this, as in everything else in Nature, there shall be gradation and harmony, – then these rudimentary organs are necessary, and are an essential part of the system of Nature. Ere the higher Vertebrata were formed, for instance, many steps were required, and many organs had to undergo modifications from the rudimental condition in which only they had as yet existed. We still see remaining an antitypal sketch of a wing adapted for flight in the scaly flapper of the penguin, and limbs first concealed beneath the skin, and then weakly protruding from it, were the necessary gradations before others should be formed fully adapted for locomotion . . . (Wallace 1855: 195–196)

Obviously, Wallace felt that such characters anticipated future changes to be implemented on the basis of some “great law”; we now know most of them to be, evolutionarily speaking, remnant structures. Before long Wallace would adopt this correct view, but this did not stop him from continuing to look favorably on the “incipient structure” notion. In general, Wallace applied the term “incipient” to various immediately anticipatory events, for example the evolution of migration systems, morphological degeneration trends, the separation of varieties through the infertility of intercrossings, and the occasional appearance of a sport (e.g. specimens of fowls with horns). But he also continued to accept a “great law” approach to evolution in general, as summarized by DelMonte (2011):

> Wallace noted the problem of incipient evolutionary stages. He argued that incipient and intermediate stages might have little selective survival advantage, as with a partially developed wing; yet evolution progressed to new forms and greater complexity as if teleologically guided. Wallace thus predicted the problem of “irreducible complexity.” A group composed of Paleo-anthropologists and Linguists similarly argued that the physical and cognitive articulations required for human speech are so sophisticated that it is difficult to imagine intermediary systems. They described as a Neo-Darwinian tautology the argument that if a human feature existed, then it must be adaptive, otherwise it would not have survived. This is a form of Panglossian, overly-optimistic, post-hoc reasoning . . .

Wallace’s most remarkable views on incipient characters are connected to his thoughts on human evolution, and most particularly to the evolution of higher consciousness. In several writings he describes powers that “are so much in advance of their [i.e., savages] needs that they could not have been evolved by natural selection” (Wallace 1879:478). This is not a matter we can explore in great depth here, but it is important to understand that Wallace felt:

> The rapid progress of civilization under favourable conditions, would not be possible, were not the organ of the mind of man prepared in advance, fully developed as regards size, structure, and proportions, and only needing a few generations of use and habit to co-ordinate its complex functions. The naked and sensitive skin, by necessitating clothing and houses, would lead to the more rapid development of man’s inventive and constructive faculties; and, by leading to a more refined feeling of personal modesty, may have influenced, to a considerable extent, his moral nature. The erect form of man, by freeing the hands from all locomotive uses, has been necessary for his intellectual advancement; and the extreme perfection of his hands, has alone rendered possible that excellence in all the arts of civilization which raises him so far above the savage, and is perhaps but the forerunner of a higher intellectual and moral advancement. The perfection of his vocal organs has first led to the formation of articulate speech, and then to the development of those exquisitely toned sounds, which are only appreciated by the higher races, and which are probably destined for more elevated uses and more refined enjoyment, in a higher condition than we have yet attained to. So, those faculties which enable us to transcend time and

> space, and to realize the wonderful conceptions of mathematics and philosophy, or which give us an intense yearning for abstract truth (all of which were occasionally manifested at such an early period of human history as to be far in advance of any of the few practical applications which have since grown out if them), are evidently essential to the perfect development of man as a spiritual being, but are utterly inconceivable as having been produced through the action of a law which looks only, and can look only, to the immediate material welfare of the individual or the race (Wallace 1870a: 358–360).

This became his explanation for the occasional emergence of mediumistic and other paranormal powers, which he viewed to be incipient abilities – that is, abilities that would become more common in the future as evolution's destiny played out.

4 More Recondite Forces

Two oft-expressed themes in Wallace's literary output are the closely related ideas that (1) a theory should not have to explain everything, and (2) there are always "more recondite" forces at work in nature. These philosophical points also seem indebted to Humboldt, as one of the earlier-quoted passages from *Cosmos* shows. Wallace used the "doesn't explain everything" caveat at least a dozen times in his writings, including this one from 1867:

> It is, therefore, no objection to a theory that it does not explain everything, but rather the contrary. A true theory will certainly enable us to understand many of the phenomena of life, but owing to our necessarily imperfect knowledge of past causes and events, there must always remain complicated knots that we cannot disentangle, and dark mysteries on which we can throw but a straggling ray of light (Wallace 1867a: 309).

Wallace found this idea useful in various contexts at various times, for example, in a defense of Darwinian logic (Wallace 1864:111), a discussion of the limits of applicability of natural selection (Wallace 1870a: 333), another such discussion (Wallace 1870b: 9), a defense of spiritualism (Wallace 1885a: 328), and a denial of the all-applicableness of the theory of evolution (Wallace 1908b: 1–2). The passage quoted above concerned a biogeographical matter.

A similar catholicity is to be found in his use of the term "recondite." This has two basic meanings according to the *OED*: a structure or habit removed or hidden from view (now rare), or, removed from ordinary apprehension, understanding, or knowledge. Wallace seems not to have applied the word in its now rare sense (though that usage often involved biological structures or habits). Of his 15 or so uses of the term, the four given below are typical:

This great principle [natural selection] gives us a clue which we can follow out in the study of many recondite phenomena, and leads us to seek a meaning and a purpose of some definite character in minutiæ which we should be otherwise almost sure to pass over as insignificant or unimportant (Wallace 1867b: 3).

> The flood of light that has been thrown on the obscurest and most recondite of the forces and forms of Nature by the researches of the last few years, has led many acute and speculative intellects to believe that the time has arrived when the hitherto insoluble problems of

> the origin of life and of mind may receive a possible and intelligible, if not a demonstrable, solution (Wallace 1869a: 105).
>
> . . . they [philosophers and men of science] have yet, for many years, refused to accept any facts or experiments which go to prove the existence of recondite powers in the human mind, or the action of minds not in a visible body (Wallace 1871: 29).
>
> Equally absurd is the allegation that some of the phenomena of Spiritualism "contradict the laws of nature," since there is no law of nature yet known to us but may be apparently contravened by the action of more recondite laws or forces (Wallace 1885b: 809).

It is apparent from both these samples and the ones given earlier that Wallace's opinion on the existence of "more recondite forces" changed very little over his career. A further indication of this is offered by his continuing allusion to possible extenuating circumstances related to "local causes."

5 Local Causes

Although Wallace immediately recognized the potential in the natural selection concept to explain a wide range of phenomena, he was not sure early on just how far it could be extended. As a result, when he was unable to come up with an explanation for a particular detail of adaptation, he fell into the habit of alluding to possible "unknown local causes" as being responsible. Interestingly, there is none of this in his writings before the advent of natural selection, and one cannot help but suspect that afterward he was "leaving the door open" for the development of further theory.

His earliest writings on this subject appeared in the famous monograph on Papilionidae, first delivered as a presentation before the Linnean Society in 1864. In this he reports:

> But even the conjectural explanation now given fails us in the other cases of local modification. Why the species of the western islands should be smaller than those further east, – why those of Amboyna should exceed in size those of Gilolo and New Guinea – why the tailed species of India should begin to lose that appendage in the islands, and retain no trace of it on the borders of the Pacific, are questions which we cannot at present attempt to answer. That they depend, however, on some general principle is certain, because analogous facts have been observed in other parts of the world (Wallace 1865: 19).

In 1869, in *The Malay Archipelago* he writes:

> Many groups of insects appear to be especially subject to local influences, their forms and colors changing with each change of conditions, or even with a change of locality where the conditions seem almost identical (Wallace 1869b: 284).

In 1876, in the first half of his lecture given as President of the Biology Section of the British Association for the Advancement of Science meeting, devoted entirely to the subject, he writes:

> I have argued, and still believe, that the need of protection is a far more efficient cause of variation of colour than is generally suspected; but there are evidently other causes at work, and one of these seems to be an influence depending strictly on locality, whose nature we

> cannot yet understand, but whose effects are everywhere to be seen when carefully searched for (Wallace 1876: 101–102).

The next year (1877), he observed:

> Another real, though as yet inexplicable cause of diversity of colour, is to be found in the influence of locality. It is observed that species of totally distinct groups are coloured alike in one district, while in another district the allied species all undergo the same change of colour . . . The most probable cause for these simultaneous variations would seem to be the presence of peculiar elements or chemical compounds in the soil, the water, or the atmosphere, or of special organic substances in the vegetation; and a wide field is thus offered for chemical investigation in connection with this interesting subject (Wallace 1877: 407).

A few years later, however, Wallace came upon a new theory of mimicry developed by the naturalist Fritz Müller (Wallace 1882), which quickly wiped away many of his remaining reservations about the ability of natural selection to explain certain details of adaptation. From this point onward he would have little to say about "unknown local causes."

6 Conclusion

In reviewing the general path that Wallace took to natural selection and beyond, one sees significant evidence of a Humboldtian influence. This gave him a strong initial philosophical position that could be linked to applied studies in the field, but it also caused him to misinterpret the relation of adaptations to evolutionary change for more than 10 years. And, even once he had come up with a more apt interpretation, he remained attached to the idea that environment might be secondarily influencing evolution in ways extending beyond natural selection. His very interest in biogeography, the most complex of all the sciences, attests to this, as do his positions on more restricted subjects. Take, for example, his greater attention than Darwin's to "environmental selection" forces such as temperature and precipitation, his theory that bird coloration was largely related to selection for drabness of females as a protective mechanism, and his attention to special protective coloration relationships, including mimicry (in which instance the mimicked species is, effectively, an element of the environment). So too, his attention to glacial theory, and even his late-career arguments as to what possibly could live where in the universe.

Another effect of the "more recondite forces" notion inherited from Humboldt was Wallace's continuing reluctance to observe a strict form of materialism, both before and after the Ternate essay. There is not a shred of evidence that as of 1858 Wallace felt that natural selection could explain the existence of humankind's "higher" mental faculties (Smith 2008), and one suspects that beyond the ethnological observations that helped lead him to his actual opinion, the "more recondite forces" stance was also a contributing influence. His adoption of spiritualism in 1866 was thus a function of these predispositions, and not the cause of them.

The Humboldt-Wallace relationship is one that deserves much more attention than it has so far received. That it has not is a function of simple oversight, the assumption that the main Humboldtian influence was of a "traveling naturalist inspiration" sort, and the only sporadic references Wallace made to Humboldt later in life. The last of these three reasons may trouble some observers, but it must be remembered that Humboldtian science was a philosophy and method, not a specific theory. Thus Wallace's direct references to Humboldt typically concerned facts the older naturalist collected, and not interpretations of process.

For Wallace, it can be seen, "incipience" was an ongoing "working hypothesis" about the nature of nature. He never was able to construct an appropriate model of final causes – that is to say, one from which actual science could emerge – but, after Humboldt, he remained unsure that all of the answers were already at hand.

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Alfred Russel Wallace and His Collections in the Malay Archipelago, with a Proposal for International Cooperation to Produce a Digital Catalogue

Earl of Cranbrook and Darren J. Mann

Abstract During 8 years (1854–1862) spent in the Malay Archipelago, Alfred Russel Wallace's main object was to acquire specimens of 'natural history' for his personal collections and for sale to museums and amateur enthusiasts. His final list amounted to 310 specimens of mammals, 8050 birds, 100 reptiles (a group in which he included amphibians), 7500 molluscan shells, 13,100 Lepidoptera, 83,200 Coleoptera and 13,400 other insects, totalling 125,660 "specimens of natural history". His field records of these collections held by the libraries of the Natural History Museum and the Linnean Society of London have been digitised and are available on line, as is his *Journal*, a chronological record of his travels from Bali to Buru. As an alternative archive of Wallace's achievement, this paper focuses on the origin and later history of his specimens, their impact on the scientific and naturalist community and their permanent significance in zoological nomenclature. His collecting practices and field skills are examined, along with the contribution of his assistants. His London agent Samuel Stevens played an important role in publicising Wallace's achievements during his travels and, as his specimens arrived, in disposing of duplicates to wealthy buyers, while retaining the best for his personal collection. Many new scientific names were described in lists and catalogs by authors Including, in some instances, Wallace himself. Records are traced to confirm the present whereabouts of specimens that can be located and authenticated. These specimens are still valuable for regional and national policy-making in matters such as nature conservation and species protection, and useful for practical applications, e.g. in integrated pest management. A bold initiative is proposed to make this resource widely available where it is needed by providing digitised images

The main object of all my journeys was to obtain specimens of natural history, both for my private collections and to supply duplicates to museums and amateurs (Wallace 1869, Preface).

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of these specimens and making these available on the web. It is suggested that the Sarawak State government, in co-operation with the Natural History Museum, London, and Oxford University Museum, could take a lead, perhaps through ASEAN scientific cooperation. An exercise to compile and disseminate a comprehensive digitised catalog of Wallace's Archipelago collections, with emphasis on the irreplaceable type specimens, would be a fitting centennial memorial for his indefatigable enterprise. It would also provide an invaluable asset for regional biologists, zoogeographers, conservationists and wildlife managers.

1 Introduction

Reflecting on his career in old age, Alfred Russel Wallace (henceforth ARW) claimed that the years[1] spent in the Malay Archipelago "constituted the central and controlling incident of my life" (Wallace 1905, 1: 336). During his travels he maintained an active correspondence[2] with his agent, Samuel Stevens, his family, friends and professional colleagues and acquaintances, including Charles Darwin (Berra 2013).[3] He also sent an impressive number of works for publication: progress reports on his collections (Wallace 1855a, c, 1856a, b, 1858), descriptions of new species (Wallace 1855b, 1860a), his developing ideas on classification and zoogeography (Wallace 1856c, 1859, 1860b) and, of course, his influential papers on the moot topic of the origin of species (Wallace 1855d; Darwin and Wallace 1858). Although his letters and publications were important for communicating his thoughts and emerging theories during his travels (Fagan 2008; Cranbrook 2013), writing was subsidiary to ARW's chief objective which was the accumulation of a rich and varied collection of natural history specimens as a means of securing his livelihood. By his own account, his collections in the Archipelago ultimately amounted to 310 specimens of mammals, 8,050 birds, 100 reptiles (a group in which he included amphibians), 7,500 molluscan shells, 13,100 Lepidoptera, 83,200 Coleoptera and 13,400 other insects, totalling 125,660 "specimens of natural history" (Wallace 1869: Preface).

From the start of his travels, in Singapore in April 1854, ARW kept field records of his collections in small notebooks. Two of these, generally known as the *Species Registry*, are now in the Natural History Museum, London.[4] The Linnean Society of London holds four further notebooks of similar size and appearance, three of which contain mainly lists and descriptions of species and specimens. The fourth, which has been described as the *Species Notebook* (McKinney 1972), is filled with a mix of short jottings, passages from his readings, field observations and reflections on

[1] From arrival at Singapore on 18th April 1854 to final departure on 8th February 1862.

[2] Available online through the NHM Wallace Correspondence Project, http://www.nhm.ac.uk/research-curation/scientific-resources/collections/library-collections/wallace-letters-online/database.html

[3] See also http://wallace-online.org

[4] Z MSS 89, O WAL.

biological topics including zoogeography and the origin of species. This notebook has been reproduced in facsimile, with annotations, by Costa (2013). The Linnean also holds four slightly larger volumes of a *Journal*.[5] The *Journal* does not cover the entire period of ARW's travels in the Archipelago but starts, after some miscellaneous notes, with his arrival at Bileling on the north coast of Bali on 13th June 1856 and closes, on a torn last page of the fourth notebook, on leaving the village of Kayeli, Buru, 19th May 1861. The main text consists of sequentially numbered entries, varying in length from a single paragraph to several pages, covering his travels and collections – often written in retrospect. The whole was transcribed by Pearson (2005) and images of the original are now available on line.[6] Unlike the narrative in *The Malay Archipelago* (Wallace 1869, henceforth *MA*), this *Journal* is a chronological record of ARW's travels.[7] It later provided source material for narrative passages of *MA*. Apart from the first volume, its pages have been cancelled by oblique lines, presumably as they were transcribed. The *Journal* is a contemporary record of what he did, when, where and with whom. For this reason, it is cited as primary source material in the following pages.

Given the wealth of biographical literature treating his life, his writings, his character and opinions (including George 1979; McKinney 1972; Clements 1983; Wilson 2000; Raby 2001; Shermer 2002; Slotten 2004; Smith 2004; Smith and Beccaloni 2008; van Wyhe 2013), ARW's specimens provide an alternative material legacy of enduring value. In his time, mid-nineteenth century, ARW's collections had a marked impact on the scientific and naturalist community, among whom there was intense curiosity about the diversity of animal life in those parts of the world newly reached by exploration, trade and expanding colonial rule, particularly the tropics. Many of his specimens were described as types of species new to science (including syntypes and holotypes), giving them permanent significance in zoological nomenclature. In the following pages, an account is given on ARW's practices in acquiring his varied collections, their reception in Britain and, as far as can be ascertained, the present location of surviving specimens.

The richness and variety of ARW's natural history collections from the Malay Archipelago reflected multiple factors. One was the efficiency of his preparations and effectiveness of his equipment for collecting, preserving and identifying target groups of animals. Paramount was his personal field skills and dedication as a naturalist-collector, and his delight in the richness of animal life – especially when dead in his hands! A moderating influence (because he needed sales, to cover current expenses and to provide future income) was his perception of the market value

[5] Linn Soc library ms 178a,b,c,d, referred to as the *Malay Archipelago Journal*.

[6] Linnean-online.org. Wallace notebooks. 54017–54020. Where there are spelling changes, cross references were provided by Pearson (2005).

[7] Wallace (1869: Preface): "I visited some islands two or three times at distant intervals, and in some cases had to make the same voyage four times over. A chronological arrangement would have puzzled my readers. They would never have known where they were; and my frequent references to the groups of islands classed in accordance with the peculiarities of the animal productions and of their human inhabitants, would have been hardly intelligible." His itinerary has been summarised by Collar and Prys-Jones (2013).

of different organisms. Very relevant were the abilities of assistants, on whom he came to rely to a considerable extent (Cranbrook and Marshall 2014). A decisive key to the success of his enterprise lay in the promotional and marketing proficiency of Samuel Stevens, who handled the specimens once they reached London. These are the first subjects covered below. This section is followed by an overview of the subsequent dispersal of his collections, the published lists and catalogs by authors Including, in some instances, ARW himself, with a preliminary account of the present whereabouts of specimens that can be located and authenticated. There is emphasis on Sarawak, as the first island destination that ARW visited, and the location where he spent a longer time and made collections as remarkable as at any other place in the Archipelago.

ARW's spelling of places and personal names is generally followed, but has occasionally been changed to modern usage. For brevity, the following abbreviations are used: ARW = Alfred Russel Wallace himself; *MA* = *The Malay archipelago* (Wallace 1869); *Journal* = Linnean Society library MS178a, b, c, d; BM= the British Museum, which later moved from Bloomsbury to South Kensington and became the British Museum (Natural History), and is now the Natural History Museum.

2 Wallace, the Collector

2.1 Preparations

In 1852, having salvaged what he could of four exacting years in Amazonia and the Rio Negro as a naturalist-collector, ARW retained his "earnest desire to visit a tropical country, to behold the luxuriance of animal and vegetable life… and to see with my own eyes all those wonders" (Wallace 1853: Preface). After balancing alternative options, he resolved to make his second venture into the under-collected tropical region of island South-east Asia. Two events may have aroused a special interest in Borneo. First, in an exchange of correspondence in April 1853, Rajah James Brooke wrote that he would be glad to see ARW in Sarawak.[8] Second, on a trip to the west country, ARW met L.L. Dillwyn who was in correspondence with James Motley, a civil engineer stationed on Labuan Island, 1851–1854, with whom he produced a joint publication on the natural history of Labuan and the adjacent Borneo mainland (Motley and Dillwyn 1855; Laverty 2013).[9]

Thirty years old and an experienced traveller, ARW made preparations for the expedition. He invested in reference books: Doubleday and Westwood (1846–1852) and Boisduval (1836) to identify butterflies (George 1979), and Prince Lucien

[8] British Library, Add. MS 46411.

[9] Dillwyn and Motley cooperated in the production of the planned first (but in the event, sole) number. In 1854, Motley moved to Banjarmasin (from where he sent bird skins to Wallace), but here he was murdered, with his family, in 1860 during an event generally called the "Malay insurrection".

Bonaparte's *Conspectus Generum Avium* (Bonaparte 1850, 1857) for birds. The last, he later described as "a large octavo volume of 800 pages, containing a well-arranged catalogue of all the known species of birds up to 1850, with references to descriptions and figures, and the native country and distribution of each species". With the first volume to hand while examining the collections in the BM, he added marginal notes on the distinguishing characters of birds expected in the Malay Archipelago. As a result, he later claimed: "during my whole eight years' collecting in the East, I could almost always identify every bird already described, and if I could not do so, was pretty sure that it was a new or undescribed species" (Wallace 1905: 327).[10]

He ordered labels for his specimens. For pinned insects, he obtained small, blank round discs. When used, the locality was written on individual labels, generally in abbreviated form: e.g. **SAR** for Sarawak (Baker 1995: 173, Table 2). Much later, he recalled that, "The small round locality labels I put on all my insects which were pinned, and either I or my assistant Charles Allen[11] wrote them. I enclose you a list of them as near as I can remember. All were collected by myself except those from Mysol, Salwatty, and a few from Flores, where C Allen went alone, but I selected the series and labelled them where required myself, so that for the whole of my collections, if they have not been changed, I am sure of the Locality tickets being right. Any other labels than the small round ones are not mine, unless perhaps in some very rare cases".[12]

For birds and other vertebrates, he ordered rectangular parchment tags preprinted with the heading ***Collected by A. R. Wallace 185***, leaving the last digit of the year to be added in due course. As his stay in the Archipelago extended beyond the decade, he obtained a second version, ***Collected by A. R. Wallace 186*** and an alternative, ***Collected for A. R. Wallace 186*** (Cranbrook et al. 2005). Any of these distinctive labels attached to a specimen, invertebrate or vertebrate, confirms its authenticity, but not necessarily that ARW was himself the collector. For instance, among 19 Dusky friarbirds *Philemon fuscicapillus* collected on Morty Island (Morotai) by Charles Allen (see below), the pre-printed labels still attached to ten include both versions, *Collected by … 186* and *Collected for … 186*, all completed by hand by ARW (Besson 2012).

To defray the cost of travel to the East, ARW sought help from the president of the Royal Geographical Society,[13] Sir Roderick Murchison, who ultimately obtained passages for ARW and Charles Allen by the P & O 'overland' route. This involved

[10] After ARW's death, this book was acquired from the sale of his library by Thomas Henry Riches who presented it, with the later index by Finsch (1865), to the Linnean Society, In its present state the book consists of both volumes, bound in brown buckram, with the title on the spine in gold lettering, simply CONSPECTUS/GENERUM AVIUM/BONAPARTE. It was repaired and rebacked in November 2008. Linnean library shelf mark 598.c BON.

[11] Charles Martin Allen, was "a London boy, the son of a carpenter who had done a little work for my sister, and whose parents were willing for him to go with me and learn to be a collector" (Wallace 1905 i:340). ARW thought Charles was an under-sized 16-year-old, but in fact he was born June 1839–thus only 14 at the time (van Wyhe 2013: 41).

[12] ARW, Letter to Poulton March 15th 1896 (Oxford University Museum archive).

[13] ARW was elected a Fellow of the Royal Geographical Society in February 1854.

sailing to Alexandria, onward by boat to Cairo, then in four-horsed, two-wheeled 'omnibuses' with six passengers each, for the desert road to Suez. Here they re-embarked via Aden to Galle (Sri Lanka), where they transhipped again to another P & O paddle steamer for the final stage to Singapore (van Wyhe 2013). Here ARW found accommodation in the French Jesuit Mission[14] and also met Rajah Sir James Brooke, currently in Singapore, who repeated his offer of hospitality in Sarawak.[15]

Having experienced the support and personal kindness of Samuel Stevens as agent during and after his years in Brazil, ARW renewed this agreement. Stevens (1817–1899) operated as a Natural History Agent from 24 Bloomsbury Street, London, conveniently close to the British Museum. His brother, J. C. Stevens, was an auctioneer with premises in King Street. Samuel Stevens retired in 1867, selling his business to Edmond T. Higgins. As well as acting as his agent for the sale of natural history specimens, and thereby funding ARW's travels and further collecting, Stevens obtained and shipped supplies and equipment, and even dealt with a broken pair of spectacles.[16] Importantly, Stevens was also a respected member of several scientific bodies, where he mingled with leading scientists and 'amateur' naturalists, some of whom indulged their passion by lavish purchases. Several were probably as knowledgeable as the staff of the museums they patronised. As ARW progressed through the Archipelago, his letters were read and his specimens were exhibited at meetings of the Entomological Society, the Linnean Society and the Zoological Society of London, and his progress was charted in naturalists' journals such as the *Zoologist* and *Annals and Magazine of Natural History* – both of which also accepted and published contributions directly from him.

Successive shipments of specimens by ARW to Stevens during his travels have been cataloged from records in his notebooks by Baker (2001). Consignments could be sent by the more expensive but faster 'overland' route, the reciprocal of ARW's P & O outward journey involving the land link between Cairo and Suez,[17] but ARW generally used the cheaper sea journey round the Cape of Good Hope which took about 4 weeks longer. As specimens began to arrive and were displayed at society meetings by Stevens, the calibre and quantity of ARW's collections roused excite-

[14] There is still a church and active community centre on the site, although the surrounding country no longer consists of hills topped by stands of virgin forest, "much frequented by wood-cutters and sawyers", which offered excellent opportunities for collecting.

[15] The Rajah was in Singapore from the end of August to 3rd December 1854, attending the Commission of Enquiry into his affairs, appointed by Parliament. The two Commissioners, the Advocate General of India, C. H. Prinsep, and a government agent H. N. Devereux, sat from 11th September to 21st November, and their final report was favourable to Brooke (Runciman 1960).

[16] Letter ARW to Stevens, from Singapore, 10th March 1856: My Dear Mr Stevens, I have received your letter of Jan. 6th, announcing the arrival in good order of the Insects by the "Connubia". At the same time I got the parcel of Books etc. which had been delayed a month as usual at Ceylon. The other shoes etc. do not send till I want something else. Do not send me more B.M. Catalogues, except new ones of Coleoptera, Birds, and Butterflies. The moths have scarcely 50 Indian species in it. I send in the box a pair broken spectacles. Get repaired at the makers, and get another pair exactly like to be sent in next parcel".

[17] In a letter to Stevens (29 October 1858) ARW proposed to send first specimens of his new bird of Paradise (Wallace's Standardwing) by this route (van Wyhe 2013:265–266).

ment among the naturalist community, professional and amateur. Rich collectors were soon paying high prices for these exotic specimens to fill their cabinets, and they and their professional colleagues launched enthusiastically into cataloguing and describing the abundance of new species. The level of activity generated by ARW's collections while he was still travelling into ever less congenial destinations in the Archipelago[18] is demonstrated by the wealth of publications on his material from 1855 onwards (Smith and Beccaloni 2008).

2.2 In the Field

ARW was an inspired collector. Insects were his first love, mainly beetles and butterflies, but not excluding other orders; birds also ranked highly. His field equipment was simple: nets for insects and guns for birds.[19] Soon after arriving in Singapore, he and Charles were out in the forest on Bukit Timah: "Insects were exceedingly abundant and very interesting, and every day furnished scores of new and curious forms". He decked himself with collector's paraphernalia: "[a] large collecting box hung by straps over my shoulder, a pair of pliers for Hymenoptera, two bottles with spirits, one large and wide-mouthed for average Coleoptera &c., the other very small for minute and active insects .... These bottles are carried in pockets in my hunting-shirt, and are attached by strings around my neck, and the corks are each secured to the bottle by a short string" (Wallace 1855c). His catch in the first 2 months in Singapore included 700 species of beetles, of which 130 were Longicornia (Cerambycidae) (*MA*), much esteemed by 'amateurs'[20] and therefore prime targets for the naturalist-collector.

From the start of his travels, he sought to maximise the numbers of species represented in his collections. His periodic reports to Stevens and the naturalist community emphasised the diversity of his catch: for example, Singapore and Malacca combined, Coleoptera 940 species, Lepidoptera 353 species (including 273 butterflies), Hymenoptera 173, Hemiptera and Homoptera 228, Neuroptera 72 (Wallace 1855a); on the Aru Islands, Coleoptera 572 species, Lepidoptera 229, Hymenoptera 214, Diptera 185, Hemiptera and Homoptera 130, Orthoptera 18, Neuroptera 18 (Wallace 1857, 1858).

Despite set-backs, bouts of illness, and logistical difficulties, his pleasure in this chosen way of life did not wane, and he pursued a disciplined and selective approach

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[18] Criticised for collecting so few birds of Paradise in New Guinea, ARW called it "a horribly wild country" where he would have been totally unsafe outside the settlement of Dorey (Anonymous 1857: 113).

[19] At Lombok in 1856: "After an early breakfast we went out to explore, taking guns and insect nets" (*Journal* #5).

[20] ARW used this word in its true meaning of a person who loves his subject, rather than its modern, slightly derogatory sense of unprofessionalism.

to collecting throughout his travels.[21] His delight showed on New Year's day 1857, his first on Kei Island: "This has been a luxurious day for me as a Naturalist. I have wandered in the forests of an island, which I believe no Naturalist has trodden before me. I obtained about 50 species of insects & four birds none of which I had ever found before though I was acquainted with a few of the Lepidoptera. Among the beetles was a magnificent black *Curculis* blue & black banded and & several pretty insects of a small size. A magnificent yellow and black *Papilio* and the curious *Hamadryas*, the sole representative in the East of the S. American Heliconidae also rewarded my excursion" (*Journal* #51).

At first, ARW's manner of life in the field was constrained by limited finances. Both the *Journal* and *MA* contain a heartfelt passage, written at Labuan Tring, Lombok, in July 1856, on the difficulties faced by "a travelling collector of limited means like myself": "One small room has to serve for eating sleeping and working, for storehouse and dissecting room; – in it are no shelves cupboards chairs or tables, ants swarm in every part of it & dogs, cats and fowls enter it at pleasure. Besides this it is the parlour and reception room of my host & I am obliged to consult a little his convenience & that of the numerous guests who visit us. My principal piece of furniture is a box which serves me as a dining table, a seat while skinning birds, and is the receptacle of the birds when skinned and dried. To keep them free from the ants we have borrowed an old bench the four legs of which place in cocoa-nut shells filled with water keep us tolerably free from them. These comprise literally the only places where any thing can be put away, & they are generally well occupied by two insect boxes and about a hundred bird skins, … All the animal substances moreover require some time to dry thoroughly, [and] emit a very disagreeable odour whilst doing so … I can assert from long experience that to make anything like extensive collections of birds & insects, keeping brief notes of the most interesting facts connected with them will fill up the time of one person, with two or three native assistants. He absolutely cannot do much else, and is often even obliged to abridge his notes in order to secure the safe preservation of his specimens" (*Journal* # 18).

[21] Thus, the morning after arriving at Dobbo, Aru Is. (January 9th 1857): "I set off for the jungle … My day's captures determined in my mind the success of my Aru journey in an Entomological view. I had taken 30 species of Lepidoptera, a larger number than I had captured since leaving the prolific banks of the Amazon, & my delight may be imagined on having among them some of the rare and handsome species only known by a few specimens form N. Guinea. … Of the other orders I was not so successful obtaining only 17 species of beetles & 20 of all other orders, with nothing remarkable among them except a pretty Longicorn beetle of the rare genus *Tinestiterinis* & a magnificent bug." (*Journal* # 58). Again, in 1858, on a brief stop at Kaioa Is.: "I found a few interesting insects most however of forms & species I was already acquainted with from Ternate & Gilolo. One beautiful new beetle of the genus *Eurycephalus* was however a great prize to me. … on the felled and burnt logs … I found [a] host of interesting Buprestidae of six species only one of which however was new to me & the lot by no means so beautiful as those of Amboyna". The following day, he obtained "about 70 species of beetles of which at least a dozen were new to me & many others rare & interesting" (*Journal* # 155).

Insect pests were a perpetual menace [22] and his health was also affected, sometimes severely.[23]

Of ARW's collecting procedures, watch and wait was most productive, but he adapted to his quarry. He searched suitable habitat by hand,[24] and learnt to use local fruit as baits. Thus, in Celebes, "I found that rotten jack-fruit were very attractive to many beetles, and used to split them partly open and lay them about in the forest near my house to rot". None the less, in Celebes he found "the great & interesting tribe of beetles very scarce, many families absent and those that I could obtain very minute. The Diptera and Hymenoptera however were abundant & in great variety & present a number of new & very curious species. The beautiful and rare butterflies of Celebes were the principal object of my search and I found many species new to me" (*Journal* #107).[25]

Such successes could have a physical effect. On Batchian in 1858 he "saw a very large black butterfly marked with white and yellow spots, which I knew at one to be a new species of the giant *Ornithoptera*[26] the bird-winged butterflies the pride of the

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[22] At Dorey: Small black ants "swarm on my table and as I am at work setting out minute insects they carry them off from beneath my nose & even tear them from the cards on which they have been gummed", and blow flies settle "in swarms on my bird skins when first put out to dry & filling their plumage with masses of eggs which if neglected the next day produced maggots. They would get under the wings or under the body of the bird where it rested on the drying board, sometimes raising it up half an inch by the mass of eggs deposited in a few hours all glued to the fibres of the feathers so as to make it a work of much time & patience to get them off without injuring the bird." (ARW Journal #147).

[23] In Ceram: "an inflammatory eruption, brought about by the constant attack of small acari-like harvest-bugs, for which the forests of Ceram are famous, and also by the want of nourishing food while in that island. At one time I was covered with severe boils. I had them on my eye, cheek, armpits, elbows, back, thighs, knees, and ankles, so that I was unable to sit or walk, and had great difficulty in finding a side to lay upon without pain. This continues for some weeks, fresh ones coming out as fast as others got well; but good living and sea-baths ultimately cured them" (*MA*).

[24] In 1858, in New Guinea: "on the last day of June, I brought home no less than 95 distinct kinds of beetles…It was a fine hot day, and I devoted it to a search among dead leaves, beating foliage, and hunting under rotten bark, in all the best situations I had discovered in my walks. I was out from ten in the morning to three in the afternoon, and it took me six hours' work at home to pin and set out all the specimens, and to separate the species. Although I had already been working on this spot daily for two months and a half, and had obtained over 800 species of Coleoptera, this day's work added 32 new ones" (Wallace 1908:510).

[25] The butterflies of Celebes were also hard to catch: "..they were so active & shy as to render it very difficult to capture them. Almost the only place where I could obtain them with any certainty was in the beds of the streams in the forests. Here at damp and muddy pools or even on the dry rocks all sorts of insects could be found. In the adjacent forests are some of the most beautiful butterflies in the world. Three species of the magnificent Ornithopterae measuring seven or eight inches across the wings & beautifully marked with spots or masses of intense satiny yellow on a black ground. They wheel through the thickets with a strong sailing flight & it is only occasionally that a specimen can be captured. About the damp places are to be seen swarms of the beautiful blue banded papilios, the superb metallic green peranthus and pretty little rare swallow tail, all of which, though very active I succeeded in getting very perfect specimens" (*Journal* #107).

[26] On reaching England the new butterfly, Wallace's Golden Birdwing, was formally named *Ornithoptera croesus* by G. R. Gray (1859c). It has a wing span exceeding 15 cm.

Indian Archipelago … At length after two months and a half I hit upon a flowering shrub which attracted these noble insects and after several days watching obtained both the female & the male. The latter I was delighted to find to be perfectly new & most magnificent insect perhaps the most gorgeously coloured butterfly in existence … The brilliancy of this colour is indescribable, & none but a naturalist can appreciate the intense excitement I experienced on at length capturing it. On taking it from my net & opening the glorious wings my heart beat violently the blood rushed to my head & I have never been so near fainting when in apprehension of instant death, as from the excitement produced by what will to most people appear a very absurd & inadequate cause. I escaped however with a headache for the rest of the day." (*Journal* #164).

Each day's catch was routinely processed in the evening.[27] The records of insect collections in the *Species Registry* notebooks are meticulous. For each locality, individual specimens were entered by serial number (repeated on the circular labels), in separate lists for different orders. In early days, notably in Sarawak, key identification features for new or unfamiliar species were illustrated by miniature sketches.

Birds rivalled beetles as desiderata. To obtain birds and mammals, his chosen weapon was the firearm. He was originally equipped with two double-barrelled guns, evidently muzzle-loaded and cap-fired. The smaller gun (80-bore) must normally have been loaded with fine shot to collect birds with minimal damage to the skin and plumage. Both barrels of the larger gun could take a single ball.[28] At Macassar in July 1857, he received a new gun from England. At Ternate in March 1858, among ARW's list of stores prepared for the trip to New Guinea there were two double-barrelled guns, one single barrelled (presumably the addition) and one Colt revolver, with 15 lbs of powder, 6 bags of shot nos. 2–10, 4,000 caps and a bag of bullets (*Journal* #128). In May 1860 at the little island of Kilwaru, "the metropolis of the Bugis traders of the far east", among other goods from Singapore he bought two muskets – not for collecting, but "to satisfy the fears of my crew who insisted on the necessity of being armed against attacks of pirates etc." Shortly thereafter, when abandoned by his locally-hired crew, these muskets were fired as signals of distress, and later as ship-to-shore warning signals (*Journal* #214, 215, 222). Finally, in 1862, ARW's two double-barrelled guns (probably the original pair) became a parting gift to his most loyal assistant, Ali (Wallace 1905).

A passage in *MA* (Wallace 1869, i: 248) not presaged in the *Journal*, shows ARW using a bird-hunter's technique to get "the beautiful ground thrushes (*Pitta concinna*)" on Lombok in 1856: "They were so shy that it was very difficult to get a shot at them, and it was only after a good deal of practice that I discovered how to

[27] On Kaioa again: "When I sat down to work the house was surrounded with men women & children lost in amazement at my extraordinary & inexplicable operations, & when I proceeded to write the name of the place on small circular tickets & attach one to each insect, even the comparatively civilised old Kapala, the Mohamedan priest & some Malay traders could not repress signs of their astonishment" (*Journal* #155).

[28] When in Sarawak, hunting orang-utans, "I got a shot at it, and the second barrel caused it to fall down almost dead, the two balls having entered the body" (*MA*).

do it. The habit of these birds was to hop about on the ground, picking up insects, and on the least alarm to run into the densest thicket or take flight close along the ground. At intervals they utter a peculiar cry of two notes which once heard is easily recognised … My practice was, therefore to walk cautiously along the narrow pathways with which the country abounded, and on detecting any sign of the Pitta's vicinity to stand motionless and give a gentle whistle continually, imitating the notes as near as possible....having my gun raised and ready for a shot, a second glimpse would enable me to secure my prize, and admire its soft fluffy plumage and lovely colours."

While ARW might go out in the morning carrying a gun himself, more often he concentrated on insects and delegated the bird hunt to assistants. In 1857 on Aru Is, "On the second day after my arrival, my boys[29] returned from the jungle with a most beautiful specimen of that superb little creature the King Bird of Paradise *Paradisea regia* of Linnaeus. Thus one of the great objects of my coming so far was accomplished! My admiration and delight over this exquisite winged form quite amused my Aru hosts who saw nothing more in the 'Burong rajah' than we do in the Robin or the Chaffinch" (*Journal* #70). There was greater excitement when, on Batchian in October 1858, he recorded the first specimen of Wallace's Standardwing: "In the first few days my men did not bring many birds, but there was one which greatly surprised & delighted me. This was a quite new species allied to the birds of Paradise which though of general sombre plumage was remarkable for its throat and breast & lateral shield of plumes of an intense & brilliant metallic green, & for two white feathers springing from each shoulder and capable of being erected vertically on each side of the body. These give the bird a most extraordinary appearance & are altogether unlike any thing yet known" (*Journal* #159).[30]

In Sarawak, as the subtitle of *MA* indicates, one of ARW's chief objects "was to see the Orang-utan (or great man-like ape of Borneo) in his native haunts, to study his habits, and obtain good specimens". The stories of orang-utan hunts that occupy much of *MA* chapter An Inordinate Fondness for Beetles. The Hero's Journey of Alfred Russel Wallace in Southeast Asia are not easy to stomach, but were written for a readership that expected savage encounters. When hunting orang-utans he normally carried the larger gun but on his third, unexpected encounter, he was armed only with the small gun. This he fired none the less, but succeeded only in enraging the ape which escaped, wounded. Altogether, ARW obtained 17 freshly killed orang-utans, of which he himself shot 16 (Cranbrook et al. 2005), and the skeletons of two others. Of necessity, the carcasses were processed very promptly. Charley [Allen]

[29] In *MA* this story appears in a more florid version, naming "my boy Baderoon" (Wallace 1869 ii:221–222).

[30] The account in *MA* ii: 40, gives credit to Ali for bringing in this new bird, and is elegiac by comparison with this first version. However, writing to Stevens shortly afterwards (29th Oct. 1858) ARW was exultant:"..a new Bird of Paradise! of a new genus!! quite unlike anything yet known, very curious and very handsome !!! When I get a couple of pairs I will send them overland to see what a new Bird of Paradise will really fetch. I expect £25 each ! … I consider it the greatest discovery I have yet made "(Raby 2001:143).

assisted in skinning and preparation of the skeleton of the largest male, finally felled after six shots of solid ball.[31] ARW had "a great iron pan, in which I boiled the bones to make skeletons" while skins were preserved in a cask of alcohol.

The bird and mammal collections were also listed in the *Species Registry*. For these groups, however, ARW was more ready to make a provisional identification, at least to genus level. Orang-utans were numbered and listed separately, with anatomical measurements, mostly one individual per page scattered among the pages of other collections. For remaining mammals, and for birds, each 'species' was allotted a serial number. This number was written (with the genus or species name, if known or conjectured) on the distinctive pre-printed label or, in a few cases, on a temporary tag from other materials. Subsequent catches of the same kind at the same location received the same number. Lists in the *Species Registry* therefore recorded the number of species from each locality, not the number of specimens. Some misidentifications occurred. Thus, of three Greater racquet-tailed drongos *Dicrurus paradiseus* taken in Sarawak, ARW gave one field number to two skins with one or two racquets present and, not recognising the similarity, another number to a third bird that had lost both racquets. The records of Sarawak mammals in the *Species Registry* begin with #1 *Cynomolgus*, accompanied by a fulsome note on the appearance and habits of this common monkey, the long-tailed macaque, but such field observations soon declined and ultimately ceased (Cranbrook et al. 2005).

Like most collectors, ARW did not fail to make use of the carcasses! Again at Batchian – "On the last day of my stay one of my hunters succeeded in finding & shooting the rare and beautiful Nicobar pigeon which I have been so long in search of. None of the people here had ever seen it which shows it is very rare. My specimen was a female in very fine plumage, I skinned it myself and had the meat for supper" (*Journal* #172).

3 The Collections

3.1 Vertebrates

Conforming with his policy of building up a personal collection, ARW divided the specimens between those for his "Private" use and duplicates available for sale. "The groups thus reserved were the birds, butterflies, beetles and land shells" (Wallace 1905, i: 385). General instructions to Stevens were to reserve a superior set of specimens for ARW's private collection and raise funds by the sale of others (Bastin 1989). It appears that Stevens exercised a degree of discretion in following these rules. Among birds from the shipments of skins from Malacca, Singapore and

[31] "On examination, we found he had been dreadfully wounded. Both legs were broken, one hip joint and the root of the spine completely shattered, and two bullets were found in his neck and jaws. … I was occupied with Charley the whole of the next day, preparing the skin and boiling the bones to make a perfect skeleton."(*MA*).

Sarawak, he retained the first set and disposed of duplicates to private collectors. However, the BM was close at hand to Stevens' premises and, starting with the receipt of specimens from Lombok, it was arranged that staff of the Zoology Department should be first to see ARW's latest consignments. "The understanding between the traveller and George Robert Gray[32] was, that the latter should describe the collections in their entirety, which was done. The first set Dr. Wallace retained, and the second set was to go to the British Museum. These separate series were selected by the traveller, and the types of the new species remained in the care of Mr. Samuel Stevens, until the return of Dr. Wallace" (Sharpe 1906: 489).[33] However, in an era before the formulation of the Code of Zoological Nomenclature in 1895 (Melville 1995) these arrangements caused later difficulties in the recognition of type specimens. The decision was ultimately made that the duplicates of new species retained by the Museum had status as syntypes with Wallace's personal specimens but, if no duplicate was accessioned, the sole type was returned to Stevens to hold for ARW. If later acquired by BM on the purchase of ARW's private collection, this was recognised as holotype (Warren 1966).[34]

In 1857, when the first consignment of birds from Lombok arrived, John Gould[35] was a frequent habitué of the British Museum and, presumably because he was working on his glorious monographs of kingfishers and pittas, he was given the opportunity to describe two new species: *Halcyon fulgidus* and *Pitta concinna* (Gould 1857a). In this instance, the types were retained by Gould. After being exhibited at a meeting of the Zoological Society on 10 November 1857, Gould (1857b) described *Spilornis rufipectus*, collected at Macassar by ARW; he also saw and commented on the two birds of paradise (*Paradisea apoda* and *P. regia*) from Aru Island (Gould 1858).

When ARW discovered his Standardwing Bird of Paradise on Batchian (Bacan) Island, he wrote at once to Stevens, with a sketch. This was read and displayed at a meeting of the Zoological Society of London in March 1859 (Wallace 1859), and Gray (1859a) proposed the name *Paradisea wallacii* based on ARW's sketch. When specimens arrived, the bird was described and illustrated by Gould (1859: plate 52), who proposed the new genus *Semioptera*. Gray was considered to have precedence by a couple of months (Warren and Harrison 1971) and, after BM bought ARW's retained collection in 1873, Sharpe (1877: 179) designated a male (reg. no. 1873.5.12.14) as type of Gray's species name, while accepting Gould's subsequent genus name.

The system worked more smoothly with other consignments. Thus, G.R. Gray (1858a) rapidly cataloged successive collections from Aru and Ké (Kei) Islands,

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[32] Assistant in the Zoological Department of the British Museum.

[33] Sharpe was appointed Assistant in the Zoological Department of the British Museum in 1872, in charge of the ornithological collection, in succession to G. R. Gray (who died in May of that year).

[34] For instance, *Habroptila wallacii* from East Gilolo (Gould 1860) was not immediately accessioned, and the Museum had to wait until the type was acquired in 1873 with ARW's personal collection.

[35] Among other distinctions, Gould was a Vice-President of the Zoological Society of London.

followed by those from New Guinea (Gray 1859b), the Moluccas (Gray 1860), and Waigiou, Mysol and Gagie (Gray 1861),[36] in each case describing hitherto unknown species. By 1865, when the final consignment was dealt with under this arrangement, 1,018 skins had been bought by the BM, adding many species to the bird collection (Table 1). Stevens also sold duplicates to prominent British private collectors, several of whom ultimately gave, sold or bequeathed to BM their collections, among which were ARW's bird skins. Further trade by Stevens with other dealers and intermediaries resulted in a wide distribution of ARW specimens which can be found, in small numbers, in museums throughout the world. For instance, Yamashina Institute for Ornithology, Tokyo, holds two skins,[37] Morotai friarbird *Philemon fuscicapillus* (Y10.50381) and Rusty pitohui *Pitohui fuscicapillus* (Y10.39588), of which the first bears an original ARW label of the form *Collected by A. R. Wallace 186*. The specimen was collected by Charles Allen, acting for ARW, who did not himself visit the Moluccan island of Morotai (which he spelled 'Morty'), while both have labels indicating Museum Boucard[38] as their source. More complicated transactions are exemplified by the history of the Asian brown flycatcher skin now in the Raffles Museum of Biodiversity Research, Singapore (van Wyhe and Rookmaaker 2013). By varied but similar means, birds collected by ARW have become distributed among many museums, including the US National Museum (Smithsonian) which holds ten such skins.[39]

ARW's mammal specimens were much less numerous than birds, and procedures for their disposal were less orderly. There were fewer private collectors interested in mammals. Notable was Robert F. Tomes, who specialised in bats and purchased ARW's collection, including specimens from Sarawak. Stevens exhibited new arrivals at meetings of the Zoological Society, some of which were subsequently sold to the BM, where J. E. Gray[40] took charge of mammals. In the history of the collections, for 1856, the "first consignment from Mr. A.R. Wallace" was among "the principal additions of the year" (Thomas 1906: 8). Wallace (1856a) claimed to have collected 35 mammal species in Sarawak, among them several interesting rarities such as the otter-civet "*Potamophilus*" (now *Cynogale bennettii*) and wild cats. The *Species Registry*, however, numbers only 32 species (excluding orang-utans). Of these, 22 were provisionally identified by systematic or vernacular name but the remainder were unspecified, being bulked as: *About 10 species more*

[36] Specimens from this consignment were exhibited by S. Stevens at the meeting of the Zoological Society held on 12th November, 1861.

[37] http://decochan.net/index.php?p=5

[38] Adolphe Boucard, a Frenchman, was more a trader than collector. His large collection went to the Museum National d'Histoire Naturelle, Paris. His labels are easy to recognise, as they are written in violet ink and bear a large, red, stemless "B". They are not very informative, since many of his skins came through the feather trade. Boucard used to write "type" on the labels of specimens which he considered as being typical of the species, possibly a trick to enhance their value. As he also described a few taxa, mostly hummingbirds, this led to considerable confusion (J-F. Voisin, *in litt*. 13th Jan 2014).

[39] http://collections.mnh.si.edu/search/birds

[40] Keeper of Zoology at the British Museum, 1840–1875.

Table 1 Direct purchase by the British Museum of Wallace's bird specimens from the Malay Archipelago; data from Sharpe (1906)

Year	Locality	Vendor	No.	Reg. nos.	Notes
1857	Lombok	S. Stevens	50[a]	57.6.13, 1–50	"This was the first collection sent from the Malay Archipelago by Dr. A. R. Wallace"
1857–1858	Makassar	S. Stevens	74	57.8.3,4–19, 58.12.2,38–96	New to the [BM] collection: *Gazzola typica*, *Macropteryx wallacei*, *Hypothymis puella*, *Geocichla erythronota*, *Lalage leucopygialia*, *Penelopedes exarrhatus*
1858	Aru Islands and Key Islands	S. Stevens	150	58.3.10, 1.150	
1859	Amboina	S. Stevens	16	59.3.25,1–5 59.3.30, 1–11	Including *Cyanalcyon lazuli* new to the collection
1859	Dorey, New Guinea	S. Stevens	74	59.4.5, 1–7[4]	New to the collection *Corone orru*, *Gymnocorax senex*, *Pseudorrhectes ferrugineus*, *Chalcophaps stephani* and *Mino dumonti*
1859	Batchian	S. Stevens	4	59.6.13, 1–4	4 specimens of *Semioptera wallacei*
1860	Batchian	S. Stevens	103	60.2.4, 1–103	Added: *Ceyx uropygialis*, *Alcyone affinis*, *Hermotimia auriceps*, *Dicaeum schistaceiceps*, *Lalage aurea*, *Melitograis giloloensis*, *Carpophaga basilica*, *Grauculus papuensis*, *Piezorhynchus nigrimentum*, *Pitta cyanota* and *P. rufiventris*
1860	Timor, E.Gilolo, Ternate	S. Stevens	79	60.9.5, 1–79	New: *Oreicola melanoleuca*, *Megaloprepia formosa*, *Eulipoa wallacei*, *Aprosmictus hypophonius*, *Pitta maxima*,*Rhipidura rufiventris*, *Philemon timorensis*
1860	Celebes	S. Stevens	46	60.9.6, 1–46	New: *Ptilopus gularis*, *P. formosus*, *Carpophaps radiata*, *Myristicivora luctuosa*, *Macropygia albicapilla*, *Chalcophaps stephani*, *Coracias temmincki*, *Pelargopsis melanorhyncha*, *Lyncornis macropterus*, *Scissirostrum dubium*, *Prionochilus platurus* and *Hypotaenidia celebensis*
1860	Ceram	S. Stevens	27	60.12.6, 1–27	New: *Baza reinwardti*, *Philemon subcorniculatus*, *Ceyx lepida*, *Eclectus cardinalis*

(continued)

Table 1 (continued)

Year	Locality	Vendor	No.	Reg. nos.	Notes
1861	Ceram, Waigiou, Mysol, etc	S. Stevens	116	61.12.11, 1–116	New: *Philemon novaeguineae*, *Rhectes uropygialis*, *R. cerviniventris*, *Pseudorhectes leucorhymchus*, *P. ferrugineus*, *Machaerorhynchus albifrons*, *Monarcha nigrimentum*, *Piezorhynchus aruensis*, *P. guttulatus*, *Todopsis wallacei*, *Microeca flavovirescens*, *Edoliisoma schistaceiceps*, *Pachycephala griseonota*, *Collocalia esculenta*, *Paradisea sanguineum*, *Geoffroyus rhodops*
1862	East Timor	S. Stevens	114	62.3.20, 1–114	New: *Ptilotis maculate*, *Philemon inornatus*, *Myzomela vulnerata*, *Dicaeum mackloti*, *Halcyon australasiae*, *Rhipidura semicollaris*, *R. rufiventris*, *Ptistes jonquilaceus*, *Artamides personatus*, *Pachycephala calliope*, *Lalage timoriensis*, *Turacoena modesta*, *Geopilia maugeri*
1862	Morotai, Gilolo, Ternate, New Guinea, Salawati	S. Stevens	35	62.2.11, 1–35	New: *Tanisptera doris*, *Aeluroedus buccoides*, *Locustella fasciolata*,*Todopsis cyanocephala*, *Erythrura trichroa*, *Piezorhynchus bimaculatus*, *Oriolus phaeochromus*, *Criniger chloris*, *Philemon fuscicapillus*, *Lycocorax pyrrhopterus* *Cyclopsittacus desmaresti*, *Ptilopus monachus*, *Henicophaps albifrons*, *Habroptila wallacei*, *Eutrygon terrestris*
1862	Sula Islands	S. Stevens	30	62.12.21, 1–30	New: *Loriculus sclateri*, *Psitteuteles flavoviridis*, *Oriolus frontalis*, *Criniger longirostris*, *Pitta crassirostris*, *Pelargopsis melanorhynchus*, *Chibia pectoralis*, *Artamus monachus*, *Hypotaenidia sulcirostris*, *Rallina minahassa*
1863	Bouru	S. Stevens	15	63.2.16, 29–43	New: *Pitta rubrinucha*, *Rhipidura bouruensis*, *Philemon moluccensis*, *Oriolus bouruensis*, *Edoliisoma marginaturm*, *Criniger mystacalis*, *Athene hantu*, *Myristicivora melanura*, *Tanygnathus affinis*, *Ninox squamipila*

1863	Flores	S. Stevens	25	63.12.16, 1–25	New: *Rhipidura diluta*, *Pachycephala fulvotincta*, *Taeniopygia insularis*, *Sporaeginthus flavidiventris*, *Zosterops aureifrons*, *Dicaeum ignifer*, *Osmotreron floris*, *Accipiter sylvestris*
1865	Various Molucca islands	S. Stevens	29	65.9.7, 1–29	
1873	Malay Peninsula and Archipelago	A.R. Wallace	2,474	73.5.12, 1–2,474	"This was Dr. Wallace's celebrated collection from the Malay Peninsula and Archipelago, Celebes and the Molucca Islands, and New Guinea" (Sharpe 1906: 505). 44 type specimens included

[a]66 skins mentioned under the year 1857 (Sharpe 1906: 252) but later 50 under S. Stevens (Sharpe 1906: 488), the latter number matching the registered series

Actually already in the collection, see 1860 from Timor, above *from* '*Peter*' (Cranbrook et al. 2005, Table 2a). A note at the end of the *Species Registry* entry ("2 Cats & *Potamophilus barbatus* from Simunjan 3 sculls private") suggests that these were specimens chosen by ARW to be held in his personal collection.

In September 1856, Stevens sold to the BM a small, mixed lot of vertebrates from Sarawak, including 17 mammal skins, comprising five typical squirrels,[41] one flying squirrel, three murine rodents and a cat. Compared with the *Species Registry* list, however, there were several absentees, including some noted by Wallace (1856a) for their particular interest. The BM did not receive: '*Macacus cynomolgus*' = long-tailed macaque *Macaca fascicularis*; '*Sciurus ephippium*' = giant squirrel *Ratufa affinis*; two '*Gymnurus* (*Rafflesii*)' = moonrat *Echinosorex gymnurus*; '*Potamophilus barbatus*' = otter-civet *Cynogale bennettii*; mouse deer, *Tragulus* sp., nor '*Galeopithecus volans*' = colugo or flying lemur *Galeopithecus variegatus*, and only one of four felids listed. It must be assumed that these attractive specimens were reserved by Stevens for ARW's private collection. One was subsequently acquired by the BM: a black-eared pigmy squirrel *Nannosciurus melanotis*, bought from Stevens in 1864. The fate of others remains unknown.

Also received by BM in September 1856 was the skull of a sun bear *Ursus* (*Helarctos*) *malayanus* shipped from Sadong on 21 July 1855 (Cranbrook et al. 2005, Table 4), possibly the "scull" marked private in the *Species Registry*. A couple of months later the BM obtained the first of ARW's orang-utan specimens. His notebooks show that the pickled skins of orang-utans, together with the dried skeletons, were shipped from Sarawak to Samuel Stevens in several consignments, as expeditiously as possible, and promptly sold. The BM register records five specimens bought from Stevens as two lots: in November 1856, a stuffed adult[42] and skull, identified as '*Simia morio*', and a stuffed young '*Simia satyrus*', followed in January 1857 by a skeleton and a stuffed specimen of '*Simia morio*' (Cranbrook et al. 2005, Table 5).[43] The two mounted specimens of 1856 both have a visible seam down the front. The stuffing material is mostly straw, with a small amount of a more fibrous, finer (almost wool-like) substance in the hands and fingers. No bones remain in the hands, and apparently none in the arms.

Other than the BM, Wallace's marginal notes name the Derby Museum (City of Liverpool) as the purchaser of five skins and skulls, and two skeletons, for the large sum of £150, as follows: ♀, dry skeleton and skin in 'arrack', the term for commercially produced ethanol for human consumption; ♀, skeleton and skin in arrack; ♂,

[41] One of which was promptly named as a new species, *Sciurus macrotis*, by J.E. Gray (1856).

[42] The attached label identifies this dramatic standing mount as: "The spm from which Wallace's description was taken". It has now been restored and is exhibited as part of the 2013 Wallace Trail in the Natural History Museum.

[43] In marginal annotations to the summary tabulation of his collection of orang-utans in the *Species Registry*, Wallace noted two purchases by the BM: firstly, for £46 altogether, a female and infant, probably the subjects of the sad tale repeated in several places: in a letter home (NHM WP1/3/34), Wallace (1856b, *MA*, 1905: 343–345); and, secondly, for £50, a 'small' male from Semabang (Cranbrook et al. 2005: Table 3). The last of these has not been rediscovered in the Natural History Museum.

dry skeleton and skin in arrack; ♂, 'small, Simunjan'; and ♀, evidently juvenile, skin in arrack (Cranbrook et al. 2005, Table 3). Of these, only a skull and a skin remain in the present Liverpool Museum collections, recorded as having been acquired through S. Stevens in March 1857.[44] The skin, now dry, remains folded as originally received and thereby demonstrates Wallace's procedure for preservation in alcohol and subsequent despatch. It can be assumed that the BM skins, shipped in liquid preservation, were also folded in this manner. The delay of 1 or more months between arrival of the specimens and their receipt at the Museum, as 'stuffed' mounts, implies that Stevens was responsible for the taxidermy before sale.[45]

At the meeting of the Zoological Society of London on 23 February 1858, two phalangers of the genus *Cuscus* sent by ARW from the Aru Islands were exhibited, and described as new species *C. ornatus* and *C. celebensis* by J. E. Gray (1858a). Further collections from the Aru Islands were reported by J. E. Gray (1858b), and from Batchian and other Moluccan islands by J. E. Gray (1860). These, and a later collection (Gray 1863), were retained by BM.

The skin of the huge python pulled from ARW's house on Amboyna (*MA*) was preserved, and is now owned by the Linnean Society of London, but he paid limited attention to the collection of reptiles and amphibians. Fifteen assorted specimens from Sarawak were bought from Stevens by BM in 1856. New species were noted by J.E. Gray (1862), and ARW's specimens were later mentioned by Günther (1872) in his account of the reptiles of Borneo. There was no other specialised report, but ARW's specimens from the Malay Archipelago were noted in the BM catalogs of Günther (1858a, b, 1865) and Boulenger (1889, 1893, 1894).

3.2 *Invertebrates*

Land shells were among ARW's declared special interests and he collected widely around the Archipelago, accumulating 7,500 specimens (*MA*: Preface). An early shipment from Sarawak included a consignment which Stevens was instructed to sell promptly. Charles Allen also collected land shells for ARW in the Moluccas in 1860–1861 (Rookmaaker and van Wyhe 2012). The main private enthusiast of that time was Hugh Cuming. There are citations of ARW specimens, many of them types of new species, in a succession of papers cataloguing Cuming's huge collection, produced during the 1860s by authors including Adams, Pfeiffer (1862a, b), Deshayes, and others. After his return, ARW himself listed 125 species by then in the ownership of W.W. Saunders, presumably having been 'private' specimens retained by Stevens. The description of 14 new species among this collection was

[44] Reg. no. F.P.M.31a, a skull only, taken from a lost mounted specimen 85a, and 18.3.57.5, ♂, skin and skull. The skull of the latter specimen, which is a juvenile, has been halved by a longitudinal cut.

[45] Among the mammals, the flying squirrel is still mounted, and the condition of some other skins suggest that they have been dismounted. Further research is needed to clarify the matter.

Table 2 Entomological specimens collected by A.R. Wallace bought directly by the British Museum (1855–1863), summarised from Baker (1995: Table 2)

Lepidopt	Coleopt	Hymenopt	Diptera	Orthopt	Neuropt	Hemipt	Apterigo	Total
1204	3,847	920	678	158	62	845	15	7,758

entrusted to the specialist, H. Adams, and these shells were illustrated in a single plate engraved by Sowerby (Wallace 1865a).

Throughout his travels in the Archipelago, ARW's personal attention was closely directed towards the curation of his insect specimens. Promptly shipped to Stevens, important new examples were displayed at meetings of the Entomological Society (e.g. Wallace 1855b) or the Zoological Society, and the name of Mr. A.R. Wallace rapidly became familiar among members of the naturalist community.[46] Baker (1995) has shown that, from the first consignments from Singapore and Malacca, to the last from New Guinea, Salwatty and Bouru, in every case the BM received entomological specimens across the range of orders, ultimately amounting to 7,758 specimens (Table 2).

The BM may have been forced to bid against private collectors of considerable means. Baker (1995) reported the minimum payment for mixed insect collections at 1 shilling[47] per specimen, for beetles 2s. 6d per specimen (with exceptions such as stag beetles *Lucanus* at 10s. each).[48] Butterflies were costly at 4s.6d. each, again with exceptional prices for new rarities, such as £6 per pair paid in October–November 1860 for the huge golden birdwing caught on Batchian that roused physical reactions in ARW, named *Papilio* (*Ornithoptera*) *Croesus* by G.R. Gray (1859c).

Stevens continued to reserve prime specimens for ARW's personal collection, but specialist collectors were encouraged to inspect new arrivals and to buy duplicates. A considerable collection of ARW's butterflies was obtained directly from Stevens by W.C. Hewitson, who described those in his personal holding combined with the retained private collection (Hewitson 1859, 1862). Among prominent private collectors who obtained major portions of his beetle specimens was Francis Polkinghorne Pascoe, one-time President of the Entomological Society of London, who specialised in Longicorn beetles. Pascoe bought much, if not all ARW's specimens of this group. His monumental catalog of ARW's Longicornia occupied an entire volume of the *Transactions of the Entomological Society* (Pascoe 1864–1869), treating more than a thousand species, of which at least 900 were previously undescribed and new to European cabinets (*MA*: Preface). The foremost expert on phytophagous beetles (= Chrysomeloidea), Joseph S. Baly, published companion papers cataloguing ARW's specimens of this superfamily in various entomological outlets, culminating in a 300-page revision of the 'Phytophaga' of the Malay

[46] After his return, in 1864 ARW was elected a Vice President of the Entomological Society.

[47] One shilling (s.) = 12 pence (d.). 20s. = one pound sterling (£1) = approx. 5 Straits dollars at that time.

[48] By comparison, each number of the *Journal of the Linnean Society*: *Zoology*, in which many of these collections were listed, cost 2s., for approximately 50 pages.

Archipelago (Baly 1865). Between them, Pascoe and Baly described more than 300 new species from Sarawak collections (Polaszek and Cranbrook 2006). Edwin Brown bought ARW's Cetoniidae. Other coleopteran groups, notably jewel beetles Buprestidae and click beetles Elateridae, reached continental entomologists including E. Fleutiaux and R. Oberthuer (Polaszek and Cranbrook 2006).

F. Moore (1859) included ARW's early collections in his catalog of silk-producing moths, but a major proportion of ARW's moth collection was acquired by William Wilson Saunders[49] who contracted to buy insects other than beetles and butterflies. Saunders (1861) produced a paper on the curious horned flies (Glaubrechta and Kotrbab 2001), but mainly "caused the larger proportion of [the specimens] to be described by good entomologists" (*MA*: Preface). Some Diptera were sent by Stevens to the French specialist Jacques M.F. Bigot (1818–1893), and others to the German C.E.A. Gerstäcker[50] (Baker 2001). Other Diptera, Heterocerous Lepidoptera (i.e., moths) and Homoptera, were passed by Saunders to Francis Walker, who was paid by result: £1 for each new genus and 1s. for each new species described (Baker 1995:180). Unsurprisingly, Walker rapidly produced a succession of catalogs of ARW's collections published in the *Journal of Proceedings of the Linnean Society of London* from 1859 to 1865, describing many new taxa. His catalog of the famously vast series of moths lamp-lighted at Rajah James Brooke's hilltop bungalow, Peninjau, in Sarawak, described more than 100 new genera and nearly 400 new species, occupying over 160 pages (Walker 1862–1864). Simultaneously, in a serious of papers in the same journal, Walker also cataloged ARW's large collections of Diptera (Walker 1861, 1864a, b) and, separately, Homoptera (Walker 1858). His final synoptic list of ARW's Diptera collected in the Archipelago occupied 23 pages, showing the occurrence, by location, of more than 950 species (Walker 1866). The quality of Walker's work was challenged, to the extent that an obituary notice charged him with doing "an amount of injury to entomology almost inconceivable in its immensity" (Baker 1995: 180). A broader view of his life has since mollified this assessment, and most of his Sarawak moth taxa have stood the test of rigorous investigation (J. Holloway, quoted by Polaszek and Cranbrook 2006).

Frederick Smith[51] was chosen by Saunders to catalog ARW's Hymenoptera. Commencing promptly in November 1857 with a report on those collected in Singapore, Malacca and Sarawak (Smith 1857–1858), and ending with the descriptions of new species from Sumatra, Sula, Gilolo, Salwatty and New Guinea, Smith duly produced a succession of papers alongside those of Walker in the *Journal of the Proceedings of the Linnean Society of London* from vol. 2, no. 6, with a catalog

[49] W. Wilson Saunders was an underwriter at Lloyd's of London. President of the Entomological Society from 1841–1842 to 1856–1857; Treasurer of the Linnean Society of London 1861–1873; Fellow of the Royal Society from 1853.

[50] Carl Eduard Adolph Gerstäcker (1828–1895) was Curator of the Zoological Museum of Humboldt University, Berlin, from 1857 to 1876.

[51] Frederick Smith. Born 1805. Curator of the Collections and Library of the Entomological Society of London 1841–1850; Assistant in the Zoological Department, BM 1850–1875; Assistant Keeper of Zoology 1875 until his death in 1879.

of Sarawak specimens (Smith 1857–1858) to vol. 8, no. 30 (Smith 1865). A concluding catalog, with a foreword by ARW, was published in 1873 (Smith 1873).

4 The Returned Traveller

On his return from the Malay Archipelago in 1862, ARW found himself "surrounded by a room full of packing-cases, containing the collections that I had from time to time sent home for my private use. These comprised nearly 3,000 bird skins, of about a thousand species; and at least 20,000 beetles and butterflies, of about 7,000 species; besides some quadrupeds and land shells" (*MA*: Preface). He also found that, through the efforts of Samuel Stevens and based on this very considerable volume of published reports, catalogs and descriptions of his collections, he was well known as an industrious and effective provider of new and valuable specimens from an under-explored region of the world.

More than this, as a result of his published works, he had gained a reputation as an innovative theorist in biology. Written during his travels, his paper on avian systematics (Wallace 1856c) had emphasised the importance of morphological features. His review of the distributions of birds of the Archipelago (Wallace 1859) had built on the pioneering work of Sclater (1858) and established biogeography as a discipline. Drawing on his reserved private collections, he now embarked on extended studies of systematics and zoogeography of birds (Wallace 1864a, b, 1865b, c), butterflies and beetles. His review of the Eastern members of the butterfly family Pieridae (Wallace 1867a) included the description of 45 new species, by no means all his own additions, confirming that he was working in the BM with full access to the collections. The treatment of this family was geographical, and picked up the challenge by Pascoe who had asserted that the division of the Malay Archipelago into Indian and Australian zoogeographical regions did not hold good for invertebrates as it does for 'higher' animals, i.e., birds and mammals. ARW also took a zoogeographical viewpoint in his catalog of the beetle family Cetoniidae of the Archipelago (Wallace 1868), again making it clear that, in addition to his own specimens, he was incorporating material in the BM and in the collection of Major Parry.[52] ARW argued that, despite large overlap in species composition, for the beetle faunas east and west, respectively of "a line drawn on the east side of the Philippines, curving to the west of Celebes, and passing between the islands of Baly and Lombock, will divide the Indian from the Australian region" (Wallace 1867a: 304). In placing the boundary here, at the deep water divide, ARW did not assert that the line marked an impermeable barrier. Rather, his figures emphasised the gradual nature of the faunal transition, with the Line representing an averaged point at which source of the majority of species turned from the west to the east. His own name was not yet attached to this famous Line.

[52] Major Frederick J.S. Parry specialised in the stag beetles, Lucanidae.

By 1869, ARW had published 30 scientific papers based on his collections,[53] which he considered sufficient groundwork to justify a book for general readership, *The Malay Archipelago* (Wallace 1869: Preface). During the 1870s, his reputation was confirmed by a succession of books published by Macmillan, drawing on his experiences in Amazonia and the Malay Archipelago but also reflecting, and responding to the writings of other authors who were engaged in the great debate on natural selection, including Charles Darwin. These Macmillan publications demonstrate his contribution to contemporary thought on natural selection (Wallace 1870), zoogeography (Wallace 1876), especially reflecting the selective influence of the tropical environment (Wallace 1878)[54] and the consequences of isolation (Wallace 1880). He also added to the literature on animal coloration and mimicry (Wallace 1867b, 1879). Remarkably, ARW's division of the world into six zoogeographical regions has only recently been amended by analysis based on advanced computing power, combined with modern concepts of phylogeny (Holt et al. 2013).

During this time, other specialists made use of his specimens in broader zoological reviews. For instance, prominent among the private buyer of duplicates sold by Stevens was Viscount Walden (later Marquess of Tweeddale). Among other new species described from his collection, he named *Mulleripicus wallacei* (Tweeddale 1877). The Keeper of Zoology at BM, in a review of Asiatic squirrels, described ARW's specimens from Sarawak as a new genus (*Rheithrosciurus*) and new species (*Macroxus sarawakensis*) (Gray 1867) and, lacking further examples, finally described a Sarawak cat as *Felis badia* (Gray 1874). Later still, the distinctness of two small rodents from Sadong, registered simply as *Mus*, was recognised by Thomas (1893), and they became type and paratype of *Chiropodomys major*.

5 Dispersal and Reassembly

5.1 Vertebrates

Ultimately, ARW had worked his way through his collections, and his interests moved away from systematics and biogeography. In 1873 he sold to BM most of his retained bird collection from the Malay Archipelago, amounting to 2474 skins, "containing the types of all the new species described by Mr. G. R. Gray and Dr. A. R. Wallace himself" (Sharpe 1906).[55] These, however, were not the final items of ARW's birds to reach this museum. Several of the great private collectors of the period who had acquired skins from Stevens subsequently passed their collections to BM, by gift, bequest or sale. The types of *Halcyon fulgidus* and *Pitta concinna* (Gould 1857b), retained by Gould, passed to BM after his death when Gould's large

[53] See http://wallace-online.org

[54] ARW (1878) *Tropical nature and other essays*. London, Macmillan and Co.

[55] ARW also chose this occasion to let the Museum have 27 hawks and owls from his Amazonian collection (Sharpe 1906).

private collection of 6,315 specimens was purchased in 1881 (Sharpe 1906: 375; Warren 1966: 104; Warren and Harrison 1971: 126). After his death, the Marquess of Tweeddale's huge collection of 20,186 Asiatic birds, including ARW specimens, was donated to BM in 1888 by his nephew, Col. R.G. Wardlaw Ramsay (Sharpe 1906: 445). Other private collectors who bought ARW bird skins that ultimately came to BM by gift or bequest included Henry Seebohm[56] and R. B. Sharpe.[57]

Some of Wallace's birds from the Malay Archipelago were acquired by Canon H. B. Tristram,[58] whose collection was ultimately sold to the Derby Museum, Liverpool. A few skins and skeletal preparations were also sold to Professor Alfred Newton[59] and are now in the University Museum of Zoology, Cambridge. In the 1890s, the BM gave duplicates, including skins from ARW's personal collection, to the Burslem Art Museum, and to Princeton Museum, USA. The former institution no longer exists, and the fate of its collections is obscure. Princeton has been able to locate ARW's specimens in its remaining holding, but also disposed of a portion of its collections to the Field Museum of Natural History, Chicago. The Field Museum now holds 13 ARW skins, mostly from Princeton but also obtained by exchange with the American Museum of Natural History (Appendix A). Still at the American Museum of Natural History are 35 skins collected in the Archipelago between 1859 and 1862 (several from the Moluccas attributable to Charles Allen), almost all of which were part of the purchase of the Rothschild collection in the early 1930s (Cracraft, personal communication, 2014). The National Museum of Natural History, Paris, holds some bird skins collected by ARW but there is no list of them, "and the accession catalogues are most of the time not very explicit about the origins of our specimens" (Voisin, personal communication, 2014). Most poignant is a group of bird skins, the residue of ARW's private collection that he saved for his own pleasure, obtained after his death by Mr Parkinson Curtis by whom, in turn, they were bequeathed to the Dorset County Museum (Appendix B).

After the death of Tomes in 1904, among the 500 mammal specimens purchased by BM from his executors there was a large number of bats collected by ARW (Thomas 1906), and also one treeshrew from Sarawak (Cranbrook et al. 2005). According to Thomas (1906) the BM held a final total of 123 mammal specimens from ARW's collections in the Malay Archipelago of which, before his return, J. E. Gray had described new species (including *Mus xanthurus*, *Mus celebensis*,

[56] Henry Seebohm (1832–1895) was a member of a prominent Quaker family involved in a variety of businesses, including banking, steel-making, and the wool trade. A respected amateur ornithologist, his publications included *A History of British Birds* (1883), *The Geographical Distribution of the family Charadriidae* (1887), *The Birds of the Japanese Empire* (1890), and (posthumously) *A Monograph of the Turdidae* (1898) and *The birds of Siberia* (1901).

[57] When Sharpe was appointed to succeed G.R. Gray in 1872, obeying "the rule of the Civil Service, which very properly prohibits the keeping of private collections of any group to the custody of which an officer is appointed" (Sharpe 1906: 481), he added his existing bird collection to the British Museum.

[58] Among other distinctions, the co-founder of the British Ornithologists' Union, publishers of the periodical *Ibis.*

[59] Among other posts, Newton held a travelling fellowship of Magdalene College, Cambridge.

Phalanger celebensis, *Phalanger ornatus* and *Phascogale wallacei*). The present BM holding is 205 specimens (Daphne M. Hills, 2013 unpublished), i.e., two thirds (66 %) of ARW's total collection of mammals. The flying squirrel and a cuscus are still mounted, and the condition of several other skins indicates that they have been dismounted. It is also apparent that, in some cases at least, ARW left the skulls in situ (as is still conventional for birds), cutting the occipital region to extract brain tissue. Further research is needed to evaluate the condition of these and other vertebrate specimens, and to trace items missing from the BM collection.

5.2 Invertebrates

The BM progressively acquired many of ARW's invertebrate specimens, as whole or part of large holdings originally the property of private collectors. Thus, Cuming's collection of 82,992 shells was acquired by BM in 1866 (Smith 1906).[60] Given time, ARW's specimens could in theory be found by diligent search among that huge acquisition.

After ARW returned to England, Hewitson completed the purchase of his butterflies, and compiled a catalog. He wrote, "The very valuable collection of Satyridae, Ericinidae, Lycaenidae and Hesperidae amassed by the indefatigable industry of Mr. Wallace having been transferred to my keeping, I am happy to comply with his wishes by compiling a list of species, with notice of all their varieties and localities" (Hewitson 1865). Hewitson died in 1878 and bequeathed to the BM his entire collection of exotic butterflies, consisting of 24,625 specimens, including most of the types collected by ARW (Waterhouse 1906: 569).

Other large private holdings of ARW's insect specimens also passed to BM as their owners, or their heirs, decided to part with their collections. On the death of F.P. Pascoe in 1893, BM purchased his entire collection of some 48,500 beetles, of which 3,191 were types of Pascoe's named species (Waterhouse 1906: 594). J.S Baly's collection of 28,000 phytophagous beetles was also obtained by BM through progressive purchases between 1880 and 1905 (Waterhouse 1906: 580). W.W. Saunders was a generous benefactor, in 1865 presenting his collections of 3207 Hemiptera and, in 1868, 2000 Neuroptera and 5000 Diptera, among which were series collected by ARW in the Malay Archipelago (Waterhouse 1906: 565, 595). Brown's collections were auctioned in Stevens's rooms in 1877 when the BM bought lots of Cetoniidae, including all Wallace's types (Waterhouse 1906: 582).

[60] "The actual number of species and types was never estimated, but when we regard the twenty volumes of Reeve's 'Conchologia Iconica', the five volumes of Sowerby's 'Thesaurus Conchyliorum', and the numerous papers by Pfeiffer, Broderip, H. and A. Adams, Dehayes and others, all descriptive of this collection, we get some idea of the interest attaching to it. This collection of shells was the main object of Mr. Cuming's life. He not only devoted several years of personal collecting to its formation, but he purchased largely, and obtained very many species by exchange with foreign museums and private collectors in all parts of the world" (Smith 1906:710)

An important private collector who bought ARW specimens direct from Stevens was Frederick William Hope FLS, FRS (1797–1862). In 1849 Hope endowed a chair of Zoology at Oxford University, nominating as the first Hope Professor John Obadiah Westwood (1805–1893), who also curated Hope's collection. Westwood himself bought more of ARW's insects[61] and thus, in Oxford University Museum, began the second most important British collection of ARW specimens (Appendix B).

Saunders' collection of 'exotic' Hymenoptera, amounting to 12,415 specimens arranged by Frederick Smith, was sold through E.W. Janson and acquired by Oxford University Museum in 1875 (Baker 1995). Smith's personal collection of about 25,000 non-British specimens (including ARW material) was dispersed after his death in 1879. The BM purchased a first selection of 3445 of his Hymenoptera, including all his types. The remainder passed in to the hands of the Rev. Farren White, whose collection of 17,451 Hymenoptera, chiefly aculeate, was ultimately presented to BM by his widow in 1899 (Waterhouse 1906: 577). Some specimens, after a variety of intermediate owners, also reached the Oxford University Museum (Baker 1995).

As time has passed, others of ARW's specimens have been transferred by exchange, gift or sale, and incorporated into the collections of museums in Europe, USA, Australia and Singapore. Among British institutions, the Hunterian, University of Glasgow, holds several labelled cerambycids from the Malay Archipelago, including *Chaeromorpha wallacei* from Borneo (i.e. Sarawak) still pinned to an original circular white label (Breitling and Hancock 2014: pl. 4). A list of institutions known to hold ARW specimens has been put online by George Beccaloni.[62] Despite these dispersals, the BM undoubtedly now holds the major proportion of ARW's vertebrate and invertebrate specimens from the Malay Archipelago, with Oxford a close second in entomology.

6 Epitome

The period from 1854 to 1862, while ARW was collecting in the Malay Archipelago, marked a revolution in human understanding of nature and natural processes regulating the evolution and distribution of species. Through his experiences in the Malay Peninsula, Singapore and the islands that extend to New Guinea, supplemented and strengthened by the information contained in his varied collections of vertebrate and invertebrate animals of that region, Wallace himself contributed powerfully to this intellectual watershed. His collections still provide potentially unmatched base-line information on the biodiversity resource, and are thus vitally

[61] "Westwood, having but a small amount for purchases, used to buy damaged specimens at a low price & patch them up. He did this very cleverly, but you must have come across some." ARW, Letter to Poulton, 26 March 1896 (Oxford Museum archive).

[62] http://wallacefund.info/wallace-specimens

important in the region for systematics and taxonomy. The information provided by these specimens is also valuable for regional and national policy-making in matters such as nature conservation and species protection, and useful for practical applications, e.g. in integrated pest management.

As shown above, a large proportion of ARW's collections ultimately ended up at BM. Moreover, when the opportunity arose, BM Trustees made special efforts to obtain the type specimens, which are of special importance in all these fields of research and policy. Of 310 specimens of mammals that ARW claimed to have collected (*MA*: Preface), 205 (66 %) are in the BM (Hills unpublished). Of c. 8050 birds, direct purchases by G.R. Gray (1,018 skins) combined with the acquisition of ARW's private collection (2474 skins) indicates a minimum of 3492 (43 %), undoubtedly raised by subsequent gifts and purchases from individual collectors. No figure for the number of 'herptiles' is yet obtainable but, for this group, the comparatively small numbers make it an exacting but not insurmountable task to discover and recognise ARW's surviving specimens.

Among invertebrates, the immense numbers involved (7500 shells, 13,100 Lepidoptera, 83,200 Coleoptera and 13,400 other insects), make the reassembly of ARW's collections a much more demanding aspiration. Moreover, the recognition of individual specimens has been hampered by changes in labelling and mounting as collections passed from hand to hand among private collectors, before ultimately reaching BM (Baker 1995). Some large collections in BM, such as Cuming's land shells, remain only partially registered. A UK Parliamentary inquiry in 1990–1992 highlighted concerns among the scientific community that the standards of curation at BM had declined as a result of financial constraints (House of Lords 1992 1: 33). The deposition from the BM itself admitted that there were serious storage and curatorial problems, that the condition of biological specimens can deteriorate, and that retarding this process is expensive (House of Lords 1992 *Written evidence* 1: 155–156).

7 A New Initiative in Sarawak

In the course of the House of Lords inquiry, the Director of Australian National Parks and Wildlife Service emphasised the special concerns among former colonial countries about the state of type specimens collected in their territories, and aired proposals for joint curatorial care (P. Bridgewater in House of Lords 1992). The listing by Polaszek and Cranbrook (2006) of insect species described from ARW's Sarawak collections has provided a start for an exercise to locate, redescribe and create digital images of types collected in Sarawak. A bolder initiative, in conjunction with BM and Oxford University Museum, could provide a model for further collective action by the national governments of Indonesia, Malaysia, Singapore and Timor-Leste, perhaps through ASEAN scientific cooperation. An exercise to compile and disseminate a comprehensive catalog of ARW's Archipelago collections, with emphasis on the irreplaceable type specimens, would be a fitting centennial memorial for the indefatigable enterprise of Alfred Russel Wallace and also an invaluable asset for regional biologists, zoogeographers, conservationists and wildlife managers in all nation states of the region.

Acknowledgments Cranbrook is grateful to the Natural History Museum authorities who have given him access to the magnificent library where the duty officer has invariably been helpful. For assistance in examining the collections, much help was also received from George Beccaloni, leading scholar and protector of Wallace's legacy, from Roberto Portelo-Miguez (mammals) and Robert Prŷs-Jones (birds). Daphne Hills has kindly made available her full list of Wallace's mammal specimens in the Natural History Museum. Successive Librarians of the Linnean Society of London, Gina Douglas and Lynda Brooks, have provided ready help. At the Liverpool Museum, Clemency Fisher kindly made available Wallace specimens in this collection, notably orang-utans. Jenny Cripps kindly provided the full list of ARW's bird skins in the Dorset County Museum, and Ben Marks kindly abstracted a list of bird skins in the Field Museum of Natural History, Chicago.

Appendix A: ARW Skins in the Field Museum of Natural History, Chicago. Information Provided by Ben Marks, Curator of Ornithology

FMNH 98708 – *Megalaima henricii henricii* – A R Wallace – 1859 – skin
FMNH 98995 – *Dicrurus hottentottus bimaensis* – A R Wallace – skin
FMNH 304574 – *Pycnonotus finlaysoni finlaysoni* – A R Wallace – 1862 – skin
FMNH 304584 – *Pycnonotus plumosus plumosus* – A R Wallace – 1854 – skin
FMNH 304585 – *Pycnonotus plumosus plumosus* – A R Wallace – 1854 – skin
FMNH 304613 – *Hypsipetes malaccensis* – A R Wallace – 186? – skin
FMNH 304647 – *Chloropsis sonnerati zosterops* – A R Wallace – skin
FMNH 304651 – *Chloropsis sonnerati zosterops* – A R Wallace – 1854 – skin
FMNH 305166 – *Copsychus pyrropygus* – A R Wallace – skin
FMNH 409589 – *Ptilinopus perlatus zonurus* – A R Wallace – skin
FMNH 303452 – *Dinopium javanense javanense* – A R Wallace – skin
FMNH 280815 – *Paradisaea apoda apoda* – A R Wallace – skin
FMNH 310220 – *Semioptera wallacei wallacei* – A R Wallace – skin

Appendix B: Birds from the Malay Archipelago in the Alfred Russel Wallace Bird Collection at the Dorset County Museum

Date	Name		Place	Acc no
0	Black-headed Pitta	*Pitta novae-guineae/? Pitta soldida*	Celebes (Sulawesi)	V1055
0	Blue-faced Parrot-finch	*Erythrura trichora*	Ternate	V1054
0	Vernal Hanging Parrot	*Coriculus vernalis*	Sula Is.?	V1070
1854	Many-coloured Barbet	*Megalaima rafflesii*	Malacca	V1075
1854	Red-breasted Bee-eater	*Nyctiornis amicta*	Malacca	V1074
1856	Blue-winged Pitta	*Pitta brachyura/ Pitta moluccensis*	Lombok	V1067
1856	Rainbow Bee-eater	*Merops ornatus*	Lombok	V1063
1858	Beautiful Paradise Kingfisher	*Tanysiptera galeata*	Gilolo (Halmahera)	V1082
1858	Pied Butcherbird	*Cracticus nigrogularis*	Dorey, New Guinea	V1053
1859	Great Pitta	*Pitta maxima*	East Gilolo	V1065
186?	Oriole	*Oriolus frontalis*	Soella (Sula Is.)	V1069
1860	Crinkle-coloured Manucode	*Manucodia chalybatus*	Misool (Mysol)	V1080
1861	? Starling	*Gracula pectoralis*	New Guinea	V1060
1861	Blue-capped Dove	*Ptilinopus monacha*	Gilolo (Halmahera)	V1083
1861	Crested Jay	*Platylophus galericulatus*	Sumatra	V1079
1861	Fairy Bluebird	*Irena puella*	Malacca	V1076
1861	Grey-headed Fruit Dove	*Ptilinopus hyogastra*	Gilolo (Halmahera)	V1084
1861	Little Friarbird	*Philemon citreogularis*	Gilolo (Halmahera)	V1062
1861	Little Green Pigeon	*Treron olax*	Sumatra	V1077
1861	White-collared Kingfisher	*Halcyon chloris*	Sula	V1071
1861	Perfect Lorikeet	*Trichoglossus euteles*	E.Timor	V1087
1861	Racquet-tailed Treepie	*Crypsirina temia*	E. Java	V1068
1861	Rail Babbler	*Eupetes macrocerus*	Malacca	V1073
1861	Trumpet Bird	*Phonygammus keraudrenii*	New Guinea	V1059
1862	Black and Red Broadbill	*Cymbirhynchus macrorhynchos*	Sumatra	V1078
1862	Black and Yellow Broadbill	*Eurylaimus ochromalus*	Malacca	V1072
1862	Olive-backed Sunbird	*Nectarinia jugularis*	Flores	V1066
1862	Timor Sunbird	*Nectarinia solaris*	Flores	V1056

Appendix C: ARW Specimens in the Oxford University Museum of Natural History. Compiled by Darren Mann, Head of Life Collections

1858 20 diurnal Lepidoptera from Celebes. Purchased from Stevens by F.W. Hope
1858 Insects from Sarawak and the Aru Islands. Purchased from Stevens by F. W. Hope
1859. Insects from Borneo, Amboyna, Dorey, Batchian, Ternate, and Gilolo. Purchased from Stevens by F. W. Hope
1860. Insects from Sarawak. Purchased from Stevens by F. W. Hope
1862. Insects from Mysol and Waigiou. Purchased from Stevens
1863. Two larvae and one pupa of *Mormolyce phyllodes.* Presented by J.O. Westwood
1863. Insects from Sumatra, New Guinea, and Mysol. Purchased from S. Stevens
1865. Entire private collection of Melolonthidae, Rutelidae, Trogidae, Aphodiidae, and genus *Valgus* (514 specimens) from the Malayan Archipelago, also his private collection of Eumorphidae (201 specimens), Pselaphidae, and Scydmaenidae (29 specimens), from the same islands (£28. 16s)
1866. Private collection of Clavicorn Coleoptera made in the Malayan Archipelago (£10)
1866. Three specimens of *Iridotania* from Kaisa, Ternate, and New Guinea (through W. W. Saunders)
1866. Entire private collection of Cleridae formed in the Malayan Archipelago containing 697 specimens, also Staphylinidae containing 523 specimens, purchased £35
1867. Purchased from Mr. Walker (on acct of W. W. Saunders) 73 Diptera, 29 Homoptera from the Malayan Archipelago collected by A. R. Wallace and described by Messrs. Walker and Stil, from Mr. Saunders Collection and 15 Cercopidae from ditto (at 10d each)
1868. Various insects from Wallace collection. Purchased from Mr Higgins, purchased £2 7s, 7s, 12s, £1, 12s, 3s, 4s
1869. Private collection of Heteromerous Coleoptera, purchased £32 10s
1871. 271 butterflies. Purchased from Mr Hewitson from collection of A. R. Wallace, £26 14s
1871. Assorted insects selected from Wallace collection. Purchased from Mr. Higgins, £8 19s 9d
1874. Malay collection: three *Sospita*, two *Mycalesis*, and 40 small butterflies chiefly *Polyommatus*. Purchased from Mr Hewitson, £1.4s
1874. A few Coleoptera amongst specimens purchased from W. W. Saunders
1876. His private Collection of the following families of Malayan Coleoptera. Price £40.0.0. Anthribidae 1,080 specimens, Brenthidae 605, Malacodermata 909+ 35 half eaten individuals, Hydrophilidae &c. 107, Passalidae 86, Coprides 199, Dynastidae 19 Oryctes-68 other genera. Total 3,073
1877. 104 Carabidae from Malay Archipelago, included in lot 345 purchased at sale of Edwin Brown's collection
1896. Butterflies from Malay Archipelago in Godman-Salvin collection

Appendix D: Bird Skins Collected by A. R. Wallace in the Collection of the Oxford Museum of Natural History, Compiled by Darren Mann

Ref no	Name	Sex	Age	Locality	Collector	Method of acquisition	Acquisition
06385	*Aplonis panayensis strigata*	♀	Adult	Sarawak	Wallace	Pascoe collection	1909
14731	*Coracina papuensis melanolora*[a]	?	Adult	Gilolo (Halmahera, Moluccas)	Wallace	British Trust for Ornithology Collections, Tring, obtained for O.U.M. and presented by Dr. C.M. Perrins, Edward Grey Institute, Oxford	09 Dec 1969
11525	*Pitohui ferrugineus ferrugineus*	?	Adult	Misol Isl.	Wallace	C.M.N. White collection	1950
12362	*Nectarina solaris*[b]	♂	Adult	Flores	Wallace	Pascoe collection	1909

[a]*Campephaga melanolora* G.R. Gray
[b]Wallace AR (1863) A list of birds inhabiting the Islands of Timor, Flores and Lombok with descriptions of the new species p 486. Most likely collected by Charles Allen, as Wallace did not visit Flores

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Alfred Russel Wallace, Nature's Prophet: From Natural Selection to Natural Theology

Michael A. Flannery

Abstract Despite considerable research into this famed naturalist's life and work, the metaphysical views of Alfred Russel Wallace (1823–1913) remain controversial. This paper reviews Wallace's refurbishment of the argument from design, placing him within the highly charged intersection of biology and religion. Wallace's own evolution from nature to natural theology can be readily demonstrated in writings dating from 1843 to his death in 1913. Numerous works reveal Wallace as nature's prophet, a teleological visionary inspired by his unique experiences as a prodigious collector of species and keen observer of nature in South America and the Malay Archipelago. Furthermore, Wallace's refurbishment of the argument from design, eschewing the special creation of William Paley (1743–1805) for a more nuanced version of creative and purposeful theistic evolution, represented one of the most innovative contributions of its kind in the Victorian/Edwardian eras, influencing a later generation of scientists and intellectuals.

1 Whither This Prophet?

Alfred Russel Wallace (1823–1913) a prophet? A sorting out of meanings will help set the context. Various Hebrew terms can serve for prophet: rō'eh and *hōzeh* are generally rendered "seer," while *nāvi* is stronger, usually meaning one who speaks for God. But in the usage here Wallace is best viewed as a Greek *prophētē*, an interpreter much as the Greeks had interpreters for the muses, oracles, and gods. Thus, Wallace should not be seen as drawing a text from his observations of nature through which God openly spoke, but rather as an adept reader of patterns, codes and clues that he learned to abductively decipher. In the end this prophētē came to a comprehensive design inference (Wallace 1910b: 395–396):

> What I should imagine the highest intelligence engaged in the work (and this not the Infinite) to have done would be so to constitute the substance of our universe that it would

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> afford the *materials* and the best *conditions* for the development of life; and also, under the simple laws of variation, increase, and survival, would automatically lead to the maximum of variety, beauty, and use for man, when the time came for his appearance; and that all this should take place with the minimum of guidance beyond that necessary for the actual working of the life-machinery of all the organisms that were produced under these laws. Some such conception seems to me to be in harmony with the universal teaching of nature—everywhere an almost infinite variety, not as a detailed design (as when it was supposed that God made every valley and mountain, every insect and every serpent), but as a foreseen result of the constitution of the universe. The vast whole is therefore a manifestation of his power perhaps of his very self—but by the agency of his ministering angels through many descending grades of intelligence and power.

There was nothing new here for Wallace. Though he was never a professing Christian, Wallace had been increasingly prone to discerning design and purpose in nature. Some have insisted that Wallace's move in this direction was a product of his turn toward spiritualism in the mid-1860s (Kottler 1974; Turner 1974; Raby 2001), a movement that included some of the Victorian generation's best and brightest among its ranks.[1] There is some evidence for this. When, in the 1869 April issue of the *Quarterly Review*, Wallace famously broke with Darwin over the special attributes of man—calling upon no less than an "Overruling Intelligence" (Wallace 1869: 394) for the unique emergence and attributes of *Homo sapiens*—Darwin's contumacious colleague explained himself in a letter dated 18 April 1869: "My opinions on the subject have been modified solely by the consideration of a series of remarkable phenomena, physical and mental, which I have now had every opportunity of fully testing, and which demonstrate the existence of forces and influences not yet recognised by science" (Marchant 1916: 1:245). This comment notwithstanding, deeper reflection might have suggested other antecedents, more particularly an inclination against reductionist materialism in favor of a more neo-Platonic and ultimately theistic view of nature and the universe that long preceded his "heretical" article in the *Quarterly*.

Wallace claimed to have his first evidence for the existence of spirits during a séance on 22 July 1865 (Wallace 1895: 133). But Wallace's progressive march towards a teleological view of nature well preceded this. For example, in examining the habitat and habits of the orangutan while in Borneo he chided his colleagues for demanding a naturalistic purpose for everything in nature (Wallace 1856: 30):

> Naturalists are too apt to imagine, when they cannot discover, a use for everything in nature: they are not even content to let beauty be a sufficient use, but hunt after some purpose to which even that can be applied by the animal itself, as if one of the noblest and most refining parts of man's nature, the love of beauty for its own sake, would not be perceptible in the works of a Supreme Creator.

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[1] The Victorian period saw the rise of a spiritualist movement that included some first-rate and noteworthy scientists, such as philologist Frederic Myers, chemist William Crookes, philosopher/logician James Hervey Hyslop, Nobel laureates Lord Rayleigh (who discovered argon gas) and Charles Richet (first to describe anaphylactic shock), and famed psychologist William James. For details, see Blum (2007).

Citing *Plurality of worlds* (1855) by William Whewell (1794–1866) and Edward Hitchcock (1793–1864), both prominent creationists, Wallace suggested that beauty was an intrinsic part of creation itself well before his dabbling in spiritualism. The orangutans of Borneo seemed nearly human, but Wallace discerned profound differences that Darwin could not. Could the orangutan appreciate the beauty of nature in the same sense that man could? Herein lay an unbridgeable divide that would deeply impress Wallace when he later turned his attentions to human beings.

The important point to remember in this context, however, is that as Wallace developed his evolutionary theory, spiritualism and natural selection were complementary of a larger teleological world. The notion of Wallace the wide-eyed spiritualist and Wallace the rigorous scientist—the "two Wallaces" hypothesis—is simply wrong. More accurate is the assessment that Wallace "was an integrated personality whose worldview incorporated diverse fields and synthesized them into a comprehensive framework" (Fichman 2004: 188). The key lay in the explanatory power of utility not only within but across species and even kingdoms. For Darwin the principle of utility, aided only by sexual selection and pangenesis, "explained" all of evolution. By contrast, Wallace's view might best be called "intelligent evolution," defined as "a theory of common descent based upon natural selection strictly bounded by the principle of utility within a larger teleological and theistic framework" (Flannery 2011b:22).

As early as 1843, as a young man of 20, Wallace asked in a surviving note, "can any reflecting mind have a doubt that, by improving to the utmost the nobler faculties of our nature in this world, we shall be the better fitted to enter upon and enjoy whatever new state of being the future may have in store?" (Wallace 1906:1:203). Martin Fichman has commented that this early musing reflected Wallace's tendency to cast his worldview even then towards "the broader framework of a purposeful cosmology" (Fichman 2004:79). Reflecting upon a "new state of being" was, after all, surely not destined to fertilize a materialistic mindset. Moreover, the question he posed would consume the remainder of his life. More than 60 years later, a few years before his death, Wallace would write to Mrs. Fisher (Arabella Buckley) on 6 March 1909, "Another point I am becoming more and more impressed with is, a teleology of fundamental laws and forces rendering the development of the infinity of life-forms possible (and certain) in place of the old teleology applied to the production of species" (Marchant 1916: 2:99). One year later he would culminate this view with the publication of *The world of life: a manifestation of creative power, directive mind and ultimate purpose*.

Wallace's long journey to *The world of life* commenced in an exotic part of the world—in the Malay Archipelago. Like all prophētæ Wallace needed to begin by reading the text before he could interpret it, and among the verdant forests teeming with colorful and exotic flora and fauna, in many cases unique in the world, what a truly resplendent and magisterial text it was!

2 Reading Nature's Text

Wallace's interest in what was then called transmutation began when he read *Vestiges of the natural history of creation*, a cosmological work written anonymously and published in 1844, later discovered to have come from the journalist/publisher Robert Chambers (1802–1871). Chambers speculated that the universe, from the solar system to the earth (including all species and man himself), evolved from lower forms. In December of 1845 Wallace wrote to his friend Walter Henry Bates (1825–1892), calling it "an ingenious hypothesis strongly supported by some striking facts and analogies, but which remains to be proved . . . ." (Wallace 1906: 1:254). This impelled Wallace to confirm Chambers' "ingenious hypothesis" from evidence in nature itself. It would, thought Wallace, only take someone willing and able to see it.

By the spring of 1848 Wallace had fueled a sufficient wander lust in his beetle-collecting friend Bates to convince him to embark upon an expedition to Brazil, a trip that would last more than 4 years. He and Bates eventually split up, but Wallace would spend his time profitably, living among the Indians of the Uaupés River Valley, exploring the remote regions of the Rio Negro and Orinoco rivers in the heart of the Amazon, and collecting an estimated 10,000 specimens (Fagan 2007). Unfortunately, a shipboard fire on the Helen during his return to England left him barely escaping with his life and virtually empty-handed when he returned in October of 1852. Although not a complete loss, it was close to it. Except for some of his journals and drawings, Wallace lost everything—specimens of butterflies, beetles, ants, river tortoises (many he believed to be new), "little known" fishes, skeletons and skins of an ant eater and manatee, and a menagerie of live monkeys and exotic birds were all gone (Wallace 1852).

Dissatisfied with his losses and his inability to resolve the question of transmutation, Wallace resolved to embark upon another voyage, this time to the Malay Archipelago. This 8-year adventure from March of 1854 to his return to England in March of 1862, Wallace would call "the central and controlling incident in my life" (Wallace 1906:1:336). The details of this fascinating and indeed historic expedition have already been well covered in the literature (Raby 2001; Fichman 2004; Slotten 2004; Flannery 2011a), including Wallace himself (1876), but of specific interest here are those insights leading the way to Wallace unlocking the secret of transmutation, which Darwin would acknowledge as the co-discovery of the theory of natural selection.

Wallace's collecting was not a mere hobbyist's amusement; it was his livelihood. His financial success depended upon his ability to collect sufficient specimens to earn a profit through his agent Samuel Stevens' sales. Thus, only two things—weather or illness—could ever slow Wallace down sufficiently to turn his attentions from the practical pursuits of obtaining, mounting, skinning, and stuffing rare and exotic species (the rarer and more exotic the better) toward theorizing about the diversity of life. It is not surprising then that the first major breakthrough came while he was in Sarawak on the island of Borneo during the rainy season of 1855. It arrived in the form of a paper titled, "On the law which has regulated the introduction of new species." From four geographical and five geological principles, Wallace deduced that, "*Every species has come into existence coincident both in space and time with a pre–existing closely allied species* [italics in the original]" (Wallace 1855: 196). The significance of Wallace's "Sarawak Law" was immense. Iain McCalman has called it "the first ever British scientific paper to claim that animals had descended from a common ancestor and then produced closely similar variations which evolved into distinct species" (McCalman 2009: 266).

A few immediately recognized its implications. Bates, Wallace's former partner in South America, called it "like truth itself," an argument so tightly reasoned that it "embraces the whole difficulty, and anticipates and annihilates all objections" (Slotten 2004:135). Famed geologist Sir Charles Lyell (1797–1875) took note too, and urged his friend and colleague at Down House to do likewise or risk losing priority to this Spice Island naturalist. Edward Blyth (1810–1873), curator of the Museum of the Royal Asiatic Society of Bengal in Calcutta, also recommended the paper to Darwin (Marchant 1916: 1:141–143). But curiously many missed the paper's significance (Darwin included).[2] Darwin's leading biographer believes he was too self-absorbed to see the connection: "he was not prepared to see the possibility that someone else might be hesitantly circling around before arriving at the same theory. His own work, not Wallace's, was primary" (Browne 1995:538). Although largely ignored at the time, Wallace noted with some pride that years later Thomas Henry Huxley (1825–1895) admitted, "On reading it afresh I have been astonished to recollect how small was the impression it made" (Wallace 1906: 1:355).

The second great breakthrough came while ill—during bouts of malarial fever to be specific—on the island of Gilolo in late February in the form of a letter to Darwin. Wallace likely finished the letter and sent it from Ternate in the Moluccas island group in March or April with Darwin receiving it on 18 June 1858. The letter titled "On the tendency of varieties to depart indefinitely from the original type", shook Darwin to his core, after all he had been working quietly on the problem for years and now this from someone who many regarded as a mere "species haggler" from an unknown island in a remote corner of the world. Darwin immediately rushed a letter to Lyell: "I never saw a more striking coincidence. If Wallace had my M.S. sketch written out in 1842 he could not have made a better short abstract! Even his terms now stand as heads of my chapters." Unable to conceal his distress, he ended, "So now all my originality . . . will be smashed . . . ." (Darwin 1897: 1:473).

The rest of the story is well known. Putting their collective heads together Lyell and Darwin's other close confidant, Joseph Dalton Hooker (1817–1911), decided to present portions of Darwin's work with Wallace's letter at the next meeting of the Linnean Society on 1 July 1858. The papers were read with both Darwin and

[2] Marchant reproduced the complete letter from Darwin to Wallace dated 22 December 1857. The substance of Darwin's reply seems dismissive and off-putting: "Though agreeing with you on your conclusion in the paper, I believe I go much farther than you; but it is too long a subject to enter on my speculative notions" (Marchant 1916: 1:141–142).

Wallace *in abstentia*; the former burying his infant son, the latter wholly unaware halfway round the world. Sixteen months later Darwin would publish *On the origin of species*. Wallace found out about the joint reading months later and was highly "gratified" of the notice the three had taken of his letter, observing with unconcealed pride, "This insures me the acquaintance of these eminent men on my return home" (Wallace 1906: 1:365). With this introduction to England's scientific elite Wallace went from "species haggler" to naturalist, a recognition that the self-taught explorer probably never could have achieved on his own, especially in class-conscious London.

More importantly for posterity is the question, how similar really were Wallace's and Darwin's evolutionary theories? Most authorities today recognize significant differences in their respective ideas (Gayon 1998; Kutschera 2003; Bulmer 2005; Fagan 2007). Darwin stressed examples of domestication in making his argument; Wallace rejected this notion and insisted that domestic stocks were inherently unnatural and were the result of intentional selective breeding and protective shielding from the normal selection pressures of nature. This was a significant difference. Jean Gayon has argued that Darwin's domestication examples were not simply metaphorical pedagogical devices, they were essential to the theory itself (Gayon 1998: 59). Domesticated animals returned to the wild, Wallace observed, either perished or reverted to their original type. Darwin tried to cite examples from the plant and animal kingdoms to demonstrate natural selection too; Wallace used only insects and vertebrates to make his argument. Also, Darwin emphasized individual struggle amidst varying and random selection pressures; Wallace tended to stress competition among demographic groups and between species.

While generally true, this last point must be approached with caution. Melinda Fagan has correctly observed that Wallace emphasized groups, but this is because his collecting routine demanded quantity. In effect, he had to collect twice; once for his agent Samuel Stevens to sell and once for himself. Wallace collected hundreds of thousands of specimens over his 12 years of exploration, and it allowed him to see animals within the larger context of groups and populations. As mentioned earlier, collecting was Wallace's livelihood; not so for Darwin, who could meticulously examine individual variations without the need of keeping a steady stream of specimens flowing to an agent for sale. However, as Fagan notes, it is wrong to see Wallace solely as a group selectionist. "As in Wallace's other writings from the field," she adds, "the individual and group levels are linked via the notion of abundance, the number of individuals composing a group. . . . Thus 'continuance of the species and the keeping up of the average number of individuals' amount to the same thing" (Fagan 2007:629). Michael Bulmer agrees, "Wallace's variations did not differ from each other much more than Darwin's individual differences" (Bulmer 2005:132).

The final difference worth noting here is how the two naturalists saw their theories functioning practically in nature. For Darwin, natural selection was cast as the drive train for species diversification; for Wallace, however, the operative feature of natural selection was in the elimination of the unfit. Charles H. Smith has pointed out that Wallace's view of natural selection as an exterminating rather than a building force—the elimination of the unfit—avoids Darwin's rather awkward tautology that "survival of the fittest" means only that the fittest survive. Indeed, he observes that "Wallace's conceptualization, focusing on an elimination (or extermination) of the unfit driving mechanism, might represent a better vehicle for relating natural selection to other evolution-related phenomena such as mass extinction, divergence, speciation and the origins of variation itself" (Smith 2012: 203). It might well be confirmed at the molecular level as the principle that loss-of-function mutations are the "first rule of adaptive evolution" (Behe 2010).

Suffice it to say that although both men were enthusiastic readers of nature's text they really examined it in different languages; Darwin, in the language of the intricate details of individual competition and struggle in geologic time, read with the eye of well-schooled privilege; Wallace, in the language of demographic groups populated by individual species within the broader geographical landscape, read with the working-class eye of an autodidact from the school of hard knocks. Thus the stories they told came to be very different. But at the time no one seemed to notice at the poorly attended Linnean Society meeting where Darwin and Wallace's respective papers were first read.

3 Interpreting Nature's Text

Although it was not obvious in 1858, the different intellectual worlds with which Darwin and Wallace were familiar were bound to erupt in schism. Imbued with notions of radical materialism at Edinburgh's freethinking Plinian Society 32 years earlier, a very young teenage Darwin (attempting unsuccessfully to train for a career in medicine) cast his science in the mold of methodological naturalism tutored by his university mentor Robert Edmond Grant (1793–1874). Not only did the young Charles learn about aquatic invertebrates from Grant, he also learned that there was "no spiritual power behind nature's throne. The origin and evolution of life were due simply to physical and chemical forces, all obeying natural laws" (Desmond and Moore 1991: 34). Later, while Darwin was compiling his notebooks, it is clear that he was drinking from the wells of skepticism provided by David Hume (1711–1776) and of positivism by Auguste Comte (1798–1857).[3]

Wallace's early mentors were a very different lot. From his youthful days with his brother in the working class districts of London he was instilled with the radical idealism of Robert Owen (1771–1858), whose views about social reform would in some measure always stay with him. Through Owen's son, Robert Dale Owen

[3] On Darwin's references to Hume, see Paul H. Barrett, Peter J. Gautrey, Sandra Herbert, et. al., transcribers and editors, *Charles Darwin's notebooks*, 1836–1844 (Ithaca, NY: Cornell University Press; British Museum, 1987), pp. 321, 325, 545, 559, 591, 592, 596. On Darwin's references to Comte, see *Charles Darwin's notebooks*, pp. 535, 539, 553, 566, 608. For more on Hume's and Comte's influences on Darwin, see William B. Huntley (1972) and Sylvan S. Schweber (1979) respectively.

(1801–1877), he would be introduced to the spiritualism of Emanuel Swedenborg (1688–1772). Though Wallace never declared himself a Swedenborgian, it is clear that he took his other-worldly revelations seriously. Yet it would be wrong to say that spiritualism formed a religious faith for Wallace, instead his growing theistic and scientific beliefs became a powerful synergy for his evolutionary teleology. Indeed, as one historian has aptly put it, "Wallace's scientific theism was his faith" (Fichman 2004: 162).

When, much to the chagrin of Darwin, Wallace rejected the idea that man's special attributes—abstract reasoning, love of music, appreciation of the numinous, empathy, etc.—could be produced solely by the processes of natural selection, and instead called upon an "Overruling Intelligence," it was actually based upon Darwin's own principle of utility in nature (Darwin 1859: 121), which Darwin described as variation "useful to each being's own welfare . . . preserved in the struggle for life" by the "strong principle of inheritance."

Wallace's position was really rather simple. Wallace pointed to the human intellect as being too great to be produced simply by natural selection because, by definition, the principle of utility as described by Darwin himself would be an effective barrier to its development. In what sense, Wallace asked, does the ability to reason abstractly, perform mathematics, play music, create art, or any of a number of uniquely human abilities and propensities afford a survival advantage in nature? Lacking a convincing answer, some other cause or action must be invoked. That cause of action Wallace called "an Overruling Intelligence."

The 1869 break with Darwin was not sudden. It could be seen in a line of reasoning that began with a paper Wallace read on "The origin of human races and the antiquity of man" before the Anthropological Society 5 years earlier. In this paper Wallace asked, "Can this theory [of natural selection] be applied in any way to the question of the origin of the races of man? or is there anything in human nature that takes him out of the category of those organic existences, over whose successive mutations it has had such powerful sway? There is, as a general rule [among animals]," Wallace noted, "no mutual assistance between adults, which enables them to tide over a period of sickness. Neither is there any division of labour; each must fulfill all the conditions of its existence, and, therefore, 'natural selection' keeps all up to a pretty uniform standard. But in man, as we now behold him," he added, "this is different. He is social and sympathetic" (Wallace 1864: clxii). For Wallace, at some point in the distant past the hominid form, devoid of sociability, sympathy, or anything approaching human reason, acquired a brain with the capacity for all of those things, at which point natural selection ceased to operate upon human physical structures. Man was no longer slave to the capricious tyranny of natural selection but conquered it through his extraordinary mental capacities. Wallace saw in man not continuity with nature but indeed something special (Wallace 1864: clxviii):

> Here, then, we see the true grandeur and dignity of man. On this view of his special attributes, we may admit that even those who claim for him a position as an order, a class, or a sub-kingdom by himself, have some reason on their side. He is, indeed, a being apart, since he is not influenced by the great laws which irresistibly modify all other organic beings.

> Nay more; this victory which he has gained for himself gives him a directing influence over other existences. Man has not only escaped 'natural selection' himself, but he actually is able to take away some of that power from nature which, before his appearance, she universally exercised.

Darwin should have seen trouble brewing in Wallace's address, but like the Sarawak Law paper he missed its implications. True, Wallace still reserved a place for natural selection in developing the mind of *Homo sapiens*, but its net effect was to sever the whole idea of the continuity of man and beast. It is odd then that Darwin considered it the best paper to ever appear in the society's journal. Just as Darwin was shocked to receive the Ternate letter, he was now flabbergasted at Wallace's abandonment of naturalism in the April 1869 issue of the *Quarterly review*. "I groan over man," he wailed, "and you the author of the best paper that ever appeared in the *Anthropological Review*! Eheu! Eheu! Eheu!—Your miserable friend, C. Darwin" (Marchant 1916: 1:252).

Perhaps Darwin's dismay was all the stronger because this defection came on the heels of an ardent and able defense of evolution in 1867 against George Douglas Campbell (1823–1900), 8th Duke of Argyll, and his book, *The reign of law*, which criticized natural selection and instead argued for the direct intervention of a divine Creator. Wallace would have none of Campbell's neo-Paleanism—*almost* none—and it is this almost that is most interesting. Typically Wallace's famous "Creation by law" reply to the Duke is considered a "closely argued but courteous demolition job" or a "trounce of outmoded views" (Raby 2001: 196; Slotten 2004: 260).[4] But a careful reading of Wallace suggests nothing quite so devastating. Wallace simply pointed out that nature did not require a Creator's *constant* interference. Wallace seemed to suggest it *did* require a Creator. Wallace indicated a front-loading of nature with laws designed to produce certain ends. In this sense life depends upon "general laws, and not on a continual supervision and re-arrangement of details." Wallace declared, "As a matter of feeling and religion, I hold this to be a far higher conception of the Creator and of the Universe that [sic] that which may be called the 'continual interference' hypothesis" (Wallace 1871: 268). Wallace continually referred to "the Creator" and a "creative mind" in the essay, and much later Wallace would discuss a "creative mind" not in the context of "feeling and religion" but as a matter of science in *The world of life*. Taken in its entirety the essay was not simply a reply to the Duke's neo-Palean musings but a proglomenon for Wallace's larger teleological vision. Even more interesting, when Wallace reprinted "Creation by law" in his collected essays 3 years later he added a table of "demonstrations" of evolution by natural selection, which he defined as "meaning simply, that on the whole those die who are least fitted to maintain their existence" (Wallace 1871:302). As mentioned earlier, natural selection for Wallace was largely a subtractive, eliminating force in nature.

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[4] "Creation by law" originally appeared in the October 1867 issue of *The quarterly journal of science*. Wallace reprinted it with certain revisions and additions in his collected works, *Contributions to the theory of natural selection*, first published in 1870 and reissued 1 year later "with corrections and additions."

So if natural selection was a force of extermination, what could account for a being as complex as man? Here Wallace ventured upon a fuller explanation of his views in “The limits of natural selection as applied to man” (Wallace 1871: 332–371). The unique physical features of *Homo sapiens* (nakedness, sensitive skin, bipedalism with hands freed for use, the ulnar opposition of the hand) and their special mental capacities required something beyond natural selection. Turning the tables on Darwin’s own domestication analogy (after all, the breeding of fancy pigeons was if nothing else *purposeful*), Wallace concluded, “The inference I would draw from this class of phenomena is, that a superior intelligence has guided the development of man in a definite direction, and for a special purpose, just as man guides the development of many animals and vegetable forms” (Wallace 1871:359).

Thus, Wallace would profoundly disagree with Darwin’s major premise in *Descent of man* that “the difference in the mind between man and the higher animals, great as it is, is certainly one of degree and not of kind” (Darwin 1871: 101). His disagreement had nothing to do with the age of man. Wallace was quite willing—even eager—to allow the great age of man, perhaps he thought even back millions of years to the Miocene period. But lack of confirmatory evidence remained a problem. Nevertheless, it would leave Wallace’s thesis of the unique nature of man unaffected. On 6 September 1876, as president of the biology section D, Wallace addressed his colleagues at the British Association for the Advancement of Science on the “Rise and progress of modern views as to the antiquity and origin of man” (Wallace 1877: 114):

> If, then, continued researches in all parts of Europe and Asia fail to bring to light any proofs of his [mankind’s] presence, it will be at least a presumption that he came into existence at a much later date, and by a much more rapid process of development. In that case it will be a fair argument that, just as he is in his mental and moral nature, his capacities and aspirations, so infinitely raised above the brutes, so his origin is due, in part, to distinct and higher agencies than such as have affected their development.

Interestingly, Wallace defended his view that some “higher agencies” were required to account for the “mental and moral nature” of man by referring to Roman Catholic zoologist St. George Mivart (1827–1900), noting that Mivart “fully adopts it [naturalistic evolutionary processes] as regards physical structure, reserving his opposition for those parts of the theory which would deduce man’s whole intellectual and moral nature from the same source and by a similar mode of development” (Wallace 1877: 112). He and Mivart had sparred over a number of evolutionary issues, but in this they were one.

If life can be said to be governed by laws front-loaded from the beginning, and natural selection is essentially a negative subtractive force of extinction, what then is responsible for the creation of life? How have these “higher agencies” operated in the creation of life generally and man particularly? What are these “higher agencies”? These questions would increasingly consume Wallace’s attention.

The “how” of these questions was answered in Wallace’s *Darwinism*, his most complete exposition of evolution as he understood it. While the majority of the book was precisely what its subtitle indicated, “an exposition of the theory of natural selection with some of its applications,” chapter 15, “Darwinism applied to man,” formed a dramatic departure from his colleague who authored *The descent of man*. Wallace pointed out all of the things he had mentioned earlier, namely, that the complex and unique attributes of *Homo sapiens* could not be accounted for by the processes of natural selection. Furthermore, two other features of the natural world could not have been produced by natural selection, he argued: sentience in animals and the origin of life itself. Here only some "spiritual influx" could account for such complex processes (Wallace 1889: 476). Darwin would have certainly bemoaned this chapter, but he was spared what he would have doubtlessly regarded as Wallace's unscientific indiscretions, having died 7 years earlier.

The oddest thing about *Darwinism* wasn't chapter 15 (this chapter presented no major surprises for anyone familiar with Wallace over the past 20 years), it was the title itself. Wallace surely knew that he departed from Darwin significantly, so why he chose this title is peculiar. His old friend Herbert Spencer (1820–1903) thought so too. Noting his receipt of the volume, Spencer conveyed his surprise and disappointment, writing, "I regret that you have used the title 'Darwinism,' for notwithstanding your qualification of its meaning you will, by using it, tend greatly to confirm the erroneous conception almost universally current" (Marchant 1916: 2, 57).

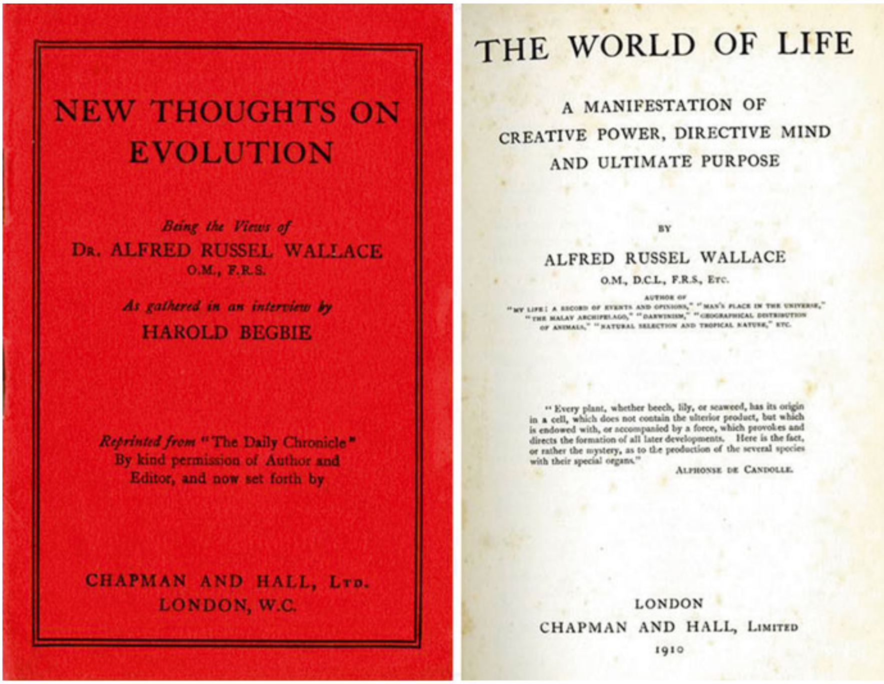
The most likely answer is that Wallace selectively chose not to emphasize the metaphysical differences between Darwin and himself. He had already been ostracized enough for his outspoken support of spiritualism; he probably concluded that any additional highlighting of explicit differences along these lines would only do harm. Additionally, Wallace tended to see Darwin's theory as synonymous with natural selection itself. This caused him to minimize his important conclusion that the origin of life, animal consciousness, and mankind's moral and mental natures were inexplicable by a naturalistic process. "These views caused much distress to the mind of Darwin," he explained, "but, as I have shown, they do not in the least affect the general doctrine of natural selection" (Wallace 1906: 2:17). Of course the fact is they *do* affect the theory of natural selection because an essential question with regard to its operations is its extent and its explanatory power. If natural selection (along with a couple of other wholly naturalistic subsidiary theories like sexual selection and pangenesis) essentially explains all of life, then Darwin's statements that he was "inclined to look at everything as resulting from designed laws, with the details, whether good or bad, left to the working out of what we may call chance" (Darwin 1897: 2:105), or that "There seems to be no more design in the variability of organic beings, and in the action of natural selection, than in the course which the wind blows" (Darwin 1897: 1:278–279), make perfect sense. But for Wallace this was precisely what evolution was not. One can only conclude that Wallace recognized this difference but that he probably chose to ignore it for strategic reasons.

It remains worth pointing out that the differences in the two men's theories noted from the beginning—the analogy to domesticated breeds that Wallace always considered false, Darwin's reference to plants that Wallace at least initially ignored, and Darwin's emphasis upon time (i.e., transmutations occurring very slowly and incrementally), which was not emphasized by Wallace—grew into huge departures as their respective evolutionary ideas developed. Darwin's favored example of developing dogs, horses, and pigeons through selective breeding as perfect examples of evolution "in action" would later be picked up by his cousin Francis Galton in eugenics. Because such nature over nurture applications made little sense to Wallace, he would completely reject eugenic manipulations of humanity toward some contrived notion of racial "fitness" as "the meddlesome interference of an arrogant scientific priestcraft" (Marchant 1916: 2:261). Darwin's immediate application of his theory across plant and animal kingdoms suggested a broad sweep across all of life for common descent by means of natural selection, but Wallace (while not denying its application to plants) would be more discerning in his distinctions between plants and sentient life, a discernment that would reveal itself even more fully in his distinction of man from animals. Finally, as Wallace's address before the British Association for the Advancement of Science demonstrated, time mattered little to the teleological aspects of his theory. While Wallace generally agreed with Darwin that evolution transpired through slow incremental steps in an earth millions of years old, the case of humanity's ancient or relatively recent development mattered little. In fact, if a more recent view prevailed, the saltationist implications would demand some teleological guidance even more urgently. Upon such seemingly minor differences major metaphysical differences were built.

Toward the end of his life, Wallace elaborated upon his metaphysical ideas in three books. First was *Man's place in the universe* (1903), a cosmology emphasizing the uniqueness of humanity against the so-called Copernican principle, the notion (misattributed to Nicolaus Copernicus) that the vastness of the universe suggests that neither the earth nor its inhabitants hold a privileged place in the cosmos. Wallace elaborated a fine-tuning of the universe argument, concluding that the earth was likely the only habitable planet and surely the only planet capable of higher life forms. Thus, for Wallace, mankind was not only unique in the earthly world, he was likely unique in the universe as well. As for the biological world, Wallace then produced his grand evolutionary synthesis, *The world of life*. Wallace now saw "an ultimate Purpose, in the very existence of the whole vast life-world in all its long course of evolution throughout the eons of geological time." (Wallace 1910b: vii).

The following selections from *The world of life* and *New thoughts on evolution* demonstrate Wallace unequivocal commitment to design in the natural world (Fig. 1):

- On the origin of life. "[T]here was at some stage in this history of the earth, after the cooling process, a definite act of creation. Something came from the outside. Power was exercised from without. In a word, life was given to the earth" (Wallace 1910a: 6).
- On the living cell. "What we must assume in this case is not merely a force, but some agency which can and does so apply, and direct, and guide, and co-ordinate a great variety of forces . . . . What we absolutely require and must postulate is, a Mind far higher, greater, more powerful than any of the fragmentary minds we see around us, a Mind not only adequate to direct and regulate all the forces at work in living organisms, but which is itself the source of all those forces and energies, as well as of the more fundamental forces of the whole material universe" (Wallace 1910b: 337–338).


NEW THOUGHTS ON
EVOLUTION

Being the Views of
DR. ALFRED RUSSEL WALLACE
O.M., F.R.S.

As gathered in an interview by
HAROLD BEGBIE

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THE WORLD OF LIFE

A MANIFESTATION OF
CREATIVE POWER, DIRECTIVE MIND
AND ULTIMATE PURPOSE

BY

ALFRED RUSSEL WALLACE
O.M., D.C.L., F.R.S., ETC.

AUTHOR OF
"MY LIFE: A RECORD OF EVENTS AND OPINIONS," "MAN'S PLACE IN THE UNIVERSE,"
"THE MALAY ARCHIPELAGO," "DARWINISM," "GEOGRAPHICAL DISTRIBUTION
OF ANIMALS," "NATURAL SELECTION AND TROPICAL NATURE," ETC.

"Every plant, whether beech, lily, or seaweed, has its origin in a cell, which does not contain the ulterior product, but which is endowed with, or accompanied by a force, which provokes and directs the formation of all later developments. Here is the fact, or rather the mystery, as to the production of the several species with their special organs."

ALPHONSE DE CANDOLLE.

LONDON
CHAPMAN AND HALL, LIMITED
1910

Figure 1 *New Thoughts on Evolution* was issued as a promotional pamphlet by Chapman and Hall for *The World of Life*. Images courtesy of the Reynolds-Finley Historical Library, University of Alabama at Birmingham.

- On the bird's wing. "Looking at it as a whole, the bird's wing seems to me to be, of all the mere mechanical organs of any living thing, that which most clearly implies the working out of a preconceived design" (Wallace 1910b: 287).
- On plant growth and insect metamorphosis. Certain "phenomena occur during the growth of the plant, which are, as I suggested from other facts, comparable in complexity with those of the metamorphosis of the higher insects, and, therefore, equally requiring the agency of some high directive power for an adequate rational explanation of them" (Wallace 1910b: 332).
- On man. "I hold that there was a subsequent act of creation, a giving to man, when he had emerged from his ape-like ancestry, of a spirit or soul. Nothing in evolution can account for the soul of man. The difference between man and the other animals is unbridgeable" (Wallace 1910a:7).

This was clearly not Paley's natural theology with its interventionist Creator forming species each suited uniquely to their place and environment. The creative processes were angelic efficient causes (Wallace 1910b: 392) leading towards an ultimately unknowable final cause, not first cause interventions. But in some sense it wasn't far from Paley. Regarding life Wallace *did*, in fact, believe in an act of creation.

Finally, the year of his death, Wallace put together the social implications of what by then had truly become a natural theology in *Social environment and moral progress*. The “spiritual influx” he appealed to nearly a quarter century before had now become a “divine influx” (Wallace 1913: 92, 115, 119), demonstrating the long influence of Emanuel Swedenborg (1688–1772), whom he considered a “great philosopher and seer” (Wallace 1913:137). The “higher” and “lower” races of Wallace’s Victorian generation had now found a moral and intellectual equality in innately *human* traits (Wallace 1913: 31–35). In the end, Wallace himself came to rely upon sexual selection, but not Darwin’s brand. Instead Wallace came to a view of society’s advancement through a teleological evolution guided by the intelligent sexual selection of women unencumbered by the artificial constrains of patriarchal social conventions (Wallace 1913: 147–149). This required removing any and all constraints upon women’s roles in science, business, the arts, or politics. For Wallace, universal suffrage was just one step in granting to women their rightful place in the evolutionary advancement of mankind.

Wallace’s natural theology was at heart idealistic. It suggested a libertarian socialism in which society was constituted so as to encourage the free cooperation of all members, with women having the economic independence to possess a free and unfettered choice in marriage. Wallace, an avowed socialist who supported land nationalization, was no proponent of absolute state control over society—that government really was best that governed least—but it would take a system premised upon cooperation rather than competition. Only in that way could the purposes of evolution be achieved and realized. Some have called Wallace a mystic, but his was a natural theology of idealism not of mysticism. For example, he thought that reincarnation and theosophy were “purely imaginative” and irrational. Nor was Wallace a pantheist or panentheist. He was unimpressed by Henri Bergson’s (1859–1941) precursors to process philosophy.[5] So what were the components of Wallace natural theology? In a letter to his close friend and biographer Reverend James Marchant (1867–1956) written just before his death, Wallace spelled out succinctly and in no uncertain terms his natural theology:

> The completely materialistic mind of my youth and early manhood has been slowly moulded into the socialistic, spiritualistic, and *theistic mind* [emphasis added] I now exhibit—a mind which is, as my scientific friends think, so weak and credulous in its declining years, as to believe that fruit and flowers, domestic animals, glorious birds and insects, wool, cotton, sugar and rubber, metals and gems, were all foreseen and foreordained for the education and enjoyment of man. The whole cumulative argument of my “World of Life” is that in its every detail it calls for the agency of a mind . . . enormously above and beyond any human mind . . . whether thus Unknown Reality is a single Being and acts everywhere in the universe as direct creator, organizer, and director or every minutest motion . . . or through “infinite grades of beings”, as I suggest, comes to much the same

[5] Alfred North Whitehead (1861–1947) founded process philosophy and acknowledged his tremendous debt to Bergson, but in a letter to Oxford’s Hope Professor of Zoology, Edward Bagnall Poulton (28 May 1912), Wallace dismissed Bergson’s “vague ideas” of “an internal development force . . . of no real value as an explanation of Nature” (Marchant 1916: 2:107–108). On theosophy and reincarnation, see his letter to “Mrs. Fisher” (née Arabella Buckley), 9 April 1897 (Marchant 1916: 2:218–219).

> thing. Mine seems a more clear and intelligible supposition . . . and it is the teaching of the Bible, of Swedenborg, and of Milton. (Marchant 1916: 2:195)

Wallace's three references are fascinating and insightful. First is his biblical appeal.

Wallace rejected key Christian doctrines such as sin, atonement, judgment, and damnation, but he was not averse to passages he thought appropriate such as Psalm 8:5 when he referred to, "Man himself . . . 'a little lower than the angels,' and, like them, destined to a permanent progressive existence in a World of Life" (Wallace 1910b: 400). Wallace was not particular about his terms either: "I believe all this [natural world] to be [under] the guidance of beings superior to us in power and intelligence. Call them spirits, angels, gods, or what you will; the name is of no importance," he declared in a New York Times interview, adding, "I cannot comprehend how any just and unprejudiced mind, fully aware of this amazing activity, can persuade itself to believe that the whole thing is a blind and unintelligent accident" (Wallace 1911).

As mentioned earlier, Wallace's reference to Swedenborg was also of considerable influence in his natural theology, but his final mention of Milton is perhaps even more interesting. Milton in some senses straddled pre-modern and modern theology. One is reminded of the nine heavenly orders described in the celestial hierarchy. Attributed to Dionysius the Areopagate (ca. fifth century), the idea of an ordered ranking of angels "whose obedience and ministry God employs to execute all the purposes which he had decreed" was championed by Thomas Aquinas and numerous lesser divines for more than a thousand years (Patrides 1959: 155). The seventeenth-century poet was one of the last to extensively acknowledge that the angels are "distinguisht and quaterniond into their celestiall Princedomes and Satrapies" (Patrides 1959: 163), and this fit with Wallace's teleological model. Wallace rejected man as a fallen and sinful creature who needed a Redeemer, yet the biblical hierarchies harkened to a scala naturæ that clearly appealed to Wallace.

Wallace's cosmology and biology formed an important and coherent challenge to the ascendant Victorian materialism, confirming recent scholarship suggesting that the angelic hierarchy lived on well past the Reformation (Mohamed 2004). Thus, Wallace's natural theology presents a Janus-faced view. Looking to science for a new and powerful foundation upon which to build a natural theology for the future, he filled in those details by taking, in several respects, a premodern approach.

Today we find the debate continues over the nature of science and the biological paradigm. Mathematician and philosopher William A. Dembski admits that much of premodern thought was worth discarding, but notes that only premodernity entails "a worldview rich enough to accommodate divine agency" (Dembski 1999: 45). Wallace, then, becomes a linchpin between past and present. To see exactly how, a few words on Wallace's impact upon later generations are in order.

4 Wallace's Legacy

Because Wallace drew from biblical sources in his natural theology, it should come as little surprise that his ideas found a welcome reception among theologians. John Magens Mello (1836–1915), vicar of Mapperley, was captivated by Wallace's *World of life* and wrote a pamphlet, "The mystery of life and mind," extolling its virtues. The reverend Mello found no contradictions in Wallace's spirit-driven world (Flannery 2011b: 238):

> To whatever extent any may be disposed to accept or reject these views [of Wallace's] upon Creation, we must all of us admit, if we do not set aside the teaching of Holy Scriptures, that there are in the Universe Spiritual Intelligences besides Man; Beings over and over again referred to in the Bible; and we are here taught that by God's appointment they have special duties and work to perform in connection with this World and with us Men. Our Lord Himself speaks to us in no uncertain terms of the Ministry of Angels, and of the interest they take in Human life.

Similarly, James Orr (1844–1913), an important conservative evangelical Presbyterian, reiterated Wallace's three points that chance and/or necessity could not account for—the origin of life, the transition of strictly organic life to conscious life forms, and human personality imbued with rational and moral natures (Orr 1917: 1:345–347). In this same category belongs the devout Catholic playwright and poet Paul Claudel (1868–1955). In fact, Claudel's faith was restored by *Man's place in the universe*. Initially shaken in his youth by the thought that man may not be alone in the universe, Claudel was won over by Wallace's tight reasoning and careful demolition of the Copernican Principle. He would later write (in words that could have been penned by Wallace himself) that God "Wanted also, near to his heart, /Beyond visible things, /To reserve to himself as servants/The inextinguishable order/Of beings in which all was spirit" (Nichols 2011: 3, 167, 168).

As one might expect, Wallace left his mark among scientists as well. Physicist and fellow spiritualist Sir Oliver Lodge (1851–1940), who Wallace knew and corresponded with, wrote two books that show Wallace's influence: *Man and the universe* (1908) and *Evolution and creation* (1926). Rejecting Darwin's animal/man continuity of kind, Lodge (like Wallace) saw in man "a being . . . with the ingredients of divinity" (Lodge 1926:158). Even more interesting is South African physician/paleontologist Robert Broom (1866–1951), whose book *The coming of man* (1933) presents a teleological evolution remarkably similar to Wallace. Broom acknowledged this similarity despite the fact that he claimed never to have read *The world of life*. But he was generally familiar with Wallace's ideas and observed that since life forms seem to have ceased evolving, "it looks as if the agencies that directed evolution are no longer active on earth, or at least that their activities are different. Possibly they are no longer interested in bodily evolutions, but engaged in the more important work of evolving higher types of human personality" (Broom 1933: 226). Finally is astronomer Fred Hoyle (1915–2001). Hoyle rejected Darwinian evolution, suggesting that to follow the theory to its logical conclusion would lead to self-destruction. With repeated references to Wallace, he instead believed that the "information-rich" universe suggested "a connecting chain of intelligence, extending downward from the largest universal scale . . . and thence by a series of further links to humans upon the Earth" (Hoyle 1983:245).

In the end, all of these voices testify that the ghost of Wallace still haunts the certainties of the most ardent Darwinian materialists because life, and especially personhood and qualia, in the words of one historian, remains their "unsolved problem" (Smith 2010). Wallace's relevance persists because he spoke to the human enigma—recognizing it as resolvable only in a spiritual context—and exposed the hubris of those who thought otherwise. If this was uncomfortable for many and exacted upon Wallace a professional price, it was also said long before him that a "prophet has no honor in his own country."

Wallace's friend and biographer James Marchant (1867–1956) was most accurate when he wrote, "He had the vision of the prophet allied with the wisdom of the philosopher and the calm mental detachment of the man of science" (Marchant 1916: 2:258). He was indeed *nature's prophet*, for he had taken from nature's text and proclaimed an evolution of the earth and cosmos that incorporated natural selection, geology, anthropology, and biogeography into a teleological framework that eschewed Darwinian reductionism in favor of a broader scientific vision.

But what of that broader scientific vision? Many would not call Wallace's vision "scientific." Naturalists would argue that invoking such recondite forces as a "Mind" or "Overruling Intelligence" is inadmissible in the court of scientific inquiry because such supernatural explanations are preemptively precluded; only naturalistic explanations (those that can be empirically measured and demonstrated) count. All else is speculation. Biologist William George Thiselton-Dyer (1843–1928), representing the new generation of scientists who had thrown off all the older creationist assumptions and commitments, said precisely this to Wallace upon reading his *World of life*. "Science," he insisted, "can only explain nature as it reveals itself to the senses in terms of consciousness." For him this was science's "practical working basis." While appreciative of those seeking metaphysical answers, "I keep scientific explanations and spiritual craving separate," he added. He concluded by chiding Wallace for claiming that scientists "shirk the problem" because it is not a problem they are asked to solve (Marchant 1916: 2:107). Wallace disagreed, saying that he felt he had demonstrated that an "ever-present Mind" works "by and through the primal forces of nature by means of Natural Selection" (Marchant 1916: 2:108).

In some important ways the two colleagues were talking past one another. The great divide between them was the role or legitimacy of methodological naturalism. Darwin's *Origin* was persuasive precisely because of its commitments to methodological naturalism (Dilley 2013). But at its heart this is a philosophical and not a scientific question. James Martin Research Fellow in the Institute for Science and Ethics at Oxford University, Stephen Clarke, has, in fact, proposed that naturalists have no grounds upon which to oppose the supernatural and that their tendency to single out the supernatural for particular condemnation is a "mysterious" objection. "Because the supernatural cannot be excluded from science, and because the naturalist must defer to science about ontological as well as methodological matters," Clarke concludes, "the naturalist has no grounds for stipulating against the supernatural in her ontology" (Clarke 2009: 140–141). Bruce L. Gordon essentially agrees, suggesting that eight observations from current biochemistry, molecular biology, and genetics (observations, of course, not available to Wallace) suggest that "defenders of transcendence in nature" are justified in concluding that unguided neo-Darwinian evolution is "a demonstrably insufficient and untenable explanation" for the origin and diversity of life (Gordon 2011: 28–29). If Clarke and Gordon are correct, Wallace's *entire* body of work deserves fresh examination.

Whether one agrees or not, it must be admitted that Wallace's impact has not been insignificant nor is it likely to vanish any time soon. We are still reminded by thoughtful analysts today that in many ways life and the special capacities of human beings remain as resistant to a wholly naturalistic explanation as ever (Denton 2002; Le Fanu 2009; Nagel 2012). Hoyle said it best, "we shall need to understand why it is that the mysterious sanctity described by Wallace still persists, beckoning us to the Elysian fields, if only we will follow" (Hoyle 1983: 251).

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An Inordinate Fondness for Beetles. The Hero's Journey of Alfred Russel Wallace

Paul Spencer Sochaczewski

Abstract Alfred Russel Wallace was a self-taught (he left school at 13) British naturalist, a self-described "beetle collector" who explored 4 years in the Amazon and 8 years in Southeast Asia. During his Asian sojourn in the mid-nineteenth century he covered some 22,500 km through territories which are now Malaysia, Singapore and Indonesia. Wallace made his voyages without formal government support, without a floating base camp (like Charles Darwin had with HMS Beagle), without infrastructure, and without much cash. During his epic journey Wallace caught, skinned and pickled 125,660 specimens of "natural productions" including 212 new species of birds, 900 new species of beetles and 200 new species of ants. Consider just the logistics – how could one man, on a tight budget and without organizational support, often living rough in rainforests, collect, identify, mount, preserve and transport 8,000 bird skins and 100,000 insects? If Wallace did nothing more than collect and identify new species he would have left an important scientific legacy. But the breadth of his interests raised him to the top tier of scientists.

His travels through the Malay Archipelago, supported by his knowledge of geology, helped him develop his understanding of the dynamics of island biology. He observed that the "natural productions" he found in western Indonesia and Peninsular Malaysia were different to those in eastern Indonesia, due to changing sea levels and a combination of shallow seas and deep oceanic trenches. By studying these differences he developed a west-east boundary which came to be known as the "Wallace Line," the dividing point between (western) Southeast Asian fauna (elephants, tigers, monkeys and apes, hornbills) and fauna of the (eastern) Austro-Malayan realm (kangaroos, birds of paradise, marsupials). He campaigned against: vaccination, vivisection, "flat earth," gambling, foreign aid, welfare state, "junk" food, sweatshops, "red-tapism," child labor, and women's labor in coal mines. He promoted: women's liberation, food and drug controls, income tax, labor unions, food stamps, and a minimum wage.

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And what led Wallace to develop his contributions to the theory of natural selection, first the Sarawak Law (written during the period he spent in Sarawak as the guest of the White Rajah of Sarawak, James Brooke), and then the famous Ternate Paper in which he outlined the concept "the fittest would survive."? Wallace sent the Ternate Paper to Charles Darwin (who up to that point had not published one word on evolution) and at that point the conspiracy theorists get involved. Did Darwin and Wallace arrive at their similar ideas independently? Did Wallace get sidelined in the quest for priority by the more prominent and well-placed Darwin?

1 Introduction

Imagine Alfred Russel Wallace studying the maps in the Royal Geographical Society in London. It was late in January 1853, around the time of his 30th birthday, and he had recently returned from a 4-year adventure in the Amazon basin. In Brazil he tasted the thrill of collecting (and the difficulties and isolation of living in the poorly-explored tropics). More practically, he saw that he could make a modest living by sending specimens to his beetle agent in London for sale to British collectors. He encountered "savage man." He wrote several scientific papers and began his climb up the British scientific hierarchy. But like all heroes' journeys, his return home to England was bittersweet – he lost most of his collection and just about lost his life when the leaky brig on which he was sailing caught fire and sank 700 miles east of Bermuda.

Wallace was relieved to be back on *terrra firma* and happy to enjoy home cooking, but nevertheless needed to get back on his horse and travel again. But where? Return to South America, perhaps the Andes this time? Central America? The Congo basin? The Indian subcontinent? Oceania? No doubt he considered these destinations and any one of them would have been a suitable choice for the curious young man. So why did he choose to apply for a grant from the Royal Geographical Society for support to travel to the Malay Archipelago? Partly because that region offered the chance for him to gather additional evidence to develop his as-yet-unpublished theory of evolution, partly the fact that the Malay Archipelago had an abundance of unusual insects, birds and animals which he could collect, pickle and sell for a good profit in England.

But I like to think that Wallace, talking with people who had seen more of the world than he had, was moved by another consideration: the sheer poetry of destinations in the Malay Archipelago.

2 Travels in the Malay Archipelago

Sumatra and Ternate. Yogyakarta and Malacca. Singapore and Sarawak. Banda Naira and Bandung and Bencoolen. Names to excite the spirit. And nourishing the spirit was as much a Wallace trait as deciphering the mysteries of natural history and man's place in the universe.

Wallace got his travel grant – first class passage to Singapore – and between 1854 and 1862 spent 8 years in territories and colonies which are now Singapore, Malaysia and Indonesia.

The Malay Archipelago is the book he wrote about his Asian travels. It is, by any standard, one of the great travel books.

But what makes this work so impressive?

First, there is the boyish adventure of it all – not all of it cakes and ale. Wallace left school at 13, wandered in the British countryside collecting beetles, learned surveying from his brother and then saved up a pittance to travel far, initially to the Amazon and then to Southeast Asia where he often lived rough and isolated in alien lands without a formal support structure. Wallace needed at least a dozen men to move camp, something he did more than a hundred times during his 8 years in Asia. Charles Darwin, by contrast, used the H.M.S. Beagle as a floating base camp where he could return after a relatively brief shore exploration to the comfort of decent food, camaraderie, and clean clothes (although, to be fair, he had to share a cramped cabin with the ship's eccentric captain Robert Fitzroy). But Wallace faced problems more significant than moving camp. He persisted in spite of almost constant, and sometimes life-threatening, irritations like malaria, capsizing, incessant rain, infections, fungal invasions, giant snakes and thieving hired help.

Wallace wasn't a brave explorer in the Speke or Burton mold. Wallace admitted in his autobiography, perhaps a touch disingenuously: "[My deficiencies] have been my want of assertiveness and of physical courage, which combined with delicacy of the nervous system and of bodily constitution, and a general disinclination to much exertion, physical or mental, have caused that shyness, reticence, and love of solitude which, though often misunderstood and leading to unpleasant results, have, perhaps, on the whole, been beneficial to me."

Second, while exploring the Malay Archipelago Wallace came up with some of the more important scientific breakthroughs of the Victorian age. He identified how geological changes resulted in western and eastern Indonesia having different faunas, and different races of man – the dividing line he identified later become known as the Wallace Line, with elephants, tigers, monkeys and hornbills to the west and kangaroos, birds of paradise and marsupials to the east. He noted how changing sea levels created unique island species. He elaborated on the principle of mimicry, first posited by his Amazon travel companion Henry Walter Bates. And, in his most recognized accomplishment, he developed a groundbreaking theory of how natural selection leads to the evolution of species.

Third, he was an underdog on a classic hero's journey. In social terms, Wallace fought above his weight. He came from a middle class (and cash poor) upbringing but quickly came into contact with the aristocracy of the British scientific establishment. *The Malay Archipelago* helped establish Wallace as a scientific force.

Fourth, he cast his intellectual net widely; in the book he asks whether the tribal people he lived amongst were really more civilized than their European cousins, whether colonialism was a force for good for people in the tropics, what was the role of women in creating more equitable and productive societies, and whether the British social model represented the pinnacle of social evolution. He was remarkably productive – his lifetime output is a staggering 769 publications, including 508 scientific papers and 22 books, totaling some 10,000 pages of printed matter.

Fifth, he was flexible, able to be calculating and sentimental. We like our heroes to be complex and unpredictable. Notably, he writes how he shot an adult female orangutan to obtain her skin and skeleton and finding, when she fell from the tree, that she had been nursing a baby, which survived the fall. He adopted the infant and gushed: "I must tell you of the addition to my household of an orphan baby … which I have nursed now more than a month … I am afraid you would call it an ugly baby, for it has dark brown skin and red hair, very large mouth … I can safely say, what so many have said before with much less truth, 'There never was such a baby as my baby,' and I am sure nobody ever had such a dear little duck of a darling of a little brown hairy baby before." Sounding like a doting grandfather, he tells how he raised the infant and the antics of the baby orangutan and its playmate, a hare-lip monkey. Ultimately, the small red ape died, and Wallace, practical to the last, calmly boiled the corpse to obtain a valuable skeleton that he could sell in England.

Lastly, what makes the book special is Wallace's voice. While Wallace maintains a straight-forward tone in much of the book, his exuberance for life erupts frequently, particularly when he describes the thrill of discovering a new species of butterfly or beetle. In one of several such passages he describes the rush he felt when he captured a new butterfly on the isolated island of Bacan: "The beauty and brilliancy of this insect are indescribable, and none but a naturalist can understand the intense excitement I experienced when I at length captured it. On taking it out of my net and opening the glorious wings, my heart began to beat violently, the blood rushed to my head, and I felt much more like fainting than I have done when in apprehension of immediate death. I had a headache the rest of the day, so great was the excitement produced by what will appear to most people a very inadequate cause."

In geographic terms, the Malay Archipelago covers the region that now includes Malaysia, Singapore, Indonesia, Brunei, the Philippines and East Timor; some descriptions of the region include Papua New Guinea. Wallace never made it to the Philippines as originally intended; Malaysia, Singapore and Indonesia were his home for 8 years.

The Malay Archipelago is sometimes called Insular Southeast Asia; more than 25,000 islands in all. Wallace visited some 30 of them, some huge and well-known like Sumatra, Java and Borneo, others tiny and so obscure – like Watubela, Waigeo, Bacan – that most people today in the cosmopolitan Indonesian capital of Jakarta would have difficulty finding them on a map.

Wallace wrote: "This Malayan region is indeed remarkable in many respects. It is the largest Archipelago in the world. It contains the two largest islands in the world, one of which, Borneo, could embrace within its limits the whole of the British Isles from the Land's End to the Orkneys, and surround them on every side with a green ocean of tropical forest. It contains, in the great volcanic belt that runs through its whole extent, a vast number of active volcanoes, and is unequalled for the frequency of its eruptions and earthquakes....

> In the animal world, the most remarkable productions are the man-like orang-utang, found only in Borneo [Wallace was wrong, the animal also is found in Sumatra], and the lovely birds of Paradise, confined to the remote islands of New Guinea; while edible birds' nests and mother-of-pearl-shell are valuable and interesting products almost restricted to this region.

It is also a region of bewildering cultural diversity; indeed it is a truism that cultural diversity parallels biological diversity. Wallace compiled 57 vocabularies during his 8 years in Asia. By some standards he was merely scratching the surface, since Indonesia alone is home to some 735 languages (no one is quite sure of the exact number). According to one source, 637 of those languages are as endangered as the region's tigers, rhinos, orangutans and Komodo dragons, with each having less than 100,000 native speakers.

Like a modern baseball fan, Wallace was fascinated by numbers and statistics, indeed, he calculated his success to a large extent on what kind of numbers he could put up.

He traveled some 22,400 km (14,000 miles) and collected an astonishing 125,660 specimens; when these got sorted out he had discovered among them 900 new species of beetles, 200 new species of ants, and among the butterflies 50 new species of the Family Pieridae and 96 of the 130 known species of the Family Papilionidae.

He kept meticulous field notes and in his careful hand noted the statistics of his achievements:

> On good nights [in Sarawak] I was able to capture from a hundred to two hundred and fifty moths, and these comprised on each occasion from half to two-thirds that number of distinct species.
>
> When I arrived at the mines [in Sarawak] … I had collected in the four preceding months 320 different kinds of beetles. In less than a fortnight I had doubled this number, an average of about 24 new species every day.
>
> [Bacan island] was a glorious spot, and one which will always live in my memory as exhibiting the insect-life of the tropics in unexampled luxuriance … October 15th, 33 species of beetles; 16th, 70 species; 17th, 47 species; 18th, 40 species; 19th, 56 species – in all about a hundred species, of which forty were new to me.

Let's put Wallace's collecting into context. Even today, with our Tupperware containers and plastic bags, with our Gore Tex, with nylon tents and solar powered generators and internet connections to the world's taxonomic literature, with freeze-dried food and water purification systems and a thousand other helpful gadgets, gizmos and tools, it's uncomfortable to spend a night or two in the rainforest, particularly during the rainy season. The moisture seeps in everywhere, nasty biting bugs slip through the mosquito net, and sleep is uncomfortable and fitful. Wallace of course had none of our modern gadgets. Just making himself comfortable would have been difficult. Then try to understand how he managed several related tasks, each tricky in itself: collecting, taxonomy, preservation. How did he manage to skin thousands of birds and store them without camp dogs eating the carcasses? How did he pin tiny critters like ants and beetles in collecting bottles? How did he stop ants from eating his butterflies? How did he skin an orangutan and then butcher the corpse and boil away the muscles and flesh to get a taxonomically-useful, and commercially-viable skeleton? (The camp gear he lugged around included a giant skillet and kegs of local rice alcohol to preserve orangutan skeletons – the level of alcohol dipped dramatically if Wallace didn't keep the moonshine out of the reach of his porters). How did he pack all those specimens, knowing that they would have to endure extremes of heat and cold on a multi-month journey to reach his beetle agent Samuel Stevens in London?

History portrays explorers as fearless individuals who brave the elements alone, stoic, unflappable, and with immense strength of character and fortitude. But, actually, all explorers, the great as well as the ignored, rely on often-unheralded people to assist in their odyssey. Magellan had Enrique of Malacca, Lewis and Clark had Sacagawea.

Alfred Russel Wallace had Ali, and without Ali's assistance it is unlikely Wallace would have been as successful as he was.

Ali was perhaps fourteen and living in Sarawak when Wallace hired him as a cook and assistant. Ali accompanied Wallace on most of his Asian travels. Ali took on increased responsibility; he learned to collect and mount specimens and soon was organizing travel (just imagine the negotiations with self-important village chiefs, unreliable porters and laborers, and greedy merchants, whose eyes no doubt grew large when they saw a white man like Alfred come to buy supplies). I don't want to overstate Ali's importance, after all, he was just a naïve teenager when he started out, but Ali did become a valuable and trusted operations officer and friend. Wallace called him "my faithful companion."

3 Wallace's Legacy

In spite of his numerous accomplishments public attention almost always reverts to a discussion of Wallace's relation with Charles Darwin.

Outside of biology circles, Wallace is best-known, if he is recognized at all, for developing the theory of natural selection. Indeed, in his autobiography he wrote that one of his objectives in travelling to the Amazon, and later to Southeast Asia, was because "I begin to feel rather dissatisfied with a mere local [UK] collection; little is to be learnt by it. I should like to take some one family to study thoroughly, principally with a view to the theory of the origin of species." His first published notes on such a theory were written while Wallace was holed-up during the rainy season in the Borneo bungalow of James Brooke, the White Rajah of Sarawak. The appropriately termed Sarawak Law, published in 1855, states a principle that to a modern reader sounds almost simplistic: "Every species has come into existence coincident both in time and space with a pre-existing closely allied species".

Three years later, Wallace, suffering from a malarial fit, wrote what has become known as the Ternate Paper, a fully-thought out ten-page scientific paper that proposed a theory which Herbert Spencer later coined "the survival of the fittest." In his autobiography Wallace described his eureka-moment: "Why do some die and some live? And the answer was clearly, that on the whole the best fitted live. From the effects of disease the most healthy escape; from enemies, the strongest, the swiftest, or the most cunning … Then it suddenly flashed upon me that this self-acting process would necessarily *improve the race*, because in every generation the inferior would inevitably be killed off and the superior would remain – that is, *the fittest would survive* … I waited anxiously for the termination of my fit so that I might at once make notes for a paper on the subject. [italics Wallace]".

In the spring of 1858 Wallace sent his Ternate Paper to Charles Darwin. Darwin was astonished (and likely disturbed) by Wallace's well-thought out paper and wrote to his friend, the noted geologist Charles Lyell: "I never saw a more striking coincidence; if Wallace had had my manuscript sketch, written out in 1842, he could not have made a better short abstract of it." Darwin sought the advice of Lyell and botanist Joseph Hooker. With Darwin's approval, Lyell and Hooker called a special meeting of the Linnean Society in London and read Wallace's paper along with two shorter unpublished communications from Darwin. Up to that time Darwin had not published one word on evolution, although he had been working for years on the question of how species evolve. Some people think that Darwin, in spite of collecting evidence for years, did not understand the mechanism until Wallace inadvertently gave it to him. Some people argue that Darwin (and his friends) were so concerned with maintaining priority that they sidelined Wallace.

Historian Daniel J. Boorstin writes: "If a Greek dramatist had contrived two characters to show how fate could bring men by opposite paths to the same destination, he could hardly have done better than invent Darwin and Wallace. Darwin, the elder by a dozen years, had been dedicated by his wealthy family to a career in the Church. All his life Darwin did his best to follow Lyell's advice 'never to get entangled in a controversy, as it rarely did any good and caused a miserable loss of time and temper.' Tediously gathering specimens and evidence over two decades, Darwin seemed led to his theory of natural selection almost against his will. The impoverished Wallace, inspired early with a suspicion of religion and all established institutions, was hasty to embrace theories and plunge into controversy. When he was only 22, Robert Chambers' popular *Vestiges of the Natural History of Creation* had converted Wallace to an unshakable conviction that species arose through a process of evolution, and his trip to the Amazon was for facts to convince others. By his later trip through the Malay Archipelago … he aimed to gather conclusive evidence … Wallace's essay "On the Law which Has Regulated the Introduction of New Species" (Sarawak Law) was published 3 years before the paper he sent to Darwin," Boorstin said. "The facts of geographical distribution that provided the cautious Darwin with questions supplied the brash Wallace with answers".

The fact is that Wallace never directly challenged Darwin's claim to priority. Just the opposite. Using three different typefaces Wallace dedicated *The Malay Archipelago*: "To Charles Darwin, author of 'The Origin of Species,' I dedicate this book, not only as a token of personal esteem and friendship, but also to express my deep admiration for his genius and his works." In *The Malay Archipelago* itself Wallace mentions neither the Sarawak Law nor the Ternate Paper.

In spite of Wallace's decision to let Darwin do the heavy lifting in regards to evolutionary theory (or perhaps because of it) Wallace rose to the top ranks of British scientists.

Charles H. Smith, professor of Library Public Services and science librarian at Western Kentucky University, who runs a respected website devoted to Wallace, feels that Wallace was lauded during his lifetime and immediately thereafter, and his relative anonymity to modern readers is a recent phenomenon. Smith says: "At the time of his death in 1913 he may well have been the most famous scientist in the world … [observers referred] to him in the following glowing terms: 'England's greatest living naturalist'; 'the acknowledged dean of the world's scientists'; '[one of the two] most important and significant figures of the nineteenth century."

Like all good travel books *The Malay Archipelago* entertains. It teaches us something about the places being visited. It has layers of narrative, insight and unanswered questions. And most important, it shines a light into the psyche of the writer.

I have been following Wallace's trail for some 40 years. I wish I could travel in time and chat with this quirky, opinionated yet private man. Failing that, I carry a tattered copy of *The Malay Archipelago* and find comfort and stimulation in its pages.

Final Years and Death of Alfred Russel Wallace. 100 Years Later

John G. Wilson

Abstract This paper introduces us to the great naturalist Alfred Russel Wallace, and his time in Sarawak. It was here in Sarawak that Wallace achieved so much, and laid the foundation for the idea of natural selection. He lived to the great age of 90 years, continually writing up to the time of his death. His funeral and grave in the south of England are briefly described. But it is the writings of some of his visitors in his last few years that give us a true picture of the man with his overwhelming love of all things in the natural world. One of Wallace's visitors at this time was from Australia. He was my great uncle, who as a young man came to see his famous uncle towards the end of his life. My great grandfather was Wallace's cousin. Many of Wallace's ideas were controversial and none more so than his views on health and disease. He also believed in the existence of an 'all powerful being' or a Divine power in the universe to explain the wonder and mystery of life. Late in life Wallace received the acclaim he well deserved, receiving many public honours, which he received somewhat reluctantly, preferring to lead a quiet life at home. It is fitting we celebrate here in Sarawak the life of this much overlooked co-discoverer of the theory of evolution.

1 Introduction

Alfred Russel Wallace (Fig. 1) died on 7th November 1913 at the great age of 90. The year 2013 was the centenary of his death and is the reason we celebrated his life and the time he spent in Sarawak at Wallace Conference, held in Kuching.

Wallace had a long and productive life devoted to science. He was perhaps the last distinguished representative of an old type of naturalist, traveller, biologist, geographer, with a mind always seeking to discover the cause of things. He had little knowledge of modern chemistry, morphology or genetics now much used in zoological research. He was an avid and resourceful collector of facts about Nature, but not of scientific honors, which came his way in spite of himself, towards the end of

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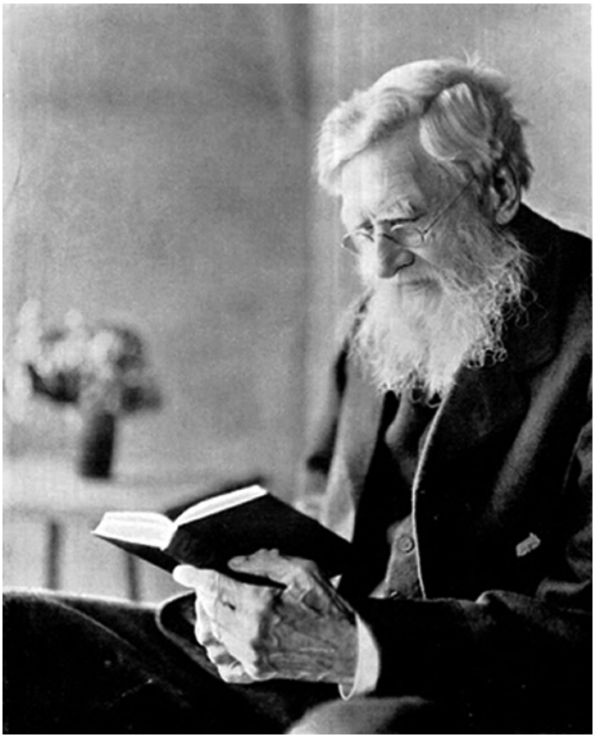

Fig. 1 Alfred Russel Wallace about 1910 aged 87 years

his life. Nevertheless he was a complete and happy man. He was a man of paradox. He was a precise and meticulous scientist, but also believed in phrenology and miracles. He was a man of great human sympathies, always ready to champion the cause of the oppressed, and to make the world a better place in which to live. He was a gentle man, reflective by nature, and had no ambition to shine forth among his fellow men.

In Sarawak he not only collected an enormous number of new species, but was beginning to formulate his ideas on the origin of species. He wrote his important Sarawak Law paper at the base of Gunung Santubong in 1855. In his travels he lived with the local Dyak people in their huts with skulls above his head. He greatly admired their simple way of life, and their life-style had a great influence on him.

After spending 8 years in the Malay Archipelago he arrived home and virtually spent the rest of his life writing books and articles, not only on evolution and natural selection, but on all sorts of subjects. He moved house many times continually looking for a milder climate as he continually suffered from asthma. In the past he had suffered from many attacks of malaria and other tropical illnesses from which he nearly died while in the Amazon It is amazing that he lived to such a great age.

2 Old Orchard

Wallace spent his last few years in the peaceful surroundings of his home, *Old Orchard*, at Broadstone, which is about 12 km from Bournemouth, in the south of England (Fig. 2). He had lived for 10 years at Parkstone and then decided to move because of the growth of buildings around him. In 1901 at the age of 78 years, he built *Old Orchard*. He bought the materials himself, and employed men to build the house. In 1903 he wrote of *the charming lodge in a wilderness I have got here*, *in which to end my days on earth. I assure you I am enjoying it*, *perhaps more than I should ever have done at an earlier period*.

His home *Old Orchard* in Broadstone has now been bulldozed to make way for a new housing estate. There is a street named Wallace Court in the area where the house and garden once were. There is a large eucalypt tree, which is thriving in one of the houses on the estate. It is a native tree of the Australian region, to the East of *Wallace*'*s Line*. Although he was more interested in alpine plant species at this time in his garden, I like to think of him planting this tree to remind us of the geographical division that he first described.

Fig. 2 Old Orchard where Wallace lived from 1902 to 1913

3 Writings

Although Wallace never changed his views on natural selection, his writing towards the end of his life was mainly philosophical. In 1910 he published *The World of Life*, which provoked great interest, and is one of his greatest books. In it he stresses the theme of "Purpose in the Universe", which is under the control of an all-powerful being. This is a belief he had held for some time. Wallace continued to write right up to the time of his death. In his last years he wrote two works *Social Environment and Moral Progress* and *The Revolt of Democracy*, the latter in his 90th year.

Wallace wrote 22 books as well as numerous articles and letters. He kept up with his many interests writing to the Land Nationalization Society, the anti-vaccination league, local newspapers and magazines on women's rights and many other issues. Spiritualism was one of his many interests. This alienated him from him from his scientific friends. He continued to crusade his socialist ideas throughout his life, and was forever hopeful that his reforms may help the poorer members of society. It was said that his pen was never dry!

4 Health and Disease

Wallace had always held strong views about the relationship of health to social and hygienic conditions. He argued that many forms of disease had been abolished by the improvement in the living conditions of the people. This was particularly true of the infectious forms of disease, and had been the basis of much of his objection to the practice of vaccination. It was far more important in his view that the cause of the disease should be removed than one should rely on methods of alleviation.

Although Wallace does not mention Louis Pasteur (1822–1895), he must have been conversant with the controversy that his Germ Theory of Disease was causing, as they lived at the same time. It fitted in well with the evolutionary ideas of the struggle for existence and survival of the fittest. It was man against the germs, man against man, nation against nation, animal against animal. We had to destroy the germs or they would destroy us. It was the most natural thing in the world for people to think that germs and men were mortal enemies. The battle lines were drawn. Most of the proponents of the theory of evolution accepted the germ theory of disease, however Wallace was not so keen.

Wallace argued in favour of the co-existence between man and his germs, as against the popular idea of competition and aggression between them. His objection to the idea of germ-causation of disease was based on the ground that "nothing in nature is not useful". He believed in the natural state of man's existence in society, that there was an innate harmony within nature *harmonia naturae*. Governments and man's interference were usually harmful.

He felt that the conflict between the host and the microbe served no useful purpose. He continually stressed that the healthy, adequately fed person was well placed to cope with the onslaught of these germs, and could co-exist with them.

> Wallace wrote: *The only doctrine on this matter worthy of an evolutionist, or a believer in God, is that health of body and mind are the only natural safeguards against disease; and that securing the conditions for such health for every individual is the one and only test of a true civilization.*

His arguments are now proving to make some sense. We are now seeing how we seem to be losing the race against disease with the use of antibiotics. As each new antibiotic is used it is not long before resistance occurs, rendering the drug useless in the fight against that particular "germ". This has prompted researchers now to follow a different approach with the accent in promoting good health of the patient rather than the use of multiple drugs. There is little doubt that one's own resistance to disease largely depends on the maintenance of standards of good health. I believe the medical profession are now coming to understand this.

5 Final Years

Towards the end of his life his favourite pastime, apart from writing was his garden. This was always "pure enjoyment". He never experimented on plants, nor studied their minute structure. To see them grow and noting their infinite variety of form and behaviour was a delight in itself.

He said:

> I have suddenly developed a sad mania for Alpine plants ..... the very first time in my life.....a bit of ground really suitable for them.....I have already got such a fine lot of plants, about 20 species of Primulas and 150 of Alpines generally.

His keeness and vitality kept him young up to the end of his long life. To his children he seemed never to grow old, and was said to have "the spirit of a boy of 16 years". He was forever looking forward, and never complaining about the past.

He said:

> If we do but get average weather next summer I hope to see a number of my best things in flower, which I have been waiting for this 5 to 10 years.

6 Some Visitors

As Wallace grew older he could not move about much so many of his old friends came to visit him at Broadstone. A frequent visitor was Professor Raphael Meldola, whom Wallace had known for over 30 years since living at Godalming in Surrey when he became interested in The Land Nationalization Society. Professor E.B Poulton of the Linnean Society was also a great supporter.

The Rev. James Marchant was a frequent visitor and subsequently wrote the first biography of Wallace, *Alfred Russel Wallace Letters and Reminiscences* in two volumes published a few years after his death (Marchant 1916).

Another and different visitor who came to see Wallace at this time was Ernest. C. Wilson, from Australia. He was my great uncle and the youngest son of Wallace's cousin Charles Wilson who had emigrated to South Australia with his parents in 1838. The young Wilson was staying with his uncle John W. Billiatt at Ottery St. Mary in Devon and wrote to Wallace. Wallace wrote back:

> We shall be very glad to see you and put you up for a night or two if you can cycle to us. It is only about 60 miles from your present place-an easy day's ride for a young man. Come as early as you like after Wednesday next as my daughter will be then at home. I am just now very busy building a new house, making a new garden. …Send a card the day before to let us know when to expect you….
>
> Signed Alfred R Wallace

There were others who came to visit Wallace and many who corresponded with him, particularly sending telegrams and letters on his birthdays as he grew older. He encouraged young naturalists, and one who went to Brazil gave up as he felt it was wrong to take the life of beautiful birds and insects. In the end Wallace had to agree with him!

Another visitor was Sir William Barrett who wrote of his visit in the last year of Wallace's life:

> …Dr Wallace then, pointing to the beautiful expanse of garden woodland and sea which was visible from the large study windows, burst forth with vigorous gesticulation and flashing eyes: "Just think! All this wonderful beauty and diversity of nature results from the operation of a few simple laws. In my early unregenerate days I used to think only material forces and natural laws were operative throughout the world. But these I now see are hopelessly inadequate to explain this mystery and wonder and variety of life. I am as you know, thoroughly convinced that behind and beyond all elementary processes there is a guiding and directive force; a Divine power or hierarchy of powers, ever controlling these processes so that they are tending to more abundant and higher types of life".

7 Death

Just before his 91st birthday, when he was still writing "how good the world was", he began to get weaker. Dr Scott the family doctor was called. After nearly a week of slowly fading, this great man died. It was on 7th November 1913.

As Rev. James Marchant wrote:

> …death came to him in his sleep as a gentle deliverer, opened the door into the larger and fuller life into which he tried to penetrate and in which he truly believed.
>
> He was amongst the foremost scientific men of the Victorian age and with his death that great period came to an end.

Alfred Russel Wallace was buried in a little cemetery just outside Broadstone, not far from his home. It had been suggested that he be buried in Westminster Abbey, but the family did not wish this. As Marchant records:

> He was laid to rest with touching simplicity in the little cemetery of Broadstone, on a pine-clad hill swept by ocean breezes.

Attending the service were his son William, his daughter Violet, and Miss Mitten, his sister-in-law. His wife Annie was unable to attend, as she was an invalid, suffering from severe arthritis. The Bishop of Salisbury, Dr Ridgeway conducted the service. Among those present were Professor Raphael Meldona and Professor E.B. Poulton representing The Royal Society and the Linnean Society together with Dr Scott, and Mr Joseph Hyder representing the Land Nationalization Society. It was a small, private, family funeral, much as he would have wanted (Fig. 3).

On the top of the Purbeck marble gravestone base has been erected a large fossilized tree trunk, from the local Portland beds. It reaches up to at least 3 or 4 m, and is a strange sight among the other gravestones in the cemetery. It was found on a local beach near Poole Harbour, and transported to the grave. This was probably done by his family to highlight his interest in natural history. Perhaps it was to make his grave stand out from the rest in the cemetery. For whatever reason, it certainly is unique, and unlike any other.

Fig. 3 The cortege on the way to the Broadstone cemetery

In August 1983, I was taken to the grave by one of Wallace's grandsons, who commented on the fact that, as he was not a church going man, this old fossilized tree-trunk seemed appropriate (Wilson 2000). His name is inscribed on the side of the base of the tombstone in clear lettering:

Alfred Russel Wallace. O.M.
Born Jan. 8th.1823. Died Nov. 7th.1913.

Wallace's wife, Annie, died a year later, and was buried with her husband.

8 The Grave

For many years the grave lay unattended and became overgrown with creepers and in need of repair. In April 2000 the Linnean Society decided to raise money to upgrade the grave-site as well as securing tenure which was due to run out shortly. A small ceremony was held both in the Wallace theatre in Bournemouth and at the grave-site to honor the great man and to commemorate the occasion (Wilson unpublished).

9 Honors

Although Wallace achieved fame at the time of his famous paper of 1858, when he was 33 years old, he subsequently faded from view being so overshadowed by Darwin. After his return from the East, he became a member of several scientific bodies, such as the Entomological Society, but public honor was not forthcoming. In 1882 he was awarded a Doctor of Law by the Dublin University, and in 1889 a Doctor of Civil Law by the Oxford University. He shunned all public honor, which has been put down to a natural shyness. In 1893 Sir Joseph Hooker put him up for membership of The Royal Society of London. Wallace was very reluctant to accept this, and much interesting correspondence ensued. He was written to severely, "*I have a certificate ready, you only have to say the word.....To dissociate yourself from The Royal Society really amounts to doing it an injury*". He was finally persuaded to accept the honour of Fellow of the Royal Society. Towards the end of his life however honours were poured upon him.

He was the first recipient of the Linnean Society's Darwin-Wallace gold medal (Fig. 4), which had been struck in 1908 to celebrate the Jubilee Celebration of that "boring" meeting of the Society in July 1858. He spoke at that meeting giving his own account of that "flash of insight" that came to him in Ternate in the Spice Islands during an attack of malaria. It was his account of Natural Selection that he sent to Charles Darwin..

Fig. 4 The Darwin-Wallace gold medal

He described himself as “young man in a hurry”, and as usual gave all the credit to Darwin. Once more he displayed the supreme example of humility and self-effacement. Neither his wife, son or daughter attended that meeting, which is hard to understand. He was ultimately awarded the Copley Medal of The Royal Society, which is their greatest honour.

Finally, in 1908 his greatest accolade was announced in the Birthday Honours. It was The Order of Merit. The Order of Merit is the highest civil distinction bestowed in Britain. This Order, which takes precedence over some 11 Orders of Knighthood, was established in 1902, and is the unfettered gift of the Sovereign. It is limited to those who have rendered meritorious service and only 24 persons may hold the Order at any one time. The name of Alfred Russel Wallace is found among distinguished company, including Florence Nightingale (1907), Bertrand Russell (1949), Britain’s greatest philosopher of recent times and Margaret Thatcher (1990), the first woman to become Prime Minister of Great Britain. Wallace was in his 85th year when he was awarded this honour, but did not attend in person to receive it. These medals remain the proud possessions of his grandsons John and Richard Wallace.

In Westminster Abbey there is a memorial medallion to Alfred Russel Wallace. It stands between Charles Darwin and Sir Isaac Newton. This was requested some years after his death. It seems appropriate that, although not buried in Westminster Abbey like Darwin, he is placed among the great scientists of the Age (Fig. 5).

Fig. 5 The medallion in Westminster Abbey, next to Charles Darwin

10 Postscript

Perhaps the greatest example of recent awareness of his great contribution to Natural History is the planned erecting of a life-sized bronze statue in the British Natural History Museum. 100 years ago when Wallace died several memorials were contemplated, but only the plaque in Westminster Abbey was arranged at that time. Now 100 years later a long overdue memorial is to be seen in its rightful place alongside other great men of science.

Acknowledgments The illustrations have come from the website of the Wallace Foundation at the British Natural History Museum in London: https://picasaweb.google.com/WallaceMemorialFund/misc.images.

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Southeast Asian and Australasian Herpetological Collections from the Eighteenth and Nineteenth Centuries in the Zoological Museum of Berlin

Aaron M. Bauer

Abstract The Zoological Museum in Berlin (Museum für Naturkunde) houses one of the most extensive herpetological collections in Europe. Important material from Southeast Asia and especially the Indo-Australian Archipelago accumulated steadily following the museum's founding in 1810. The earliest parts of the collection, stemming from the natural history cabinets of Marcus Elieser Bloch, Friedrich Heinrich Graf von Borcke and others, are represented by eighteenth century material, mostly without specific locality. Throughout the early decades of the nineteenth century amphibians and reptiles reached Berlin from a number of collectors, both German and foreign. The most important of these were Fedor Jagor and Eduard von Martens, both contemporaries of Alfred Russel Wallace. Additional important material was obtained by exchange or purchase from museums and natural history dealers from across Europe. Among approximately 625 specimens from Southeast Asia catalogued into the Zoological Museum before about 1870 are specimens representing types of at least 44 nominal species of amphibians and reptiles. The majority of these were described by Wilhelm Peters, director of the Zoological Museum, whose later collaboration with Giacomo Doria in Genoa further strengthened the collection through the addition of many specimens from Sarawak. Berlin Southeast Asian collectors and localities are reviewed and the identity and status of confirmed and putative type material from the region is evaluated.

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1 Introduction

Alfred Russel Wallace's years in the Malay Archipelago (1854–1862) marked a period of herpetological exploration and discovery in the region. Much of this is associated with the activities European colonial empires extant at the time. Most notably, Britain in Malaya, Singapore, and North Borneo, and the Netherlands in the remainder of the islands of the Sunda Shelf and beyond. Portugal likewise had a foothold in East Timor, but conducted little fundamental zoological research in this period (Kaiser et al. 2011). France, a world leader in science of the period, was only beginning its involvement in Indochina, but herpetological material was obtained through private collectors and others.

Germany was not a colonial empire at the time of Wallace's travels, and indeed was not yet united as single European state, although the Kingdom of Prussia, with its capitol in Berlin, was certainly a major power. Nonetheless, German and especially Prussian contributions to the herpetology of Southeast Asia were not inconsequential. Specifically, collectors associated with the Zoological Museum of Berlin (ZMB, today the Museum für Naturkunde), were important in obtaining, naming, and documenting the amphibians and reptiles of the region. In this paper I review the contribution of Berlin herpetologists to our understanding of the herpetofauna until the mid-1860s. I include in the geographic area of consideration the mainland areas from Myanmar (Burma) east to Indochina and the Malay Peninsula and the islands of the Indo-Australian Archipelago as far as the Lesser Sundas and western New Guinea. I exclude the Philippines which, although well studied by Berlin-based naturalists (e.g., Fedor Jagor, Carl Semper), was not within Wallace's sphere of activity.

2 Methods

Data were obtained directly from the original hand-written catalogue of the ZMB herpetological collection compiled by Martin Carl Hinrich Lichtenstein (1780–1857), beginning in 1856 and continued by Wilhelm C.H. Peters (1815–1883; Fig. 1) until his death. Data regarding collector, original and type status was taken from this source and supplemented by information from the original published descriptions of new taxa and from published narratives of relevant voyages. This catalogue was initiated in conjunction with the preparation of the published list of Berlin herpetological holdings in the *Nomenclator Reptilium et Amphibiorum* (Lichtenstein and von Martens 1856) and replaced earlier lists of specimens which did not use a continuous numbering system for the entire collection. In the ZMB catalogue the first 3750 numbers were assigned to material already in the collection during the time of Lichtenstein's directorship (1813–1857) and the first 3706 of these were ordered by taxonomic group (see Bauer 1999 "1998" for a breakdown of numbers assigned to each group). From entry 3707 onwards specimens were entered as they were received or worked upon by Peters and others. At least 625 specimens among the first 7000

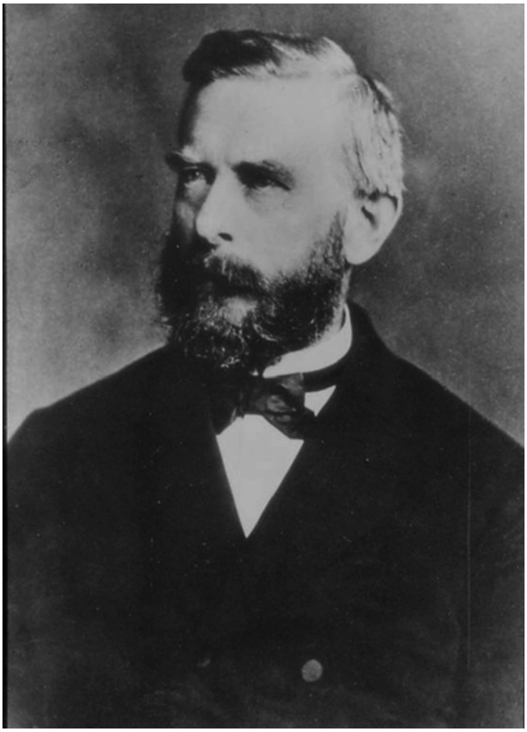

Fig. 1 Wilhelm Peters, during his period of directorship of the Zoological Museum in Berlin. Image courtesy of Hannelore Landsberg (Museum für Naturkunde Archiv)

ZMB registration numbers correspond to amphibians and reptiles from the area under consideration. This includes material accessioned through approximately 1870. Although this was chosen as an arbitrary cutoff, due to time lags in the registering of material, this date would allow for the inclusion of all or most specimens actually collected through the mid-1860s. However, some of this material was not described until considerably later, e.g. *Clemmys gibbera* (Peters 1874).

Southeast Asian material in Berlin can be divided by its sources. A small number of specimens stem from the early collections of the museum. Others were obtained through purchase or exchange with natural history dealers and other institutions. The majority, however, come from collectors acting directly or indirectly on the behalf of the Zoological Museum. The contributions of each of these sources will be treated in turn, with special emphasis on specimens that served as the types of new taxa.

3 Early Collections

The earliest Southeast Asian material in the collection stems from the foundational material of the museum. These are from the collections of Marcus Elieser Bloch (1723–1799), Friedrich Heinrich Graf von Borcke (1776–1825), and Johann Centurius Hoffmann Graf von Hoffmannsegg (1766–1849). Bloch's herpetological material consisted of about 380 specimens, of which more than 200 are still present in the ZMB collection (Bauer 1999 “1998”; Günther 2001). It was obtained from collectors and correspondents from around the world, and included some material from tropical Asia, most significantly, the types of the skink *Lacerta serpens* [syn. *Lygosoma quadrupes* (Linnaeus 1766)], the only reptile described by Bloch (1776) himself and Bauer and Günther (2006; see Table 1). In addition, the holotype of *Draco fimbriatus* Kuhl 1820 was derived from Bloch’s collection. Von Hoffmansegg’s collection was not herpetologically rich, but it nonetheless did provide the type specimen for one species of Javan snake, *Dipsas hoffmanseggii* Peters 1867 [syn. *Boiga nigriceps* (Günther 1863)]. Graf von Borcke’s herpetological collection was largely obtained, through a series of purchases, from the famous cabinet of Albertus Seba (1665–1736) (Bauer and Günther 2013, 2014), who illustrated many of his specimens in his *Thesaurus* (1734–1765). Other specimens from von Borcke’s collection were figured by Merrem (1790). Merrem’s (1790) figure of the “Unregelmäßige Natter” is based on ZMB 2583 and through the illustration this specimen serves as the holotype of both *Coluber irregularis* Bechstein 1802 and *Hurria pseudoboiga* Daudin 1803 [now *Boiga irregularis*] (see Bauer and Günther 2013 for an explanation of this complex connection). Other specimens may also have been the models for other Seba and Merrem images used as iconotypes, although their type status remains ambiguous (see Table 1, footnote 25). Most of the older herpetological material present in Berlin is associated with only the most basic data, and this is especially true of these foundational collections. Indeed, some specimens bear only the locality “Ostindien” or “Indien” and the only specific island locality given is Java. In no case are these specimens associated with a collector or collection date.

4 Exchanges and Purchases

Another category of specimens are those obtained through exchange or purchase from other museums. Under both Lichtenstein and Peters, the Museum carried out extensive exchanges with other leading institutions throughout Europe, as well as with smaller collections, chiefly in Germany. Material from the Indo-Australian Archipelago was obtained from Paris, London, Stockholm, Munich, Halle, and especially Leiden (Fig. 2). In some cases only the collection is noted as a source, but in others the responsible curator or director was specifically listed in the ZMB catalogue. Thus, Coenraad Jacob Temminck (1778–1858) and Hermann Schlegel (1804–1884) are often acknowledged for specimens from Leiden, Johann Georg Wagler (1800–1832) for early material received from Munich, Albert Karl Ludwig Gotthilf Günther (1830–1914) for material from London, and Séraphin Braconnier (1812–1884) for specimens from Paris. In the case of Leiden three specific collectors of the material are mentioned by name: Heinrich Kuhl (1797–1821), Eltio Alegondas Forsten (1811–1843) and Salomon Müller (1804–1863), all of whom were sent to the Dutch East Indies by Temminck to collect; of these only Müller returned alive to Europe (see Adler 2012).

Table 1 Herpetological taxa from Southeast Asia and the Indo-Australian Archipelago that entered the Zoological Museum Berlin (ZMB) collections before approximately 1865 and represented by confirmed or putative type material

Family	Original name	Author	Current name	Source	Locality	ZMB type(s)
Bufonidae	*Hylaplesia borbonica*	Tschudi (1838)	*Leptophryne borbonica*	Leiden	Java	Syntype: ZMB 4487[a]
Bufonidae	*Bufo claviger*	Peters (1863)	*Ingerophrynus claviger*	von Martens	Benkulu, Sumatra	Lectotype: ZMB 4863[b]; Paralectotypes: ZMB 37322
Dicroglossidae	*Phrynoglossus Martensii*	Peters (1867)	*Occidozyga martensii*	von Martens	Bangkok	Holotype: ZMB 5645
Dicroglossidae	*Rana brevipalmatta*	Peters (1871)	*Fejervarya brevipalmata*	purch. Cutler	Pegu[c]	Holotype: ZMB 6130 (not located)
Microhylidae	*Diplopelma disciferum*	Peters (1867)	*Microhyla achatina*	Mus. Halle	Java	Lectotype: ZMB 4434[d]
Microhylidae	*Phrynomantis fusca*	Peters (1867)	*Callulops fuscus*	von Martens	Amboina	Syntypes: ZMB 5648 (2 specimens)
Microhylidae	*Calohyla sundana*	Peters (1867)	*Metaphrynella sundana*	Hooft via von Martens	Pontianak, Borneo	Syntypes: ZMB 5635 (2 specimens)
Ranidae	*Hyla chalconotus*	Schlegel (1837)	*Hylarana chalconota*	Leiden	Java	Syntypes: ZMB 4462[e] (2 specimens)
Ranidae	*Hyla erythraeus*	Schlegel (1837)	*Hylarana erythraea*	Leiden	Banca	Syntype?: ZMB 4463[f]
Ranidae	*Polypedates raniceps*	Peters (1871)	*Hylarana raniceps*	von Martens/Doria	Pulo Matjan, Borneo	Paralectotypes: ZMB 5020, ZMB 54894[g]
Ranidae	*Limnodytes celebensis*	Peters (1872a)	*Hylarana celebensis*	Leiden, coll. Forsten	Manado, Celebes	Holotype: ZMB 5745
Rhacophoridae	*Polypedates Mackloti*	Peters (1871)	*Buergeria buergeri*	Schlegel	Java[h]	Holotype: ZMB 3157

(continued)

Table 1 (continued)

Family	Original name	Author	Current name	Source	Locality	ZMB type(s)
Rhacophoridae	*Hyla aurifasciata*	Schlegel (1837)	*Philautus aurifasciatus*	Leiden, coll. S. Müller	Java	Paralectotype: ZMB 4465[i]
Geoemydidae	*Clemmys (Heteroclemmys) gibbera*	Peters (1874)	*Orlitia borneensis*	von Martens	Pulo Matjan, Borneo	Holotype: ZMB 5022
Trionychidae	*Emyda scutata*	Peters (1868)	*Lissemys scutata*	purch. Gerrard	Pegu	Holotype: ZMB 6029
Agamidae	*Draco fimbriatus*	Kuhl (1820)	*Draco fimbriatus*	Bloch	Java	Holotype: ZMB 713[j]
Agamidae	*Otocryptis (Aphaniotis) fusca*	Peters (1864)	*Aphaniotis fusca*	Japan Expedition	Malacca	Holotype: ZMB 5032
Agamidae	*Otocryptis* (*Japalura*) *nigrilabris*	Peters (1864)	*Phoxophrys nigrilabris*	von Martrens	Pulo Matjan, Borneo	Holotype: ZMB 5023 (not located)
Dibamidae	*Typhlosaurus Martensii*	Peters (1864)	*Dibamus novaeguineae*	von Martens	Ternate	Syntypes: ZMB 5026, 5027 (not located)
Lacetidae	*Tachydromus sexlineatus* var. *aeneofuscus*	Peters (1863)	*Takydromus sexlineatus*	von Martens	Bangkok	Holotype: ZMB 4534
Scincidae	*Chelomeles sumatrensis*	Bleeker (1860)	*Larutia sumatrensis*	Bleeker	Agam, Sumatra	Syntype: ZMB 4055[k]
Scincidae	*Euprepes* (*Mabuya*) *samoensis var. moluccensis*	Peters (1864)	*Emoia sorex*	von Martens	Moti	Holotype: ZMB 5104
Scincidae	*Euprepes* (*Riopa*) *punctatostriatus*[l]	Peters (1864)	*Lygosoma bowringii*	Jagor	Singapore	Holotype: ZMB 7013
Scincidae	*Heteropus Schlegelii*	Peters (1864)	*Carlia leucotaenia*	von Martens/ Leiden	Amboina/Timor	ZMB 4951[m]/ZMB 4981 (2 specimens)

Scincidae	*Lacerta serpens*	Bloch (1776)	*Lygosoma quadrupes*	Bloch	Ostindien	Syntype: ZMB 1276[n]
Scincidae	*Zonurus novae Guineae*	Schlegel (1834)	*Tribolonotus novaeguineae*	Leiden, coll. Müller	Neu Guinea	Syntype?: ZMB 4474[o]
Typhlopidae	*Typhlops flaviventer*	Peters (1864)	*Ramphotyphlops flaviventer*	von Martens	Ternate	Holotype: ZMB 5029
Typhlopidae	*Typhlops nigro-albus*	Duméril and Bibron (1844)	*Argyrophis muelleri*	Paris	Sumatra	Syntype?: ZMB 4114[p]
Cylindrophiidae	*Tortrix rufa* var. *Celebica*	Schlegel (1844)	*Cylindrophis melanotus*	Leiden	Celebes	Holotype?: ZMB 4049[q]
Colubridae	*Calamaria maculolineata*	Peters (1863)	*Calamaria margaritophora*	Gaymans via von Martens	Kepahiang, Sumatra	Holotype: ZMB 4884
Colubridae	*Calamaria vermiformis*	Duméril et al. (1854)	*Calamaria lumbricoidea*	Paris	Java	Syntype?: ZMB 4118[r]
Colubridae	*Coluber irregularis*	Bechstein (1802)	*Boiga irregularis*	von Borcke	"Indien"	Holotype: ZMB 2583[s]
Colubridae	*Dendrophis formosus*	Boie (1827)	*Dendrelaphis formosus*	Leiden	Padang	Syntype?: ZMB 4047[t]
Colubridae	*Dipsas drapiezii var. bancana*	Peters (1867)	*Boiga drapiezii*	Müller via von Martens	Banca	Holotype: ZMB 4543
Colubridae	*Dipsas hoffmanseggii*	Peters (1867)	*Boiga nigriceps*	von Hoffmansegg	Java	Holotype: ZMB 2585
Elapidae	*Calliophis furcatus var. nigrotaeniatus*	Peters (1863)	*Calliophis intestinalis lineata*	Gaymans via von Martens	Kepahiang, Sumatra	Syntypes: ZMB 4885, ZMB 4906 (not located)
Elapidae	*Hydrophis tenuicollis*	Peters (1873)	*Hydrophis cyanocinctus*	Wessel	Java	Holotype: ZMB 5727

(continued)

Table 1 (continued)

Family	Original name	Author	Current name	Source	Locality	ZMB type(s)
Elapidae	*Naja* (*Hamadryas*) *scutata*	Peters (1861)	*Notechis scutatus*	Jagor	Java[u]	Holotype: ZMB 2815 (lost)
Elapidae	*Stephanohydra fusca*	Tschudi (1837)	*Aipysurus fuscus*	Schönlein	Celebes[v]	Holotype: ZMB 2824
Homalopsidae	*Hydrodipsas elapiformis*	Peters (1859)	*Cantoria violacea*	Jagor	Sarawak, Borneo	Holotype: ZMB 2492
Homalopsidae	*Hypsirhina* (*Eurostus*) *Jagorii*	Peters (1863)	*Enhydris jagorii*	Jagor	Siam	Holotype: ZMB 4746
Natricidae	*Styporhynchus truncatus*	Peters (1863)	*Tropidonophis truncatus*	von Martens	Dodinga, Djololo/ Wahai, Ceram	Syntypes: ZMB 4883, ZMB 67263 (ex ZMB 4883)[w]
Natricidae	*Tropidonotus maculatus*	Peters (1871)	*Amphiesma petersii*	Hallmann	Ostindien	Syntype: ZMB 7008[x]
Pareatidae	*Asthenodipsas malaccana*	Peters (1864)	*Asthenodipsas malaccanus*	Baumgarten	Malacca	Holotype: ZMB 5041

[a]Other types in Leiden (Gassó Miracle et al. 2007); this specimen not previously noted as having type status
[b]Lectotype designated by Bauer et al. (1995). Other paralectotype: FMNH 73840 (ex ZMB)
[c]Locality probably in error (Boulenger 1905)
[d]Lectotype designated by Bauer et al. (1996). Paralectotype(s): Halle
[e]Other types in Leiden (Gassó Miracle et al. 2007); these specimens not previously noted as having type status
[f]Other types in Leiden (Gassó Miracle et al. 2007) and Paris (Ohler and Mallick 2003 "2002"); this specimen not previously noted as having type status. Doubtful, as "Banca" is not among the stated type localities
[g]Lectotype and another paralectotype in Genoa; designation by Capocaccia (1957)
[h]If the synonymy of Ahl (1931) is correct, the locality associated with the type is in error as the species is endemic to Japan
[i]Other types in Leiden (Gassó Miracle et al. 2007). Lectotype designated by Bossuyt and Dubois (2001)
[j]Denzer et al. (1997) considered ZMB 713 as a holotype and ZMB 712 (exchanged to CAS in 1924) as a paratype. However, 712 was obtained from Temminck in Leiden after Kuhl's description, which is based on a single Berlin specimen
[k]At least one other syntype is in BMNH. Authorship of this name is often attributed to Günther (see Bauer et al. 2003)
[l]The title of Peters' paper uses the epithet *punctatolineatus* and the holotype is listed as such in the ZMB catalogue

[m]ZMB 54382–86 are listed as originally part of 4591 in the ZMB catalogue, however the description explicitly notes only two specimens each from Amboina and Timor (Bauer et al. 2003)

[n]There were originally two syntypes of *L. serpens* but it is uncertain if the second ever entered the ZMB collection, as the description predates the founding of the museum by several decades (Bauer et al. 2003; Bauer and Günther 2006)

[o]Brygoo (1985) and Bauer et al. (2003) identified possible syntypes in several collections, but it is difficult to determine the extent of the original type series

[p]McDiarmid et al. (1999) considered MNHN 6991 as the holotype of this taxon, however, it is clear that the description is based on three specimens. ZMB 4114 is consistent with the type data and may have been an exchanged syntype. Bauer et al. (2002) considered its status as a type questionable

[q]From the type description the number of type specimens cannot be determined. McDiamrid et al. (1999) considered the type(s) as unlocated. Although it is unclear why the type would be in Berlin, rather than Leiden, the ZMB catalogue indicates this specimen as the type. Bauer et al. (2002) considered its status questionable

[r]Duméril et al. (1854) mention many specimens of this species in Paris. The ZMB specimen is likely an exchanged specimen from this series

[s]This same specimen also serves as the holotype of *Hurria pseudoboiga* Daudin 1802. Both Bechstein and Daudin linked their new names to the same figure by Merrem (1790), which in turn has been determined to be based on ZMB 2583 (see Bauer and Günther 2013). In addition, several other Berlin specimens are plausible matches to illustrations by Seba (1735–1765) that served as iconotypes of other taxa: ZMB 727, Java, *Draco volans* Linnaeus 1758; ZMB 2506, "Ostindien," *Coluber horridus* Daudin1803 [syn. *Homalopsis buccata* (Linnaeus 1758)]. However, as a definite match between these specimens and the plates cited in the descriptions cannot be confirmed with any certainty these specimens can be considered putative types at best. Three von Borcke specimens of *Naja naja* (Linnaeus 1758) are putative matches for the iconotypes of as many as six different nominal taxa (see Bauer and Günther 2013, Table 1). However, this species only reaches the periphery of the region under consideration (Myanmar) and it is much more likely that the specimens (ZMB 2795–2797), which have the locality "Ostindien," originated from further west

[t]A specimen in Leiden (RMNH 877) has been identified as the probable holotype (Vogel and van Rooijen 2007; Wallach et al. 2014). Although Boie's description gives details for only a single specimen, it is not possible to determine if there were additional types, thus the status of this Berlin specimen is questionable

[u]Locality probably in error; species is believed to be an Australian endemic. Rawlinson (1991) designated a neotype (NMV D47618)

[v]Cogger (1975) considered the type locality as a probable error; the species is known with certainty from western Australian waters

[w]Bauer et al. (1995) incorrectly listed ZMB 5031 as an additional type following the ZMB catalogue, but this specimen has a different provenance (Ceram) and only two Dodinga specimens are noted in the description

[x]ZMB 7105 and MSNG 30085(2) are additional syntypes collected by Doria in Sarawak

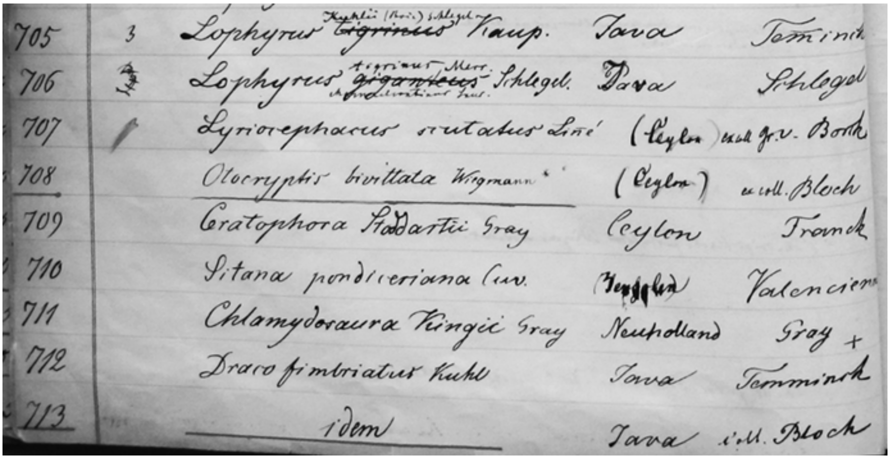
705 3 Lophyrus ~~tigrinus~~ Kaup. Java Temminck
706 3 Lophyrus ~~giganteus~~ Schlegel. Java Schlegel
707 1 Lyriocephalus scutatus Linné (Ceylon) Bork
708 Otocryptis bivittata Wiegmann (Ceylon) e coll. Bloch
709 Ceratophora Stoddartii Gray Ceylon Franck
710 Sitana ponticeriana Cuv. Valenciennes
711 Chlamydosaurus Kingii Gray Neuholland Gray +
712 Draco fimbriatus Kuhl Java Temminck
713 idem Java e coll. Bloch

Fig. 2 Excerpt from the Zoological Museum of Berlin herpetological collection catalogue showing the entries for several specimens from Java, including the type of *Draco fimbriatus* from the Bloch collection, and several exchanged specimens obtained from Temminck and Schlegel in Leiden

Among the types from the region, 13 taxa were based on exchanged material, some of which was described by Lichtenstein or Peters, and others which are syntypes of taxa described earlier by Schlegel, Boie, or Tschudi (Leiden) or by Duméril, Bibron and Duméril (Paris). Not surprisingly, given the Dutch control of the Malay Archipelago, the majority of exchanged specimens, including the majority of exchanged types, came from Leiden (see Table 1).

Other specimens were obtained by purchase from commercial natural history dealers. These establishments were common in the period and the practice of purchasing scientific material of interest was widespread among natural history museums. One source of specimens for Berlin was the Museum Godeffroy in Hamburg which, despite having a curator and publishing its own journal, existed in part as a money-making venture. Its published catalogues were, in large part, price lists of specimens available for purchase (Evenhuis 2007). It had been founded in 1861 by Johann Cesar Godeffroy VI, whose family ran a shipping business and had extensive overseas contacts, particularly in the Pacific (Spoehr 1963; Scheps 2005). At least eight additional dealers also sold material to Wilhelm Peters, among them the famous firms of Carl Ludwig Salmin in Hamburg and Edward Gerrard in London. Additional suppliers included J. G. W. Brandt (Hamburg), Gustav Adolph Frank (Amsterdam), Ludwig Parreys (Vienna), Carl Wessel, E. Cutler (London), and Keitel [?]. Although the majority of these specimens are not of particular importance, at least one specimen, purported to be a type, collected in Cambodia by Henri Mouhot (1826–1861), the French naturalist and explorer of Indochina, was purchased via Gerrard. Mouhot's travels were sponsored by the Royal Geographic Society and the Zoological Society of London and important parts of his collections were also purchased by the British Museum (Günther 1912).

5 Major Collectors

Two major collectors are chiefly responsible for the Southeast Asian herpetological specimens that reached Berlin in Wallace's time. The first was Andreas Fedor Jagor (1816–1900). Chiefly an ethnographer, he led expeditions to the region in 1857–61, 1873–1876, and 1890–1893. ZMB herpetological material from Jagor is present from Java, Thailand, Melaka and Singapore (as well as Hong Kong, the Philippines and other areas). His first expedition, which generated the specimens discussed here, was nearly 5 years in length and began in Singapore, Malacca and Java, from which most of his herpetological material was derived (Jagor 1866). His later trips were also chiefly to the Indo-Australian Archipelago.

The second collector was Eduard Karl von Martens (1831–1904; Fig. 3) (see Adler 2012 regarding the correct version of his name). Von Martens was chiefly a malacologist. He was trained at the universities of Tübingen and Stuttgart, and received his doctorate from the former institution in 1855. He became an assistant (1856), and later (1859) curator of invertebrates at the Zoological Museum in Berlin. Eventually he became a professor (1874) and director of the Museum (1887). As a young man he travelled on the ship *Thetis* on the Prussian Expedition to East Asia (1860–1862)—also known as the "Japan Expedition"—a mission to open up trade with east Asia and, secondarily, to collect scientific material for study. The *Thetis*

Fig. 3 Eduard von Martens, the most important contributor of Indo-Australian herpetofauna to the Berlin Museum in the early 1860s. Portrait from the late nineteenth century from Meissner (1901)

reached the Sunda Straits in July 1860, spent September 1860 through February 1861 in Japan, and carried on to China, Taiwan, the Philippines, Celebes, Java and Siam. However, von Martens left the *Thetis* in March 1862 in Singapore following a disagreement with Friedrich Albrecht Graf zu Eulenberg, leader of the expedition, and continued his own explorations and collecting in the Indo-Australian Archipelago, visiting Java, Banka, Sumatra, Celebes, the Molukkas (Ternate, Amboina, Banda group), Timor, Flores, and Borneo. He spent more than 3 months each on Sumatra and Borneo and eventually returned to Germany in December 1864 (Meissner 1901; Hoppe 1990).

In contrast to most of the other early herpetological material present in Berlin, that collected by von Martens is typically accompanied by rather specific (for the time) collecting localities. Von Martens (1876) provided this information in an extensive "Verzeichniss der gesammwlten oder beobachteten Wirbelthiere," in which 147 reptiles and 32 amphibians (125 and 16, respectively, from the present area of consideration) were recorded. By this time nearly all the herpetological novelties from the trip had already described by Peters, who had helped obtain support for the zoological work of the expedition. Peters also had worked up the mammals and fishes of the expedition, while Jean Louis Cabanis (1816–1906), the curator of ornithology in Berlin, took responsibility for the birds.

In some cases von Martens served as a conduit for collections made by others he encountered in his travels. They were noted by von Martens in his book and usually also by Wilhelm Peters in his descriptions and in the ZMB catalogue entries. These collectors (names and titles and areas of collection as given by von Martens 1876) were: Capt. Müller (Banka), Dr. Rebentisch (Java), Dr. Wienecke (Atapupu, Timor), Cressonnier (Batavia), Dr. z'Hooft (Pontianak, Borneo), Dr. Mock (Banka), Major de Kock (Batavia, Bandong), Dr. Greiner (Malang, Java), Markwald (Siam), Dr. Gaymans (Kepahiang and Tibingtingi, Sumatra), Dr. Beyen (Wahai, Ceram), Dr. von Richthofen (Ostküste des Golfs von Siam), Dr. Hubus (Singkawang and Sambas, Borneo), Thiess (Bangkok), Dr. Broers (Tibingtingi, Sumatra), Commodore Sundewall [naval commander of the Prussian expedition] (Java), Dr. Tressling (Sambas, Borneo), Gersen (Muara-Enim, Sumatra), Foremann (Benkulen, Sumatra), Ducosta (Bangkok), Otto Schottmüller [Gardner on the Eulenberg Expedition] (Anjer), Dumont (Bengkayang, Borneo), and Dr. Schneider (Banka). Dr. Johswich, surgeon on the *Thetis*, apparently donated material directly to the Zoological Museum, as he is listed in the ZMB catalogue as a donor, but is not included in von Marten's list as a contributor to his collections.

Not all of von Martens specimens appear in the ZMB catalogue and it is likely that duplicate specimens may have been exchanged to other institutions, and some listings may have been sight records only. In addition to localities noted based in the ZMB catalogues, von Martens also recorded herpetological material from Simaharadscha, Siam; East Coast of the Gulf of Siam; Bukit-tima near Singapore; Batjan; Adenare; Surabaya, Java; Kajeli, Buru; Batu-lubar on Danau-Sriang Lake, Borneo; Pomangkat, Borneo; and Maros, Celebes.

In addition to Jagor and von Martens, other collectors were Hugh Cuming (1791–1865) a British field collector who traveled to Singapore and Malacca in the 1830s and Pieter Bleeker (1819–1878), a Dutch ichthyologist and herpetologist who amassed collections from throughout the Indo-Australian Archipelago from his base in Java. Cuming established a natural history dealership in London in 1839 and presumably the Berlin specimens were obtained from him by purchase. Bleeker also sold his collections, with much of the herpetological material going to the British Museum, although it is unclear if his specimens in Berlin were donated or purchased. Specimens from Rodolfo Amando Philippi (1808–1904), a Berlin-trained professor in Kassel who is most well-known for his work after his emigration to Chile in 1851 and from Johann Lukas Schönlein (1793–1864), a noted physician, were donations of material they had received rather than collected themselves. Additional material was derived from a diversity of other collectors and donors, most of which are not readily identifiable beyond their designations given in the ZMB catalogue: Drs. Arndt, Dirksen, and Hellmann, Lieutenant Berendt, W. Baumgarten, Bekker, Beyerhaus, Göring, Kleinwoorth, Meyer, Nagel, and Schweigger.

6 Southeast Asian and Indo-Australian Material

Exclusive of the extremely vague localities of “Indien” and “Ostindien” associated with some of the earliest Berlin collections, the material from Southeast Asia and the Indo-Australian Archipelago represented in the ZMB collection until the time of Wallace is listed below:

6.1 Mainland Southeast Asia

Burma [Myanmar] (32 specimens): Mergui (8); Pegu (23); Rangoon [Yangon] (1).
Siam [Thailand] (56 specimens): Bangkok (37); Chartaboum (1); Phetchaburi (3); Si Maha Racha (1); unspecified (14).
Cambodia (1 specimen).
Cochinchina (2 specimens).
Malacca (44 specimens) Malaccafluß (1); unspecified (43).
Singapore (16 specimens).

6.2 Indo-Australian Archipelago

“Indische Archipel” (7 specimens): Sunda Inseln (5); Sundasee (1); unspecified (1).

6.2.1 Greater Sundas

Java (249 specimens): Anjer = Anyer [Banten] (2); Bandung [West Java] (2); Batavia = Jakarta [Special Capital Region] (4); Buitenzorg = Bogor [West Java] (1); Malang [East Java] (3); Pasuruan [East Java] (1); Samarang = Semarang [Central Java] (7); unspecified (229).
Sumatra (31 specimens): Agam (1); Bengkulu (5); Luburaman (3); Padang (1); Lahat (3); Kepahiang (9); Muara Enim (1); Tibingtingi (4); unspecified (4).
Borneo (63 specimens): Sarawak (15); Sambas (4); Sintang (3); Mandhor (1); Lempai (1); Pontianak (15); Banjarmasin (2); Bengkayang (3); Pulau Matjan (7); Singkawang (1); unspecified (11).

6.2.2 Sahul

Celebes [Sulawesi] (13 specimens): Gorontalo (2), Manado (1); unspecified (11).
Bangka (32 specimens): Muntok (4); unspecified (28).
Maluku Islands
Molukka (1 specimen).
Halmahera (1 specimen): Dodinga [South Jailolo, West Halmahera] (1).
Moti (3 specimens). Ceram [Seram] (7 specimens): Elpaputih Bay (2); Wahai (4); unspecified (1).
Ambon (32 specimens).
Bacan (1 specimen).
Ternate (7 specimens).
Lesser Sundas
Timor (23 specimens): Kupang (6), Atapupu (6); unspecified (11).
Flores (2 specimens): Larantuka (2).

6.2.3 New Guinea

New Guinea (3 Specimens)

Predictably for the period, the greatest number of specimens was derived from Java, which had a long established European presence and was a point of call for nearly all collectors in the region. Modest collections from Borneo and Sumatra and smaller islands in the Dutch East Indies largely reflect the activities of von Martens as well as exchanges from Leiden, whereas those from Siam and Malacca stem, in part, from Jagor's voyage. Burmese material was mostly purchased, some through the Museum Godeffroy. Nearly all specific localities within islands reflect the precision of von Martens' records. For the time period the geographic coverage is quite comprehensive, except for Indochina.

7 Type Specimens

Putative types of at least 44 herpetological species in Berlin are based on Southeast Asian or Indo-Australian material collected during or prior to the period of Wallace's activity in tropical Asia. Twenty-eight of these were described by Wilhelm Peters, of which 16 were based on von Martens' material, and 3 on Jagor's material. Sixteen species descriptions were based on material obtained from other museums: Paris, Halle, and especially Leiden, and these were described by Schlegel, Boie, Duméril and Bibron, Tschudi, and Bleeker, as well as by Wilhelm Peters. While there is no question about the type status of material representing species described by Peters, it is often difficult or impossible to verify the type status of specimens described by others and subsequently received through exchange. In the mid-nineteenth century, prior to the formal establishment of the International Code of Zoological Nomenclature, the type concept was often loosely interpreted. Corresponding curators may have intentionally or inadvertently claimed that material was part of a type series when it was not, or the term "typical" may have been intended to indicate only that a specimen was similar to the named form (i.e., not a "variety").

Two taxa described from the region are unambiguously extralimital and, therefore, despite their published type localities cannot have been derived from the region under consideration. The types of *Hoplobatrachus reinhardtii* (Peters 1867) = *Pelophylax nigromaculatus* (Syntypes: ZMB 5900, ZMB 62987 [ex ZMB 5900]) were described from material from the specimen dealer Carl Wessel as being from "Malacca oder China." However the species does not occur in tropical Asia and the type locality was restricted to "China" by Liu (1950). The holotype of *Simotes semicinctus* Peters 1862 (ZMB 4553) was presumably obtained from the "Mission Barman" and has a published type locality of "? Borneo." This name was long forgotten, but was subsequently considered a valid species of *Oligodon* (Wallach and Bauer 1997), before being synonymized with *Coronella austriaca*, a European species, by Tillack et al. (2008).

Both confirmed and questionable types are presented in Table 1, with footnotes flagging cases of uncertainty or other noteworthy issues. In addition to these, there are a number of additional cases of Southeast Asian or Indo-Australian specimens incorrectly noted as types in the ZMB catalogue. These are briefly noted here to avoid any future confusion:

Both Wilhelm Peters, in his annotations in the ZMB type catalogue, and Denzer et al. (1997) considered ZMB 5678 as a paratype of *Dilophyrus mentager* Günther 1861. The specimen is from Chartaboum, Siam and was collected by Henri Mouhot. However, Mouhot's collections were sold through the dealer Gerrard and it appears likely that this specimen was not seen by Günther, whose type in the BMNH would have been purchased separately.

The Berlin catalogue lists ZMB 1298 (two specimens) as types of *Tropidolepisma kuhlii* Lichtenstein and von Martens 1856 from Timor and received from Leiden. This is a *nomen nudum*, however, and Lichtenstein and von Martens attribute authorship to Schlegel. This is probably a shelf name that was never published. The relevant specimens are referable to *Eutropis carinata* (Schneider 1801).

ZMB 4049 is indicated in the catalogue as a type of *Typhlops multilineatus* Schlegel 1839 (= *Ramphotyphlops multilineatus*) obtained from Leiden and collected from Ceram. However, the type locality of this species is in western New Guinea and a single holotype (MNHN 1067) has been identified in Paris (McDiarmid et al. 1999; Wallach et al. 2014).

ZMB 3816, from Amboina, purchased from the natural history dealer Parreys, is listed in the ZMB catalogue as the type of *Leptophis doleschalii* Jan. However, this is not the name of a described species. The specimen is referable to *Chrysopelea rhodopleuron*.

The Berlin catalogue lists ZMB 4048 as a type of *Dipsas pallida* (= *Boiga irregularis* Bechstein 1802) with authorship attributed Schlegel. However, the species was actually described by Jan (1863), who acknowledged the name as a Schlegel manuscript or shelf name. Jan explicitly mentions that his specimens were from Breslau (Wrocław) and Neuchatel, thus the Berlin specimen cannot be one of the types.

The Berlin catalogue lists ZMB 1542 and ZMB 67257 (ex ZMB 1542) as types of *Xenodermus javanicus* (Reinhardt 1836) from the collection of von Hoffmansegg (although the annotation indicates "ex orig. *Xenodermus javanicus* Dum. Bibr. Erpet. gén. ref."). However, the original description (Reinhardt 1836) makes it clear that there was but a single holotype (given as ZMUC R5941 by Reinhardt (1997) and as ZMUC 5481 by Wallach et al. (2014)). This distinctive snake was subsequently commented upon by Wiegmann (1837) and a Berlin specimen from the collection of Graf von Hoffmansegg, was mentioned by Reinhardt (1843) as having been subsequently obtained. In fact, as noted by Peters (1867), von Hoffmanegg's collections are among the founding collections of the Berlin Museum. Thus, although the Berlin material is not part of the type series, it actually predates the Copenhagen holotype, which was not collected until 1834.

8 Later Collections

The Berlin Museum's involvement in the herpetology of Southeast Asia, and especially the Indo-Australian Archipelago expanded dramatically after the era of Wallace. Beginning in 1871, Wilhelm Peters began publishing on material from the region collected by the Marquis Giacomo Doria (1840–1913), founder of the Museo Civico di Storia Naturale in Genoa. This resulted in numerous descriptions starting with those from Doria's own travels (Peters 1871), then those of both Doria and Odoardo Beccari (1843–1920) in Sarawak (Peters 1872c). Ultimately, Peters coauthored with Doria a major work, one of his longest and one of very few with a coauthor, describing the extensive material collected by Beccari, D'Albertis and Bruijn in the Malay Archipelago (Peters and Doria 1878). Herpetological material from Doria's initial expedition to the Indo-Australian Archipelago (1865–1868) began arriving in Berlin in the late 1860s and material was still being accessioned until the time of Peters' death in 1883. In all, hundreds of specimens, including type material of more than 40 species, were added to the Berlin collection through this fruitful collaboration. There were also publications based on the collections of Adolf Bernhard Meyer (1840–1911) made in 1870–1871 in Gorontalo, Sulawesi and the Togian Islands (Peters 1872a, b). Peters also published on material collected on the 1874–1876 expedition of SMS *Gazelle*, which also included specimens from the region, particularly Timor, Amboina and New Guinea (Peters 1876).

9 Conclusions

Despite Germany's lack of a colonial empire in Asia, an important collection of herpetological specimens from the Indo-Australian Archipelago and adjacent regions was amassed at the Zoological Museum in Berlin by the middle of the nineteenth century. This was derived from a diversity of sources, including historical collections, the donations of many individuals—most significantly Eduard von Martins, and judicious purchases and exchanges with other institutions. The collection is of special note and value because of the many type specimens it contains, some stemming from each of the major sources noted. Although the sources of the type material are varied, the majority of type descriptions are the work of one man, Wilhelm Peters, who dominated German herpetology in the second half of the nineteenth century and under whose directorship the Berlin Museum grew to be one of the leading collections in Europe (Bauer et al. 1995).

Alfred Russel Wallace is the most well-known explorer and collector of the Malay Archipelago of his generation and his contributions to the development of evolutionary thought and other fields clearly elevate him among his contemporaries. However, his activities in the region were complemented by those of other, less acclaimed travelers. Collectively, the fruits of their labors provided context to the more fragmentary information gathered by earlier researchers and served as the foundation for the modern understanding of biodiversity and ecological and evolutionary processes in tropical Asia.

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Part II
Natural History and Systematics

Phylogenetics and Systematics of Animal Life

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Abstract Phylogenetics is the study of evolutionary relationships among groups of organisms, and systematics the study of the diversity of organisms and the relationships among them. The relationships are presented in evolutionary trees. In addition to morphological data, gene-enzyme systems were used extensively in earlier days for phylogenetic and systematic studies. Currently, molecular sequencing data are commonly used for phylogenetics and systematics. Cytogenetic data in some cases also serve as good parameters for differentiating sibling/cryptic species. In general, sound systematics and phylogenetics are important and relevant to various fields of biology. This review discusses selected taxonomic groups in which identification has proven problematic based on morhphological characters. The role of phylogenetics and systematics is illustrated by nematode parasites of the genus *Angiostrongylus*, stingless bees of the genus *Tetragonilla*, tephritid fruit flies of *Bactrocera caudata* complex, crab-eating frogs of *Fejervarya cancrivora* complex, and murid rats of the genera *Hapalomys* and *Maxomys*.

1 Introduction

Phylogenetics is the study of evolutionary relationships among groups of organisms. Systematics may be defined as "the entire field dealing with the kinds of animals [organisms], their distribution, classification, and evolution" (Blackwelder and Boyden 1952), and "the scientific study of the kinds and diversity of organisms and

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of any and all relationships among them" (Simpson 1961). It includes taxonomy, "the theoretical study of classification, including its bases, principles, and rules", and classification, "the ordering of animals [organisms] into groups (or sets) on the basis of their relationships" (Simpson 1961).

Both phylogenetics and systematics concern the study of relationships among taxa. The relationships are presented in evolutionary trees. In addition to morphological data, gene-enzyme systems were used extensively in earlier days for phylogenetic and systematic studies. Currently, molecular sequencing data are commonly used for phylogenetics and systematics. Cytogenetic data in some cases also serve as good parameters for differentiating sibling/cryptic species. In general, sound systematics and phylogenetics are important and relevant to various fields of biology, including biodiversity and conservation, and other scientific disciplines.

This review discusses selected taxonomic groups in which identification has proven problematic based on morphological characters. They are cryptic or sibling species (referred to as species complex), i.e. closely related species that appear as a single species based on morphological characters. The role of phylogenetics and systematics is illustrated by nematode parasites of the genus *Angiostrongylus*, stingless bees of the genus *Tetragonilla*, tephritid fruit flies of *Bactrocera caudata* complex, crab-eating frogs of *Fejervarya cancrivora* complex, and murid rats of the genera *Hapalomys* and *Maxomys*.

2 Nematode Parasites Genus *Angiostrongylus*

The *Angiostrongylus* lungworms are of public health and veterinary concerns in many countries. They are bursate nematodes of the family Angiostrongylidae, superfamily Metastrongyloidea. Of the *Angiostrongylus* lungworms, the rat lungworm, *A. cantonensis* (Chen 1935) is a food-borne zoonotic parasite of public health importance in many countries of the tropics and subtropics (Eamsobhana and Tungtrongchitr 2005; Eamsobhana 2006).

A related species, *A. malaysiensis* Bhaibulaya and Cross 1971 in Southeast Asia and Japan, has not been confirmed to infect humans but human infection from the species remains a possibility. When first documented, it was referred to as *A. cantonensis* (Bhaibulaya and Cross 1971). With taxonomic revision, the taxa in Sarawak, Sabah and Peninsular Malaysia, earlier attributed to *A. cantonensis* have been shown to be *A. malaysiensis* (Eamsobhana 2006).

Another congenric species, *A. costaricensis* (Morera and Céspedes 1971) in the Americas (from southern United States to northern Argentina in South America), causes abdominal or intestinal angiostrongyliasis which mimics appendicitis, with eosinophilia (Graeff-Teixeira 2010; Graeff-Teixeira et al. 2009). This species does not occur in the Old World.

Apart from the species of human public health importance, the French heartworm *A. vasorum* (Baillet 1866) is of veterinary concerns. This parasite infects wild and domestic canids and causes canine angiostrongylosis (Conboy 2000; Morgan et al. 2005). It is enzootic to Western Europe but has been found in many parts of the world.

Molecular differentiation of *A. cantonensis* and its phylogenetic relationship to other *Angiostrongylus* species have been achieved by polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) (Calderia et al. 2003) and DNA sequences of 66-kDa protein gene (Eamsobhana et al. 2010a), internal transcribed spacer 2 (ITS-2) (Jefferies et al. 2009; Foronda et al. 2010), cytochrome *c* oxidase subunit I (COI) (Eamsobhana et al. 2010b; Tokiwa et al. 2012), and small subunit (SSU) ribosomal RNA (Fontanilla and Wade 2008; van Megen et al. 2009; Tokiwa et al. 2012).

Based on SSU rDNA sequences (van Megen et al. 2009), 66-kDa protein gene (Eamsobhana et al. 2010a) and COI sequences (Eamsobhana et al. 2010b), *A. cantonensis* shows closest affinity to *A. malaysiensis* compared to other congeneric species.

Phylogenetic analyses of COI nucleotide sequences indicate two distinct genetic lineages each for *A. costaricensis* and *A. vasorum* (Jeffries et al. 2009, 2010; Eamsobhana et al. 2010b; Fig. 1). The genetic distances between these allopatric taxa are many folds larger than intraspecific distances (Table 1), indicating the component taxa are valid cryptic species.

The COI sequences of the georgraphic isolates of *A. cantonensis* (Fig. 1) indicate that the Thailand isolate is most likely not involved in dispersal to other areas. On the other hand, most of the Brazil isolates might have been introduced from Japan. The dispersal of the parasite from China (Fujian and Guangdong) and Taiwan to Japan (Honshu Island), and vice-versa, needs to be confirmed.

3 Stingless Bees of the Genus *Tetragonilla*

Stingless honey bees are members of the Apidae. There are some 30 species in Malaysia. The genus *Tetragonilla* was erected by Moure (1961) for the taxa of the *atripes* species group of stingless bees, comprising the taxa *atripes*, *collina*, *fuscibasis* and *rufibasalis*. Although the component taxa were accorded specific status, he was of the opinion that *fuscibasis* could be a Bornean subspecies of *collina*.

The four taxa of the *atripes* species group were regarded by Schwarz (1939) as varieties of *Trigona* (*Tetragona*) *atripes*. Schwarz was also of the opinion that "… it is possible that *fuscibasis* instead of being a variety of *collina* is merely the callow stage of that insect".

Taxonomic treatments had placed the *atripes* species group as members of the subgenus *Tetragona* of the genus *Trigona* (Schwarz 1939; Wille 1979), the subgenus *Tetragonilla* (Sakagami 1975) and the subgenus *Tetragonula* (Sakagami et al. 1985). At present the species group is accorded generic status, viz. *Tetragonilla* as originally proposed by Moure (1961). The phylogeny based on five genes (16S, ArgK, EF-1α, opsin and 28S) indicates close affinity of *Tetragonilla* to the genus *Tetragonula* (Rasmussen and Cameron 2010). Of the component taxa, *T. atripes* clusters with *T. rufibasalis* and *T. collina* with *T. fuscibasis*.

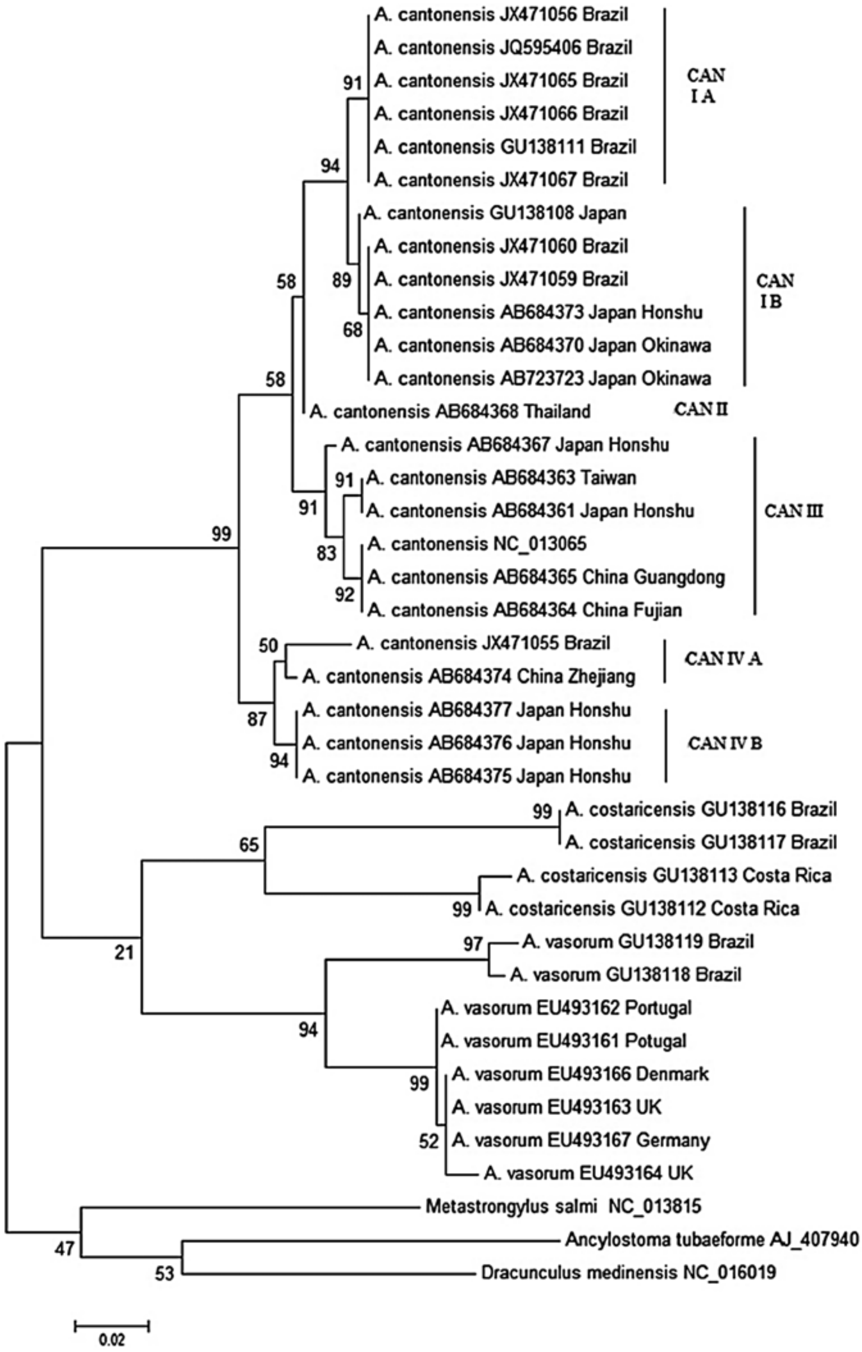

Fig. 1 Phylogenetic tree of *Angiostrongylus* lungworms (with *Metastrongylus salmi*, *Ancylostoma tubaeforme* and *Dracunculus medinensis* as outgroups) generated by the Maximum Likelihood method based on partial COI mtDNA nucleotide sequences conducted in MEGA5 (Tamura et al. 2011)

Table 1 Genetic distance (uncorrected 'p' distance) between taxa of *Angiostrongylus costaricensis* and *Angiostrongylus vasorum* (based on COI sequences listed in Fig. 1)

	A. costaricensis		*A. vasorum*	
Taxon	Brazil	Costa Rica	Brazil	Europe
A. costaricensis Brazil	0			
A. costaricensis Costa Rica	0.1316–0.0088	0.1423		
A. vasorum Brazil	0.1608	0.1605–0.1717	0.0118	
A. vasorum Europe	0.1528–0.1639	0.1639–0.1715	0.0810–0.0878	0.0000–0.0118

Table 2 Genetic idemntity (Nei's *I*, above diagonal) and genetic distance (*D*, below diagonal) among the component taxa of the genus *Tetragonilla* of Malaysian stingless bees based on 17 enzyme loci (After Yong 1991)

Species	*T. atripes*	*T. collina*	*T. fuscibasis*	*T. rufibasalis*
T. atripes	–	0.58	0.62	0.65
T. collina	0.54	–	0.66	0.76
T. fuscibasis	0.48	0.42	–	0.73
T. rufibasalis	0.43	0.27	0.31	–

The four component taxa of *Tetragonilla* (*Trigona atripes* species group in earlier literature) could be unequivocally separated from one another based on 17 enzyme loci (Yong 1991). The genetic identity values (Table 2) indicate closest affinity between *T. collina* and *T. rufibasalis* (I=0.76, D=0.27), and most distant between *T. collina* and *T. atripes* (I=0.58, D=0.54). It is noteworthy that *T. collina* and *T. fuscibasis* which are morphologically rather similar, are genetically more distant compared to *T. rufibasalis*.

4 Tephritid Fruit Flies of the *Bactrocera caudata* Complex

Tephritid fruit flies are of economic importance, with some 200 species considered as pests, causing direct losses to a wide variety of fruit, vegetable and flower crops (Carroll et al. 2002). The larvae of about 35 % of the species attack soft fruits, and about 40 % of species develop in the flowers of Asteraceae (White and Elson-Harris 1992). Among the species attacking Asteraceae flowers is *Bactrocera caudata*

Fig. 1 (continued) using the Tamura-Nei model (1993). The tree with the highest log likelihood (−1700.7916) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 39 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All positions containing gaps and missing data were eliminated. There were a total of 342 positions in the final dataset

Table 3 Percentage of uncorrected ‘p’ distances between mainland Asia (Peninsular Malaysia) and Indonesia (Bali and Lombok) samples of *Bactrocera caudata* based on combined COI and 16S rDNA sequences (After Lim et al. 2012)

Taxon	1	2	3	4
1. *B. caudata* (UM, P. Malaysia)	–			
2. *B. caudata* (Carey Island, PM)	0.09	–		
3. *B. caudata* (Lombok)	4.45	4.46	–	
4. *B. caudata* (Lombok)	4.45	4.46	0.00	–
5. *B. caudata* (Bali)	4.45	4.46	0.00	0.00

(Fabricius). It has a Paleartic and Oriental distribution, occurring in India, Sri Lanka, Myanmar, Thailand, Vietnam, China, Malaysia, Brunei and Indonesia (Sumatra, Java, Bali, Lombok, Flores) (Carroll et al. 2002; Lim et al. 2012).

The partial DNA sequences of cytochrome *c* oxidase subunit I (COI) and 16S rRNA genes reveal distincet genetic lineages of *B. caudata* from mainland Asia and Indonesia (Bali and Lombok), without common haplotype between them (Lim et al. 2012). The uncorrected ‘p’ distances for COI, 16S and combined COI-16S sequences between *B. caudata* of Malaysia-Thailand-China and *B. caudata* of Bali-Lombok are distinctly different from intraspecific ‘p’ distance (Table 3). Both the *B. caudata* lineages are distinctly separated from related species in the subgenus *Zeugodacus* – *B. ascita*, *B. scutellata*, *B. ishigakiensis*, *B. diaphora*, *B. tau*, *B. cucurbitae*, and *B. depressa*. Molecular phylogenetic analysis indicates that the *B. caudata* lineages are closely related to *B. ascita* sp. B, and form a clade with *B. scutellata*, *B. ishigakiensis*, *B. diaphora* and *B. ascita* sp. A.

The taxon in Lombok (east of Wallace’s Line) is most likely an alien introduction from neighboring island(s), such as through Bali.

5 Crab-Eating Frogs of the *Fejervarya cancrivora* Complex

The crab-eating frogs are widely distributed in Asia (Frost 2013). Gene-enzyme systems (17 enzymes, 26 loci) and mtDNA sequences (16S rRNA and cytochrome b genes) reveal the occurrence of three distinct genetic lineages: (1) Mangrove-type in Bangladesh, Thailand and Philippines; (2) Large-type in Malaysia and Indonesia (Sumatra, Java, Bangka); and (3) Sulawesi-type in West Java and Sulawesi (Kurniawan et al. 2010).

Genetic distances based on these enzyme loci and mitochondrial genes (Table 4) indicate that the three genetic lineages are valid cryptic species. Of the three taxa, the Large-type has closer affinty to the Sulawesi-type, in good agreement with geographical distribution. The Large-type is the nominal *F. cancrivora* and the Mangrove-type attributed to *F. moodiei* (Hasan et al. 2012). Indeed molecular markers indicate considerable numbers of cryptic species in many groups of amphibians (Hasan et al. 2012; Kurashi et al. 2012).

Table 4 Genetic distance of three taxa/types of *Fejevarya cancricora* complex based on 26 enzyme loci (Nei's D, above diagnoal) and mtDNA sequences (16S rRNA/cytb, uncorrected 'p' distance in percentage, below diagonal) (After Kurniawan et al. 2010)

Taxon/Type	Mangrove	Large	Sulawesi
Mangrove	–	0.510 ± 0.025	0.586 ± 0.036
Large	9.10 ± 0.25/14.64 ± 0.59	–	0.197 ± 0.012
Sulawesi	10.22 ± 0.24/16.38 ± 0.49	5.78 ± 0.21/12.88 ± 0.28	–

6 Murid Rodents

6.1 Marmoset Rats Genus Hapalomys

Marmoset rats are currently represented by two nominal species: *Hapalomys delacouri* Thomas (Lesser Marmoset Rat or Delacour's Marmoset Rat) and *Hapalomys longicaudatus* Blyth (Greater Marmoset Rat) (Musser and Carleton 2005). Two subspecies of *H. delacouri* were recognized based on tail pilosity and some cranial and dental dimensions: *H. d. delacouri* from C. Vietnam and *C. d. pasquieri* from Laos (Corbet and Hill 1992).

The karyotype of *H. delacouri* from Thailand consists of 2n = 48 chromosomes and Nfa = 92 (Badenhorst et al. 2009). On the other hand, the karyotype of the Vietnam *H. delacouri* is 2N = 38 and Nfa = 48 (Abramov et al. 2012). The significantly different karyotypes indicate the two taxa are distinct cryptic species. As the type locality of *H. delacouri* is S. Vietnam (Dakto), the northern Thailand taxon with 2N = 48 warrants a new specific rank. An available name is *H. pasquieri* Thomas described from Xieng Khouang, Laos (Corbet and Hill 1992; Abramov et al. 2012). However it remains to be confirmed if the two taxa are conspecific.

The usefulness of karyotype for species discrimination (Table 5) is also supported by the karyotype of a congeneric species *H. longicaudatus* which has 2N = 50 (Yong et al. 1982). Based on chromosome constitution, it appears that the Thailand *H.* '*delacour*i' has closer affinity to *H. longicaudatus*.

6.2 Spiny Rats Genus Maxomys

Spiny rats of the genus *Maxomys* are represented by some 18 species (Corbet and Hill 1992; Musser and Carleton 2005; Achmadi et al. 2012). Among them are two sibling species, *Maxomys rajah* Thomas and *Maxomys surifer* Miller (previously referred to the genus *Rattus*). Cytogentic, serological (albumin and hemoglobin) and ecological characters show that they are genetically distinct and are valid species (Yong 1969, 1972). *M. rajah* possesses 36 chromosomes and *M. surifer* 52 chromosomes (1969, 1972). Prior to that, these two species had been also regarded as colour phases of one species.

Table 5 Karyotypes of marmoset rats *Hapalomys* spp

Taxon	2N	X	Y	Ref
H. delacouri (Vietnam)	38	M	M	Abramov et al. (2012)
H. '*delacouri*' (Thailand)	48	M	M	Badenhorst et al. (2009)
H. lomgicaudatus	50	M	SA	Yong et al. (1982)

2N, diploid number; X and Y, sex chromosomes; M, metacentric; SA, subacrocentric

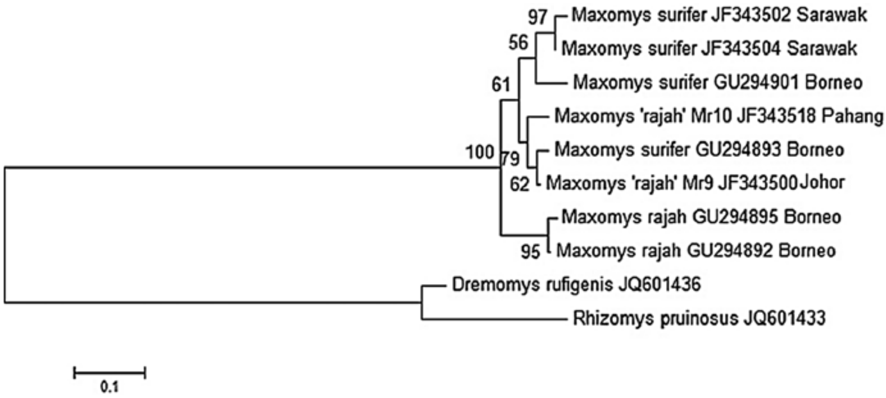

Fig. 2 Phylogenetic relationship of *Maxomys rajah* and *Maxomys surifer* (with *Dremomys rufigenis* and *Rhizomys pruinosus* as outgroups) generated by the Maximum Likelihood method based on partial COI nucleotide sequences conducted in MEGA5 (Tamura et al. 2011) using the Tamura-Nei model (1993). The tree with the highest log likelihood (–2202.5033) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 10 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All positions containing gaps and missing data were eliminated. There were a total of 471 positions in the final dataset

Among the definitive hosts of the rat lungworm *A. cantonensis* in Thailand is a spiny rat of the genus *Maxomys*, reported as *Rattus raja* (Punyagupta et al. 1970). This taxon is probably *M. surifer* as based on cytogenetic evidence, *M. rajah* does not occur in Thailand (Marshall 1977).

Phylogenetic analysis based on partial sequences of cytochrome *c* oxidase subunit I (COI) gene could not confirm the taxonomic status of some specimens attributed to *M rajah* (Tamrin and Abdullah 2011). One specimen (Mr11, Kubah National Park, Sarawak) clustered with *Leopoldamys sabanus* and *Niviventer cremoriventer*. On the other hand, two specimens from Peninsular Malaysia (Mr9 from Johor; Mr10 from Pahang) clustered with *M. surifer*. Comparison of the COI sequences of these two specimens with those of *M. surifer* and *M. rajah* indicates close affinity of these two specimens with *M. surifer* and distinctly separated from *M. rajah* (Fig. 2). This dataset does not support the two specimens to be distinct from *M. surifer*. As

Table 6 Coefficient of genetic similarity (S, Roger's formula) of *Maxomys* rats in Peninsular Malaysia based on nine erythrocyte protein loci (Data from Chan et al. 1978)

Species	*M. surifer*	*M. whiteheadi*	*M. inas*
M. rajah	0.13	0.17	0.13
M. surifer		0.25	0.15
M. whiteheadi			0.69

these specimens were singletons, the inclusion of more individuals from the same locality, or the application of multiple genes (nuclear and mitochondrial), is needed for clarification of the systematic status.

Based on nine erythrocyte protein loci, *M. rajah* is distantly related to *M. surifer* compared to two other congeneric species (*M. whiteheadi* and *M. inas*) from Peninsular Malaysia (Table 6; Chan et al. 1978). Phylogenetic analyses using two COI nucleotide sequences of different length also unequivocally separate *M. rajah* and *M. surifer* (Figs. 3 and 4). The taxa of *M. surifer* from Laos and Vietnam show closer affinity compared to the taxon from Kalimantan; the unidentified *Maxomys* species from Johor clusters with *M. surifer* and distinct from *M. rajah* (Fig. 3). However, the genetic distance ($p = 0.1281$) between the Kalimantan taxon and the Laos-Vietnam taxon indicates distinct genetic lineage. Further studies using multiple genes and extensive geographic sampling are needed to resolve this issue.

Although different phylogenetic methods unequivocally differentiate the congeneric species, the phylogentic relationships resulting from different methods may not be concordant (Figs. 4 and 5). The topology of the phylogenetic trees is also affected by the number of taxa (Figs. 3 and 4).

7 Conclusion

Phylogenetic analyses form an essential component in researching the evolutionary tree of life. Proteins and nucleotide sequences, in particular, provide large numbers of characters for phylogenetic analysis. Phylogeography, based on phylogenetic analysis, can help in the prioritization of areas of high value for conservation. Systematics (particularly correct identification) is of paramount importance in phylogenetics as well as other disciplines for sound inference, decision or judgment. The contribution and importance/relevance of systematics to various fields of biology (including biodiversity and conservation) and other scientific disciplines are succinctly reflected by the following statement regarding ecology (Elton 1947): "The extent to which progress in ecology depends upon accurate identification, and upon the existence of a sound systematic groundwork for all groups of animals, cannot be too much impressed upon the beginner in ecology. This is the essential basis of the whole thing; without it the ecologist is helpless, and the whole of his work may be rendered useless".

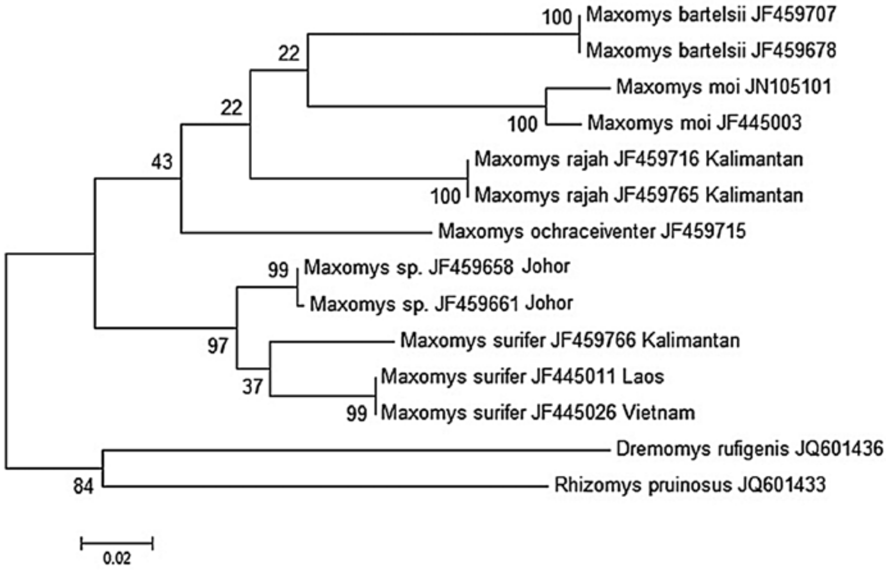

Fig. 3 Phylogenetic tree of *Maxomys* spiny rats (with *Dremomys rufigenis* and *Rhizomys pruinosus* as outgroups) generated by the Maximum Likelihood method based on relatively long partial COI nucleotide sequences conducted in MEGA5 (Tamura et al. 2011) using the Tamura-Nei model (1993). The tree with the highest log likelihood (−2692.1225) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 14 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd + Noncoding. All positions containing gaps and missing data were eliminated. There were a total of 593 positions in the final dataset

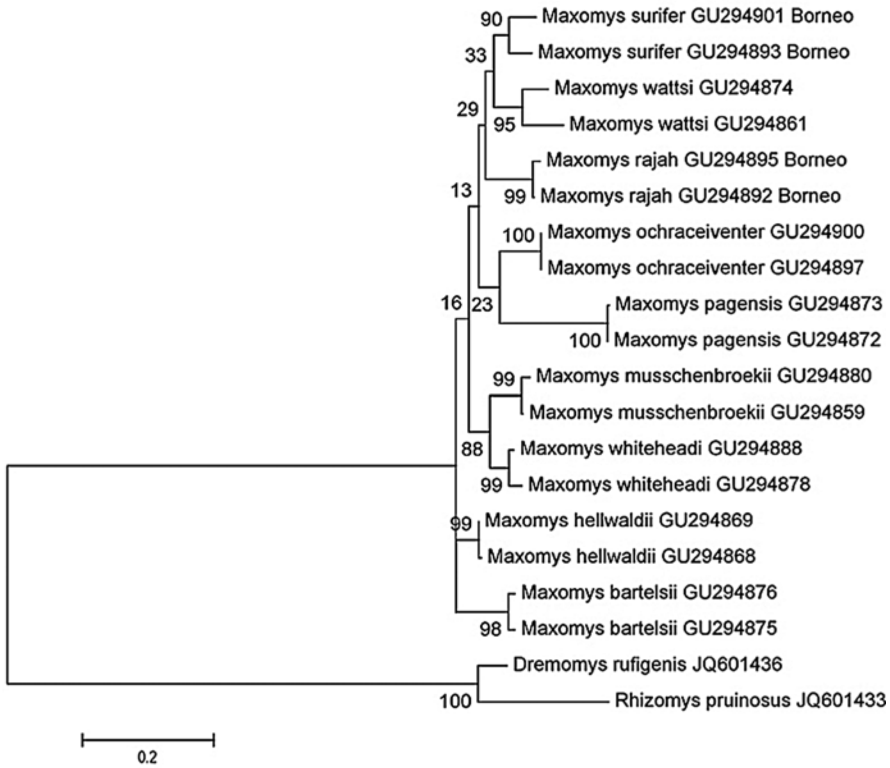

Fig. 4 Phylogenetic tree of *Maxomys* spiny rats (with *Dremomys rufigenis* and *Rhizomys pruinosus* as outgroups) generated by the Maximum Likelihood method based on relatively short partial COI nucleotide sequences conducted in MEGA5 (Tamura et al. 2011) using the Tamura-Nei model (1993). The tree with the highest log likelihood (−3452.2025) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 20 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All positions containing gaps and missing data were eliminated. There were a total of 474 positions in the final dataset

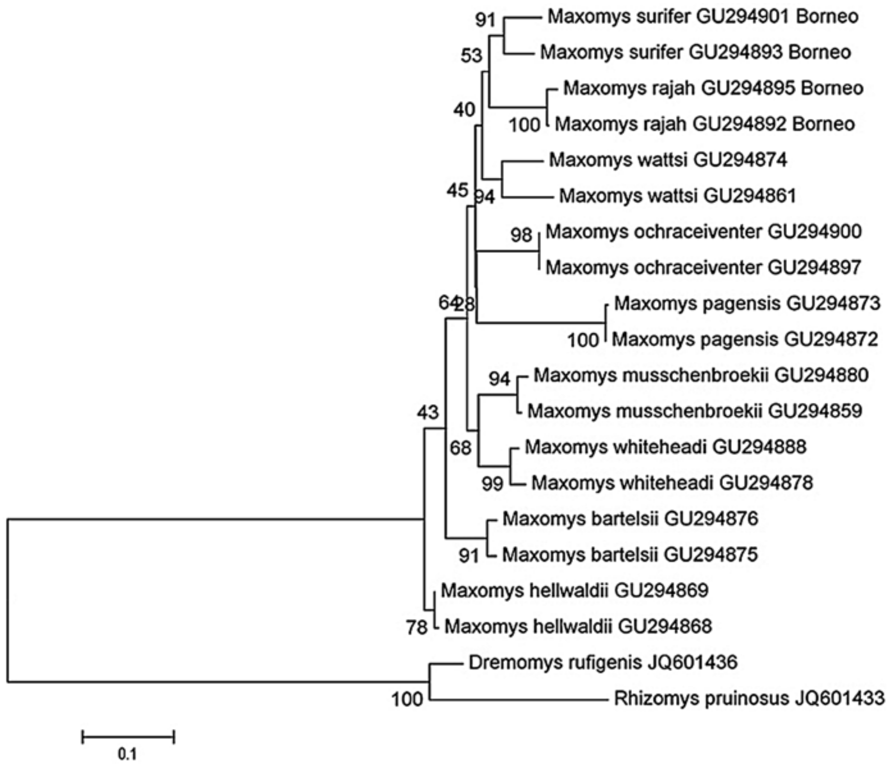

Fig. 5 Phylogenetic tree of *Maxomys* spiny rats (with *Dremomys rufigenis* and *Rhizomys pruinosus* as outgroups) generated by the Neighbor-Joining method (Saitou and Nei 1987) based on relatively short partial COI nucleotide sequences conducted in MEGA5 (Tamura et al. 2011). The optimal tree with the sum of branch length = 1.93656235 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) are shown next to the branches (Felsenstein 1985). The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Kimura 2-parameter method (Kimura 1980) and are in the units of the number of base substitutions per site. The analysis involved 20 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All positions containing gaps and missing data were eliminated. There were a total of 474 positions in the final dataset

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Ecological Characteristics of the Freshwater Crab, *Isolapotamon bauense* in One of Wallace's Collecting Sites

Jongkar Grinang, Indraneil Das, and Peter Ng

Abstract Effective conservation of biodiversity requires good ecological information on species, populations and communities. This is particularly true for the Malaysia state of Sarawak in Borneo, whose rich biological diversity remains poorly documented, with many wetland species facing serious threats resulting from habitat alteration, pollution and overexploitation. This study aims to quantify the ecological characteristics of an endemic potamid freshwater crab, *Isolapotamon bauense* Ng 1987, a species listed as 'Vulnerable' in the IUCN Red List of Threatened Species. A capture-mark-recapture exercise was conducted at two sites along a stream at Gunung Serambu in the Bau region to better understand the ecology of this species. Our results reveal a sex ratio of 1:1, whereas analysis of carapace width-weight relationship document a negative allometric growth pattern and a relatively low condition factor for intermediate sized specimens. Males and females do not differ significantly in body mass and there is no obvious sexual size dimorphism. Over the month long study, the size frequency of carapace classes indicates the population was dominated by smaller size-classes. A linear regression shows a trend in the number of crabs captured with lower air temperatures and higher relative humidity. It also suggests a strong positive correlation with the depth of associated streams, used as a proxy for soil water saturation. We use the MARK program to estimate the overall population size at 90 m^2 sampling area, utilizing Akaike's Information Criterion for model selection. The best model incorporated individual heterogeneity and the effect of rain during the survey on capture probability. The population estimate is 133 individuals with 95 % confidence interval of 106–187. Other ecological aspects of the species, such as local distribution and,

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habitat and food preferences, will need to be studied in order to develop a concise conservation plan for the species.

1 Introduction

Freshwater crabs are one of the most species-rich crustacean groups, and occur across all continents, except the islands of the Pacific and the Antarctic region (Yeo et al. 2008). Globally, over 1,280 species have been recorded, with many species endemic to small geographical areas, and an estimated 128–846 species potentially remain to be discovered (Ng and Yeo 2007; Yeo et al. 2008; Cumberlidge et al. 2009, 2011, 2012). Surprisingly, about one-sixth of the world's freshwater crabs have been threatened with extinction, as a result of habitat loss and environmental pollution (Cumberlidge et al. 2009). On the other hand, the rate of extinction of freshwater crabs may also be associated with biological characteristics of the respective species, such as high level of endemism, dietary and/or microhabitat specialization and low tolerance to rapid environmental changes (Cumberlidge and Daniels 2008; Yeo et al. 2008; Cumberlidge et al. 2009, 2011, 2012). This latter scenario is rather complex and not well understood, particularly in the Southeast Asian region, due to inadequate ecological studies.

The freshwater crabs of Sarawak have been surveyed since the early of 1900s, and are presently represented by 40 species (Ng and Grinang 2004, 2014; Ng et al. 2008; Ng 2013; Grinang and Ng 2014). Of these, four species are listed as 'Endangered' (*Ibanum pilimanus*, *Lepidothelphusa cognettii*, *Thelphusula cristicervix* and *Terrathelphusa kuchingensis*) and two species are 'Vulnerable' (*Isolapotamon bauense* and *Stygothelphusa bidiensis*) in the IUCN Red List of Threatened Species (IUCN 2013). Thirty-one species are categorized either as 'Least Concern' or 'Data Deficient', the conservation status of recently described species, as expected, being unassessed. The conservation assessment of Sarawak freshwater crabs is hampered by a lack of ecological information for its species (see Ng and Yeo 2007; McFarlane and Lundberg 2012). The first ecological work on the freshwater crabs of Sarawak was that of Collins (1980) for the semi-terrestrial species at Gunung Mulu National Park, in Miri Division, northern Sarawak. His study revealed that semi-terrestrial crabs tend to have small population size and are geographically restricted, yet play significant roles in litter communities of alluvial forests at their respective habitats. No further similar studies have addressed other species, despite the desirability of such information for conservation assessments, such as listing under the Red List Criteria (IUCN 2012).

Isolapotamon bauense was described from Gua Sireh, a limestone outcrop near the town of Serian, western Sarawak; is the largest freshwater crab known in Borneo (Ng 1987; Ng and Tan 1998). It has been classified as 'Vulnerable' and is endemic to Sarawak, but there is hardly any ecological information to help in a more effective conservation of the species. A preliminary conservation assessment of the species indicated that its population size and threats are not known (Ng and Yeo 2007;

IUCN 2013). In addition to the lack of knowledge about the species, freshwater crabs are not protected under the Wild Life Protection Ordinance of Sarawak (1998) – assessment of species protection under the WLPO 1998 has been focused on two major pressures, namely hunting and wildlife trading (Wildlife Conservation Society and Sarawak Forest Department 1996). No protection priority has been given to species that no or less pressure from hunting and wildlife trading. Protection of other species has been relying on the establishment of totally protected areas, where nearly 1 million ha of forests had been gazetted across the State for the purpose. Unfortunately, the known range of *Isolapotamon bauense* is outside the totally protected areas (Ng 1987; Ng and Grinang 2004), which are potentially subjected to land development and disturbance by agricultural activities. Our study aims to investigate various ecological characteristics of the crab, including population structure, growth pattern, condition and population size; criteria that are essential for an accurate conservation assessment of the species.

2 Materials and Methods

2.1 Study Sites

Gunung Serambu at Kampong Peninjau Lama in Bau District, Sarawak is a historical site, being associated with Sir James Brooke's cottage, where the celebrated British naturalist, Alfred Russel Wallace (1823–1913) spent much time during his explorations in Sarawak. Our study was conducted at an intermittent stream, located to the northeast of the mountain (Fig. 1). The stream channel area consists predominantly of rocky outcrops, with massive boulders lining the passages; and the vegetation comprising mixed dipterocarp forest. The stream is ephimeral, flowing only after periods of heavy rainfall, although there is year-round ground water. Two sampling sites were chosen, based on the presence of the crab during a preliminary survey in October 2012. Site 1 (01°25′55″N, 110°13′27″E; 199 m above sea level) was located at the lower slope, the size of the stream channel been 40 m long by 1 m wide. Site 2 (01°25′50″N, 110°13′04″E) was located 340 m above sea level on the upper slope of the mountain, and ca.100 m south of the Rajah Brooke's cottage site. It is 50 m long and 1 m wide at the stream channel. The total sampling area for both sites was 90 m^2.

2.2 Capture-Mark-Recapture Protocol

Ecological information of the potamid crab was obtained using capture-mark-recapture (CMR) protocol. Ten sessions of CMR, with 4 or 6 day interval, were conducted from 19 April to 27 May 2013 at Sites 1 and 2. The time interval allows for captured and uncaptured crabs to randomly mix, and relaxing potentially

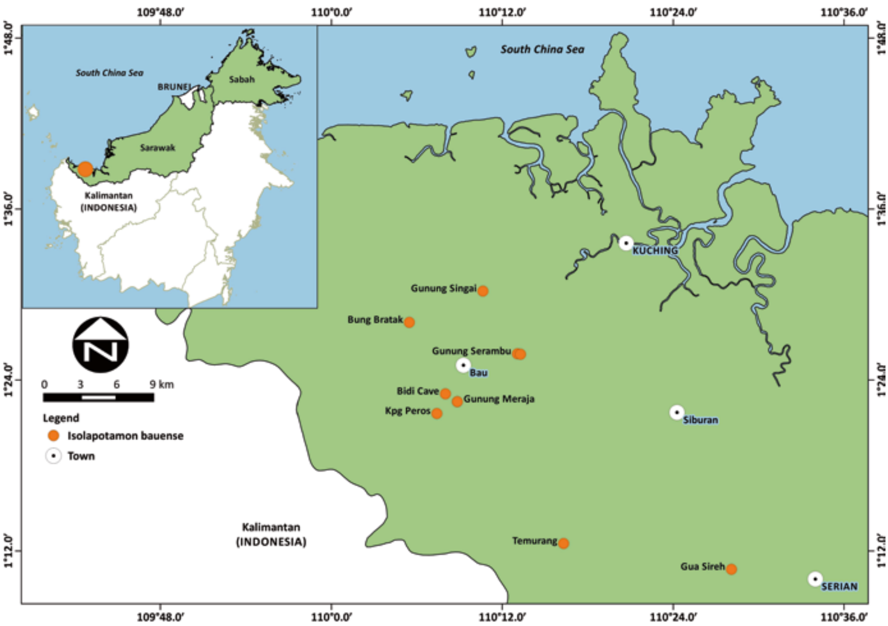

Fig. 1 Map showing location of Gunung Serambu and other known localities of *Isolapotamon bauense*.

unnatural reactions of crabs to capture. CMR was conducted between 1900 and 2300 hrs by three field personnel throughout the sampling sessions. All crabs found within the sites were hand-collected. Each individual crab was identified and the morphological characteristics, such as weight, carapace width and carapace length were measured, and sex and relative age determined by examining the shape of the abdomen. Weight and length were measured using a Shimadzu ELB200 electronic balance (to the nearest 0.01 g) and a Mitutoyo CD-8CSX digital caliper (to the nearest 0.01 mm), respectively. A waterproof oil-based paint marker was used to mark the crabs. The marking was made on the carapace that contained numbered codes. The marked crabs were released at the site where it was caught. A HOBOware Pro Version 3.3 data logger was installed at the study site to record air temperature and relative humidity. Depth of water at selected points of the intermittent stream was measured, for use as proxy for soil water saturation in relation to rain events during each sampling session.

2.3 Statistical Analyses

Ecological data associated with the crab species at the two sites were pooled for analysis of size classes, sex ratio, growth pattern and condition. The crabs were sexed and grouped into five classes in each category of weight, carapace width and carapace length. Differences in weight, carapace width and carapace length between male and female were evaluated using a non-parametric (Mann-Whitney *U*-) test. The rationale for the same was arrived at after prior runs of Shapiro-Wilk- and Levene's tests. Male to female ratio of crabs was calculated using the formula, $S_0 = (M_0 - F_0)/(M_0 + F_0)$, where M_0 and F_0 is the number of males and females in the population, respectively (Christiansen et al. 1990). Zero value indicates a population with a sex ratio of 1:1. Exact binomial test goodness of fit, specifically for a small sample size was run to test if sex ratio of the crab species being studied significantly deviated from 1:1.

Growth pattern and condition of crab was estimated using carapace width-weight relationships (CWWRs) with the formula, $W = aCW^b$, where W and CW is the weight (to the nearest 0.01 g) and carapace width (to the nearest 0.01 mm), respectively (Froese 2006). The formula was logarithmic transformed to obtain a linear expression of $Ln\,W = Ln\,a + b\,Ln\,CW$, where a and b are the intercept and slope of the straight line, respectively. Least squares regression of CWWRs was run in GraphPad Prism Version 6. The b value implies type of growth of crab, where $b=3$ is isometric, and $3 < b < 3$ is allometric. A value of $b<3$, $b=3$ or $b>3$ can also be interpreted as growth rate of crab to be poor, normal or over, respectively. The condition factor (K) was determined with a formula, $K = 10^5 W / L^3$ to evaluate the relative degree of well-being of each crab. A higher K value indicates a better condition of the crab.

Association between number of crabs captured and three covariates (i.e., air temperature, relative humidity and water depth) was determined using linear regression. Population size was estimated using closed population capture-recapture models in the program MARK. The main assumptions underlying the models are the crab population is geographically and demographically closed (i.e., no immigration, emigration, death and birth), and crabs did not lose their markings. Models used for the population estimation were M_o (null model assuming capture and recapture probabilities are constant), M_t (probability vary with time), M_b (probability vary with behavioral response to capture), M_{h2} (probability vary by individual crab or heterogeneity) and models by incorporating the covariates (Otis et al. 1978). Akaike's Information Criterion (AIC) was used for selection of best model for estimation of population. Analysis of median c-hat (ĉ) was performed to estimate overdispersion correction of the data subsequently use to assess how well the models fit the observed data.

3 Results

3.1 Population Structure

A total of 79 crabs were captured, marked and released, whereas 53 crabs (67 %) were recaptured during the ten sampling sessions. The total number of specimens captured was 43 males (55 %) and 36 (45 %) females. Analysis of size class shows a population skewed to smaller sizes (Fig. 2). The trend was clearly observed in weight structure, where the highest relative frequency occurred at size class 0.2–30.2 g. The size frequency distribution imply that population, over a period of 1 month of the current study period, was dominated by smaller size-classes. The largest individual crab caught was a male, with wet mass, carapace width and carapace length of 145.2 g, 74.8 mm and 56.8 mm, respectively. A Mann-Whitney U-test showed that size of male was not significantly different from females for all three measurements (Table 1). The size range in male population tends to be wider than female population. These results show that maximal adult size is not sex-determined. Sex ratio is 0.09, and the exact binomial test goodness of fit confirmed that this skewness was not significant, with a p-value of 0.428 (Table 1).

3.2 Growth Pattern and Condition

The carapace width-weight relationships of the population at Gunung Serambu were exponential (Fig. 3), which is appropriate for estimation of growth pattern and condition factor of both male and female populations. Regression of carapace width-weight relationships was significant at $p<0.0001$ (Table 2). Values of r^2 for males, females and both sexes combined were 0.997, 0.998 and 0.997, respectively. The estimate of parameter *b* for males (mean = 3.017, 95 % confidence interval 2.996–3.069) was significantly higher than for females (mean = 2.918, 95 % confidence interval 2.872–2.964). The equation models for males and female crabs are $\text{Ln W} = 3.017\text{Ln CW} - 8.083$ and $\text{Ln W} = 2.918\text{Ln CW} - 7.749$, respectively. The values of parameter *b* indicate that male crabs show positive allometry, whereas females show a negative allometric growth pattern. There was no evidence of a difference of condition factor among males, females or the two sexes combined (Table 2). An analysis of condition factor for the five size classes show that the value was relatively low for intermediate-sized crabs (weight 60.3–90.3 g; carapace width 36–49 mm; carapace length 28–38 mm) (Fig. 4).

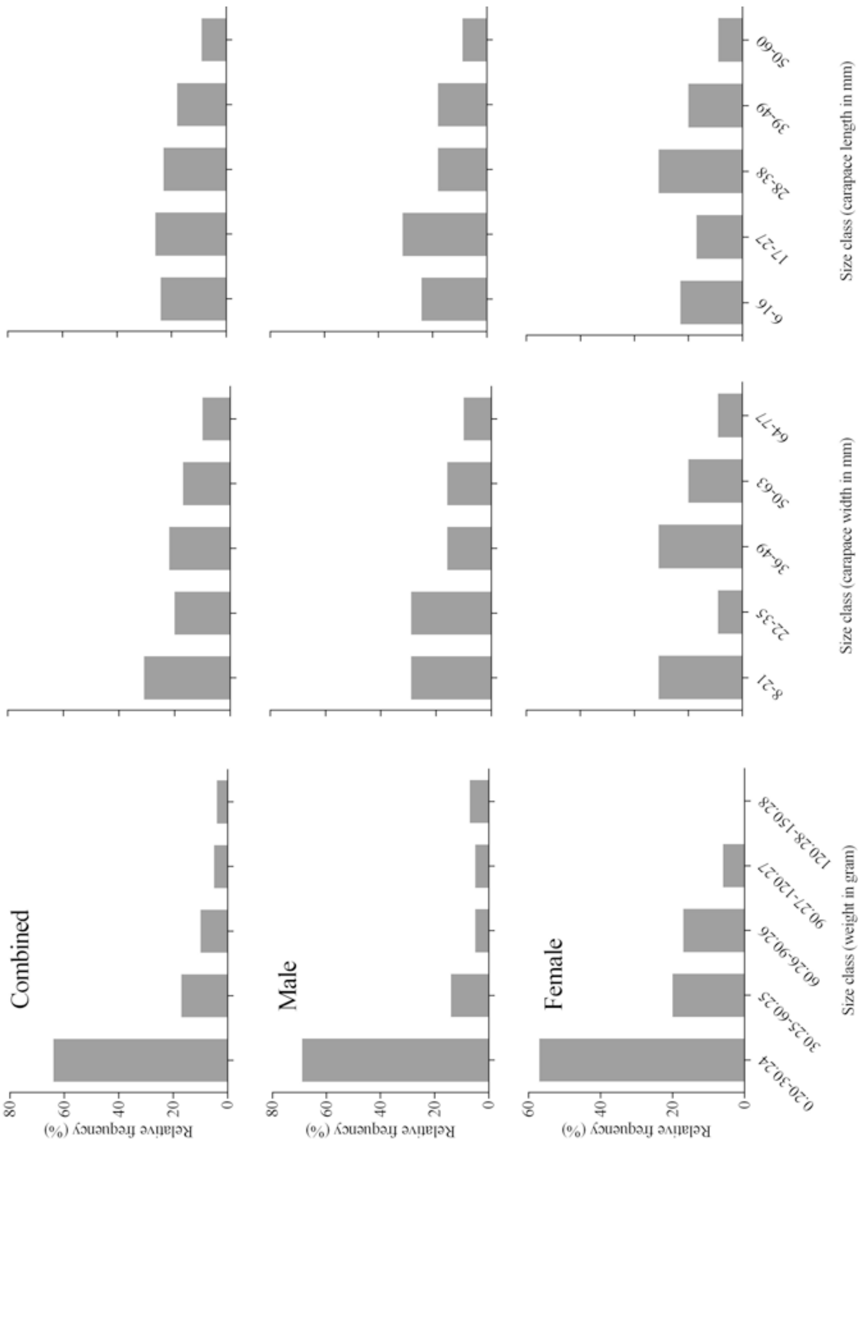

Fig. 2 Population size structure of *Isolapotamon bauense* in Gunung Serambu

Table 1 Sex ratio and morphometric differences between male and female *Isolapotamon bauense* from Gunung Serambu. Bau, Sarawak. S, L and MW for Shapiro, Levene and Mann-Whitney test, respectively. Only one ovigerous female crab (6.80 × 5.24 mm, 102.64 g) was captured at Site 1 on the second session and recaptured on the third session

	Weight (g)		Carapace width (mm)		Carapace length (mm)	
Metrics	♂ (n = 43)	♀ (n = 36)	♂ (n = 43)	♀ (n = 36)	♂ (n = 43)	♀ (n = 36)
Range	0.30–145.20	0.24–102.60	9.80–74.50	8.70–69.10	8.70–56.80	6.80–54.30
Mean + SE	29.12 ± 6.08	31.32 ± 5.24	35.81 ± 2.86	39.13 ± 3.21	27.82 ± 2.12	30.68 ± 2.37
95 % CI	16.84; 1.40	20.66; 1.97	30.04; 1.57	32.61; 5.64	23.53; 2,104	25.87; 35.49
S	p = 0.0001	p = 0.001	p = 0.006	p = 0.032	p = 0.013	p = 0.049
L	p = 0.308		p = 0.769		p = 0.837	
MW	p = 0.574		p = 0.524		p = 0.397	

Sex ratio = 0.09; Exact binomial test goodness of fit for sex ratio of 1:1, $t_{(calculated,\ n\ =\ 1)} = 0.060$, $p = 0.428$

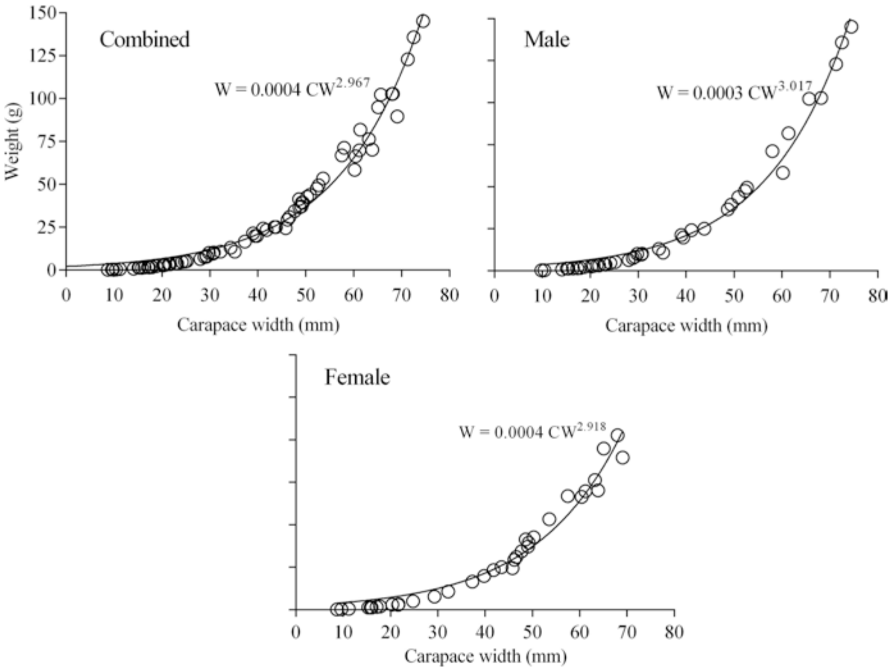

Fig. 3 Exponential growth of *Isolapotamon bauense*

Table 2 Estimated of the carapace width-weight relationship and condition factor (*K*) for *Isolapotamon bauense* with 95 % confidence interval. All regression analyses were significant, with p = 0.0001

	Carapace width-weight relationship			
Parameter	r^2	Ln a	b	*K*
Combined (n = 79)	0.997	−7.915 (−8.040;−7.789)	2.967 (2.931; 3.003)	32.71 (32.04;66.74)
Male (n = 43)	0.997	−8.083 (−8.262;−7.903)	3.017 (2.966; 3.069)	32.92 (32.02;67.54)
Female (n = 36)	0.998	−7.749 (−7.913;−7.586)	2.918 (2.872; 2.964)	32.44 (31.40;66.84)

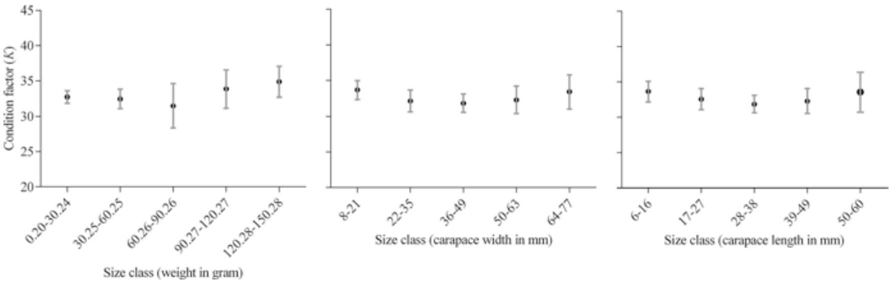

Fig. 4 Condition factor with 95 % confidence interval of *Isolapotamon bauense* for difference size classes

3.3 Population Size Estimation

The forests in Gunung Serambu are relatively less disturbed compared to other forested areas outside the protected areas system in western Sarawak, and probably plays a significant role in stabilizing air temperature and relative humidity. Data recorded for the study period show a minimum fluctuation of air temperature and relative humidity (Fig. 5). Linear regression of the parameters with crab abundance shows a trend of association (Fig. 6): the number of captures was negatively correlated with air temperature ($r^2 = 0.049$, $p = 0.537$), but positively correlated with relative humidity ($r^2 = 0.010$, $p = 0.788$), although neither relationships were significant. Finally, the number of individuals captured was strongly correlated with water depth ($r^2 = 0.828$; $p = 0.0003$).

The total individual crabs caught from Site 1 and Site 2 was 47 and 32, respectively. Our observations show that *I. bauense* does not wander far from its burrow even when foraging. No individual crab was recaptured at both sampling sites. Points where the crab recaptured were also near the point of first capture (the farthest ca. 5 m). This indicates that the population estimation exercise conducted with the assumption of a closed population was valid. The census yielded an overall population estimate of 133 individual of crabs, with a 95 % confidence interval 106–187 from an approximate area of 90 m^2 (Table 3). The estimation was derived from the best model, {Site1 = h2p1(Rain)p2(Rain) Site2 = Mo(Rain) c = p N_{site1},

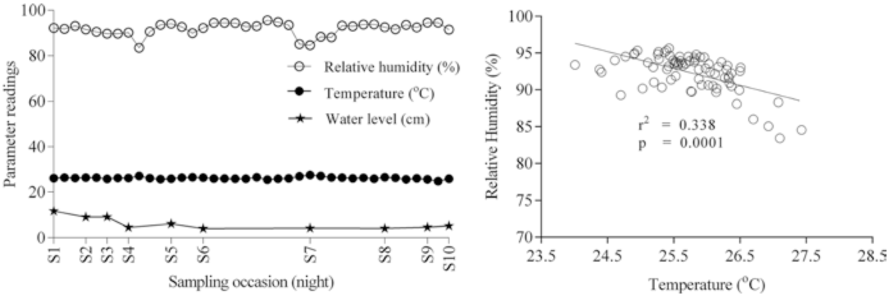

Fig. 5 Environmental variables at Gunung Serambu, Sarawak, recorded during the study period. Chart on the right shows negative correlation between relative humidity and air temperature

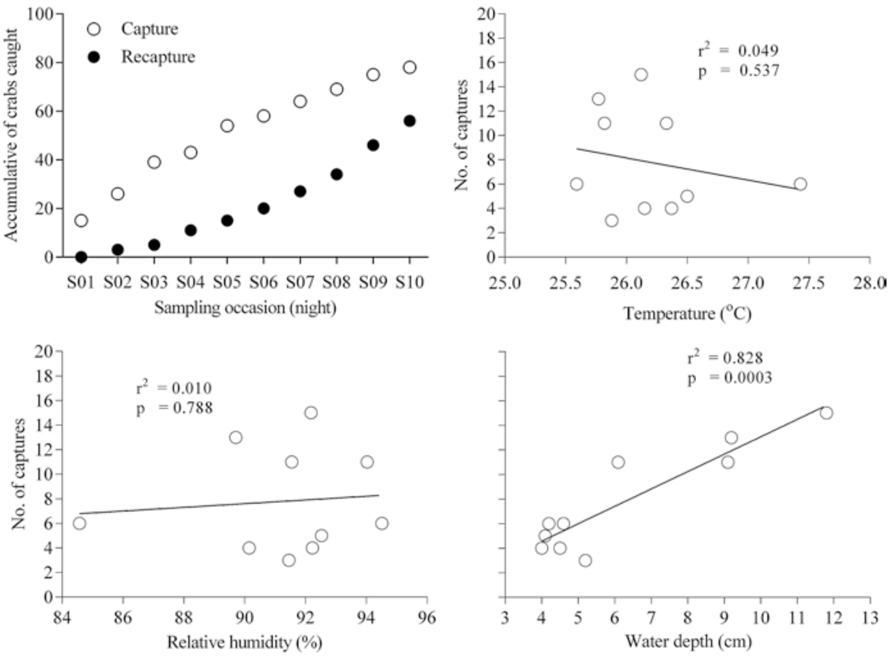

Fig. 6 Association between capture rate and three environmental variables. Chart on the top left shows accumulated number of crabs captured and recaptured in each sampling session

N_{site2}} pi2 = 1} (QAICc = 210.705; QAICc Weight = 0.7801) that incorporated individual heterogeneity and the effect of precipitation during the survey period on capture probability. The support for the best model was about five times better than the second best model (M_{h2}; QAICc = 213.775; QAICc Weight = 0.1681). Value of ΔQAICc (=3.070) indicates considerable support for real difference between the two models (see Burnham and Anderson 2002). There was no evidence of difference of estimate population size between Site 1 (N=65.95; 95 % CI 55.05–101.51) and Site 2 (N=65.48; 95 % CI 45.59–114.49).

Table 3 Estimate population size (*N*) of *Isolapotamon bauense* at Gunung Serambu, Bau, Sarawak

Models	*N* (95 % confidence interval)		QAICc	ΔQAICc	QAICc weight	No. par
	Site 1 (bottom)	Site 2 (top)				
{Site1 = h2p 1 (Rain)p 2(Rain) Site2 = Mo(Rain) c = p N_{site1},N_{site2}} pi2 = 1}	67.95 (55.05; 101.51)	65.48 (45.59; 114.49)	210.705	0.000	0.7801	7
{M_{h2}}	68.05 (55.09; 101.77)	65.65 (45.67; 114.85)	213.775	3.070	0.1681	7
{M_o}	55.77 (50.54; 68.70)	65.65 (45.67; 114.85)	216.562	5.857	0.0417	4
{M_b}	53.39 (48.56; 73.19)	48.92 (35.12; 123.91)	220.054	9.349	0.0073	6
{ρ(Rain) c = ρ N_{site1}, N_{site2}}	62.55 (54.59; 78.88)	42.43 (36.59; 55.66)	223.769	13.063	0.0011	4
{ ρ(TEM) c = ρ N_{site1},N_{site2}}	62.63 (54.63; 78.99)	42.48 (36.62; 55.75)	225.845	15.140	0.0004	4
{ ρ(WD) c = ρ N_{site1},N_{site2}}	62.63 (54.63; 79.00)	42.48 (36.62; 55.75)	225.935	15.229	0.0004	4
{ ρ(RH) c = ρ N_{site1},N_{site2}}	62.64 (54.64; 79.02)	42.49 (36.63; 55.76)	226.232	15.527	0.0003	4
{ ρ(TEM + WD) c = ρ N_{site1},N_{site2}}	62.61 (54.62; 78.97)	42.47 (36.62; 55.73)	227.424	16.719	0.0002	5
{ ρ(RH + WD) c = ρ N_{site1},N_{site2}}	62.62 (54.63; 78.98)	42.47 (36.62; 55.74)	227.573	16.719	0.0002	5
{ ρ(TEM + RH) c = ρ N_{site1},N_{site2}}	62.63 (54.63; 78.99)	42.48 (36.62; 55.75)	227.870	17.165	0.0002	5
{ ρ(TEM + RH + WD) c = ρ N_{site1},N_{site2}}	62.61 (54.62; 78.97)	42.47 (36.62; 55.73)	229.443	18.738	0.0001	5
{M_t}	55.65 (50.48; 68.50)	63.51 (44.66; 110.41)	233.715	23.010	0.0000	22
{M_{tb}}	47.47 (47.02; 60.88)	52.21 (33.05; 419.26)	255.133	44.428	0.0000	38

The c-hat (ĉ) for overdispersion correction of the models was 1.17. Total individuals caught, Site 1 = 47; Site 2 = 32
TEM temperature, *RH* relative humidity, *WD* water depth

4 Discussion

To our knowledge, this study is the first study of the ecological characteristics of a freshwater crab species in Southeast Asia, incorporating a capture-mark-recapture census technique and the employment of statistical models in estimating population size. Collins (1980) used the pitfall trapping method to assess population and biomass of a semi-terrestrial gecarcinucid crab, *Terrathelphusa loxophthalma* (as a species of *Perbrinckia*) in Gunung Mulu National Park, but did not estimate the species' population size. Nonetheless, both studies indicate comparable ecological findings. Both species show nocturnal habits, exhibit small home ranges and are burrowers. Our field observations found that *I. bauense* consume beetles, snails, slugs and seeds, as well opportunistic cannibalism. The population of *I. bauense*, with a sex ratio of 1:1 was also found in *T. loxophthalma* (cf. Collins 1980). High frequency of smaller size-classes might suggest high reproductive activity in the preceding months, followed by recruitment of young during the study period. The presence of single ovigerous crab out of 36 individual females (sample size notwithstanding) supports our hypothesis. Because our sampling method used was non-invasive, we cannot determine the size of maturity although the carapace of the ovigerous female crab was 6.80 mm wide by 5.24 mm long, and weighed 102.64 g.

The growth pattern and condition factor can be affected by food availability, habitat quality, disease, high population densities and reproductive cycles, as well overexploitation (Froese 2006). Our study shows that *I. bauense* tends to follow an isometric growth pattern, implying a proportionate increase in body weight and carapace width. The population is also in good condition with slightly low K value for the intermediate size-classes. Ideal growth pattern and good condition factor for *I. bauense* may be the result of ambient environmental condition and low anthropogenic disturbance. In comparison, the parameters b and K of *I. bauense* are comparable with that reported for the African true freshwater crab, *Sudanonautes africanus* (Potamonautidae) from western Nigeria (Bello Olusoji et al. 2009), and better than *Barytelphusa guerini* (Gecarcinucidae) from the Kham River in India (Patil and Patil 2012).

Our best model for estimating population size of *I. bauense* has incorporated individual heterogeneity and rain events, with assumption of no difference of probability between sessions, and no behavioral responses to capture. Although the assumptions are difficult to meet (Otis et al. 1978), a high degree of support of the best model to the observed data (in comparison to other models) suggest our estimation method for the population size of *I. bauense* at Gunung Serambu is sound. Heterogeneity among capture probability of individual crabs may be correlated with behavioral plasticity in the species, where the variation in behavior may be advantageous in the avoidance of competition via intraspecific resource partitioning.

The capture-mark-recapture technique has been frequently applied for estimating of population sizes of species with low mobility, such as frogs, lizards, terrestrial turtles and crayfish (Pham et al. 2007; Krishnamurthy and Reddy 2008; Nowicki et al. 2008; Dodd et al. 2012; Tenan et al. 2013), especially when an assumption of closed population, which is the basis of the method, can be reasonably met. This non-invasive method in population estimation for freshwater crabs is hardly used (see Collins 1980; Hill and O'Keeffe 1992). We reiterate that the capture-mark-recapture technique can serve as alternative approach for population estimation of freshwater crabs, especially when the distribution of the species is restricted and the species does not wander far from its burrows.

5 Conclusions

The need for detailed of ecological information in any conservation program for freshwater crabs has been discussed earlier. Ng and Yeo (2007) noted that survival of the Singaporean endemic crab, *Johora singaporensis* (Potamidae) in Bukit Timah Nature Reserve was only because of the conservation of a small patch of primary forest on the island. Other studies have indicated that good management of fragmented habitats is necessary to conserve populations, including for freshwater crabs (Brook et al. 2003). It is appears that any assessment for protection of freshwater crabs in Sarawak must include ecological attributes of the species. Our study provides key ecological data for *Isolapotamon bauense* that would be useful for conservation of the species. Other ecological aspects, such as local distribution, and detailed habitat- and food preferences will be required to develop a more comprehensive plan for the long-term conservation of the species.

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Streams in Forested Headwaters as Reservoirs of Endemicity in Bornean Amphibians

Yong Min Pui and Indraneil Das

Abstract Tropical forests are known centers of amphibian richness and endemicity. Within these forests, embedded wetlands, particularly streams and other lotic environments, are focal areas of amphibian diversity. Are specific streams or sections of streams relatively more important than others as reservoirs of species richness or endemicity? To address this question, we studied stream-dwelling amphibian assemblages within Gunung Mulu National Park, Sarawak, East Malaysia (Borneo). Six streams were selected, ranging from the headwaters of Sungei Tapin (1,800 m asl) to low elevation streams within the Sungei Melinau system, both tributaries of Sungei Tutoh. A 100 m transect was established at each stream, and standardized visual encounter surveys conducted along each transect at night. A cumulative sampling effort from 35 nights yielded a total of 262 individuals representing 41 amphibian species. Our results indicate greater endemicity in lower order streams (headwaters highest- 80 %) compared to higher order streams at lower elevations (500 m asl, 75 %; <200 m, 42–57 %). In contrast, species diversity and species richness were significantly greater at larger streams. Species composition at lower elevation streams were more similar to one another, but could be separated into discrete large stream- and small stream- assemblages. These results suggest that species composition of stream-dwelling amphibians is affected by stream elevation or stream width. Our results underline the importance of riparian habitats, especially forested headwaters, in harboring Bornean endemics, a number of which are on the global list of threatened species. These findings support prioritization of stream types and stream segments, especially within forested headwaters, as a regional conservation strategy.

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1 Introduction

The island of Borneo is known as a mega-biodiversity center, harboring a biota that is remarkably lineage-rich (MacKinnon et al. 1996; Sodhi et al. 2004). At present, around 180 amphibians are known from the island, consisting 174 species of anuran amphibians and 6 species of caecilians (Das et al. 2014; Frost 2015). These figures reveal that Bornean amphibians are exceedingly rich and show high levels of endemism, with nearly 70 % (113 species) not recorded elsewhere. The island is also the type locality for 141 species of anuran amphibians, some widely distributed, others restricted to small parts of the island. An earlier study reported that a third of the fauna as specialists of montane/submontane environments, above 750 m asl (Inger and Stuebing 2005).

The island's biodiversity is severely threatened by logging, conversion of forests into agricultural and other developments, which have destroyed large swathes of lowland rainforests (MacKinnon et al. 1996; Achard et al. 2002; Fuller et al. 2003; Curran et al. 2004). Ninety-eight species (60 %) are facing population declines, 27 species (17 %) show stable populations, and 38 species (23 %) are unassessed (IUCN 2014). These figures reveal that Bornean amphibian populations face high levels of decline, and 24.2 % of the species are classified in a threat category.

Tropical amphibians may utilize a wide range of microhabitat types, with some species showing specialisations for rocky stream, hilly terrain and non-riparian forested areas (Inger et al. 2002). Further, most highland frog species use similar microhabitats (Ramlah et al. 2002). Species may be segregated into ecological guilds in such tropical environments. Keller et al. (2009) recognised three distinct habitat guilds, comprising large stream species, waterfall and stream species, and calm stream (presumably slow-flowing) species. Faunal turnover with elevation is also known, with increasing elevation known to be related to both species diversity and richness (Das et al. 2007).

Located in northern Sarawak, East Malaysia, Gunung Mulu National Park is arguably the most spectacular National Park on Borneo. The Park, covering ca. 52,865 ha of forest, encompasses a remarkable diversity of vegetation, with 17 recognized vegetation zones. Elevational range in the Park is from 45 to 2,376 m asl. The region is drained by tributaries of two major river systems, the Limbang and the Baram, formed by numerous subcatchments (Walsh 1982) with numerous accessible established trails. The area is known to be home to over 100 species of amphibians (Malkmus 2002; Pui unpubl), making it arguably the richest amphibian hotspot in the Old World, and matching species-rich sites in the Neotropics (Donnelly and Guyer 1994). A large number of amphibian species on Mulu are, in fact, endemic to the mountain massifs (Dring 1983a, b, 1987; Inger et al. 1995; Dehling 2008, 2010, 2011). Despite the fact that trails are well established, the numerous perennial streams, intermittent and ephemeral water bodies, and the presence of intact vegetation and high amphibian diversity, spatial aspects of amphibian diversity remain unstudied. Even small-scale habitat assessment information is important for amphibian conservation because most these species are not widely distributed. This study addressed the following question: Are specific streams or sections of streams are more important than others as reservoirs of species richness or endemicity?

2 Methodology

2.1 Field Site

Field work was carried out at Gunung Mulu National Park (headquarters at 04.02.30.3N; 114.48.46.1E; 49 m asl; datum WGS84; Fig. 1) between 28 February 2008 and 31 March 2009. A total of six transect lines were established along streams (ca. 100 m long) (Fig. 2). Detailed descriptions of the survey sites are provided below following the forest classification of Anderson and Chai (1982). The Park's

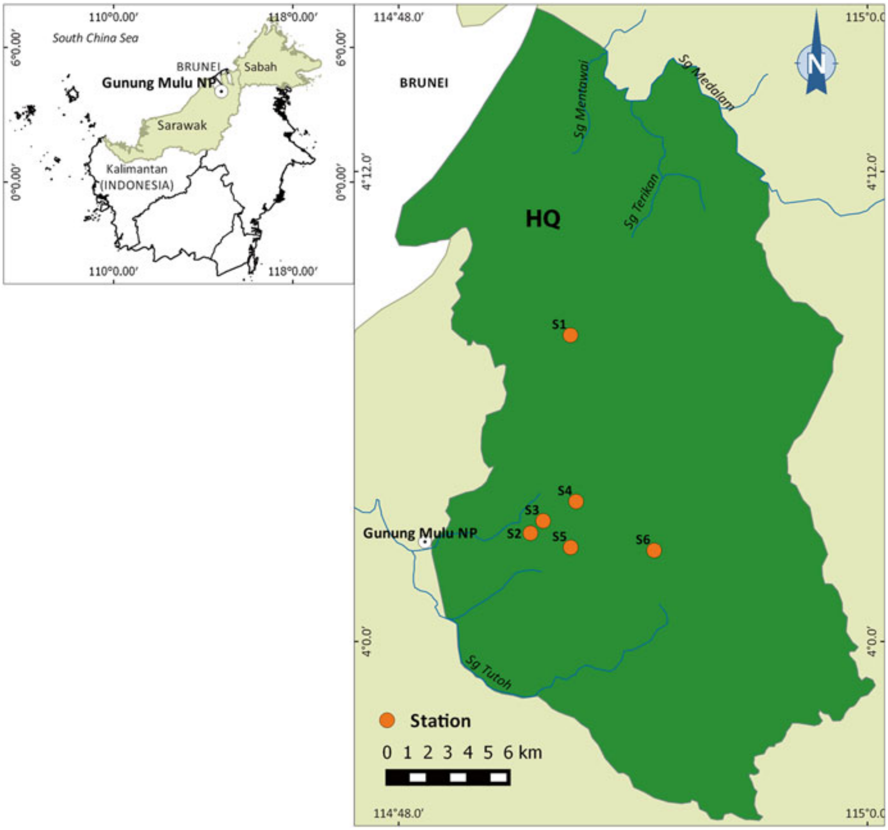

Fig. 1 Location of major areas mentioned in this study in Gunung Mulu National Park. Abbreviations; S1–S6 = survey sites 1–6, Mulu *HQ* Gunung Mulu National Park Headquarters

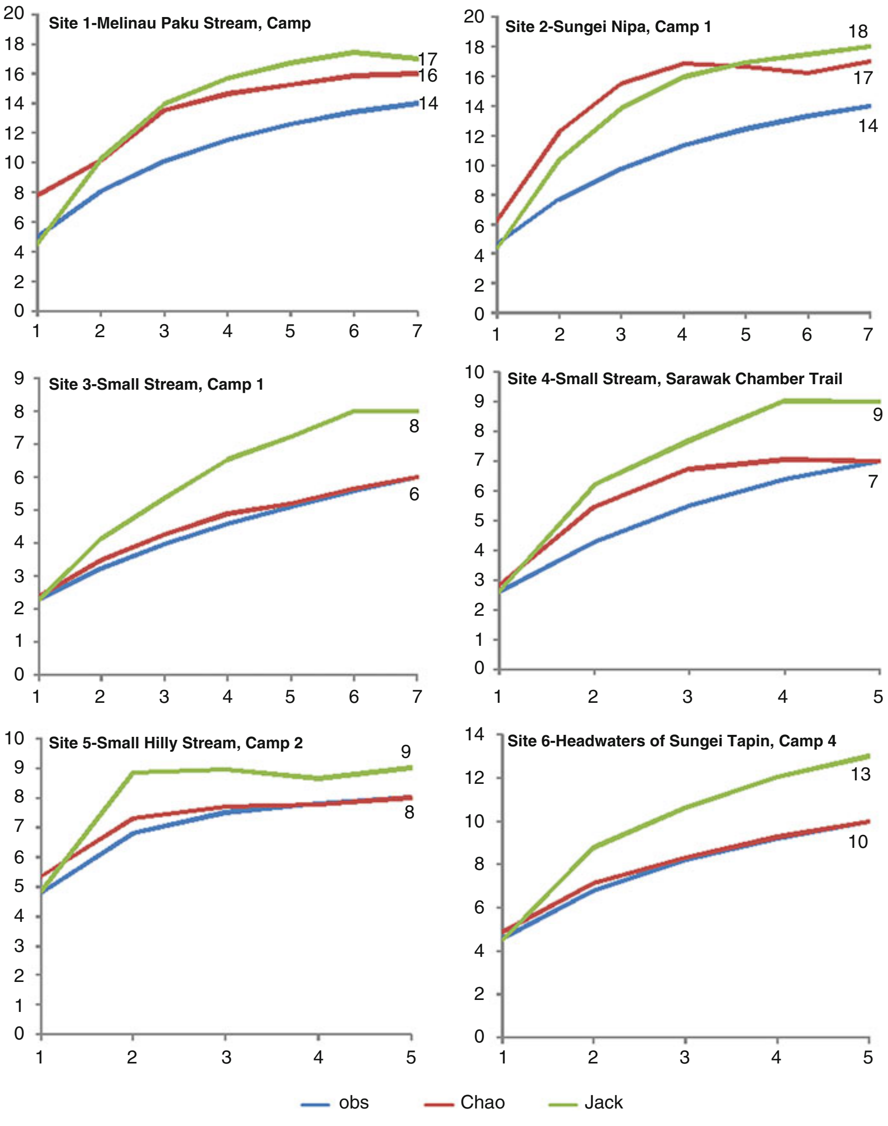

Fig. 2 Species accumulation curves for each survey site at Gunung Mulu National Park. Note: Graphs; axis-y = sampling efforts (nights) and axis-y = number of species recorded

vegetation was described by Anderson and Chai (1982) and Hazebroek and Abang Morshidi (2002). Its geology and geomorphology have been described by Waltham and Webb (1982) and Osmaston and Sweeting (1982), based on data from the Royal Geographical Society (RGS) Expedition to the Park in 1977–1978. GPS data were obtained with a Garmin® GPSMAP 60CSx device.

Site 1- Melinau Paku Stream, Camp 5. This site was located in the vicinity of Camp 5, with the 100 m stream transect established at the Melinau Paku Stream (starting point: N04°07.820′, E114°52.396′; 125 m asl). The stream has an average width of 15 m, clear water with moderately fast flowing current, and a rather open canopy along the established transect, although partially shaded along some portions of the stream. The stream bed was dominated by pebbles, and the banks covered by shrubs and saplings

Site 2- Sungei Nipa, Camp 1. This site was located in the vicinity of Camp 1 ca. 15 m from the Camp 1 hut. A 100 m transect was established at Sungei Nipa (starting point: N04°02.765′, E114°51.373′; 250 m asl). The stream had an average width of 12 m and a gradient of ca. 6–7°, with an open canopy and clear and fast-flowing water currents. It is surrounded by undisturbed mixed diterocarp forest. The stream substrate consists of gravel, boulders, and pebbles. The stream banks are of moderate height, often covered by saplings and fallen logs. This stream is referred to as 'Likoh Nipa' by the Berawan ethnic group (Proctor 1982).

Site 3- Small Stream, Camp 1. A 100 m length of stream transect was established along a small stream that is located at Camp 1 (starting point: N04°03.077′, E114°51.699′; 250 m asl). The stream is surrounded by undisturbed mixed dipterocarp forest on moderately hilly terrain, with an average width of 1.5 m; large forest-floor with numerous permanent small pools are found at 80–90 m along the transect. The stream has a shaded canopy, and the banks dominated by shrubs and saplings.

Site 4- Small Stream, Sarawak Chamber Trail. An ca. 100 m transect was established along a small stream that cuts across the Sarawak Chamber Trail (starting point: N04°03.572′, E114°51.451′; 245 m asl). The stream is surrounded by undisturbed mixed dipterocarp forest, with average width of 3 m, and has slow-flowing current with clear water and substrate composed of sand, leaf litter, gravel, and pebbles. The stream banks are abundantly clad with shrubs and saplings, and the canopy extensive, producing a substantial amount of shade along the transect.

Site 5- Small Hill Stream, Camp 2. This site is located in the vicinity of Camp 2. A ca. 50 m stream transect was established. This stream could be characterized as a moderate gradient (8–9°) hill stream (starting point: N04°02.401′, E114°52.403′; 540 m asl). The stream width averaged 2 m, minor torrents and shallows, and containing pebbles and pools. Bedrock is exposed along the stream, the banks dominated by shrubs and saplings, the canopy moderate, resulting in partial shade.

Site 6- Headwaters of Sungei Tapin, Camp 4. This site is located in the vicinity of Camp 4, where a ca. 100 m length of transect was established along the stream (starting point: N04°02.323, E114°54.542; 1,600–1,700 m asl). The stream is small, steep, and rocky, and has an average width of 2 m, with clear and moderately fast current. The streambed is dominated by bedrock and gravel, with a few fallen logs, the banks dominated by herbaceous and epiphytes, and a few saplings with branches that overhung the stream. The stream canopy was extensive, and the site was rather shaded along the established transect.

2.2 Data Collection and Analysis

Standardised visual encounter surveys (VES) were conducted along each transect between 1900 and 2200 h, in order to determine the species diversity, species richness, and relative abundance of amphibians within the selected streams. A species relative abundance (*RA*) was estimated by total number of individuals per species divided by the total number of captures. During these surveys, amphibians were observed by walking slowly along the established transect line using headlights; all amphibians encountered were collected (see Crump and Scott 1994; Heyer et al. 1994). Nomenclature of species follows Frost (2015). Voucher specimens have been deposited at the Museum of the Institute of Biodiversity and Environmental Conservation, UNIMAS.

The occurrence of amphibian species during each census at each sites was used to generate species accumulation curves. The total number of species richness was estimated from the census data using Jackknife and Chao estimators by carrying out 100 random re-ordering of censuses in Estimate S 9.1.0 (Colwell et al. 2004). PAST (Palaeontological Statistics) version 1.96 (Hammer et al. 2001) was used to generate the diversity indices (Shannon-Wiener Index and the Simpson's Diversity Index), and diversity *t*-tests were used to detect significant differences in species diversity among the sites. Unweighted Pair-Groups Method Average (UPGMA) cluster analysis was conducted following hierarchical agglomerative clustering, based on the Bray-Curtis Similarity Coefficient (Bray and Curtis 1957) on presence/not detected data of species composition across sites, using the Multivariate Statistical Package (MVSP) program by Kovach (1998).

3 Results and Discussion

The cumulative 35 night transect sampling effort yielded a total of 262 individual amphibians comprising 41 species belonging to 7 families at the 6 sites: Megophryidae with 7 species; Microhylidae with 1 species; Ranidae with 11 species; Rhacophoridae with 5 species; and Bufonidae and Dicroglossidae with 8 species each (Table 1). Species accumulative curves are shown in Fig. 2 for each sampling sites, suggested additional species (in the range of 1–3 species) are expected from each site. Species richness was greatest at Sungei Nipa (S2) with estimated of 18 species. The Melinau Paku (S1) with 17 species, followed by the headwaters of Sungei Tapin (13 species), the hilly small stream at Camp 2 and the small stream at Sarawak Chamber (9 species) and the small stream at Camp 1 (8

Table 1 Species composition and counts of amphibians collected from six survey sites in Gunung Mulu National Park

Taxon	Survey sites						O	n	RA (%)
	S1	S2	S3	S4	S5	S6			
Bufonidae									
Ansonia hanitschi[a]	–	–	–	–	–	**17 (38.6)**	1	17	6.489
Ansonia longidigita[a]	–	2 (3.8)	–	–	7 (15.2)	–	2	9	3.435
Ansonia platysoma[aEN]	–	–	–	–	6 (13.0)	–	1	6	2.290
Ansonia torrentis[b]	–	–	–	–	–	4 (9.1)	1	4	1.527
Ingephrynus divergens[a]	–	1 (1.9)	–	2 (10.5)	–	–	**2**	3	1.145
Pedostibes hosii	10 (14.5)	–	–	–	–	–	1	10	3.817
Pedostibes rugosus[a]	1 (1.4)	–	–	–	–	–	1	1	0.382
Phrynoides juxtaspera	3 (4.3)	3 (5.7)	–	–	–	–	2	6	2.290
Ceratobatrachidae									
Alcalus baluensis[a]	–	–	–	–	5 (10.9)	–	1	5	1.908
Dicroglossidae									
Limnonectes ibanorum[a]	6 (8.7)	8 (15.1)	–	–	–	–	2	14	5.344
Limnonectes ingeri[a]	1 (1.4)	–	–	–	–	–	1	1	0.382
Limnonectes kuhlii	–	–	5 (16.1)	3 (15.8)	6 (13.0)	–	3	14	5.344
Limnonectes sp.[b]	–	–	–	–	–	2 (4.5)	1	2	0.763
Limnonectes leporinus[a]	7 (10.1)	2 (3.8)	–	1 (5.3)	–	–	**3**	10	3.817
Limnonectes malesianus	–	1 (1.9)	–	2 (10.5)	–	–	**2**	3	1.145
Occidozyga baluensis	–	–	2 (6.5)	–	–	–	1	2	0.763
Occidozyga laevis	–	–	1 (3.2)	–	–	–	1	1	0.382
Megophryidae									
Leptobrachella juliandringi[a]	–	–	–	**8 (42.1)**	5 (10.9)	–	2	13	4.962
Leptobrachella parva[aVU]	–	8 (15.1)	–	–	–	–	1	8	3.053

(continued)

Table 1 (continued)

Taxon	Survey sites						O	n	RA (%)
	S1	S2	S3	S4	S5	S6			
Leptobrachella brevicrus[bVU]	–	–	–	–	–	2 (4.5)	1	2	0.763
Letopbrachium montanum[a]	–	–	–	–	–	2 (4.5)	1	2	0.763
Leptolalax dringi[b]	1 (1.4)	–	–	–	–	–	1	1	0.382
Leptolalax fritinniens[b]	–	–	–	–	–	3 (6.8)	1	3	1.145
Xenophrys dringi[a]	–	–	–	–	–	5 (11.4)	1	5	1.908
Microhylidae									
Metaphrynella sundana[a]	2 (2.9)	–	–	–	–	–	1	2	0.763
Ranidae									
Abavorana luctuosa	–	–	2 (6.5)	–	–	–	1	2	0.763
Chalcorana raniceps	13 (18.8)	1 (1.9)	–	–	–	–	**2**	14	5.344
Huia cavitympanum[a]	–	3 (5.7)	–	–	–	–	1	3	1.145
Meristogenys amoropalamus[a]	–	–	–	–	–	2 (4.5)	1	2	0.763
Odorrana hosii	1 (1.4)	1 (1.9)	–	–	–	–	2	2	0.763
Pulchrana glandulosa	–	–	–	1 (5.3)	–	–	1	1	0.382
Pulchrana picturata	2 (2.9)	1 (1.9)	–	–	1 (2.2)	–	3	4	1.527
Pulchrana signata	1 (1.4)	4 (7.5)	–	2 (10.5)	–	–	3	7	2.672
Staurois guttatus[a]	–	3 (5.7)	–	–	7 (15.2)	–	3	10	3.817
Staurois parvus[a]	–	–	–	–	9 (19.6)	–	1	9	3.435
Staurois latopalmatus[a]	**17** (**24.6**)	**15** (**28.3**)	–	–	–	–	2	32	12.214
Rhacophoridae									
Feihyla kajau[a]	–	–	**19** (**61.3**)	–	–	–	1	19	7.252
Philautus macroscelis[a]	–	–	–	–	–	6 (13.6)	1	6	2.290
Philautus tectus[a]	–	–	2 (6.5)	–	–	–	1	2	0.763
Philautus sp.[b]	–	–	–	–	–	1 (2.3)	1	1	0.382
Rhacophorus gauni[a]	4 (5.8)	–	–	–	–	–	1	4	1.527

(continued)

Table 1 (continued)

Taxon	Survey sites						O	n	RA (%)
	S1	S2	S3	S4	S5	S6			
Evenness	0.6431	0.666	0.5734	0.7639	**0.9137**	0.6927			
Total individual (n)	69	53	31	19	46	44		**262**	
Total days	7	7	7	4	5	5			
No. individuals/ day	9.86	7.57	4.43	4.75	9.2	8.8			
Species richness (observed)	14	14	6	7	8	10			
Species richness (Chao's estimation)	15	17	6	7	8	10			
Species richness (Jack's estimation)	16	18	8	9	9	13			
Endemism	7	8	3	3	6	8			
% Endemism	50	57.1	50	42.9	75	80			
Species diversity	2.198	2.233	1.236	1.677	1.989	1.935			

Species are listed in overall order of counts in each category, values in brackets represent a species relative abundance and value highlighted in bold indicate dominant species. Survey sites are S1–S6
n number of individuals, *N* overall number of species, *RA* species relative abundance in percentages, *O* number of occurrences, *EN* Endangered species, *VU* Vulnerable
[a]Borneo endemic
[b]Mulu endemic

species). Estimated species richness in this study are in the range 8–17, therefore species richness in most of the sites match those studied by Inger and Voris (1993).

In terms of overall species relative abundance (*RA*), *Staurois latopalmatus* had the greatest percentage of relative abundance (*RA* = 12.21 %). This species was followed by *Feihyla kajau* (*RA* = 7.25 %), *Ansonia hanitschi* (*RA* = 6.49 %), and *Chalcorana raniceps*, *Limnonectes ibanorum* and *L. kuhlii* (each with *RA* = 5.34 %). At some of the survey sites, certain species showed relatively high abundance and dominate the amphibian community. For instance, *S. latopalmatus* was abundant at both large streams (Sungei Nipa, S2; and, Melinau Paku Stream, S1). In contrast, the small stream at Camp 1 (S3) at low elevation was dominated by *Feihyla kajau*, and the small stream on the Sarawak Chamber trail (S4) was dominated by *Leptobrachella juliandringi*. Furthermore, the headwaters of Sungei Tapin (S6, 1,600 m asl) was dominated by *Ansonia hanitschi* (Table 1). The hilly small stream at Camp 2 appeared had no obvious dominant species, with species being more evenly distributed (S5; evenness = 0.9137).

When the local distributions of threatened or endemic species of each stream were evaluated, the endangered species *Ansonia platysoma* was found at the hilly small stream at Camp 2 (S5). Another vulnerable species, *Leptobrachella brevicrus*, occurred in the headwaters of Sungei Tapin (S6), while *Leptobrachella parva* was found to occur at the Sungei Nipa at Camp 1 (S2). For endemism, the headwaters of Sungei Tapin, located at high elevations (1,600 m), had the greatest percentage of

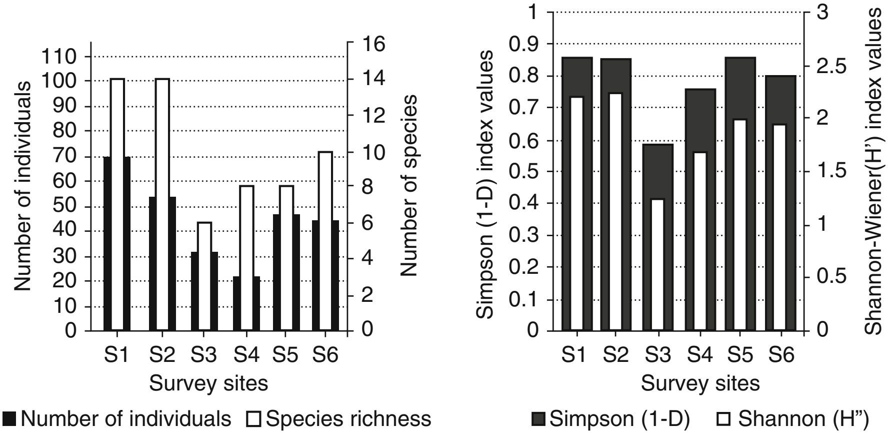

Fig. 3 Comparison of number of individuals, species richness, and species diversity indices among survey sites at Gunung Mulu National Park. Note: S1–S6 = Survey sites 1–6

endemism (80 %) compared to sites at lower elevations, including a stream at Camp 2 (500 m asl, 75 %) and other low elevation streams (>200 m, 42–57 %). High percentages of endemism (80 %) at high elevational streams (1,600 m) suggest that amphibian endemicity at Mulu is most likely concentrated along higher elevation forested streams.

In terms of species diversity, Sungei Nipa (S2) was found to be the highest ($H'=2.333$, $D\text{-}1=0.8544$), with the Melinau Paku stream (S1) slightly lower for Shannon-Wiener's (H′), but higher for Simpson's (1-D) ($H'=2.198$, $D\text{-}1=0.857$). They were, in turn, followed by the small hill stream at Camp 2 (S5) ($H'=1.989$, $D\text{-}1=0.857$), the headwaters of Sungei Tapin (S6) ($H'=1.935$, $D\text{-}1=0.7975$), the small stream at the Sarawak Chamber Trail (S4) ($H'=1.677$, $D\text{-}1=0.759$), and the small stream at Camp 1 (S3) ($H'=1.236$, $D\text{-}1=0.5848$). The Shannon diversity *t*-test indicate that only the small stream at Camp 1 (S3) differed significantly in diversity from the other streams ($p<0.05$), except for the small stream at the Sarawak Chamber Trail (S4) ($p=0.055$). This study demonstrate that large streams have greater species diversity and richness compared to small streams (Fig. 3). This may be attributed to the ability of large stream landscapes to provide favorable breeding habitats for numerous species, as well as for tadpole microhabitat/diet requirements. Some species (such as *Huia cavitympanum* and *Meristogenys* spp.) breed only in swift-flowing waters and their tadpoles live in the strongest of currents. Large streams are able to hold water for longer periods, which is important for species with long period of tadpole development, such as in species of *Limnonectes* and *Hylarana*, and *S. latopalmatus* that are restricted to clear, swift and rocky streams (Parris and McCarthy 1999; Inger and Stuebing 2005; Keller et al. 2009). Many of these species are found abundant along stream banks, and two of these, *Pedostibes hosii* and *Leptobrachella parva*, occasionally form large calling groups. This suggests that the availability of breeding habitats is a major causal factor for

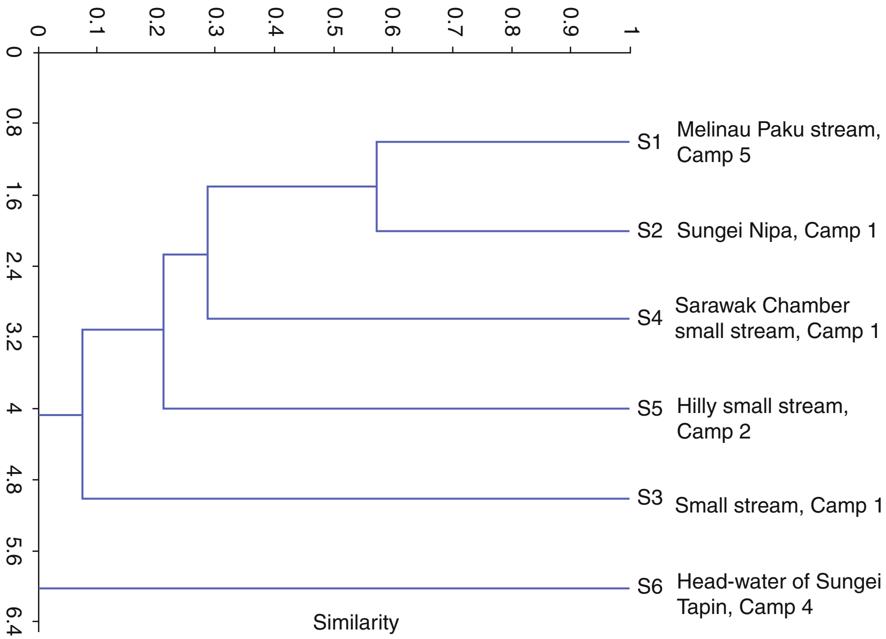

Fig. 4 Dendogram using unweighted pair-group method (*UPGMA*) cluster analysis based on similarity of amphibian species composition at selected streams in Gunung Mulu National Park

high species diversity and richness regionally. Nevertheless, other factors need to be considered. Forest landscapes, disturbance levels, availability of resources, competition, elevational and habitats types are known to influence species diversity and species composition (Duellman 1997; Faruk et al. 2013; Konopik et al. 2015).

Amphibian assemblages in selected streams at Mulu are found to be distinctly clustered into two major ecological groups (similarity coefficient = 0; Fig. 4). The fauna of survey sites at large streams (S1 and S2) are closely related to each other, and separate from smaller streams at lower elevations. The amphibian assemblage at the headwaters of Sungei Tapin, a first order stream, located at 1,600 m, shows a complete species turnover compared to those of higher order, or streams at lower elevations (below 500 m). These results suggest that species composition of higher order streams are more similar to each other, albeit differentiable into discrete large stream- and small stream- assemblages. Thus, species composition of stream-dwelling amphibians is affected by stream elevation and/or stream width.

4 Conclusion

This study highlights the role of upland forests streams as important refuges for Bornean endemic amphibians, and a majority of the endemic species at Mulu were found in such regions. These results coincided with numerous works that document highlands as refuges for many endemic amphibians globally. Species composition of stream-dwelling amphibians is affected by both stream elevation and stream width. Our results underline the importance of riparian habitats, especially low order streams in forested headwaters, in harbouring Bornean endemics, a number of which are on the global list of threatened species. They further support prioritization of stream types and stream segments, especially within the forested headwaters, as a regional conservation strategy.

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Effect of Temperature on Development: The Case of the Malayan Snail-Eating Turtle *Malayemys macrocephala*

Rangsima Pewphong, Noppadon Kitana, and Jirarach Kitana

Abstract The embryonic development in several freshwater turtles is dependent on the incubating temperature. Different incubating temperature can induce significant difference in sex ratios among turtle populations with temperature dependent sex determination. The Malayan snail-eating turtle, *Malayemys macrocephala*, is a native freshwater turtle commonly found in rice fields of Thailand. Previous morphometric analysis on this species suggested a temperature-dependent pattern of sex determination. This study aimed to examine effect of temperature on gonadal development of *M. macrocephala* using histological analysis. Turtle eggs were collected during December 2011 to February 2012 from rice fields in Phra Nakhon Si Ayutthaya province in the central part of Thailand and incubated in the laboratory at 26 °C, 29 °C and 32 °C. Results from sex identification based on gonadal structure and statistical analyses of sex ratio confirm prior observations that incubation at low temperature (26 °C) produced male-biased sex ratio, while incubation at high temperature (32 °C) produced female-biased sex ratio. Incubation at 29 °C resulted in 1 male: 1 female sex ratio, suggesting that this incubating temperature is a pivotal temperature of *M. macrocephala*. A 3×3 contingency table analysis reveals a significant association between incubating temperature and the stage of gonadal development. Interestingly, testicular development was more advanced at 32 °C than other temperatures, while developmental stage of the ovaries was more advanced at 29 °C than other temperatures. This suggested that incubating temperature can also induce significant difference in gonadal development of the freshwater turtle.

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1 Introduction

Rise in global average temperature can change both physical and biological properties in environment and may affect survival of organisms (IPCC 2007). Organisms that cannot adjust themselves to suit with the changed environment may die and become extinct (Walther et al. 2002). Freshwater turtles are susceptible to temperature change, since their embryonic development depends on incubating temperature, affecting hatching rate and development (Grant et al. 2003).

Temperature is an important factor in sex determination of many reptiles, including freshwater turtles. Many freshwater turtles exhibit temperature dependent sex determination or TSD (Valenzuela 2004). Different incubating temperature can induce significant difference in sex determination in turtle with TSD and can determine sex ratios of a turtle population (Bull et al. 1990). TSD is a process that depended on a variety of factors that interact to determine the sex ratio of offspring (Valenzuela 2004). On the other hand, sex ratio variation may affect the evolutionary stability of TSD (Bulmer and Bull 1982).

Southeast Asia has high species richness of freshwater turtles, although the extent of their susceptibility to temperature change remains unknown, due to the lack of information on gonadal development pattern. The Malayan snail-eating turtle, *Malayemys macrocephala*, is a native freshwater turtle commonly found in rice fields in the central part of Thailand. Previous morphometric analysis on this species suggested a temperature-dependent pattern of sex determination (Keithmaleesatti 2008). The current study aimed to further examine effect of temperature on gonadal development of *M. macrocephala* using histological analysis in order to confirm the temperature-dependent pattern of sex determination in this species.

2 Materials and Methods

2.1 Egg Collection

Visual encounter surveys for nests of *Malayemys macrocephala* were carried out in rice fields (UTM Zone 47P: 0653086–0659077 and 1583552–1591014) at Bang Ban District, Phra Nakhon Si Ayutthaya Province (Fig. 1), an important breeding ground of this turtle species in central part of Thailand (Keithmaleesatti 2008), during December 2011 to February 2012. Based on five field surveys, a total of 712 eggs from 126 clutches were collected. Eggs were individually numbered, placed in a styrofoam box and transported to a laboratory at the Department of Biology, Faculty of Science, Chulalongkorn University. All portions of this research project involving turtle egg collection and animal subjects were approved by the Chulalongkorn University Animal Care and Use Committee (Protocol Review Number 1323005).

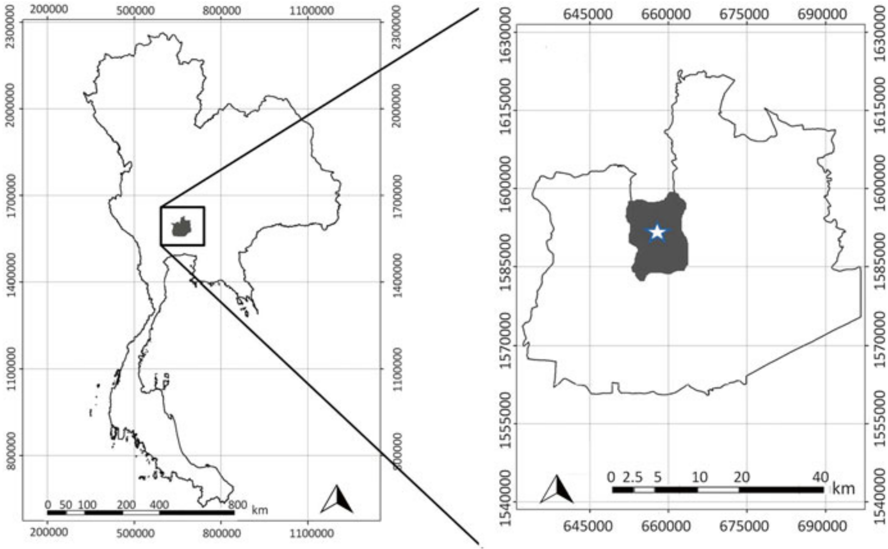

Fig. 1 Egg collection area (*star*) at Bang Ban District, Phra Nakhon Si Ayutthaya province, Thailand (UTM Zone 47P: 0653086-0659077 and 1583552-1591014)

2.2 Egg Incubation

Eggs were cleaned, weighed and randomly allocated in plastic boxes containing moistened vermiculite (1 part vermiculite: 1 part distilled water; weight: volume). The boxes were kept in microprocessor-controlled incubators (Siam Incubators System, Bangkok, Thailand) at three temperatures including 26 °C (n = 237), 29 °C (n = 237) and 32 °C (n = 238). A tray of water was placed inside each incubator to control relative humidity (>80 %). Temperature and relative humidity inside the box were monitored using a data logger (HAXO-8, LogTag Recorders, Auckland, New Zealand). Eggs were randomly sampled, weighed and dissected on weekly basis until hatch.

2.3 Embryo Collection

Upon emergence, hatching embryos were weighed and measured for carapace length. Developmental stage of turtle embryo was studied in reference to the widely used developmental stage of *Chelydra serpentina* (Yntema 1968) and *Pelodiscus sinensis* (Tokita and Kuratani 2001). After measurement, embryos were subjected to euthanasia by intraperitoneal injection with pentobarbital sodium at a dose of 600 mg/kg. Hatchlings from three temperatures including 26 °C (n = 40), 29 °C (n = 26) and 32 °C (n = 9) were fixed in Davidson's fixative for 24 h and then preserved in 70 % ethanol.

2.4 Histological Examination of Gonad

The fixed gonads from each individual were processed following standard histological techniques (Humason 1979). Gonadal tissues were infiltrated in paraffin, sectioned at 5 mm and stained with periodic acid Schiff reagent (PAS). Histological study was performed by light microscopy. Gonadal development and sex differentiation in *Malayemys macrocephala* were studied in reference to previous report of the snapping turtle, *Chelydra serpentina* (Yntema 1981). After sex of the embryos was identified by histology, sex ratio of turtle from each temperature was determined.

In addition to sex identification by histological analysis of gonadal structure, testis or ovary from each individual was further examined for stage of development. In case of testis, the stage of development was categorized into three stages primarily based on an advancement of seminiferous tubules from medullary region. For ovary, the stage of development was classified into three stages based on progression of germinal epithelium in ovarian cortex.

2.5 Statistical Analyses

For gonadal developmental stage, gonads of hatchlings from each incubating temperature were classified into three arbitrary stages (I, II or III). Then, a 3 × 3 contingency table was used to determine association between incubating temperatures (26, 29 and 32 °C) and gonadal developmental stages (I, II or III).

For sex ratio of the hatchlings, *G* statistics for the log-likelihood ratio goodness of fit test (*G* test) with Yates's correction was used to determine whether the sex ratio of turtle from each incubating temperature was best fitted to any expected sex ratio (e.g. 1:1, 1:2 or 2:1; male: female).

A significant association or goodness of fit is reported at $p < 0.05$. All statistical procedures used in this study were performed according to Zar (1998).

3 Results

3.1 Gross Morphology of Gonad

Since sex of young freshwater turtle is difficult to determine because they lack external sexual dimorphic characteristics (Ceriani and Wyneken 2008), in this study, sex of the hatchling was initially determined using gross morphology. Upon dissection of the abdominal cavity, an ovary appears as long, thin, oval shaped with a scalloped edge (Fig. 2), while a testis is fusiform in shape with a smooth edge (Fig. 3). It is of interest to note the similarity in these structures. Therefore, using

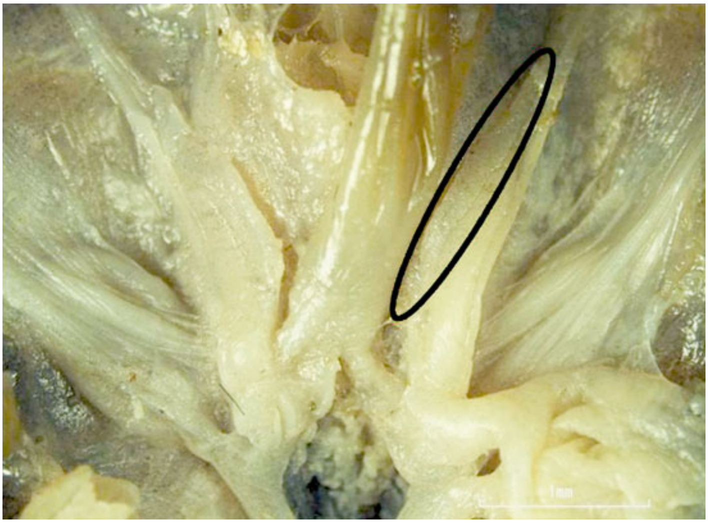

Fig. 2 Gross morphological characteristics of female gonad of *Malayemys macrocephala* hatchling at stage 26

gross morphological characteristics of the hatchling gonads alone to differentiate the sex was not enough to verify the sex of embryos.

3.2 Histological Analysis of Gonad

Because of the difficulty in using the gross morphological characteristics of the gonads to differentiate the sex of the turtle hatchlings, histological examination was used to confirm the sex of embryos. In freshwater turtle, gonad is generally fully differentiated into testes or ovaries at hatching stage. Histological study of gonadal development in *Malayemys macrocephala* was thus studied based on a previous report in the snapping turtle, *Chelydra serpentina* (Yntema 1981).

The developing testis can be divided into two zones including cortex and medulla. Histological structure of the testicular cortex was poorly developed whereas the medulla contained germ cells in mesenchyme tissue. Testicular development of the male *M. macrocephala* hatchling could be divided into three stages as described below.

- Stage I: The testicular cortex was covered with connective tissue capsule. The testicular medulla displayed wide cords of primordial germ cells (Fig. 4a, b).
- Stage II: The testicular medulla was branched out and transformed into immature seminiferous cords containing germ cells (Fig. 4c, d).
- Stage III: The testicular medulla contained many germ cells and transformed into immature seminiferous tubules (Fig. 4e, f).

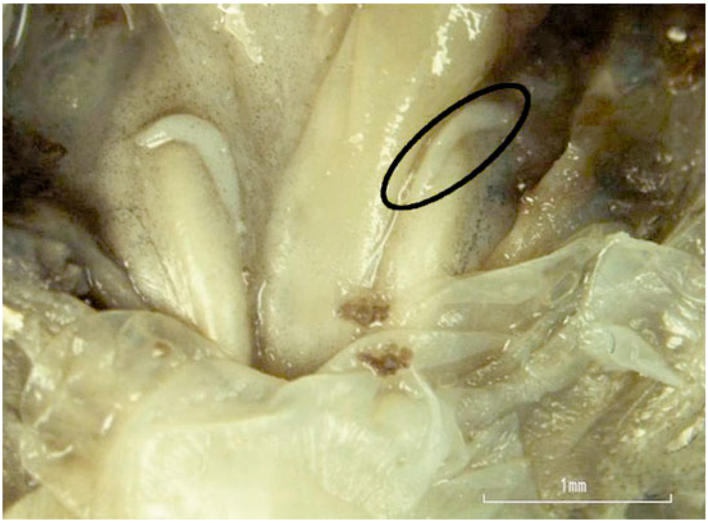

Fig. 3 Gross morphological characteristics of male gonad of *Malayemys macrocephala* hatchling at stage 26

The developing ovary can be divided into two zones including cortex and medulla. Histological structure of the ovarian cortex was advanced whereas the medulla consisted mostly of diffused mesenchyme. This character is a marker of ovary. Ovarian development of female *M. macrocephala* hatchling could be classified into three stages as described below.

- Stage I: The ovarian cortex was thin containing germ cells and separated from the internal medulla. The PAS-positive line can be seen separating between these two layers. The ovarian medulla consisted mostly of diffused mesenchyme (Fig. 5a, b).
- Stage II: The ovarian cortex become thicker containing numerous germ cells (Fig. 5c, d).
- Stage III: The ovarian cortex was well developed containing many germ cells and primary oocytes (Fig. 5e, f).

3.3 Effect of Temperature on Gonadal Developmental Stage

In male turtle, testicular development was more advanced at high temperature (32 °C) than other temperatures (26 °C and 29 °C), as evidenced from the higher proportion of stage III testis in turtles incubated at 32 °C (Fig. 6). As a result, the 3×3 contingency table analysis (Table 1) shows a significant association between incubating temperature and the stage of testicular development of *Malayemys macrocephala* ($\chi^2 = 10.14$, d.f. $= 4$, $p < 0.05$).

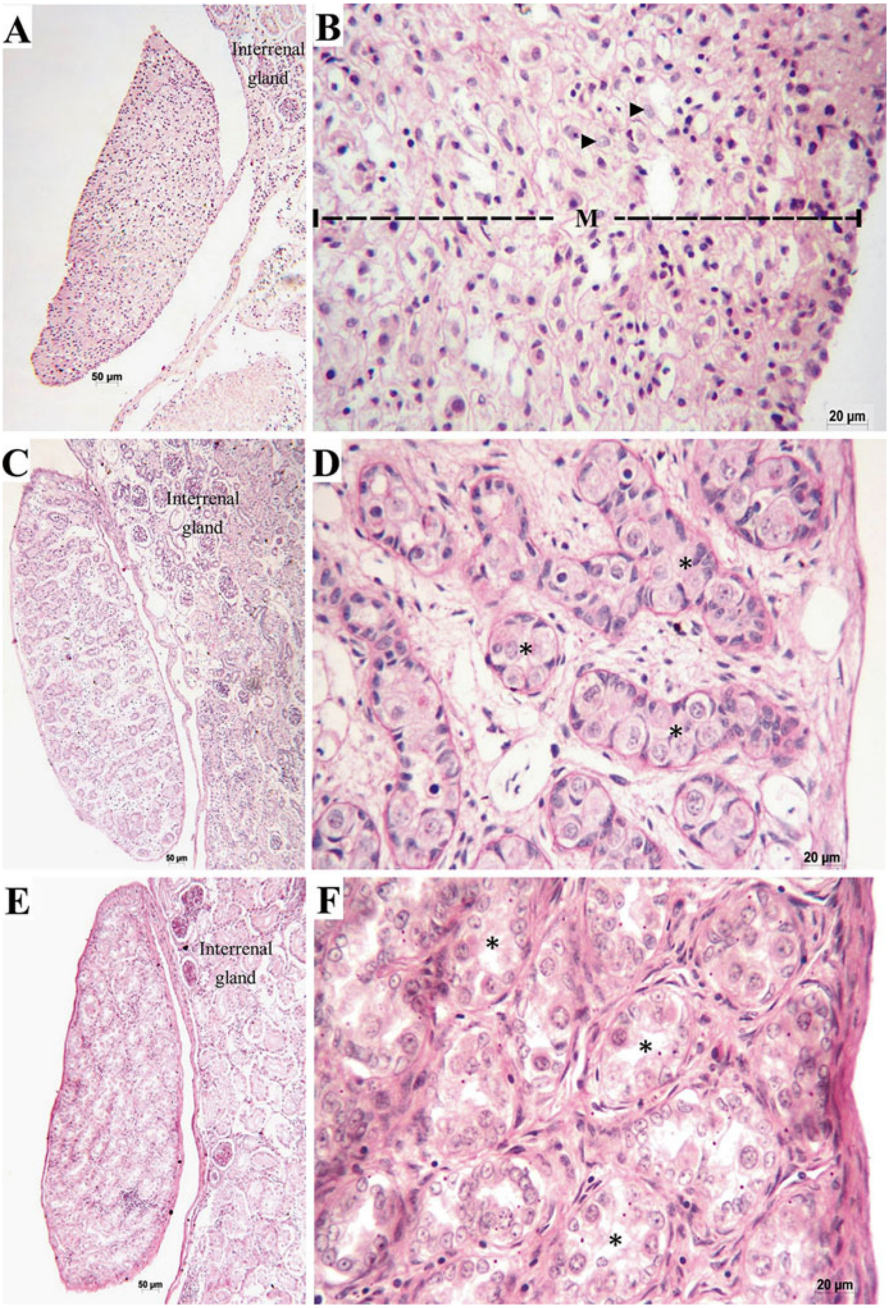

Fig. 4 Photomicrographs of testes of *Malayemys macrocephala* hatchling at different gonadal developmental stages (PAS stain). (**a**) Overall structure of the testis at stage I. (**b**) High magnification of the testis showed primordial germ cells (*arrows*) in the medulla (M). (**c**) Overall structure of the testis at stage II. (**d**) High magnification of the testis showing primary sex cords (*asterisks*). (**e**) Overall structure of the testis at stage III. (**f**) High magnification of the test is showing seminiferous tubules (*asterisks*)

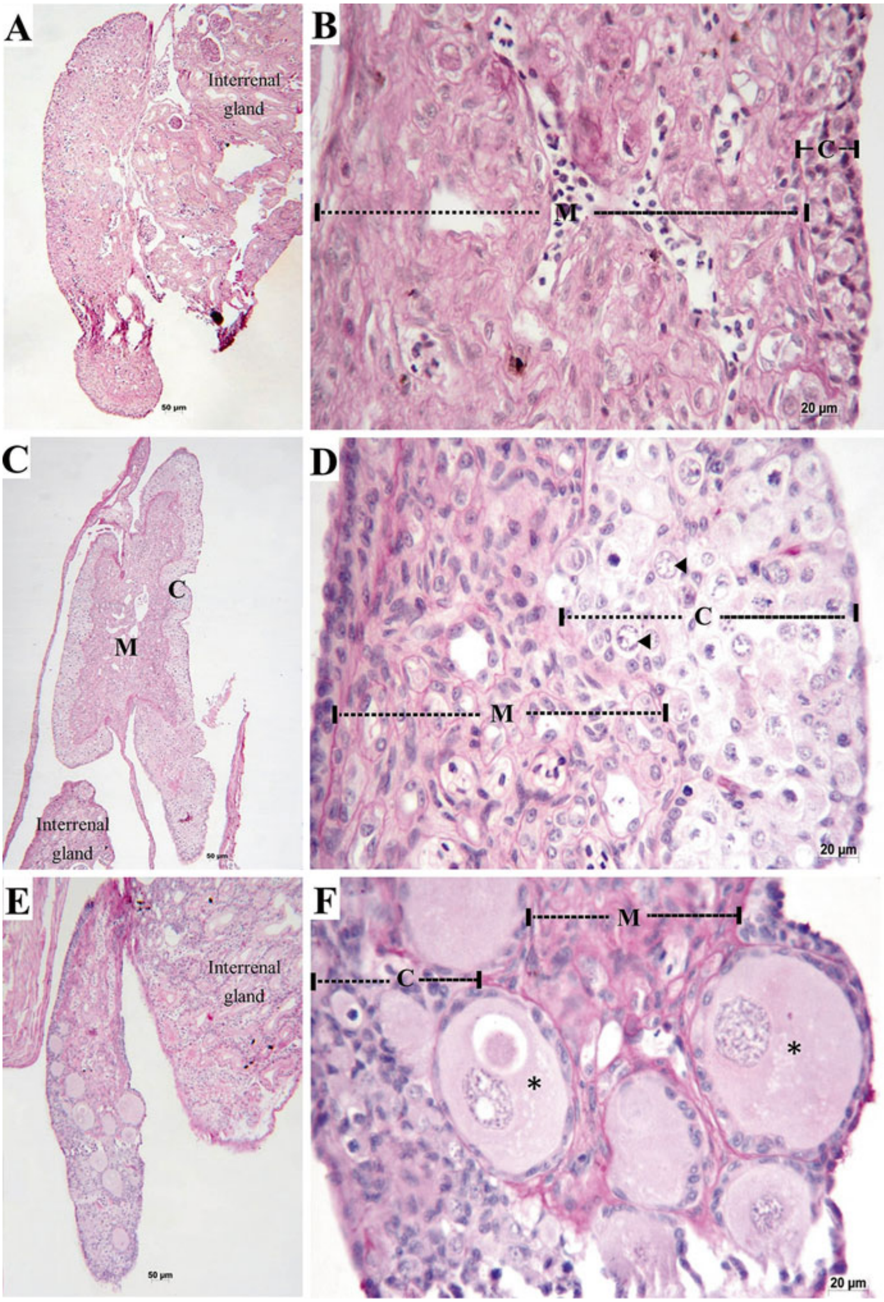

Fig. 5 Photomicrographs of ovaries of *Malayemys macrocephala* hatchling at different gonadal developmental stages (PAS stain). (**a**) Overall structure of the ovaries at stage I. (**b**) High magnification of the ovary showing primordial germ cells (*arrow*) in the thin cortex (C). (**c**) Overall structure of the ovary at stage II, medulla (M) and cortex (C) are discriminated. (**d**) High magnification of the ovary showed germ cells (*arrows*) are present in the thick cortex (C). (**e**) Overall structure of the ovary at stage III. (**f**) High magnification of the ovary showing primary oocytes in the cortex (*asterisks*)

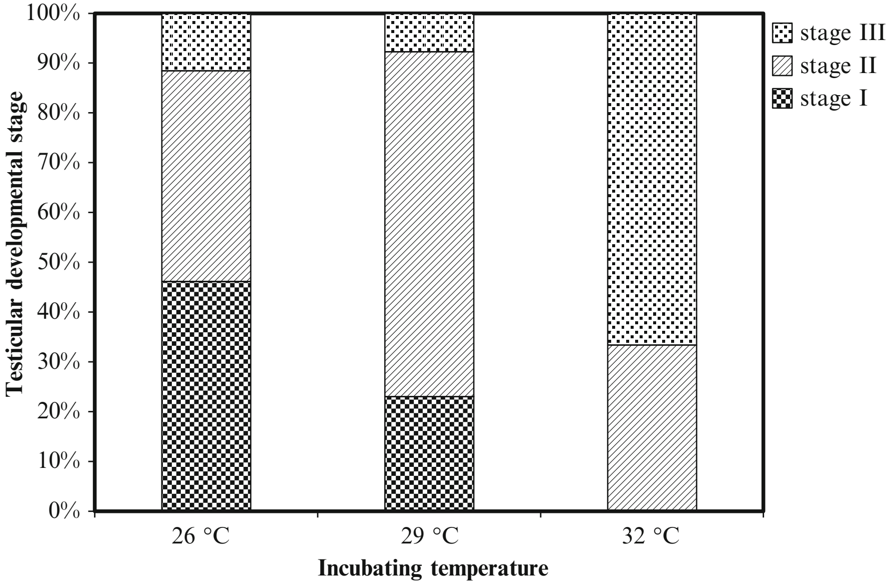

Fig. 6 Proportions of *Malayemys macrocephala* hatchling with different testicular developmental stage in each incubating temperature

Table 1 Contingency table analysis for association between incubating temperature and the stage of testicular development of *Malayemys macrocephala*. Theoretical value: $\chi^2 = 9.49$, d.f. = 4, $p = 0.05$. Calculated value: $\chi^2 = 10.14$

Testicular development		Temperature 26 °C	29 °C	32 °C	Total
Stage I	Observed (O)	12	3	0	15
	Expected (E)	9.29	4.64	1.07	
	$(0\text{-}E)^2/E$	0.79	0.58	1.07	
Stage II	Observed (O)	11	9	1	21
	Expected (E)	13	6.5	1.5	
	$(0\text{-}E)^2/E$	0.31	0.96	0.17	
Stage III	Observed	3	1	2	6
	Expected	3.71	1.86	0.43	
	$(0\text{-}E)^2/E$	0.14	0.40	5.73	

In female turtle, developmental stage of the ovaries was more advanced at pivotal temperature (29 °C) than other temperature (26 °C and 32 °C; Fig. 7). The 3 × 3 contingency table analysis (Table 2) shows a significant association between incubating temperature and the stage of ovarian development of *M. macrocephala* ($\chi^2 = 21.79$, d.f. = 4, $p < 0.05$).

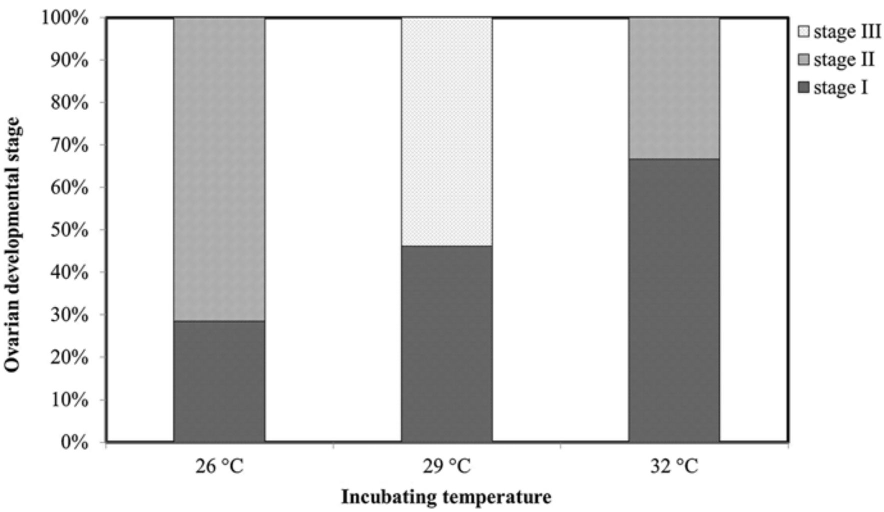

Fig. 7 Proportions of *M. macrocephala* hatchling with different ovarian developmental stage in each incubating temperature

Table 2 Contingency table analysis for association between incubating temperature and the stage of ovarian development of *Malayemys macrocephala*. Theoretical value: $\chi^2=9.49$, d.f. = 4, p = 0.05. Calculated value: $\chi^2=21.79$

Ovarian development		Temperature			Total
		26 °C	29 °C	32 °C	
Stage I	Observed (O)	4	6	4	14
	Expected (E)	5.94	5.52	2.55	
	$(0\text{-}E)^2/E$	0.63	0.04	0.82	
Stage II	Observed (O)	10	0	2	12
	Expected (E)	5.09	4.73	2.18	
	$(0\text{-}E)^2/E$	4.74	4.73	0.01	
Stage III	Observed	0	7	0	7
	Expected	2.97	2.75	1.27	
	$(0\text{-}E)^2/E$	2.97	6.57	1.27	

3.4 Effect of Temperature on Sex Ratio

Malayemys macrocephala hatched from eggs incubated at three different temperatures were examined for sex by histological examination of the gonad. Sex ratio from each incubating temperature was shown in Fig. 8 and Table 3. The result showed that low incubating temperature (26 °C) resulted in the highest proportion of male turtle whereas high temperature (32 °C) showed the highest proportion of female turtle. The result also showed that pivotal temperature (29 °C) showed the equal proportion of male and female turtles.

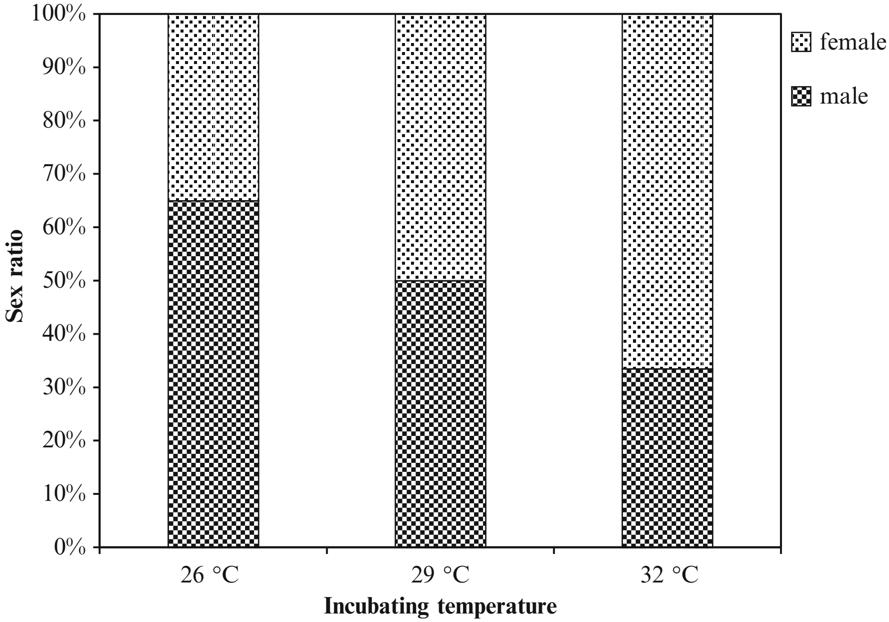

Fig. 8 Sex ratios of *M. macrocephala* hatched from eggs incubated at three different temperatures

Table 3 *G* statistics for the log-likelihood ratio goodness of fit test of sex ratio of *Malayemys macrocephala* hatched from eggs incubated at three different temperatures. The best-fitted sex ratio (*) is determined from the lowest *G* value that must be lower than the theoretical χ^2 value

	Sex ratio (male:female)		
Temperature	2:1	1:1	1:2
26 °C	0.1*	3.6	12.91
(n=40)	($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841)	($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841)	($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841)
29 °C	3.24	0.0*	3.24
(n=26)	($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841)	($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841)	($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841)
32 °C	4.5	1.0	0.0*
(n=9)	($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841)	($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841)	($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841)

G tests were performed to test for goodness of fit at three expected sex ratios of *M. macrocephala* (male-biased sex ratio, 1:1 sex ratio and female-biased sex ratio). In each temperature, the best fitted sex ratio is determined from the *G* value that must meet the following two assumptions: (1) *G* value must be lower than the theoretical χ^2 value ($\chi^2_{0.05,\ d.f.\ 1}$ = 3.841), and (2) the lowest *G* value (Zar 1998).

4 Discussion

The results indicate that incubation at low temperature (26 °C) produced male-biased sex ratio, while incubation at high temperature (32 °C) produced female-biased sex ratio. Incubation at 29 °C resulted in 1 male: 1 female sex ratio, confirming this incubating temperature as pivotal temperature for *M. macrocephala*. The result in this study is similar to study in *Chrysemys picta* (Bull et al. 1982) and *Mauremys reevesii* which showed pivotal temperature in the range of 28–30 °C (Du et al. 2007).

Many species of turtle are reported to have TSD (reviewed in Ewert et al. 2004). Incubating temperature plays important role in determining sex ratio of freshwater turtle population (Bull 1980; Bull et al. 1990). Among 79 species of turtles examined, 64 species of turtle in the world are known to have TSD (Ewert et al. 2004). For the Malayan snail-eating turtle, previous studies of *M. macrocephala* from Phra Nakhon Si Ayutthaya using morphometric analysis (Keithmaleesatti 2008) predicted that sex ratio of hatchlings showed a temperature-dependent pattern (TSD). The current research using histological analysis confirmed the pattern of temperature-dependent sex determination of this species. This result provides a new record of TSD in this tropical freshwater turtle species (Ewert et al. 2004).

5 Conclusions

Many species of oviparous reptiles, including crocodilians, turtles and lizards have shown temperature-dependent sex determination pattern. In this study, histological analysis of gonad of *Malayemys macrocephala* incubated at different temperature confirmed that the snail-eating turtle also exhibits a temperature-dependent sex determination. Incubation at low temperature (26 °C) produced male-biased sex ratio. Incubation at high temperature (32 °C) produced female-biased sex ratio. Incubation at the pivotal temperature (29 °C) resulted in 1 male: 1 female sex ratio. Furthermore, the result extended prior observations that incubating temperature was an important variable affecting differentiation of gonads into ovaries or testes as well as degree of development of the gonad in *M. macrocephala*. This information could be used to assess the impact of global trend of temperature change and potential mitigation measure to reduce this impact on the freshwater turtle in order to conserve their natural populations.

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Bird Diets in Urban Environments: The Case of the Asian Glossy Starling, *Aplonis panayensis*

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Abstract The Asian Glossy Starling, *Aplonis panayensis,* is one of the most abundant birds in Kuching City, occupying nooks and cavities of buildings and soiling the walls and floors with their droppings. To determine why they are so abundant, we focused on their dietary habits in a study conducted in Dewan Suarah area of Kuching in 2013. A total of 51 fecal samples were collected from the floor of Dewan Suarah and examined for dietary fragments. The results showed the diet comprises insects as well as plant parts. The insects are solely from the Order Hymenoptera (70 individuals), whereas the plant parts comprised figs (86 %), *Vitex* sp. (2 %) and unidentified plant materials (12 %). The Hymenopteran identified in fecal samples belong to the family Agaonidae (45 individuals), Formicidae (18 individuals), and Ormyridae (7 individuals). There is a significant difference in frequency occurrence of insects and fruits in the diet of starlings. From the fecal analysis, the insects in the diet of the starlings are mainly from the figs they have eaten. The diet of the bird is discussed in relation to the availability of food items in the surrounding areas.

1 Introduction

Pro-development government policies and rising human population has transformed the landscape of many Southeast Asian countries, including Malaysia, through deforestation and urbanization (Flint 1994). Urban population in Malaysia increased from 34 % in 1980 to 71 % in 2010 (Department of Statistics Malaysia 2012). This rapidly changing landscape has caused many animal species to lose their original

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habitat and become threatened while some have become adapted to human environment and thrived to the extent they have become a nuisance to resident human population (Chong et al. 2012). This study focuses on the diet of the Asian Glossy Starling (AGS), which has apparently adapted to urban environments.

The species is an opportunistic cavity nester competing with other native birds for nesting sites (Linz et al. 2007), and has successfully adapted to habitats that have greatly been modified by humans (Lin 2001; Sontag and Louette 2007; Chong et al. 2012). The starlings can be found nesting at airport hangers, commercial structures, and residential buildings and may affect human health when they contaminate walls and floors of buildings with their feces. They are known to roost in large flocks when suitable nesting sites are available.

In addition to the presence of suitable nesting sites, the other factors that promote the population growth of AGS would be the abundance of foods in urban areas. Various studies have explored the diet of starlings and concluded that it is a generalist and omnivorous type of species (Strange and Jayavarajasingam 1993; MacKinnon and Phillipps 1993; Smythies 1999; Bockheim and Congdon 2001) and they have been recorded to feed on soft fruits such as figs, papaya, banana and mangos (Peh and Chong 2003) and insects (Skorupaa and Hothem 1985; Corlett 1992). Information on the biology of birds such as feeding, nesting, breeding, roosting requirements and behavior are important for an effective control of population size. This paper presents the result of a preliminary study that was conducted in Kuching City between November 2012 and March 2013 to determine what food resources is available to Asian Glossy Starling (AGS) nesting at Dewan Suarah Negeri Kuching and which one is being eaten.

2 Materials and Methods

2.1 Study Area

The present study was conducted in Kuching city, Sarawak, the two sites being Taman Budaya (1°33′8″N, 110°20′47″E) and Dewan Suarah (1°24′49″N, 110°9′25″E). Taman Budaya is an urban park and heavily used by the cityfolk for recreational activities, in particular, for walking and jogging. Taman Budaya is landscaped with plants, including native species, some of which (e.g. figs) bear fruits throughout the year, and thus provide foraging opportunities for a variety of birds and mammals. Dewan Suarah is a large public building, that houses a planetarium, a tower, a library and a banquet hall. Taman Budaya is located less than 500 m from Dewan Suarah.

2.2 *Survey Methodology*

2.2.1 Point Counts at Taman Budaya

Point counts were conducted along 800 m transect line at Taman Budaya in January and March 2013. The distance between each point was 200 m to reduce the possibility of double counting. Counts were conducted at morning or evening period when the activities of birds are high. At each point, all birds seen and heard were recorded for 10 min. The point counts were repeated for 3 days at the same stations. Observations were made with the aid of a pair of 8 × 25 Nikon binocular and a digital camera. Species were identified using MacKinnon and Phillipps (1993) and Phillipps and Phillipps (2009).

2.2.2 Counting Individual Birds at Dewan Suarah

Direct counts were conducted at Dewan Suarah Negeri Kuching in February 2013. Counts were conducted at evening period when the birds start to roost. At the building, all the birds seen where recorded. Observation was been done to ensure no individual were recorded twice. The direct counts were repeated for 3 days at the same building.

2.2.3 Density Estimation of Potential Prey

Observation on potential diet was carried out at Taman Budaya, Kuching in November to December 2012 by walking along designated trails that traverse the Park. All fruiting plants and insects that were present were recorded. Direct counts of insects (by estimation) were made, and insects were identified at least to the familial level of classification. In addition, a survey was conducted in November 2013 to determine the location of fig trees within a 1000 m radius of Dewan Suarah, an area which includes Taman Budaya.

3 Fecal Examination

A total of 51 fecal samples of AGS were collected at Dewan Suarah Negeri, Kuching from the end of February to the end of March 2013. Samples were collected from roosting site where only this species had been observed roosting and no other bird had been sighted roosting there at the time. Care was taken to avoid contamination of the sample during collection.

Following the method of Rodway and Cooke (2001), collected fecal samples were dried or frozen for analysis. Feces were mixed and rinsed with 70 % ethanol to separate insects and fleshy fruits. Samples were examined under a stereoscopic microscope and photographed with the aid of a Moticam 2.0 camera. Insects were identified with the aid of entomological texts (e.g. Borror et al. 1989; Hill and Abang 2010). Insects that were counted as individuals (recovered entirely or found present as an identifiable head and other parts of body are considered an individual) were identified. The identification of insects, fleshy fruits, and seeds were done to the familal level of classification.

4 Statistical Analyses

We employed Chi-square tests to determine differences in frequency of occurrence of fruits and insects in the diet of starlings.

5 Results

A total of 29 species of birds were recorded at Taman Budaya (Table 1). The most abundant species recorded at Taman Budaya is AGS, with 132 individuals. This is followed by Yellow-vented bulbul (72 individual), Pink-necked green pigeon (38 individual), and Olive backed sunbird (26 individual). The less common species found at Taman Budaya are White-rumped shama, Plaintive cuckoo, Pied fantail, Purple-naped sunbird, Asian koel, Zebra dove, Hill myna, Yellow-belled prinia, Dusky munia, and Little spiderhunter, for which only one individual was observed during 3 days of observation. Figure 1 shows the relative abundance of fruiting plants at Taman Budaya that are available for starlings and other birds to feed on. *Areca* sp. (Areca palm, locally known as 'Pinang') shows the highest fruiting among plants available at Taman Budaya, followed by *Ficus* sp. (Fig trees, locally known as Ara) and *Vitex* sp. (local name: Leban) plants.

Additional survey in November 2013 was conducted to survey the abundance of fig trees in Kuching City within a 1 km radius from Dewan Suarah. This survey recorded 50 fig trees.

Table 3 shows insects recorded in Taman Budaya. The most abundant potential diet is the Hymenoptera (ants, wasps, and bees), followed by Isoptera (termites), Hemiptera (bugs and true bugs), Odonata (dragonflies), Diptera (flies), Orthoptera (grasshoppers and crickets) and Coleoptera (beetles).

Table 2 shows the proportion of the total number of other bird species and AGS observed at Taman Budaya and Dewan Suarah. The relative abundance of AGS at Taman Budaya is 34.6 % whereas at Dewan Suarah, is much higher at 94 %. Based on fecal examination, the diet of AGS in Kuching City consists of both insects and fruits. A total of 49 % of the fecal samples contain fruit only while another 49 % contained both fruit and insect. Only 2 % of the fecal sample contained only insect.

Table 1 List of bird species recorded at Taman Budaya, Kuching

	Family/species	Count (individuals)		Status in wildlife protection ordinance 1998
		Total count (individuals)	Occurrence	
	Columbidae			
1	Pink-necked Green Pigeon (*Treron vernans*)	38	10.0 %	Not protected
2	Spotted Dove (*Streptopelia chinensis*)	6	1.6 %	Not protected
3	Zebra Dove (*Geopelia striata*)	1	0.2 %	Not protected
	Cuculidae			
4	Greater Coucal (*Centropus sinensis*)	3	0.7 %	Not protected
5	Plaintive Cuckoo (*Cacomantis merulinus*)	1	0.2 %	Not protected
6	Asian Koel (*Eudynamys scolopacea*)	1	0.2 %	Not protected
	Alcedinidae			
7	White Collared kingfisher (*Todiramphus chloris*)	6	1.6 %	Protected
	Picidae			
8	Buff-necked Woodpecker (*Meiglyptes tukki*)	3	0.7 %	Protected
	Campephagidae			
9	Pied Triller (*Lalage nigra*)	5	1.3 %	Not protected
	Aegithinidae			
10	Common Iora (*Aegithina tiphia*)	14	3.7 %	Not protected
	Rhipiduridae			
11	Pied Fantail (*Rhipidura javanica*)	1	0.2 %	Not protected
	Muscicapidae			
12	Oriental Magpie Robin (*Copsychus saularis adamsi)*	5	1.3 %	Not protected
	Nectariniidae			
13	Olive-backed Sunbird (*Nectarinia jugularis*)	26	6.8 %	Not protected
14	Purple-naped Sunbird (*Hypogramma hypogrammicum*)	1	0.2 %	Not protected
15	Brown-throated Sunbird (*Anthreptes malacensis*)	2	0.5 %	Not protected
16	Little Spiderhunter (*Arachnothera longirostra*)	1	0.2 %	Not protected
	Dicaeidae			
17	Yellow-breasted Flowerpecker (*Prionochilus maculates*)	16	4.2 %	Not protected
	Estrildidae			
18	Dusky Munia (*Lonchura fuscans*)	1	0.2 %	Not protected

(continued)

Table 1 (continued)

	Family/species	Count (individuals) Total count (individuals)	Occurrence	Status in wildlife protection ordinance 1998
	Passeridae			
19	Eurasian Tree-sparrow (*Passer montanus*)	14	3.7 %	Not protected
	Sturnidae			
20	Asian Glossy Starling (*Aplonis panayensis*)	132	34.6 %	Not protected
21	Common Myna (*Acridotheres tristis*)	6	1.6 %	Not protected
22	Hill Myna (*Gracula religiosa*)	1	0.2 %	Protected
	Muscicapidae			
23	Rufous-chested Flycatchers	1	0.2 %	Not protected
24	White-rumped Shama (*Copsychus malabaricus*)	1	0.2 %	Not protected
	Pycnonotidae			
25	Yellow-vented bulbul (*Pycnonotus goiavier*)	72	18.8 %	Not protected
	Hirundinidae			
26	Pacific Swallow (*Hirundo tahitica*)	10	2.6 %	Not protected
	Timaliidae			
27	Chestnut-winged Babbler (*Stachyris erythroptera*)	2	0.5 %	Not protected
	Cisticolidae			
28	Yellow-belled Prinia (*Prinia flaviventris*)	1	0.2 %	Not protected
29	Rufous-Tailed Tailorbird (*Orthotomus sericeus*)	11	2.9 %	Not protected

Total family = 18 families Total species = 29 species
Total individual = 382 individuals

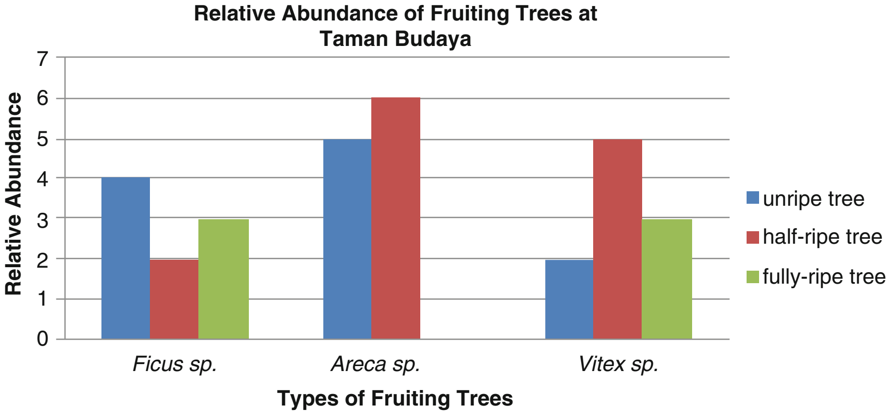

Fig. 1 Relative abundance of fruiting plants at Taman Budaya, Kuching

Table 2 Proportion of bird species recorded at Taman Budaya and Dewan Suarah Negeri Kuching

	Taman Budaya	Dewan Suarah
Total number of species	29	2
Total number of bird	382	121
Total number of AGS	132	114
Relative abundance of AGS (%)	34.6 %	94 %

Table 3 Relative abundance of insects at Taman Budaya. Sampling conducted on five occasions

Insect groups	Total count (individuals) tree		Total estimation	Relative abundance (%)
	Ground	Tree		
1. Orthoptera	21	0	21	0.13 %
2. Odonata	51	10	61	0.38 %
3. Hymenoptera	9947	5745	15,692	97.76 %
Formicidae	9928	5719	15,647	97.48 %
Other species	19	26	45	0.28 %
4. Hemiptera	56	8	64	0.40 %
5. Coleoptera	0	1	1	0.006 %
6. Diptera	35	6	41	0.26 %
7. Isoptera	170	2	172	1.07 %

Table 4 shows the diet of AGS based on fecal examination. Only one order of insects was found, that is order Hymenoptera. From order Hymenoptera, three families were identified, family Agaonidae, Ormyridae and Formicidae. The highest consumed by AGS is from the family Agaonidae (45 individuals), followed by family Formicidae (18 individuals), family Ormyridae (7 individuals). The rest is unidentified insects (five individuals).

Figs are the highest proportion in fecal samples (Table 5), where 44 out of 51 fecal samples (86 %) contained figs. *Vitex* sp. fruits were found in only 2 % of the feces although a number of *Vitex* sp. trees have ripe fruits during the time of survey. Unidentified plant materials were recorded in 12 % of the fecal samples and no palm fruits (*Areca* sp.) were observed in the fecal samples. A significance difference in the frequency of occurrence of insects and fruits in the diet of starlings was found (Chi-square test 22.16; d.f. = 1).

6 Discussions

Urbanization tends to select birds that are omnivorous, granivorous, and cavity nesting species (Mills et al. 1989; Allen and O'Conner 2000; Kluza et al. 2000). This may due to the foods that are available in urban areas and the presence of human structure that creates nesting sites that gives opportunity for urban species to roosts. Moreover, bird species that have met their food requirements within an urban setting can exhibit positive population response (Chace and Walsh 2004). Asian glossy

Table 4 Insects in the feces of the Asian glossy starling

Insects	Individuals in samples
Insects (order)	
Hymenoptera	70
Family agaonidae (fig wasps)	45
Family ormyridae (parasitic gall-making insects)	7
Family formicidae (ants)	18
Unidentified insects	5

Table 5 Fruits in diet of the Asian glossy starling

Dietary components	Samples
1. *Ficus* sp.	44 of 51 fecal samples with figs (86 %)
2. *Vitex* sp.	1 of 51 fecal samples with *Vitex* fruits (2 %)
3. Others (unidentified)	6 of 51 fecal samples with unidentified parts of plants (12 %)

starling is the most abundant bird at Taman Budaya and Dewan Suarah Negeri Kuching accounting for 34.6 % and 94 % of birds recorded, respectively, because they are able to exploit existing roosting sites and of food resources. Asian glossy starling is the most abundant urban bird found at both sites compared to other urban bird. This urban bird population structure shows that AGS are dominant where they are categorized as a winner population in terms of access to food and reproductive success (Anderies et al. 2007). Asian glossy starling seems to be well adapted in Kuching City and is believed to increase in population size. Moreover, Dewan Suarah acts as a safe nesting and roosting sites for these starlings, protecting them from adverse weather such as rain, wind and heat. The reason why other species of birds are roosting less in this building compared to starling is because starlings are opportunistic cavity nester and occupying as much of the available cavity as possible (Linz et al. 2007). Apart from that, they are aggressive species and roost in flock. They probably occupy the best cavity in the building and making the other species that are roosting in solitary and not a strong competitor to find another roosting site. Only Eurasian tree sparrow is observed roosting in same building with AGS but in fewer numbers. It may be caused by nest predation pressure created by starlings that have affected densities and distribution of other birds in that area (Emlen 1974).

Dewan Suarah Negeri Kuching is an ideal roosting place for AGS as this area is surrounded by a quite large number of fig trees including in Taman Budaya. Additional survey within 1 km radius from Dewan Suarah recorded 50 fig trees and this gives opportunity for starlings to feed. This shows that the starling go to nearby places such as Taman Budaya from their roosting site at Dewan Suarah to search for foods. According to Juricic et al. (2004), starlings have wide visual fields. They can widely forage to other places from their roosting site as long as there is food. From the results, figs seem to be a primary food resource for AGS where most of starling's diets consist of figs (86 %). Furthermore, it shows that AGS select foods that are abundant in the city such as *Ficus* sp., which can also be found at Taman Budaya.

Lim and Sodhi (2004) found that in Singapore, insectivorous birds are less dominant in highly urbanized areas and frugivores favour low-density housing areas. However, in this study, AGS was found to selects more figs (49 %) compared to insects (2 %) in highly urbanized area. It is believed that factor such as availability of foods types influences the diet of urban birds. The finding of this study shows that the diet of the starlings consists mostly of fruits and insects (49 %) and fruits (49 %). Among the fruits, figs were found in 86 % of the starling's fecal samples. A recent survey of Kuching City within 1-km radius of Dewan Suarah in November 2013 yielded 50 numbers of fig trees some of which were in fruit. Earlier studies elsewhere showed that figs feature prominently in the diet of starling (Ali and Ripley 1983; Bell 1984; Roberts 1992; Kinnaird 1995; Balasubramanian 1996). Figs are important to frugivorous animals especially during food scarcity as it is available all year round and tend to produce large crops that ripen synchronously within a tree (Janzen 1979; Lambert and Marshall 1991). Even when the foods are abundant, frugivores regularly eat fig fruits (Lambert and Marshall 1991; Kinnaird et al. 1996). Figs are unprotected which means its soft flesh can be easily eaten without any specialized handling requirements such as powerful bills, teeth or claws.

The diet of AGS exclusively contains insects from the Hymenoptera, an order with a great diversity of species and habits, ranging from parasites and predators, to pollinators of plants (Borror et al. 1989), ranging in size from minute to large-sized species, and regarded as the most evolved insects (Hills and Abang 2010). While most, such as Formicidae (ants), are found free in the environment, others, such as Agaonidae (fig wasp) live within a host (fig fruit). The presence of Formicidae (18 individuals) in the fecal samples of AGS is not unexpected, since Formicidae was the most abundant insect in Taman Budaya, especially on the ground. Zain (2011) also recorded Formicidae in the diet of AGS at the campus of Universiti Malaysia Sarawak at Kota Samarahan, Sarawak. The absence of other insect orders in the fecal samples would suggest that either these were not eaten or they were eaten but completely digested and therefore not detected. It is likely that AGS do not feed on these other insects because they are less abundant and therefore more expensive energetically to search for them. Feeding on Formicidae will incur less energy expenditure since these tend to occur in large aggregations, especially along the ground. Also, by staying in the canopy, AGS avoids potential conflict with humans and their pets, which are potential predators.

Despite Formicidae being the most abundant insect in the immediate vicinity of Dewan Suarah most of the insects found in the fecal samples are fig wasp (Agaonidae). Fig wasps were not among the insect groups recorded in Taman Budaya. It seems the starlings may have indirectly ingested the wasp when they eat the figs. Each fig seems to have its own pollinating wasp species from the family Agaonidae (Cook and Rasplus 2003).

From the fecal analysis, the main diet of AGS seem to be figs, and the insect found in the fecal samples are mainly fig wasp. The AGS does not seem to feed on the other fruits or insects that are found at Taman Budaya, except Formicidae. Feeding on Formicidae is not coincidental to consumption of figs but perhaps because this is the most abundant insect in the vicinity. Furthermore, from the fecal analysis, insects that been consumed by AGS are found not to be digested by them as these insects has been found in their feces with most of them in a complete body and partially full body. Thus, insects consumed by AGS in this study are not contributing nutrients to AGS as they were excreted in the feces.

Based on these fecal analyses, this study conclude that the diet of AGS is composed of fruits and insects. The insects are mainly from the Order Hymenoptera (70 individuals), represented by the family Agaonidae (45 individuals), Formicidae (18 individuals), and Ormyridae (7 individuals). The fruit consumed by AGS is mainly figs (86 %), followed by *Vitex* fruits (2 %). The rest are unidentified plant materials (12 %). Therefore, from the fecal analysis, the insects in the diet of AGS are mainly from the figs ingested.

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Part III
Biodiversity and Conservation

Diversity of Trees at Gunung Serambu, Bau District, Sarawak, Malaysia

Ik Wadell Ik Pahon, Alexander Kiew Sayok, and Jugah Tagi

Abstract An inventory on trees was undertaken in 12 plots of 20 × 20 m at Gunung Serambu, Bau District as part of a multidisciplinary study in 2012. Six plots were established at the upper elevation (≥500 m) of the mountain and another six along the lower elevation from the foothill (≤500 m). A total of 487 trees were enumerated consisting of 112 species from 80 genera and 43 families. Among them are three species of figs namely *Ficus schwarzii*, *F. fistulosa*, *F. grossulariodes* and a legume, *Koompassia excelsa,* which are categorized as protected in Sarawak based on Sarawak Protection Ordinance 1998. Another eight species (*Vatica micrantha*, *Artocarpus primackii*, *Knema pallens*, *Chionanthus pubicalyx*, *Mangifera pajang*, *Diospyros piscicarpa*, *Lithocarpus hallieri* and *Xanthophyllum ecarinatum*) are listed as Borneo endemic. Euphorbiaceae with 13 species and 10 genera was considered the most dominant family. The families that follow in order of decreasing dominance are Moraceae, Clusiaceae, Lauraceae and Anacardiaceae. Based on important value index (IVI), *Durio zibethinus* represents the most dominant species with IVI = 259.24 followed by *Lansium domesticum* with IVI = 242.84, while *Blumeodendron tokbrai,* a distant third*,* with IVI = 157.23. There were nine species, with IVI less than 5.0. Higher number of individuals and species were recorded at higher elevation than at the lower elevation, as shown by the Shannon index (H') = 3.69 (≥500 m) and H' = (400–500 m), respectively. Simpson index (Ds) also recorded the highest value, with Ds = 0.97 at elevation of ≥500 m. The distribution of individuals among species was more or less even in all plots with E > 0.9.

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1 Introduction

The Bidayuhs form the fourth largest ethnic group in Sarawak, and were traditionally settled on mountains, for protection from marauding enemies for centuries until 1841, when the Brooke's took the authority from the Brunei Malay Sultanate to illegalized headhunting and tribal warfare (Chang 2001). Being abandoned for almost a century, the old village sites are today quasi-pristine forming islands of tropical rainforest compared to the developed surroundings. In her journey towards development, Malaysia had rapidly transformed her forests. In general, agricultural estates, which are mainly rural, took most of the land area. City and town development and expansion took place where population concentrate and congregate. The forest fragments in the old village sites, though small in size, are increasingly important as wildlife refuge, apart from being a gene pool for the biodiversity they harbor, warranting conservation and protection.

Peninjau Hill at Gunung Serambu, located near Kuching City, Sarawak, is an old Bidayuh settlement site. Historically, faunal studies have been conducted on insects by Wallace (1876) and one specifically on butterflies by Moulton (1912). Despite its place in history and close proximity to Kuching and its institutes of higher learning and research centers, and that Odoardo Beccari, an Italian botanist, who described many plant species too visited Peninjau Hill in 1902, no structured research has been carried out on the vegetation of the site. Several floristic studies had been reported in the adjacent Bau region, such as those of Adam and Mamat (2005), Pahon (2011), and Migas (2012). This paper presents an inventory of trees, undertaken in 2012 as part of multidisciplinary assessment organized by the Institute of Biodiversity and Environmental Conservation of Universiti Malaysia Sarawak. The objective of this study is to describe the composition, distribution and diversity of trees at Gunung Serambu.

2 Methodology

2.1 Study Area

Gunung Serambu is a lowland secondary forested hill, located in Bau District in the western part of Sarawak, at 1.422°N, 110.225°E, about 35 km from Kuching, the capital city of Sarawak State (Fig. 1).

Alfred Russel Wallace spent about 4 weeks (December 1855 to January 1856) in Peninjau Hill of Gunung Serambu, collecting butterflies, moths, land shells, ferns and orchids. Bukit Peninjau is also the site of the cottage built by Rajah Brooke between the years 1848–1850. The Italian botanist, Odoardo Beccari, who made important contributions to science of the region, also visited Peninjau in 1902. Today, this fragmented habitat of old secondary forest stands intermixed with old farmlands and fruit orchards.

The hill was formerly covered with mixed dipterocarp forest with small patches of heath forest on the exposed rocky peak. The summit is at 555 m above sea level.

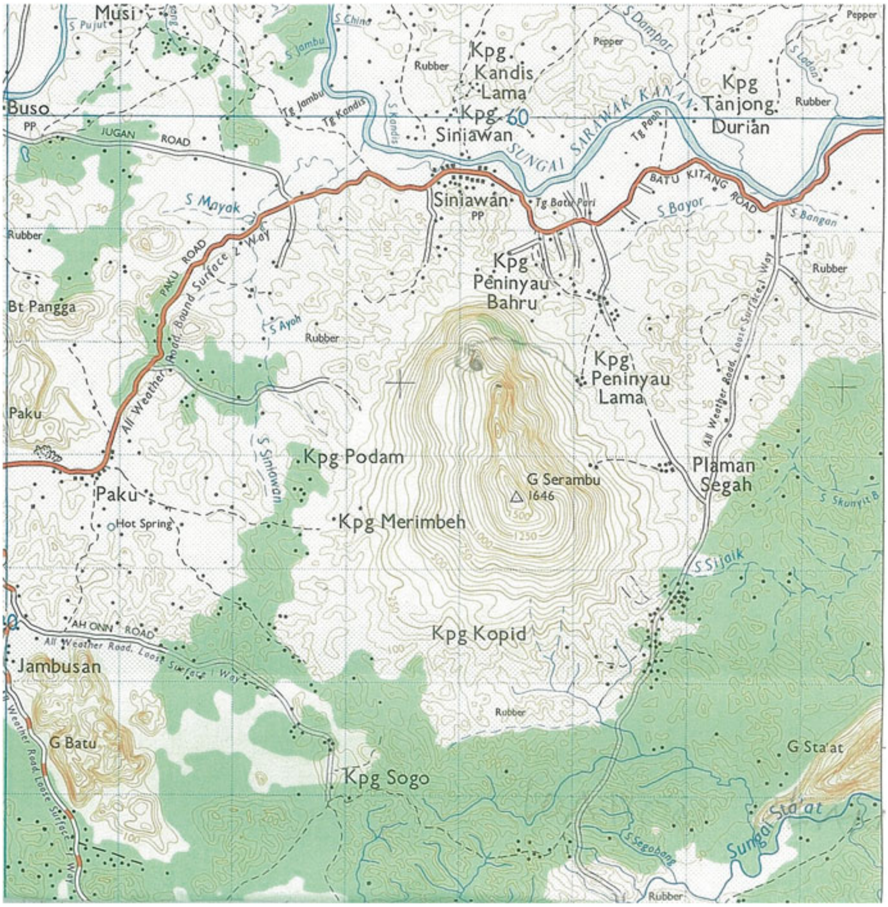

Fig. 1 Map showing the location of Gunung Serambu in Bau District, Sarawak

Much of the timber have been extracted by the local inhabitants for building houses and for other uses. Subsistence farming for hill rice was undertaken along the hill slope by the settlers but had stopped for more than 50 years. Burning of clearings for hill rice planting in the 1960s had engulfed the entire southwestern part of the hill so that smaller and younger trees dominated. At the old village site and foothill, local fruit trees dominated such as *Durio zibethinus*, *Lansium domesticum*, *Baccaurea brecteata*, *Baccaurea motleyana*, and *Mangostana,* with *Koompassia excelsa* trees and bamboo as well as various palms found scattered throughout. A majority of the old fruit trees had been planted during the first resettlement of the Serambu Bidayuh people (known as the Biroih), nearly a century ago. Most of the surrounding lowland areas are owned by the local community and are planted with various fruit trees and rubber (*Hevea basiliensis*). Further uphill, the landscape is steep and strewn with huge boulders. In between, various bamboo and palms, as well as dense understory plants, flourish. At the summit and its immediate surroundings, no records of clearing activities were observed so that the original vegetation was maintained.

The study was conducted in lowland mixed dipterocarp of old regrowth forest somewhat resembling a tropical lowland evergreen rainforest.

2.2 Sampling Method and Analyses

Twelve plots of 20 × 20 m were established along the trail at Gunung Serambu with first plot (Plot 1) just above Old Peninjau village and last plot (Plot 12) on the summit. Brief descriptions of the plots are shown in Table 1. At the steeper terrain and big boulders along the trail, some of the plots were adjusted to suit. For each tree with diameter 5 cm and above, both local and botanical name of the plants was recorded. Diameter at breast height was measured using a dbh tape and total height of trees was measured using a clinometer. Voucher specimens of twigs, leaves, flowers and fruits wherever possible, were collected and identified at Sarawak Forest Department Herbarium. Specimens were identified to the lowest taxonomic level possible. The relative frequency (Rf), relative dominance (RD), relative density (Rd), and important value (IV) were determined based on Soepadmo (1987). Three species diversity indices, including the Shannon (H'), Simpson (Ds) and Evenness (E) indices were used to compare different elevation (Magurran 1988).

3 Results and Discussions

3.1 Relative Abundance

A total of 487 individual trees were enumerated comprising of 112 species 80 genera and 43 families of trees. Four species of trees (*Ficus schwarzii*, *F. fistulosa*, *F. grossulariodes* and *Koompassia excelsa*) are categorised as protected plants species in Sarawak, according to the Sarawak Protection Ordinance 1998. Another eight species of trees recorded at Gunung Serambu were listed as Bornean endemic namely *Vatica micrantha*, *Artocarpus primackii*, *Knema pallens*, *Chionanthus pubicalyx*, *Mangifera pajang*, *Diospyros piscicarpa*, *Lithocarpus hallieri* and *Xanthophyllum ecarinatum*. A comparison was made with study conducted at Gunung Santubong as reported by Ipor et al. (2006), where 1421 trees ha^{-1} was enumerated. Gunung Santubong is generally classified as tropical lowland and submontane evergreen rainforest. However, this study did not describe in detail the composition and distribution of trees, containing nonetheless, the dominant trees at different elevations. Migas (2012) reported a total of 83 species from 325 trees at an undisturbed mixed dipterocarp forest at Gunung Jagoi, also in the Bau region, while Sayok et al. (2013; in prep) describes the understory and tree flora at Gunung Singgai, Bau, that includes 23 genera and 17 families for 131 tree species.

Table 1 Plot description for established plots in Gunung Serambu

Plot no	Coordinates		Plot description
	Latitude	Longitude	
1	1.431029°	110.228555°	Foothill of Gunung Serambu, in old orchard, mostly dominated by fruit trees (*Durio zibethinus*, *Lansium domesticum*, *Baccaurea angulata*, *Mangifera* spp.). Terrain condition: flat area, high decomposed leaf litter, litter depth of 5 cm, high moisture on forest floor. High number of understory plants such as common grass and weeds, tapioca, chilies, *Piper* sp., aroid plants, ferns, wild gingers and small clumps of *Bambusa* spp
2	1.431302°	110.227651°	Foothill of mountain. About 50 m from plot 1. Few large fruit trees observed. Mostly dominated by fruit trees (*Durio zibethinus*, *Lansium domesticum*, *Baccaurea angulata*, *Mangifera* spp.). Terrain condition: The slope was 10 %, as trail starts to ascend to the old traditional village (to Biroih village). Low decomposed leaf litter, litter depth of 3.5 cm, high moisture on forest floor, small boulders of rock also recorded outside plot. Understory plants such as seedlings of fruit trees, ferns and fern allies, grass, aroid plants, *Amorphophallus* sp
3	1.431557°	110.226366°	On ridge of mountain. Trees tall with large buttresses. Both *Durio zibethinus* and *Lansium domesticum* dominate plot area. Terrain condition: 15 % slope. Low decomposed leaf litter, litter depth of 2 cm, relatively moist forest floor. Few understory plants, such as seedlings of fruit trees, climbing ferns, palm species, *Caryota mitis* and aroids
4	1.431823°	110.225358°	Area steeper than plots 2 and 3. Mostly dominated by *Lansium domesticum* and *Hevea brasiliensis*. Terrain condition: 30 % slope. Low decomposed leaf litter, litter depth of 2.5 cm, relatively wet and moist forest floor. High number of understory plants observed, such as seedlings of *Hevea brasiliensis*, climbers, aroid plants and few clumps of bamboo. High number of large sized bamboo clumps recorded
5	1.432125°	110.224274°	Site of abandoned ancestral village. Trees high with old buttresses. High number of old fruit trees observed, such as *Durio zibethinus*, *Lansium domesticum* and *Baccaurea spp.* Terrain condition: relatively flat area. High and thick semi decomposed leaf litter on forest floor. Forest floor relatively wet and moist. Some undergrowth cleared with trees intact. High number of fruit tree seedlings observed on forest floor
6	1.432936°	110.223320°	Above site of abandoned village. Steep slope of 15 %. Low semi-decomposed or decomposed leaf litter. Litter depth of 2 cm. Certain part dry due to open canopy

(continued)

Table 1 (continued)

Plot no	Coordinates		Plot description
	Latitude	Longitude	
7	1.431973°	110.221985°	Site of old White Rajah cottage. Old secondary forest. No fruit trees observed within the area. Some patches of openings are seen at plot 8. Extent of farmed land at plot 8. Terrain condition: flat area with pockets of gentle slope. Relative dried and lesser moist forest floor. Low leaf litter with litter depth of 2 cm
8	1.430850°	110.222620°	
9	1.429722°	110.222870°	
10	1.428341°	110.223159°	About 10 m away from the 1st mountain view point. No fruit trees recorded in this plot except few *Artocarpus integer* (Tibodak) trees recorded outside plot. Most probably seedlings dispersed by squirrels. Gentle slope about 5 %. High and thick decomposed leaf litter on forest floor. Forest floor relatively wet and moist. High number of understory plants within and outside plot
11	1.427181°	110.222780°	
12	1.425920°	110.223147°	Second highest summit in Gunung Serambu. Forest floor with thick semi-decomposed/decomposed leaf litter, depth 6 cm. Forest floor with high moisture content. Terrain condition: on ridges, small flat areas. Low number of understory plants, such as seedlings, herbs, *Nepenthes ampullaria,* lichen species and parasitic plants including orchids

The Euphorbiaceae is the most dominant family within the established plots, comprising 10 genera and 13 species (Table 1). The families Lauraceae and Anacardiaceae followed a distant second and third, respectively. The largest family, based on species numbers, was also the Euphorbiaceae, with a total of 13 species or 11.30 % of the total number of species. This was followed by the Moraceae, with ten species (8.70 %) and Clusiaceae, with seven species (6.09 %). The families Lauraceae, Anacardiaceae and Myrtaceae were represented with six species each (5.22 %) within the established plots. These results agree with the studies conducted by Whitmore (1972) and Kochummen et al. (1990), that show that the Euphorbiaceae is one of the largest families of tropical forests. The 12 established plots at Gunung Serambu displayed an extremely low composition of dipterocarp although the vegetation was once classified as lowland dipterocarp forest. However, only two species of dipterocarp were recorded in this study and were found almost on top of the mountain (elevation ≥500 m). Ipor et al. (1998, 2001) also reported low numbers of dipterocarp trees in the highlands of Bario in Sarawak and the Mahua region of the Crocker Range, in Sabah.

A cumulative plot of species (Fig. 2) shows the number of species increased with decreasing rate as the number of plots increases. The species accumulation curve showed no tendency to flatten out, and new species continue to increase slowly as the plot increases within the study area. Poore (1968) mentioned that in the species-rich rainforests, tree species continue to accumulate even over 4–5 ha survey areas, particularly those species whose presence are the result of habitat conditions, or by chance.

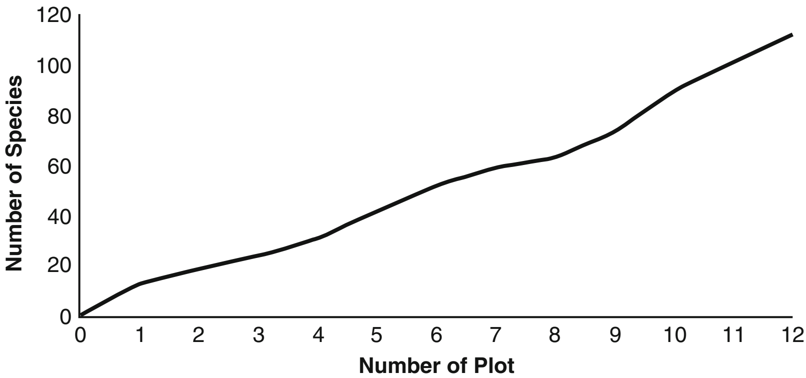

Fig. 2 Species-area curve for trees in Gunung Serambu

Table 2 Six largest families of trees within the established plots (based on species number) at Gunung Serambu

Family	No of genera	No of species
Euphorbiaceae	10	13
Moraceae	2	10
Clusiaceae	3	7
Lauraceae	6	6
Anacardiaceae	4	6
Myrtaceae	2	6

3.2 Important Value Index (IVI)

Based on their important value index (IVI) in Table 2, Durio zibethinus represents the most dominant species, with IVI = 259.24, followed by Lansium domesticum (IVI = 242.84) and Blumeodendron tokbrai (IVI = 157.23). Table 3 shows that some of the co-dominant species recorded included *Artocarpus elasticus* (IVI = 141.24), *Koompassia excelsa* (IVI = 128.04), *Adinandra dumosa* (IVI = 113.32), *Dacryodes rostrata* (IVI = 112.91) and *Symplocos adenophylla* (IVI = 76.88). Some of the least dominant species recorded in the established plots with IVI < 5 are from nine species- *Adenanthera borneense*, *Fagraea crassipes*, *Actinodaphne pruinosa*, *Saurauia heterosepala*, *Swintonia spicifera*, *Diospyros sumatrana*, *Strombosia ceylanica*, *Vitex pubescens* and *Ficus grossulariodes*. According to Ipor et al. (2006), low tree species dominant is due to fewer individual trees as well as their smaller basal area.

3.3 DBH Class Distribution

Figure 3 shows that trees can be classified into five groups based on their dbh (in cm). Class 1 (5.0–≤15.0), class 2 (15.1–≤25.0), class 3 (25.1–≤35.0), class 4 (35.1–≤45.0) and class 5 (≥45.1). The highest number of individual trees were in class 1,

Table 3 Relative frequency (*Rf*), relative dominance (*RD*) and relative density (*Rd*) and importance value index (*IVI*) of tree species with dbh 5 cm and above at Gunung Serambu

Genus	Species	Family	rF	rDom	rd	IVI
Durio	*zibethinus*	Bombacaceae	83.52	92.20	83.52	259.24
Lansium	*domesticum*	Meliaceae	69.05	104.74	69.05	242.84
Blumeodendron	*tokbrai*	Euphorbiaceae	52.79	51.66	52.79	157.23
Artocarpus	*elasticus*	Moraceae	46.07	49.10	46.07	141.24
Koompassia	*excelsa*	Fabaceae	45.85	36.33	45.85	128.04
Adinandra	*dumosa*	Theaceae	34.01	45.31	34.01	113.32
Dacryodes	*rostrata*	Burseraceae	36.38	40.14	36.38	112.91
Cratoxylum	*glaucum*	Clusiaceae	26.57	30.54	26.57	83.67
Symplocos	*adenophylla*	Symplocaceae	24.19	28.50	24.19	76.88
Vatica	*micrantha*	Dipterocarpaceae	19.63	33.66	19.63	72.93
Symplocos	*rubiginosa*	Symplocaceae	24.39	23.22	24.39	71.99
Myristica	*lowiana*	Myristicaceae	19.25	17.86	19.25	56.37
Pimeleodendron	*griffithianum*	Euphobiaceae	14.87	24.06	14.87	53.80
Ixonanthes	*petiolaris*	Ixonanthaceae	17.24	18.01	17.24	52.49
Pometia	*pinnata*	Sapindaceae	17.05	14.05	17.05	48.14
Pangium	*edule*	Flacourtiaceae	17.05	13.90	17.05	47.99
Porterandia	*anisophylla*	Rubiaceae	14.68	15.75	14.68	45.11
Barringtonia	*macrostachya*	Lecythidaceae	12.69	18.38	12.69	43.76
Artocarpus	*kemando*	Moraceae	14.62	13.10	14.62	42.34
Garcinia	*mangostana*	Clusiaceae	15.38	11.22	15.38	41.97
Swintonia	*spicifera*	Anacardiaceae	1.75	1.19	1.75	4.70
Diospyros	*sumatrana*	Ebenaceae	1.75	1.19	1.75	4.70
Strombosia	*ceylanica*	Olacaceae	1.75	1.19	1.75	4.70
Vitex	*pubescens*	Verbenaceae	1.75	1.19	1.75	4.70
Saurauia	*heterosepala*	Actinidiaceae	1.75	1.14	1.75	4.65
Adenanthera	*borneensis*	Fabaceae	1.75	1.14	1.75	4.65
Actinodaphne	*pruinosa*	Lauraceae	1.75	1.14	1.75	4.65
Fagraea	*crassipes*	Loganiaceae	1.75	1.14	1.75	4.65
Ficus	*grossulariodes*	Moraceae	1.75	1.14	1.75	4.65

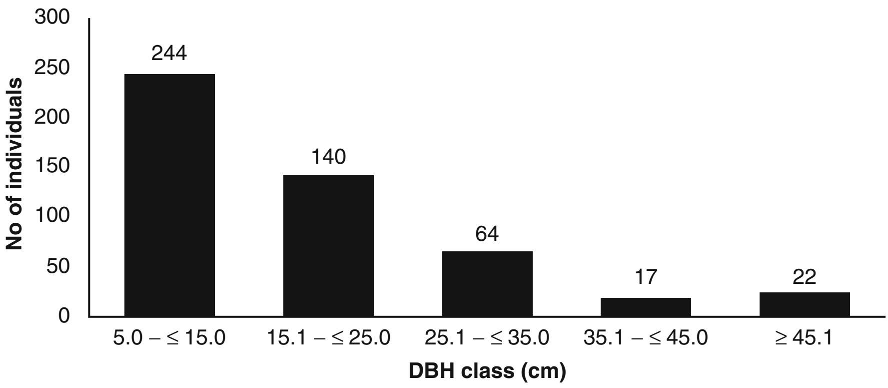

Fig. 3 dbh (cm) class distribution of trees at Gunung Serambu

with 244 individuals, followed by class 2, with 140 individual trees. The least number of individual trees recorded (17) was found in class 4. There is a decreasing trend on number of individual trees as the diameter at breast height (dbh) increases in size. Class 5 (≥45.1) cm included 22 individuals trees. The largest trees recorded in the established plots in Gunung Serambu were Dooh (*Kompassia excelsa*), with dbh 168 cm and Dien (*Durio zibethinus*), with dbh 110 cm.

3.4 Height Class Distribution

Figure 4 shows that trees can be classified in to groups based on their height (in m). Class 1 (0–≤10.0), class 2 (10.1–≤20.0), class 3 (20.1–≤30.0), class 4 (30.1–≤40.0) and class 5 (≥40.1). The highest number of trees with 261 individuals was recorded in class 2 (10.1–≤20.0) m, followed by class 1 (0–≤10.0) m, with 132 individuals and class 3 (20.1–≤30.0) m with 66 individuals. The least number of trees recorded, with 12 individuals, fall in class 5 (≥40.1) m. The tallest tree recorded in Gunung Serambu is Do'oh (*Kompassia excelsa*) with total height range from 45 to 65 m. Notably, there is a major drop in the number of individuals reaching heights of more than 20 m and a gradual decrease in numbers with increasing height class (Fig. 2).

3.5 Species Diversity and Elevations

The highest elevation for Gunung Serambu recorded was 514 m above mean sea level. To compare the species diversity based on different elevational gradients, five different elevation readings were used for this study which are 0–100 m, 100–200 m, 200–300 m, 300–400 m, 400–500 m, and more than 500 m. The highest number of individual trees was 172, recorded at elevation more than 500 m. The second highest was 116 individuals recorded at 400–500 m followed by third ranked

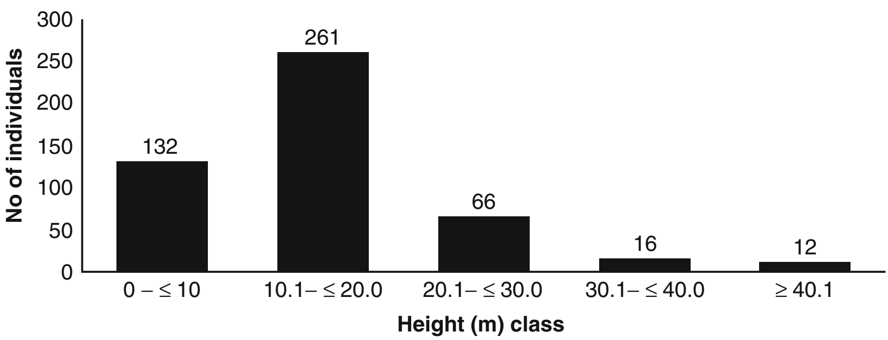

Fig. 4 Height (m) class distribution of trees at Gunung Serambu

Table 4 Tree species diversity indices for different elevations at Gunung Serambu, using the Shannon index (H′), Simpson index (Ds) and Evenness index (E)

Elevational bands (m)	Individuals (n)	Species (s)	Shannon (H′)	Simpson (Ds)	Evenness (E)
0–100	47	19	2.63	0.90	0.73
100–200	40	23	2.89	0.93	0.78
200–300	63	32	3.14	0.94	0.72
300–400	49	27	2.99	0.93	0.74
400–500	116	37	3.15	0.94	0.63
≥500	172	55	3.69	0.97	0.73

highest with 63 individuals at 200–300 m. The lowest number of individuals recorded at two elevations, which are located at the foothill of the mountain with 40 individuals (100–200 m) and 47 individuals (0–100 m).

The highest number of species found was recorded at elevations over 500 m, with 55 species, followed by 37 species at 400–500 m, 32 species at 200–300 m and 27 species at 300–400 m. The lowest number of species found was recorded for 23 species at 100–200 m and 19 species at 0–100 m.

Shannon Index (H′) showed high values at higher elevations. Table 4 shows that H′ = 3.69 at elevations over 500 m, followed by H′ = 3.15 at 400–500 m and H′ = 3.14 at 200–300 m. Low H′ values were recorded at the three lower elevational bands, 0–100 m (H′ = 2.63), 100–200 m (H′ = 2.89) and 300–400 m (H′ = 2.99). Simpson index (Ds) also indicates high values at higher elevations (≥500 m), with Ds = 0.97, while the lowest value (Ds = 0.90) was recorded at the foothills of the mountain (0–100 m). Evenness index (E) shows high value at 100–200 m, with E = 0.78, and the lowest recorded was at 400–500 m, with E = 0.63. The distribution of individuals among the species was even in all established plots (E > 0.9). Figure 4 shows that the highest elevation of Gunung Serambu (≥500 m), recorded high values of selected diversity indices, including high number of individuals, number of species, Shannon index (H′) and Simpson index (Ds).

Based on our observations, no logging or forest extraction activities were evident on the upper reaches of the mountain, as the villagers maintain them for watershed protection, and furthermore, it is difficult to access the steep terrain. The local communities of Gunung Serambu, especially villagers from Kpg. Peninjau Lama and Kpg. Peninjau Baru, live off the forest: they collect wild vegetables, wild fruits, wild honey and meat. Selected tree species provide materials for diverse use, such as housing materials, roofing, firewood, medicine and musical instrument. The forests of Gunung Serambu are also an important water catchment for some of the lowland villages.

4 Conclusions

Gunung Serambu still harbors substantial species of the tropical rainforest despite that it had been settled for a few centuries. These include several protected species under Sarawak Law and Bornean endemic species, as well as the original species of the lowland mixed dipterocarp in tropical rainforest at upper elevations. Fruit trees which dominate in the old village sites and at the lower elevation should be considered as good combination with native species as these trees will provide seasonal fruit and protect the mountain's ecosystem such as habitats for wildlife, source of clean water, and prevention of erosion. They can also be included as one of the ecotourism products. The existing spirit shown the locals to protect the forest and sustainably use it should be supported through gazettement of the area as community forest to discourage individual claims, that can lead to its fragmentation and thus its ecosystem functions.

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Diversity of Butterflies on Gunung Serambu, Sarawak, Malaysia

Sing Tyan Pang, Alexander Kiew Sayok, and Mathew Jenang

Abstract Gunung Serambu, a mountain in western Sarawak, northern Borneo, was occupied by the Bidayuh ethnic group, and abandoned about a century ago, with their settlement at the foothill of the mountain. The present study attempts to document butterflies, as part of a multidisciplinary study on this mountain, with the aim of conservation and sustainable use of the site. Three surveys of 4 days each were conducted from September 2012 to March 2013, using aerial nets and baited traps, that recorded 377 butterflies from 97 species. About 81 % (303 butterflies) of the captures were from the Nymphalidae, comprising 61 species, followed by the Lycaenidae with 24 individuals from 16 species. Baited traps captured less butterflies (163 compared to 214 by aerial traps), all from the Nymphalidae indicating that the method may have limitations in such studies. With the addition of 58 species that were considered new records, Gunung Serambu has 111 recorded species. Species accumulation curve suggest more additional records with time. Furthermore, with 46 species (more than 47 %) singletons and 21 species (22 %) doubletons, as well as the increasing species accumulation curve, longer sampling is warranted, covering different times of the year, as well as additional sites.

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1 Introduction

Butterflies play an important and numerous roles in the environment. Apart from being noticed for their attractive appearance, they are important both in their own right and as quality of life indicators, worthy on conservation and protection (Chey 2000; Warren et al 2001; Otsuka 2001). They pollinate flowers, and throughout their morphological stages, support a range of other predators and parasites, many of which are specific to individual species, or groups of species and thus form important components of the food chain as preys for birds, bats and other insectivorous animals (Andersson et al. 2002).

Intrinsically, butterflies serve as flagship species for conservation in general, and in particular, for invertebrate groups. Aesthetically, they are part of our heritage as they often portrayed as the essence of nature or as representing freedom, beauty or peace. Their fascinating life-cycles which involves transformation from egg to caterpillar to chrysalis is one of the wonders of nature and their the intricate wing patterns and iridescence, and as examples of insect migration are used in many countries to educate us about the natural world. Butterflies are an extremely important group of 'model' organisms used, for centuries, to investigate many areas of biological research, including such diverse fields as navigation, pest control, embryology, mimicry, evolution, genetics, population dynamics and biodiversity conservation. Their beauty attracts thousands of people to travel each year looking for butterflies and moths. Such ecotourism could bring valuable income to many developing countries of the world. A fine example is that of the Monarch butterfly (*Danaus plexippus*), which migrate yearly from northern United State to Mexico (Gross 2014) and is an attractions to these countries via tourism and wildlife conservation.

The issues plaguing butterflies may be similar to those causing populations of other biodiversity, such as bees and other insects to decline. The main one being the clearance of forests for development which threatens their habitats, while the use chemicals for crop protection adversely affect insects populations, including butterflies (Koh 2007). Many areas in Sarawak and elsewhere in Malaysia are facing the same fate as forests are being cleared to give way to various developmental projects. The effects of deforestation in Malaysia on various fauna, including butterflies had been extensively reported (Yule 2008; Wilcove and Koh 2010; Sarvision 2011; Chakravarty et al. 2012). They have been used as indicators in conservation planning as reported by several authors (e.g. Nelson and Andersen 1994; DeVries et al. 1997), and many of the a priori advantages of butterflies as biodiversity indicators are summarized in McGeoch (1998).

The surrounding areas of Gunung Serambu face a similar fate with those of other mountains in Bau District, where islands or fragmented areas were formed for wildlife refuge caused by the deforestation and monoculture. The present study on butterflies is part of the multidisciplinary study to document the various biodiversity at Gunung Serambu to enable its protection and conservation. Studies on insects, including butterflies was initialized a century ago by Wallace (1876), when the area was still much forested and found substantial insects, so that he concluded that his collection here was the most fruitful of all made in the Malay Archipelago. This study documents the diversity of the butterfly at a community forest, which had been anthropogenically disturbed through settlement and cultivation (Elderly Steven Sinyun, pers. comm.), but have reverted back to its presumed near original status from the abandonment for almost a century. Thus, it created a unique opportunity for a comparison between the present collection and one made a century ago.

2 Methodology

2.1 Study Site

The study was undertaken Peninjau Hill and Podam Hill of Gunung Serambu in Bau District, Sarawak. The Peninjau Hill was once the site of Bidayuhs, natives of Sarawak, settlement in four longhouse villages with a peak population of more than 500 for almost 200 years. They practiced subsistence farming mainly of rice on the hillsides for rice and later planted fruit trees and thus had transformed the original landscape from a lush tropical rain forest into the mosaic vegetation of different successional stage as well as introduced species. The villagers had moved to form 17 villages surrounding this mountain. Having been abandoned almost 100 years ago, the village sites and immediate surrounding areas are now quasi-pristine albeit with a mosaic of vegetation cover at different stages of growth amidst mature fruit trees housing rich diversity of plants and animals. At present, several villages are found at the foothill including Kampung Podam on western part of the mountain. Gunung Podam was also similarly anthropogenically modified albeit of more recent nature.

Gunung Serambu is particularly known as the site where James Brooke, whom was born 29 April 1803 and died on 11 June 1868. He was known as the First White Rajah of Sarawak and built his cottage to escape the heat of Kuching. Alfred Rusell Wallace, who later stayed in this cottage in 1855 and 1856, gathered an enormous sample collection of fauna including Lepidoptera (Wallace 1876). However, the record on collection of butterflies is poorly documented. In 1912, Moulton conducted an expedition on insects at the same location and with similar method recorded 41 species of butterfly which are presently housed in the Sarawak Museum (Moulton 1912).

2.2 Sampling

Butterfly samplings were undertaken at two sites at Gunung Serambu. The first site was located at attitude 347 m ASL (N1.43 E110.22) Peninjau Hill on the northern side of the mountain while the second was an old orchard above Podam Village, at attitude 78 m ASL (N1. 42 E.110. 21). Two aerial nets and 12 baited traps were used in the sampling. Ripe or fermented pineapples were used as baits. Captured butterflies were kept in folded envelopes and then identified to the lowest taxonomic level using the reference books of Otsuka (1988), Seki et al. (1991) and Maruyama (1991). The classification of species follows Corbet and Pendlebury (1992), Itioka et al. (2009) and Wahlberg et al. (2009).

Butterfly diversity at Gunung Serambu was tested by using Shannon Weiner Index in PAST (Hammer et al. 2001). In order to compare the diversity between three comparable sampling trips t-test, and the similarity test like Chao-Jaccard-Est Abundance-based and Chao-Sorensen-EST Abundance-using *EstimateS* Version 9.1.0 program were applied. The male and female ratio was hypothesized to be 1:1 in natural habitat. Thus, the sex ratio comparison of seven species which with collection above ten individuals of combined sexes was done by using Chi-square test (χ^2).

3 Result and Discussion

3.1 Family Composition

Altogether, 371 individuals, comprising 97 species of butterflies, were recorded over the 12 days of surveys, using both aerial nets and baited traps (Tables 1 and 2). Of these, Nymphalidae could be considered as the predominant family in Gunung Serambu (81 %) due to the higher number of captured individuals than from other four families. The high percentage was simply because there was a lot of fruit trees planted at the Gunung Serambu as well as the efficiency of the two sampling methods in capturing individuals from this family. Family Lycaenidae and Pieridae came in as the distant second and third whereby the individuals' number collected were both 6 % of all recorded. The Birdwings, Papilionidae (4 %) were ranked fourth while the family with the least number of individuals caught was the skippers, Hesperiidae with 3 %. It could be due to their small-body size resulting in collectors overlooking them during sampling. Less favored host plants found on the sites was also a possible factor leads to the low yield of these families. The low number of Birdwing butterflies sampled could be due to their fast flying skill thus avoiding the

Table 1 The composition of five butterfly families collected in Gunung Serambu based on the total number of individuals and (species) collected

Family	Total number of species	Total number of individuals
Hesperiidae	8	13
Papilionidae	5	9
Pieridae	7	28
Nymphalidae	61	302
Lycaenidae	16	19

Table 2 Total butterfly individuals recorded in the present study

No.		Total individuals recorded
	Superfamily: Hesperioidea	
	Family: Hesperiidae	
	Subfamily: Coeliadinae	
1	*Hasora vitta vita* Butler, 1870	1
	Subfamily: Pyrginae	
2	*Tagiades parra parra* Fruhstorfer 1910	1
	Subfamily: Hesperiinae	
3	*Halpe zema otsukai* Moore 1878	3
4	*Koruthaialos rubecula rubecula* Plotz 1882	1
5	*Ancistroides nigrita othonias* Hewitson 1878	2
6	*Ancistroides gemmifer dombya* Fruhstorfer 1911	3
7	*Notocrypta paralysos varians* Plotz 1882	1
8	*Baoris penicillata brenda* Evans 1937	1
	Superfamily: Papilionoidea	
	Family: Papilionidae	
	Subfamily: Papilioninae	
9	*Papilio nephelus albolineatus* Forbes 1885	2
10	*Papilio helenus enganius* Doherty 1891	2
11	*Papilio fuscus dayacus* Rothschild 1908	2
12	*Graphium agamemnon agamemnon* Linne 1758	2
	Subfamily: Leptocicinae	
13	*Pathysa antiphates itamputi* Butler 1885	1
	Family: Pieriidae	
	Subfamily: Coliadinae	
14	*Gandaca harina elis* Fruhstorfer 1910	1
15	*Eurema simulatrix tecmesa* De Niceville 1895	2
16	*Eurema sari sodalis* Moore 1886	19
17	*Eurema ada ada* Distant & Pryer 1887	1
	Subfamily: Pierinae	
18	*Delias hyparete diva* Fruhstorfer 1888	1
19	*Parenonia valeria lutescens* Butler 1879	2
20	*Leptosia nina malayana* Fruhstorfer 1910	2
	Family: Nymphalidae	
	Subfamily: Danainae	
21	*Parantica aspasia aspasia* Fabricius 1787	2
22	*Ideopsis vulgaris interposita* Fruhstorfer 1910	2
23	*Ideopsis gaura daos* Boisduval 1836*	2
24	*Idea lynceus fumata* Fruhstorfer 1897	1
25	*Euploea crameri crameri* Lucas 1853	1
26	*Euploea mulciber portia* Fruhstorfer 1904	2
27	*Euploea midamus aegyptus* Butler 1866	3

(continued)

Table 2 (continued)

No.		Total individuals recorded
	Subfamily: Satyrinae	
28	*Melanitis zitenius rufinius* Fruhstorfer 1908	45
29	*Elymnias nesaea hypereides* Fruhstorfer 1902	1
30	*Elymnias kuenstleri rileyi* Corbet 1933	1
31	*Neorina lowii lowii* Doubleday 1849	30
32	*Lethe europa kayan* Aoki & Uemura 1982	1
33	*Lethe chandica delila* Staudinger 1897	1
34	*Orsatriaena medus medus* Fabricius 1775	1
35	*Mycalesis anapita fucentia* Fruhstorfer 1911	8
36	*Mycalesis fusca adustata* Fruhstorfer 1906	6
37	*Mycalesis kina* Staudinger 1892	1
38	*Mycalesis mnasicles mnasicles* Hewitson 1864	26
39	*Mycalesis mineus macromalayana* Fruhstorfer 1911	3
40	*Mycalesis horsfieldi hermana* Fruhstorfer 1908	1
41	*Mycalesis orseis borneensis* Fruhstorfer 1906	15
42	*Erites argentina argentina* Butler 1868	9
43	*Erites elegans elegans* Butler 1868	10
44	*Ragadia makulata umbrata* Fruhstorfer 1991	21
45	*Ypthima fasciata fasciata* Hewitson 1865	6
46	*Ypthima pandocus sertorius* Fruhstorfer 1911	2
	Subfamily: Morphinae	
47	*Faunis gracilis gracilis* Butler 1867	1
48	*Faunis canens borneensis* Fruhstorfer 1905	1
49	*Faunis kirata kirata* De Niceville 1891	4
50	*Faunis stomphax stomphax* Westwood 1858	3
51	*Xanthotaenia busiris burra* Stichel 1906	5
52	*Amathusia ochraceofusca ochraceofusca* Honrath 1888	4
53	*Amathusia schoenbergi schoenbergi* Honrath 1888	1
54	*Zeuxidia amethystus wallacei* C. & R. Felder 1867	3
55	*Zeuxidia doubledayi horsfieldii* C. & R. Felder 1867	3
56	*Thauria aliris aliris* Westwood 1858	7
57	*Discophora necho cheops* C. & R. Felder 1867	8
58	*Discophora sondaica symphroina* Fruhstorfer 1911	6
	Subfamily: Heliconiinae	
59	*Cupha erymanthis erymanthis* Drury 1773	2
60	*Cethosia hypsea hypsea* Doubleday 1847	3
	Subfamily: Nymphalinae	
61	*Junonia orithya metion* Fruhstorfer 1905	1
62	*Kallima limborgi boxtoni* Moore 1879	1
	Subfamily: Limenitinae	
63	*Pantoporia aurelia aurelia* Staudinger 1886	2
64	*Neptis nata nata* Moore 1857	3

(continued)

Table 2 (continued)

No.		Total individuals recorded
65	*Neptis leucoporos cresina* Fruhstorfer 1908	1
66	*Neptis miah digita* Fruhstorfer 1905	1
67	*Athyma adunora pedanis* Fruhstorfer 1906	1
68	*Tanaecia pelea djataca* Fruhstorfer 1913	1
69	*Tanaecia munda munda* Fruhstorfer 1899	3
70	*Tanaecia clathrata coerulescens* Vollenhoeven 1862	4
71	*Tanaecia aruna aparasa* Vollenhoeven 1862	8
72	*Euthalia godarti vacillaria* Butler 1868	5
73	*Euthalia iapis ambalika* Moore 1858	8
74	*Euthalia monina bipunctata* Vollenhoeven 1862	1
75	*Dophla evelina magama* Fruhstorfer 1913	1
76	*Lexias pardalis dirteana* Corbet 1941	3
77	*Lexias canescens canescens* Butler 1868	1
	Subfamily: Pseudergolinae	
78	*Amnosia decora buluana* Fruhstorfer 1908	1
79	*Stibochiona schoenbergi* Honrath 1889	1
	Subfamily: Charaxinae	
80	*Charaxes bernadus repititus* Butler 1869	1
81	*Charaxes durnfordi everetti* Rothschild 1893	2
	Family: Lycaenidae	
	Subfamily: Miletinae	
82	*Allotinus* (*Paragerydus*) *horsfieldi permagnus* Fruhstorfer 1913	1
83	*Allotinus* (*Paragerydus*) *melos* (H. H. Druce 1896)	2
84	*Allotinus* (*Paragerydus*) *corbeti* Eliot 1956	1
	Subfamily: Polyommatinae	
85	*Discolampa ethion icenus* Fruhstorfer 1918	1
86	*Udara* (*Udara*) *cyma cyma* Toxopeus 1927	1
87	*Jamides pura tenus* Fruhstorfer 1916	1
88	*Jamides alecto ageladas* Fruhstorfer 1916	1
89	*Nacaduba hermus swatipa* Corbet 1938	2
90	*Nacaduba kurava nemana* Fruhstorfer 1916	1
	Subfamily: Lycaeninae	
91	*Heliophorus kiana* Grose-Smith 1889	1
	Subfamily: Theclinae	
92	*Iraota distanti nileia* Fruhstorfer 1904	1
93	*Loxura cassiopeia amatica* Fruhstorfer 1912	1
94	*Exooylides tharis tharisides* Fruhstorfer 1904	1
95	*Hypolycaena erylus teatus* Fruhstorfer 1912	1
96	*Deudorix staudingeri* H.H. Druce 1895	2
	Subfamily: Curetinae	
97	*Curetis regula* Evans 1954	1

catch. The most remarkable Sarawak Birdwing species, Rajah Brooke (*Trogonoptera brookiana brookiana*) was not found in this study because it was usually found by the river. The presence of the 24 species from Family Pieridae could be due to the host plants they favored.

The most abundant species caught in this study were all from Satyrinae, namely *Melanitis zitenius rufinius*, *Neorina lowii lowii*, *Mycalesis mnasicles mnasicles* and *Ragadia makuta umbrata* with 45, 30, 26 and 21 individuals, respectively. These species were effectively caught by netting and trapping due to their relatively slow and low flying characteristics as well as their preference to the fermenting fruit. For example, *N. lowii lowii* was observed to visit fallen fermented fruit, *Artocarpus indeger*, which is locally called as *Cempedak*.

Compared to the century-old records of Moulton (1912), 58 species were new record thus, bringing the number of butterfly species collected at this site to 111 species. Seventeen species were recollected, while 23 species were not found in the current study. The recaptured species consisted of Nymphalidae, including *Amnosia decora*, *Zeuxidia amethystus*, *Z. doubledayi*, *Thauria aliris*, *Ideopsis gaura daos* and *Melanitis* spp. The only species recaptured from family Pieridae, Papiliondae and Lycaenidae were *Eurema sari* and *Papilio nephelus*, respectively. Their long-time presence indicates that the long-existing of certain host plant at Gunung Serambu. Palmae, the host plant of both *Zeuxidia* spp. were found extant (Pang 2006). As for those species which were not captured in the current, the loss of the host plant might be the best to explain their absence after 100 years (Wilf et al. 2006).

The occurrence of new record for butterfly species is suspected to be the result of the rapid and intensive oil palm development in Bau areas. At least 10,532 ha of oil palm plantation developed in different areas, Bau. They are Jagoi, Bratak, Stenggang and Undan (Tuen and Amit 2012). The distance between the nearest opening land and the south of Gunung Serambu was 2.14 km. The consequences of rapid tree falling explaining the loss of host plant and changes in local climate may result in the butterflies that are highly specialized with host plant as well as forest-dwelled species as *Amathusia ochraeofusca ochraceofusca*, *A. schoenbergi schoenbergi*, *Discophora necho cheops* and *D. sondaica sondaica* to be forcibly moved to other forests, such as Gunung Serambu. In addition, new growth of weeds in a cleared land attracted more butterflies to the areas as well as adjacent area (Koh 2008). Perhaps these explained the new record of 58 species found at the site.

The newly formed assemblages of butterflies could be competing against other species and individuals. Species that were not fit in competing might fly away. The absence of 23 species could also be the consequence of the activities such as cultivation and construction carried out by the Bidayuhs' settlement in the past. As for Lycaenids and Hesperids, the butterflies with small-body size might be overlooked during the sampling days. Other possibilities could be there were changes in the surroundings which butterflies were not fit enough to adapt the changes occurred. Changes in climate would also change the flowering times at the forest as well as the foraging pattern of the pollinators at the same time (Vanbergen et al. 2013). Technique used in sampling may also influence the result as stated by Tangah et al.

(2004) showing that ground-based transect techniques can survey Satyrinae and Morphinae butterflies fairly reliably but are likely to miss the canopy component of the fauna. They also stated that movements of recaptured butterflies between traps at different heights were minimal, indicating that species are confined to certain height.

This study also discovered species with one or two individuals. Forty six species were caught with only one individual, (i.e., singletons); and 20 species with only two individuals (i.e. doubleton). Surprisingly, all singletons and doubletons came from the family of Hesperiidae and Lycaenidae. It could be the number of those species happened to be very few or they were overlooked by the collectors. In addition, the numbers of species increased throughout the 12 sampling days as clearly shown in the species accumulation curve. The combination of the accumulation curve below and the high number of singletons and doubletons indicated that there are more species to be discovered in that area. Thus, more surveys on the butterfly are necessary.

3.2 Comparison Among Samples

The most number of species and individuals were sampled in the second trip. Nevertheless, the collection in the first trip shows the highest Shannon Index (S.I) among all (S.I of 1st trip = 3.629, 2nd trip = 3.428, 3rd trip = 3.268) indicated that the butterflies at that time was the most diverse. Since sampling periods were traditionally considered to fall on the dry (first trip) and wet season (second and third trip) (Abang Kassim and Hazebroek 2000), and the samplings carried out at the same elevation during the first trip and second trip, thus the *t*-test was done by comparing only first and second trip. The statistical results showed there was no significant difference (p-value = 0.90898). The results from *EstimateS* Version 9.1.0 program also showed that the diversity of butterfly in two trips were similar to each other. Chao-Jaccard-Est Abudance-based and Chao-Sorensen-Est Abundance-based also showed that the value skewed to 1 rather than 0, 0.535 and 0.697, respectively. Number of species captured by aerial net and baited trap in each trip was estimated by rarefraction shown in Figs. 1 and 2.

Of the 97 species, 67 species were encountered within a single trip; 26, 22 and 19 species were encountered only during the first, second and third trip, respectively. Only 16 species were captured from all three trips. The inconsistence of butterfly species captured in the three sampling trips could be due to the different flowering times for different plant species which butterflies associate with. For example, *Melanitis zitenius rufinus* was reported to associate with bamboo (Corbet and Pendlebury 1992). Hence, this species were captured at all trips as bamboo was not developing seasonally. On the other hands, plants that flower seasonally might attract its nectar feeders at certain times. For instance, the presence of *Euploea* spp. that were captured only on the first trip; and *Papilio fuscus dayacus*, *P. helenus enganius* and *Neptis nata nata* captured only in second trip were specialist feeders

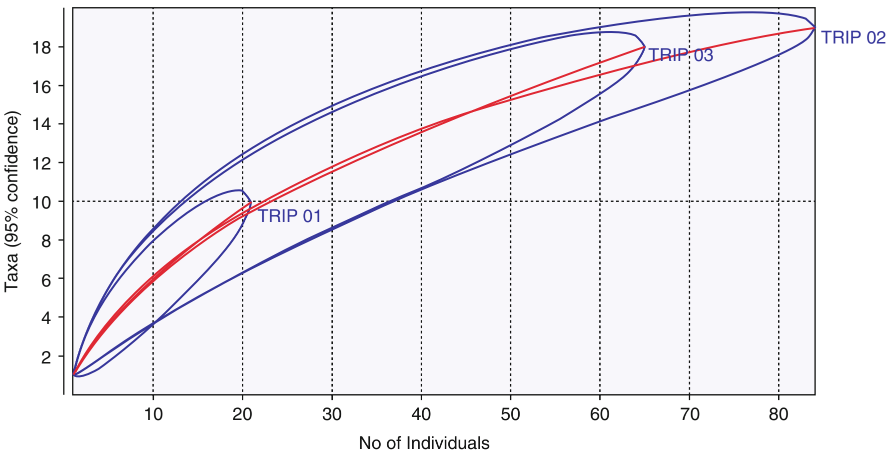

Fig. 1 Total estimated number of species captured by using aerial net in each trip at Gunung Serambu

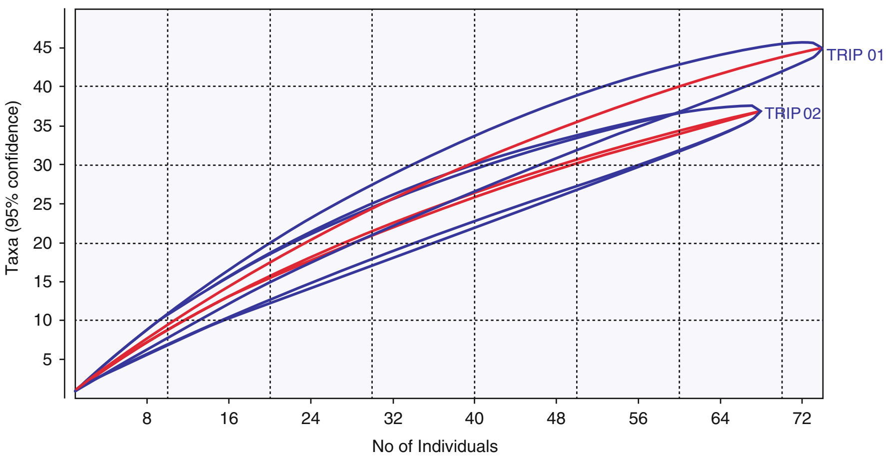

Fig. 2 Total estimated number of species captured by baited trap in each trip at Gunung Serambu

which visited to the *Clerodendron* sp., that was flowering at that time. There were also species found only during the second third trips. *Amathusia schoenbergi schoenbergi* and *Stibochiona schoenbergi*. The possible reason of the existence of these species at lower altitude area which was below 100 m ASL could be the sole food plant consumed by the larvae, *Elymnias* were only found at lower altitude.

Regardless of lack of rainfall data, there were more frequent damp weather and rainy days during the second and third trips. The higher number of both species number and individual number in the second trip can help inferred that some species were captured only on this trip. Twenty one species were found only in the second

Table 3 Comparison of males and females between nine species

	χ^2 cal	χ^2 (df = 1, 0.05)	Ho
Melanitis zitenius rufinus	0.118	3.84	Accepted
Mycalesis mnasicles mnasicles	0.383	3.84	Accepted
Neorina lowii lowii	0.300	3.84	Accepted
Ragadia makuta umbrata	0.417	3.84	Accepted
Discophora necho cheops	0.650	3.84	Accepted
Discophora sondaica symphroha	0.900	3.84	Accepted
Eurema sari sodalis	0.582	3.84	Accepted

trip. For instance, *Amathusia schoenbergi schoenbergi*, *A. ochraceofusca ochraceofusca* and *Amnosia decora buluana*. The captured-butterflies that only caught by using aerial net and only in second trip could be prefer the wetter weather or they could be simply missed by the collectors. However, the three mentioned butterflies were captured in the baited-trap indicate that their occurrence during that trip with that particular wetter condition. Nevertheless, statistical results show that the density was higher in first trip which had less rainy days.

Hamer et al. (2003) reported that a larger number of butterfly species could be sustained in logged forest than expected. The study also showed that butterfly diversity of logged forest was significantly higher than that of a primary forest during the dry season. Christharina (2011) studied the fruit-feeding butterflies in a primary forest of Kubah National Park, Sarawak and found that the number of butterfly individuals were higher in the dry season (May–July 2010) that wet season (August–November 2010).

This study suggests that despite not being a primary forest, extensive regeneration has taken place for about a century after its abandonment at Gunung Serambu (Elderly Steven Sinyun pers. comm.), and the area today serves as an important habitat for butterflies.

3.3 Sex Ratios

Comparisons of the sex between individual butterfly species reveal more males (216) than females (161). Itioka et al. (2009) saw adult males flying from primary forest to adjacent surroundings more often than adult females, indicating that males are more mobile. Despite the higher number of males, the results of the Chi-square test (χ^2) among seven selected species show that sex ratio was equal (Table 3). This is reasonable, as males and females in different family were distinctive in terms of the mating activity (Miller and Clench 1968). For example, females of subfamily Satyrinae and family Hesperiidae were reported to be active partners, while in subfamily Danainae, males were dominant in mating. Having reported this, it was assumed that the active partner would be more in number. However, the findings were not as expected. The number of the males in the mentioned families Satyrid

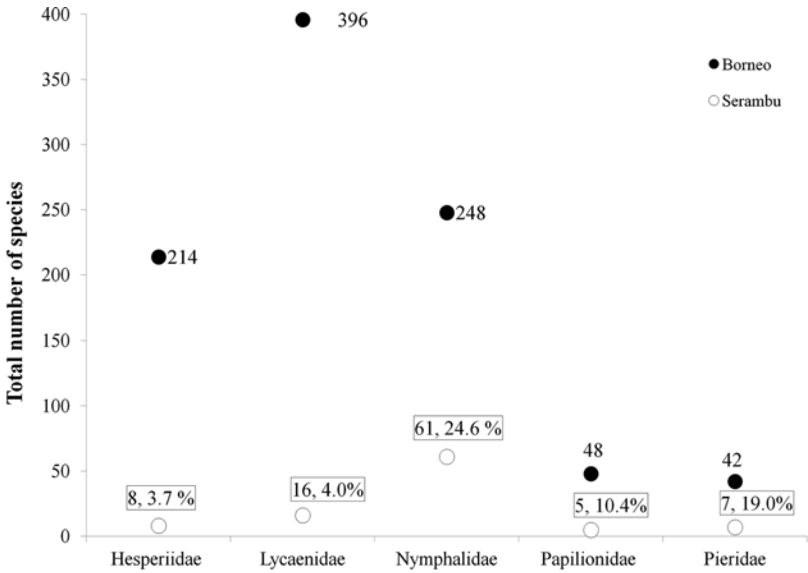

Fig. 3 Number of species of five butterfly families sampled from the Gunung Serambu in relation to the Bornean butterfly species composition (Jalil 2000)

and Hesperiids captured in this study was higher than that of females, which were 111 to 81 in the former, and eight to four individuals in the latter while in Danainae, the ratio of males to females as such six: seven. On top of that, the choice of mating time could be varied among families or even subfamilies. Overall, the mating time for butterflies were reported taking place begin in the late morning to mid-afternoon. The prolonged sampling time from morning until evening might capture not only the individuals were searching for their mating partners but also foraging butterflies.

3.4 Comparisons with Other Localities

Figure 3 compares the number of species for butterfly families collected from Gunung Serambu with the Bornean butterflies recorded by Jalil (2000). Overall, species inhabiting at Gunung Serambu comprised 10 % of the Bornean butterflies. Although Lycaenidae is the largest family (with the most number of species recorded) on Borneo, there was only 4 % of Bornean Lycaenids found in the current study. Similar to Hesperiidae, there was only 3.7 % of the total on Borneo captured at the site. Their small-body size as well as the limited number of their preferred host plants might contribute to the fact that they were not captured.

Only five species of Papilionids and eight of Pierids captured in the current study, which were 10 % and 20 % of the total species recorded on Borneo, respectively.

They were considered reasonable numbers captured as the habitat preferences are distinct among species in a family. For instance, there was no running water body found at the site which were favored by, the Rajah Brooke, *Trogonoptera brookiana* and *Graphium sarpedon luctatius* from family Papilionidae favour to be staying near to with it (Itioka et al. 2009) while *Eurema* spp. from family Pieridae was reported to favour areas with human disturbances (Tan et al. 1990). The most common Bornean species represented at Gunung Serambu was Nymphalidae. As mentioned, their fruit-feeding characteristic might be best explained the high occurrences on the site since fruit trees were abundant at the foothill of the Gunung Serambu.

In addition to the comparison with the total number of recorded Bornean species, the current collection of butterfly was compared with other well-sampled areas (see Karim and Abang 2004; Pang et al. 2004, 2009; Itioka et al. 2009; Pang and Sayok 2013). The areas included 18 Bau limestone hills, Gunung Singai and Gunung Jagoi, also in the Bau region, both known with their mixture of secondary forest and old orchard, as well as two protected areas in Sarawak, Lanjak-Entimau Wildlife Sanctuary and Lambir National Park which comprises mixed dipterocarp forest, Fig. 4 shows the overall similarity of species number captured in the current study in comparison with other studies. As expected, the species that were common among sites were Nymphalidae. Surprisingly, regardless of the similar habitat that Nymphalids inhabiting, there were less same species of the family Nymphalidae caught at Gunung Serambu with Gunung Jagoi and Gunung Singai, compared to that of found in limestone areas and dipterocarp forests. Other than that, there were more common Pieridae between Gunung Serambu and Bau limestone areas.

Covering an area of 884.4 km^2, Bau is a well-known limestone area, with at least 18 limestone hills. A comprehensive study of butterflies was conducted for 15 months (September 2001–November 2002) and yielded a total of 194 species (Karim and Abang 2004) while a rapid survey carried out near Jambusan limestone cave captured 273 individuals, comprised 86 species over five sampling days (Pang et al. 2004). *Cupha erymanthis erymanthis* and *Gandaca harina elis* are considered limestone species as they were the most caught during both studies. The absence of limestone in Gunung Serambu may explain the low capture of these two species in the current study. Likewise, the most captured species in Gunung Serambu, *Melanitis zitenius rufinus* was not found in any of the limestone areas. The low density of bamboo in those limestone areas could be the reason for the absence of this species. *M. zitenius* was known to be highly associated with bamboo. Butterfly larvae are highly specialized feeders (Karim and Abang 2004); thus the occurrence of particular host plants is crucial to the presence of adult butterflies in the area. However, 65 species are common in the areas in two studies (Karim and Abang 2004; Pang et al. 2004). It is possibly due to the flying distance of the captured butterflies that were within the areas of limestones and Gunung Serambu. The best explanation could be that their host plants exist in these areas.

Besides the settlement at Gunung Serambu, the Bidayuhs also inhabited at Gunung Singai and Gunung Jagoi; and in the same case, the mountain inhabitants have moved down to the foothills but the cultivated fruit trees remain on the mountain. Thus, the habitats in these three mountains are likely to be similar in terms of

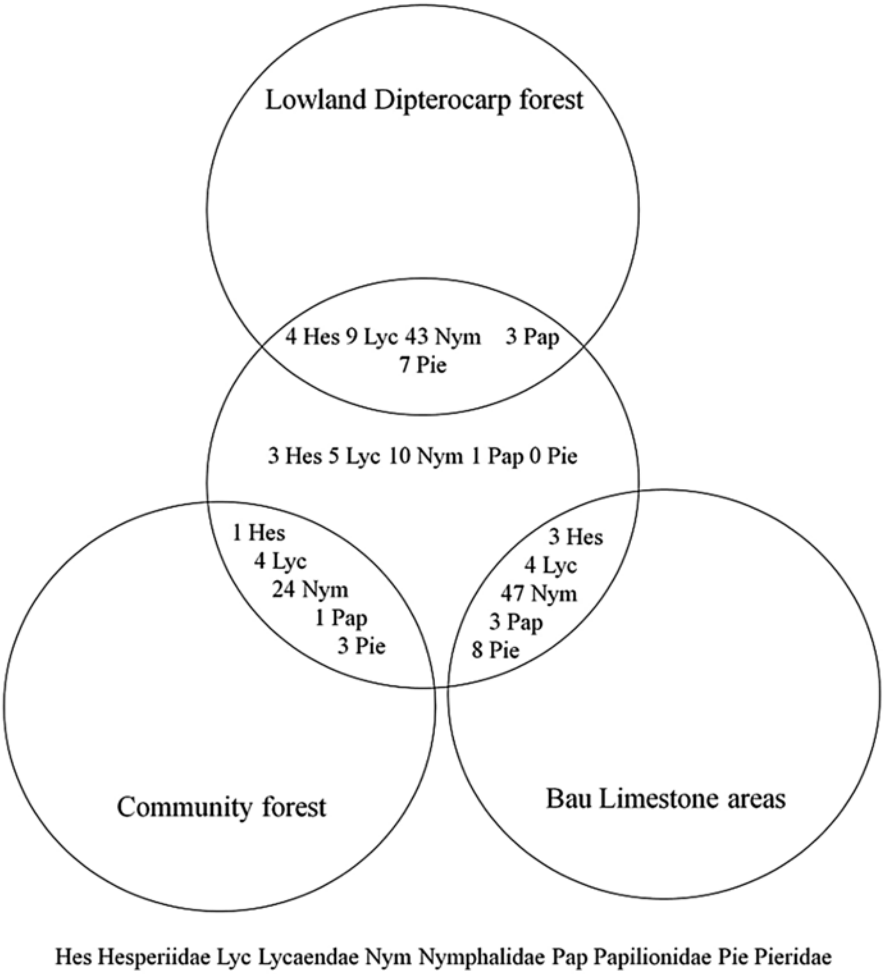

Fig. 4 Total number of species that were common among well-sampled areas. The overlapping areas indicate the number of common species between Gunung Serambu and the combined data from other sites with similar habitat. The number of five families arranged in a straight line at the center of the circle refers to the number of species discovered only in the current study

the mixture of abandoned orchard and old growth secondary forest. The other couple of butterfly surveys conducted at Gunung Singai and Gunung Jagoi (Pang and Sayok 2013). The species between Gunung Serambu and that of combined Gunung Singai and Jagoi varied despite the similarity of habitats among the areas. For example, *Cirrchoa* spp. were found at Gunung Singai and Jagoi but not in Serambu. On top of that, these sites shared the least number of common species under family Nymphalidae. Butterflies are sensitive to the changes in the surrounding (2001). It could be led by changing of the environment taken place during the oil palm cultivation carried out in the adjacent area shown above and thus drew more butterflies to settle at Gunung Serambu. In short, there were unexpectedly high number of species were housed in the secondary forest of Gunung Serambu.

It would be interesting to determine the butterfly composition in secondary forest and that of dipterocarp forest. Thus, the collection of the current study was compared with the butterflies caught at Lanjak Entimau Wildlife Sanctuary (Pang et al. 2009) and Lambir Hills National Park (Itioka et al. 2009). A total of 32 species in the current study were not found in the mentioned dipterocarp forests. For instance, all the *Neptis* spp. and rare forest-dwelling butterflies, namely *Amathusia ochraceofusca* and *A. schoenbergi* were sampled in the current study. Although Barlow et al. (2012) strongly commented that the overestimation on species richness in secondary forests compared to primary forests showed that some species sustained in the former rather than the latter.

4 Conclusions

Overall, a list 97 butterfly species were found in the current study, of which 57 are newly added to the butterfly fauna of Gunung Serambu. Thus, the two studies at Gunung Serambu have accumulated a combined number of 110 species. With the total of 61 species and 303 individuals, Nymphalidae appeared to be the most common family at Gunung Serambu. This was followed by the families Lycaenidae, Pieridae, Papilionidae and the least common family, Hesperiidae. No significant difference was found between the captured number of males and females. Despite more individuals captured at lower elevation, the butterfly diversity was slightly lower here compared to that at higher elevation. At the same elevation, the diversity of butterflies was lower during the second trip than that of the first trip, regardless of the higher captured number of species and individuals. The increase in the number of species collected from the current study indicates that additional species in Gunung Serambu may be discovered.

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The Distribution of *Buceros rhinoceros* and Awareness of Its Conservation Status

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Abstract A rapid survey on the distribution of hornbills in Santubong National Park, Sarawak, East Malaysia, was carried out in April 2013 using point sampling technique at various locations around the park. Only the Rhinoceros hornbill, *Buceros rhinoceros*, was recorded, with a total of 45 independent calls and 15 observations at 10 locations around the protected area, mostly during early mornings and late evenings from 162 h of survey. Most of Rhinoceros hornbills were observed in pairs (73 %), while a single observation recorded at least ten individuals at a location. Additionally, local communities were interviewed to collect information on the occurrence, status, ecology and perception on Hornbill conservation in Santubong National Park. A standard questionnaire was designed to meet the purpose of this study. This survey was conducted on local communities from five local villages around Santubong National Park, local and international tourist visiting touristic areas in Santubong peninsula. In general the awareness on the conservation needs and status of the hornbill is high suggesting that the communities are interested and supportive of conservation related activities. Based on the socio-economic and ecological survey, the surrounding habitat of this protected area need to be protected through park extension that will increase connectivity between nearby forest patches which in turn may ensure the long term viability of the Rhinoceros hornbill in Santubong National Park.

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1 Introduction

Sarawak constitutes approximately 17 % of Borneo, the third largest island in the world, that covers 746,337 km^2 and supports one of the richest assemblages of flora and fauna in Sundaland. A substantial proportion of Sarawak's wildlife is endemic to Borneo. This includes approximately 19 % of mammals (5 % of 98 bats species, 5 primates, 3 carnivores, 21 rodents and 2 large mammals), 20 % of snakes and 6 % of birds.

The family Bucerotidae represents the Asian Hornbills, consisting 54 species (Kemp 2005). Sarawak boast eight species of hornbills (15 % of the species), namely, Bush-crested hornbill, White crowned hornbill, Wrinkled hornbill, Wreathed hornbill, Black hornbill, Pied hornbill, Rhinoceros hornbill and Helmeted hornbill. Among these species, the Rhinoceros hornbill is regarded as Sarawak's state bird, and appears in the State's coat of arms. This species is also important in local culture, being part of ceremonies, folklores, legends, and beliefs (Bennett et al. 1997). The male Rhinoceros hornbill has reddish orange irises while the female whitish, with the tip of the casque curving upwards. This species can be easily identified in flight as it has a white tail with a black band.

Hornbills are excellent seed dispersers in tropical rainforest where declines of these species have affected large seeded tree species in this region (Chaisuriyanun et al. 2011; Kitamura 2011; Kitamura et al. 2011, 2008). Whereas isolated and fragmented forests created by logging activities alongside with illegal hunting of hornbills have caused major decline for these species in this region (Bennett et al. 1997; Poonswad et al. 2005).

This species is considered Near Threatened, according to the IUCN Red List (2015) and listed as Totally Protected in Sarawak in accordance to Sarawak Wild Life Protection Ordinance 1998, whereby offenders are liable to a fine of 25,000 Malaysian Ringgits (RM) and imprisonment for 2 years. In Peninsular Malaysia, this species also receives totally protected status under the Wildlife Conservation Act 2010, whereby offenders are liable to a maximum of 100,000 RM fine or imprisonment for a term not exceeding 3 years or both. In Sabah this species receives only Protection status where a maximum fine of 50,000 RM or imprisonment for 5 years or both. The Rhinoceros hornbill is listed in CITES Appendix II since 1990 which restricts international trade.

This large bird has a historic distribution from southern Thailand and Peninsular Malaysia, to the islands of Sumatra, Java, Borneo; the species is thought to be extinct in Singapore. This species have been recorded in tall secondary forest, mixed dipterocarp forest and swamp forest (Bennett et al. 1997; Kitamura et al. 2011; Poonswad et al. 2005). Past surveys in Santubong National Park have recorded Rhinoceros hornbill but little is known of its distribution in this protected area.

Despite the fact that the species is threatened and recognized as the State bird, little is known on its population ecology and distribution in Sarawak. Therefore a systematic study combining secondary information and field observation was initiated in Santubong National Park to identify the distribution of hornbills and to understand the perception and conservation awareness of the community. The major reason for use of interview surveys are the perceived time and cost savings and to provide a direct forum to discuss conservation issues with local communities (Mohd-Azlan et al. 2013).

2 Materials and Methods

2.1 Study Site

Gunung Santubong National Park, situated in the Santubong Peninsula, was gazetted as a National Park in 2007, and has an area of 14.1 km^2. The Park is covered mainly by mixed dipterocarp forest with patches of Kerangas and beach forest, with a mountain peak of 810 m above sea level. It is partly surrounded by privately owned forest. Santubong peninsula is a popular tourist spot among local and foreign visitors. The attractions in Santubong Peninsula include several Malay fishing villages (Kampung Santubong, Kampung Buntal, and Kampung Pasir Pandak), Sarawak Cultural Village, golf courses, Permai Rainforest Resort and the adjacent beach resort area.

2.2 Survey and Analyses

Field surveys were carried out by students and staff from the Department of Zoology, Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, the Protected Area and Biodiversity Conservation Unit of the Sarawak Forestry Corporation and Permai Rainforest Resort in Santubong National Park for a duration of 4 days from 5 to 9 April 2013. The survey used the point sampling technique, areas being strategically identified to cover as much ground as possible within the boundaries of the protected area. Observers were stationed at four to six localities simultaneously throughout the day to observe bird activities and to record calls. The date, time and GPS position where an observation and calls of hornbill were recorded. These data were later compared and scrutinized to remove similar observation and calls.

The survey on local community's perception and awareness was conducted around the protected area. This survey adopted a face-to-face interview of local communities from five local villages around Santubong National Park- Kg. Santubong (17 %), Kg. Buntal (12.7 %), Kg. Lumut (8 %), Kg. Pasir Pandak (13 %) and Kg. Pasir Panjang (3.7 %), local (40.1 %) and international tourists (5.6 %) visiting the Damai Central and Permai Rainforest Resort. The questionnaire was intended to gather information including, socio-economic characteristics, awareness and conservation of hornbills in Santubong National Park from respondents. All analysis was conducted using Statistical Package for Social Sciences (SPSS) version 21.0.

3 Results

A total of 162 h of observation from six different locations around Santubong National Park (Teluk Arang, Putri trail, Teluk Belian, Tanjung Salih, Teluk Kerangan, Red and Blue trails) translates to an average of 7.6 h surveyed per day. During this survey at least 81 species of birds including both observations and calls of the Rhinoceros hornbill were recorded. A total of 45 independent calls and 15 observations of Rhinoceros hornbill were recorded at 10 locations (Fig. 1).

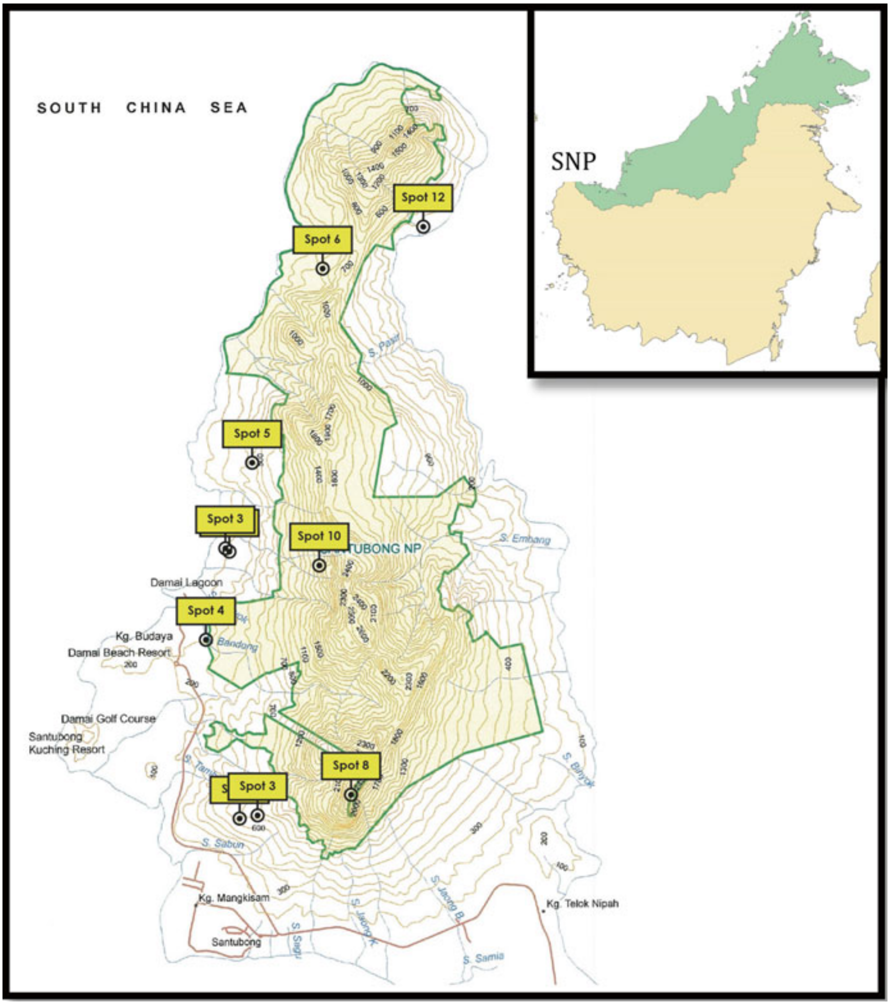

Fig. 1 Locations of Rhinoceros hornbill at Gunung Santubong National Park, Sarawak, during surveys from 5 to 9 April 2013

Peak observations and calls of the Rhinoceros hornbill were recorded during early mornings and late evenings. Most of Rhinoceros hornbills were observed in pairs (73 %), which suggest breeding season, while a single observation recorded at least ten individuals flying towards a lower elevation from Puteri trail (Fig. 1, Spot 9).

An observation of ten individuals on nearby fig tree suggesting breeding season during the survey period. A total of 323 respondents comprising 187 males (57.9 %), 136 females (42.1 %) were interviewed from various locations surrounding the protected area. Majority of the respondent were local resident (54.3 %). Most respondents had some form of formal education while only 6.5 % did not have any exposure. Respondents were mostly employed (75.6 %) and in most cases provided reliable answers, while there are several cases of unwillingness to participate in this survey. Average age of the respondents are 40.3 years old (SD = 16.3) where the majority of the respondent were from the age category of 21–40 years old (45.7 %) with a small proportion of elders aged 60 years old and above (12 %) (Table 1).

Most of the respondents felt that hornbills are synonymous with Sarawak (88.6 %), and has helped create a distinct image of the State. Most respondents felt that hornbill conservation is important because it serves as Sarawak's emblem (89.2 %) and can act as an umbrella species, whereby the protection of hornbills will help to protect other habitats and species (77.2 %), besides being a major attraction in the State (85.5 %).

Approximately 82 % of the respondents know that the hornbills are protected in Sarawak and 74 % acknowledges that it is illegal to trade hornbills or any of its parts, while 82 % understand the fact that it is illegal to hunt and keep them as pets, which suggest that a majority of the local communities are aware of related legislation.

Anecdotal reports from several elderly correspondents confirm the presence of at least seven species in the late 1940–1950s in that area. Only two of the respondents surveyed have eaten at least one species of hornbill in the past, while some of the younger respondents do not even know that hornbills exist in the area. More than 90 % of the respondents, mostly from younger generation, have not seen White crested, Bushy crested, Wrinkled, Wreathed, Black, Pied and Helmeted hornbill in this area. The only commonly reported species was the Rhinoceros hornbill (49 %), which was most frequently observed in the Santubong area (54.3 %). Most of these observations were of single individual (65 %) while the remaining records were of small groups. However, 47 % of the respondents feel that it is difficult to see a hornbill in the rainforests while 34 % think otherwise. Absence or small populations of other hornbill species in the Gunung Santubong National Park may be a reason why a majority of respondents only observed Rhinoceros hornbills. These reports are consistent with our field surveys, and suggest that hornbill identification by the local community is reliable.

Almost two-thirds (over 60 %) of the respondents somewhat agree that hornbills are threatened in Sarawak, while a small proportion think that it is not (17 %). Similarly, slightly more than half (54 %) of the respondents think that hornbills will become extinct if no conservation measures are taken, while 20 % think that horn-

Table 1 Socio-demographic profile of respondents interviewed around Gunung Santubong National Park, Sarawak

Variables	Categories	Frequence	Percent	Variables	Categories	Frequency	Percent
Gender	Male	187	57.7	Occupation	Unemployed	79	24.4
	Female	137	42.3		Self-employed/business	130	40.1
	Total	324	100.0		Public sector	34	10.5
Age group	20 years old and below	28	8.6		Private sector	38	11.7
	21–30 years old	92	28.4		Others	43	13.3
	31–40 years old	56	17.3		Total	324	100
	41–55 years old	81	25.0	Origin	Locals (Santubong, Buntal, Pasir Pandak)	176	54.3
	56–60 years old	28	8.6		Kuching	31	9.6
	Above 60 years old	39	12.0		Other places in Sarawak	62	19.1
	Total	324	100.0		Sabah	5	1.5
Income group	Below RM 800	192	59.3		Peninsula Malaysia	32	9.9
	RM 801–1000	45	13.9		Other countries	18	5.6
	RM 1001–1500	41	12.7		Total	324	100.0
	RM 1501–2000	17	5.2	Education level	No formal education	21	6.5
	RM 2001–5000	23	7.1		Primary school	60	18.7
	Above RM 5000	6	1.9		Secondary school	171	53.3
	Total	324	100.0		Diploma, etc	37	11.5
					University	32	10.0
					Total	321	100.0

bills are not in any danger. In relation to this, 29 % of the respondents do not feel that the existing protected areas will protect hornbills, while 32 % think that it is adequate.

Besides, over 80 % of the respondents feel that seeing hornbills in the wild gives them a satisfying experience and it is their responsibility to protect them for future generations (88.6 %) through financial aid (80 %) and most are willing to donate (73.8 %) and participate in volunteering programs (74 %) for conservation purposes in Sarawak. This indicates that most respondents, especially local communities, are concerned and willing to support effort towards conservation and protection of hornbills in the Santubong Peninsula. Many people feel that stiffer penalty (81 %) and more strict law enforcement (86 %) will enhance the protection of hornbills in Sarawak. Respondents are supportive of intensifying law enforcement and engaging deterrent punishment to ensure better protection of the hornbills in Sarawak. Similarly, 86 % of the respondents think that it is important for the related departments to organize programs to educate local residents and visitors to understand and support hornbill conservation in Sarawak. Essentially, there is a need to ensure and enhance effective dissemination of knowledge on conservation of hornbills in Sarawak to local communities and visitors. Eighty-seven percent of the respondents agreed that hornbill conservation in Santubong National Park would generate income through ecotourism industry and provide employment opportunities to local residents.

4 Discussion

The secondary information gathered from the interview survey appears to be reliable and consistent with the field survey. Throughout the survey only one species of hornbill, Rhinoceros hornbill was identified despite our intensive sampling. Even though the Black hornbill was reported in this area (Rahim Bugo pers. com.) it was not recorded during this survey suggesting that this species may occur at very low densities or may have become locally extinct.

Each breeding pair of Rhinoceros hornbill have been reliably estimated with a home range of 2.3 km^2 (Leighton 1986). Based on this it can be conservatively estimated that Santubong National Park could potentially accommodate only six breeding pairs. Given the fact that isolated and fragmented forest patches may not support hornbills over a long period of time, the viability of Santubong National Park to support populations of Rhinoceros hornbill in perpetuity is of question. Therefore protection of large tracts of adjacent forest patches including secondary and degraded forest within the ranging distance of this species from Santubong National Park need to be protected.

According to elders from the local community around the area, at least seven species of hornbills were frequently seen at the Santubong Peninsula, including along Santubong river. However, only the Rhinoceros hornbill was reported by local communities and visitors during our interviews. These suggest that Santubong Peninsula provides suitable habitat to support Rhinoceros hornbill and this species is relatively tolerant to fragmentation compared to other hornbills, which was previously thought to exist in this area.

In reality, accelerated land conversion to agriculture, agro-forestry and urban development has confined the residual biodiversity to protected areas and human-modified or secondary habitat (Mohd-Azlan and Lawes 2011). With protected areas being fragmented and isolated, even minor threats to these areas could potentially have large impacts on hornbills. The ability of hornbills to persist within such remnants is an issue of concern. Based on past and present experience, a decisive approach to conserving the remaining population hornbills throughout Sarawak is urgently needed. Therefore further studies are required to understand the population dynamics of hornbill in protected areas for long-term conservation and management. Restoration of degraded habitat around protected areas to increase connectivity between protected areas, which will allow movement of hornbills, is important to sustain a viable population.

Most local residents and visitors in Santubong Peninsula acknowledges the importance of hornbill conservation and are supportive of effort and programs on conservation of hornbills. Likewise, majority of the local residents and visitors are aware of laws and regulations pertaining to protection and conservation of hornbills in the State. Furthermore, the majority of local residents and visitors also realized socio-economic contribution of tourism. Precisely, this explained that empowering local residents through ecotourism is regarded as a useful tool to effectively foster environmental conservation (Amat and Abdullah 2004). Moreover, the relationship between ecotourism development and conservation in Santubong Peninsula is seen to reflect a symbiotic relationship (Budowski 1976) and potential appropriate use of environmental resources (Butler 1991).

Although the majority of local residents and visitors are aware of the importance of conserving hornbills, many feel the need to further embark on programs such as awareness campaigns and conservation exhibition, and activities including interpretative talks and tours, to better educate local residents and visitors. Obviously, this is considered a vital strategy to impart knowledge to obtain wider support and to further enhance effective conservation and protection of hornbills in the Santubong peninsula.

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Identifying Habitat Characteristics and Critical Areas for Irrawaddy Dolphin, *Orcaella brevirostris*: Implications for Conservation

Cindy Peter, Anna Norliza Zulkifli Poh, Jenny Ngeian, Andrew Alek Tuen, and Gianna Minton

Abstract Irrawaddy dolphins, *Orcaella brevirostris*, in the Kuching Bay, Sarawak, Malaysia have been subjected to pressure from cetacean-fisheries interactions, dolphin watching tourism and coastal development. However, very little information is known about their ecology and factors driving their habitat preferences. To obtain critical information on the distribution, habitat preference and range pattern of Irrawaddy dolphins in Kuching Bay, Sarawak, systematic boat-based surveys were conducted between June 2008 and October 2012. The results showed a statistically significant relationship between Irrawaddy dolphins' distribution and different categories of salinity, tide levels and distance to river mouths. Kruskal-Wallis tests confirmed that the presence of Irrawaddy dolphins in Kuching Bay had statistically significant relationships to habitat parameters of salinity (chi-square = 4.694, $p = 0.03$). Fisher's exact test indicated that Irrawaddy dolphins were statistically more likely to be present in waters within a 6 km radius of river mouths. The distribution of dolphins was also affected by tide levels as Mann-Whitney *U*-tests proved a statistically significant difference in dolphin distribution between tide levels lower than 2.0 m and tide levels higher than 2.0 m ($p = 3.153 \times 10^{-11}$). The representative range and core area of photo-identified Irrawaddy dolphins estimated using fixed kernel range was 246.42 km^2 and 37.22 km^2, respectively, with core area located in the Salak Estuary. The results obtained in this study reflect dry season distribution only, and may differ during the wet season. Nonetheless, these results highlight the

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importance of shallow coastal waters and the overlap of Irrawaddy dolphin critical habitat with that of human activities in Kuching Bay. Conservation efforts are required to minimise the effects of the pressures exerted on these animals and their habitats.

1 Introduction

Baseline data on animal distribution, habitat preference and range patterns are critical for effective conservation and management, providing answers to the basic questions of "where do they occur?" and consequently "which areas require protection?". This is particularly important in areas where coastal development is taking place or is planned in the near future. The monitoring of distribution, habitat use and abundance before, during and after development can help scientists and managers to quantify the impacts of these anthropogenic activities to the animal populations (e.g., Dähne et al. 2013).

The Kuching Bay in Sarawak, East Malaysia is home to at least four cetacean species including the Irrawaddy dolphin (*Orcaella brevirostris* Owen in Gray 1866), Indo-Pacific finless porpoise (*Neophocaena phocaenoides* Cuvier 1829), Indo-Pacific humpback dolphin (*Sousa chinensis* Osbeck 1765) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus* Ehrenberg 1833) (Minton et al. 2011, 2013). The mangrove forest, river networks, and coastal area surrounding the Kuching Bay are of economic importance, supporting activities such as gillnet fishing, aquaculture and tourism (including dolphin watching) (Ling et al. 2010; O'Connor et al. 2009). Major development taking place includes an 8 km long flood mitigation channel, currently under construction and scheduled to be operational by 2015. The channel is designed to direct floodwater from the city of Kuching into the Salak River, therefore alleviating the flooding problems during monsoon (Mah et al. 2012), but also introducing enormous quantities of freshwater possibly tainted by urban waste and discharge into core dolphin habitat. Gillnet fishing, aquaculture, dolphin watching, freshwater influxes and coastal runoff/pollution have all been identified as threats to estuarine and coastal cetacean populations worldwide (DeMaster et al. 2001; Bejder et al. 2006; Currey et al. 2009; Fury and Harrison 2011).

Boat-based surveys conducted from 2008 onward have provided baseline information on the distribution of small cetaceans (Minton et al. 2011) and population estimates for the Irrawaddy dolphin and finless porpoise (Minton et al. 2013) in the Kuching Bay. However, to accurately manage and protect this population there is a need to fully understand the factors that influence their habitat requirements on a finer scale. This paper aims (1) identify critical areas of Irrawaddy dolphin habitat in Kuching Bay by calculating the core area and representative ranges using fixed kernel method, and (2) better to understand the factors driving these habitat preferences.

2 Methods

2.1 *Study Area*

The survey area, defined as the “Kuching Bay” due to its proximity to the city of Kuching, the capital of Sarawak, East Malaysia, actually includes a wide area ranging from the Bako Peninsula on the east to Rambungan River on the west and extending up to 15 km north to include Satang Island (Fig. 1). Major rivers flowing into the bay include the Bako River, Buntal River, Santubong River, Salak River, Sibu Laut River and Rambungan River. The bay is generally shallow with a maximum depth of 10 m as far as 15 km from shore, while some river channels are more than 10 m deep with a maximum depth of 23 m recorded at Telaga Air during high tide. Salinity in the study area ranges from approximately 27 PSU in rivers and estuaries to 33 PSU in the offshore areas, while pH ranges from 7.4 to 8.8.

One of the main beaches in Kuching Bay is half way along the west coast of the Santubong Peninsula, a hotspot for both locals and tourists. There are five resorts located along the beach as well as homestay facilities in some of the fishing villages and a golf course. The study area includes portions of the Kuching Wetlands

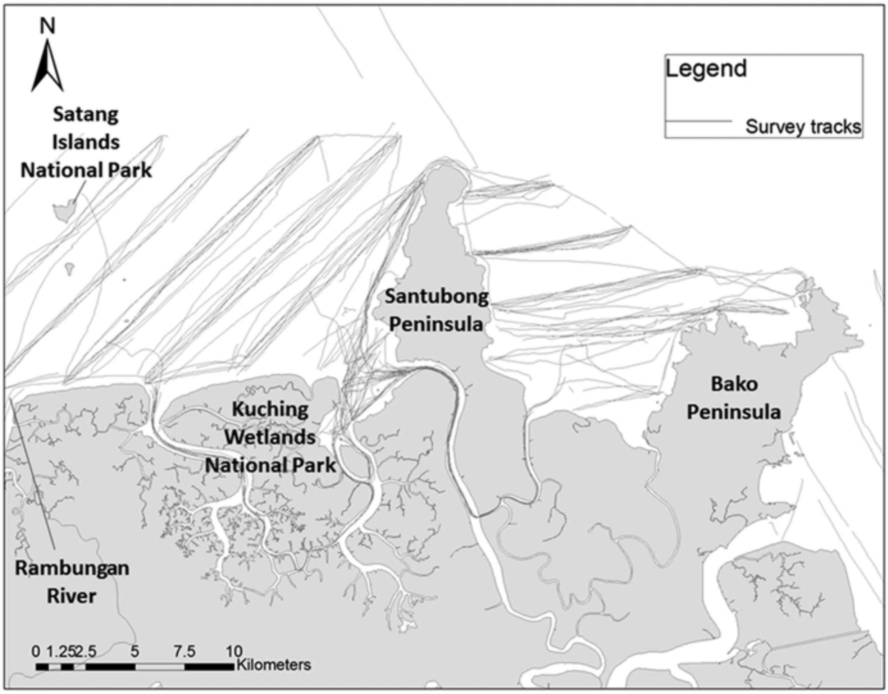

Fig. 1 Study area in Kuching Bay, showing the boat-based survey transects (on-effort portion), running ca. 45° parallel to the nearest coastline

National Park on the west side, the Talang-Satang Marine National Park approximately 10 km offshore and Bako National Park on the east. Mount Santubong National Park is located on the Santubong Peninsula.

2.2 Data Collection

Line transect surveys were conducted from March–October in 2009–2012. Surveys were conducted using open decked, fiberglass-hulled boats that ranged from 7 to 10 m-long, with double outboard engines ranging from 90 to 115 hp. Surveys followed pre-determined parallel transects in the areas along the coasts of the Santubong and Bako peninsulas with occasional surveys along the coast of Kuala Rambungan (Fig. 1). Transects extended up to 15 km offshore with a distance of 4 km between the consecutive transects. Line transects were designed to run approximately at 45° to the coast. This design allows for detection of cetacean density gradients along-shore as well as onshore/offshore (Dawson et al. 2008). Surveys were also carried out in the rivers and channels that were interconnected during all tidal states. Boats were navigated down the centre of the river.

Transects were navigated at a steady speed of 15 km per hour (eight knots). At least two experienced observers were always onboard, while supporting observers had varying degrees of experience. Observers alternated searching with the naked eye and 7 × 50 binoculars with a built-in compass, with each observer scanning arcs of approximately 100° from just past the centre line to 90° to starboard and port (e.g., Buckland et al. 2001; Parra et al. 2006). The eye-height of the observers to the water line was between 2.5 and 3.5 m.

Positional data for survey tracks and dolphin sightings were collected using a handheld GPS unit. Effort was recorded to the nearest minute to distinguish between time spent searching (on-effort), fast transits to or from the start and end points of transect lines, working with cetacean groups, fueling or meal breaks (all off-effort). Beaufort scale (as an indicator of sea conditions), swell height and visibility were recorded on each transect leg and at the end of each sighting, or upon noticeable change. Search effort was suspended during heavy rain and/or when the Beaufort scale reached 4 or higher.

Whenever splashes, blows or dark figures similar to dorsal fins or backs were spotted, search effort was suspended and observers went off-effort to confirm the sightings. Once a sighting was confirmed, the boat then left the transect to approach the sighted group and collect data on group composition, group size and behaviour following standardized data collection methods (e.g., Jefferson 2000; Parra 2006).

Water parameters were sampled at the start, midpoint and end of each transect leg. Readings of water temperature, pH, salinity and turbidity were taken using a YSI 6820V2 meter. Readings were also taken at the location of each dolphin sighting. Photographs of the dolphins' dorsal fins were taken using digital SLR cameras with 70–300 mm zoom lenses. Attempts were made to approach the animals as closely as possible without disturbing their natural behaviour and to position the boat so that photos of the left of right sides of dorsal fins could be taken from a perpendicular angle to the animal. Following Wursig and Jefferson (1990), we attempted to "take at random as many photos as possible of members of the group within constraints of time and budget". The photographs taken were not only used for range pattern analysis, the photographs were also used to estimate the population of Irrawaddy dolphins in Kuching Bay as described in Minton et al. (2013).

2.3 Data Analyses

2.3.1 Habitat Characteristics

Although boat surveys were conducted between 2008 and 2012, the habitat characteristics analysis of Irrawaddy dolphins in this paper was only carried out for the data collected from 2009 to 2010, whereas the range patterns analysis were only carried out for the data collected from 2008 to 2012.

The GPS locations of observed dolphin groups were downloaded at the end of each day using DNR Garmin® and plotted in ArcMap®. All the water sampling stations were compiled and overlaid with on-effort sightings on ArcMap®. Readings taken at all water sampling station during start, midpoint and end of each transect as well as locations of dolphin sightings while on effort were included in the analysis. Only on-effort sightings were used to avoid the bias that might be introduced by including sightings made while speeding close to shore to the start and endpoints of the transects. Each water sampling station was assigned a value of "Presence" or "Absence". A station was assigned presence (value of 1) when an Irrawaddy dolphin sighting fell within a 600 m radius of the recorded location on the same day that sampling took place. Otherwise it was assigned absence (value 0). This radius was chosen based on field experience. When working with a group of dolphins, the maximum distance they traveled during an encounter was generally 500–600 m from the original location where they were first sighted.

Values for physical characteristics like depth, distance to river mouth and distance to land were assigned to each of the sampling stations ex situ. Depth values were obtained from ArcGIS compatible rasters of British Admiralty charts purchased from and issued by Seazone®. Digitized bathymetry points were generated by manually assigning depth values to each depth point on the chart, and various functions were tested to determine the "best fit" model for interpolating depths in the study area between the known depth values of the chart. The function chosen was Inverse Distance Weighted (IDW) with 1 km grid size.

These interpolated values were used to assign depth values to all water sampling stations since a depth sounder was initially not available on the research vessel. In some instances where the depth was less than 7 m, the depth could be recorded in situ because the YSI meter, which has a maximum cable length of 7 m and had depth sensors on the instrument would reach the sea floor. Distance to river mouth was measured using Google Earth by creating a fixed mid-point in the line connecting two corners of a river mouth and measuring the distance of the sampling stations to

Table 1 Results of Kruskal-Wallis testing for the statistical significance on different parameters for stations with Irrawaddy dolphin present vs absent

Parameters	Chi-square	p-value	df
Temperature	1.077	0.299	1
pH	1.107	0.293	1
Depth	0.513	0.474	1
Distance to land	1.861	0.173	1
Salinity	4.694	0.03	1
Distance to river mouth	5.060	0.02	1

Table 2 Results of Fisher's exact testing for the statistical significance of the stratification range in depth, salinity and distance to river mouth with the distribution of presence or absence of Irrawaddy dolphins

Parameter	Bin stratifications	Number of present	Number of absent	P value of Fisher's exact test
Depth (m)	0–2.99	13	92	0.105
	3–5.99	11	53	
	6–8.99	5	1	
	9–14.6	40	42	
Salinity (PSU)	25–27.99	2	8	0.066
	28–30.99	15	70	
	31–33.99	9	80	
	34–35.99	4	69	
Salinity (PSU)	25–30.99	17	78	0.026
	31–35.99	13	149	
Distance to river mouth (km)	0	5	26	0.033
	0.036–2.99	9	59	
	3–5.99	9	40	
	6–8.99	5	32	
	9–14.32	2	70	
Distance to river mouth (km)	0.00–5.99	23	125	0.033
	6.00–14.32	7	102	

this midpoint. Sampling locations upriver were assigned a value of "0". All the physical and water characteristics parameters were stratified into bins of three units (e.g. 0–2.99 m, 3.00–5.99 m for depth; 25–27.99 PSU, 28–30.99 PSU for salinity, 0.1–2.99 km, 3.0–5.99 km for distance to river mouth) (Table 2).

The dataset of all parameters in Table 1 were tested for normality using Shapiro-Wilks test. The test showed a non-normal distribution for all habitat parameters for both presence and absence grouping, therefore the non-parametric Kruskal-Wallis tests were used to determine which parameters would be statistically significant in relation to the presence or absence of dolphins. The Fisher's exact test was then used to pinpoint the range of values of the parameters that affect the distribution of presence or absence of the dolphins.

Following the statistical analysis, the effects of tidal movement and currents on dolphins' distribution were investigated by plotting the distribution of sightings according to the tidal state at the time of sighting. The Shapiro-Wilks test showed that the sightings were not normally distributed in relation to the tide levels at tide levels of 2.0 m or lower and higher than 2.0 m. Hence the non-parametric Mann-Whitney *U* test was used to test whether the tide levels affect dolphin distribution.

2.3.2 Range Pattern

The term 'range pattern' was used instead of 'home range' due to the fact that the sightings data are only restricted to the study area and dolphins may have ranged outside of the study area. Range pattern was determined using fixed kernel estimation. Fixed kernel produces a probability distribution that describes an animal's home range based on the distribution of its observed locations (Worton 1989) and can also be used at the population level to determine critical areas or areas of high use (e.g., Ingram and Rogan 2002; Parra 2006). Sighting locations for groups of Irrawaddy dolphins were used to determine their ranging pattern. Whenever the same group of dolphins were encountered and photographed more than once in the same survey day, only the first sighting point was taken into account in order to minimize statistical dependence among sighting points.

A shape file (.shp) containing sighting data points was created and the range pattern for the Irrawaddy dolphins with the fixed kernel estimation method was calculated using Geospatial Modelling Environment (GME) version 0.7.2.1 (Beyer 2012). The least-squares cross-validation (LSCV) soothing parameter was chosen because it focuses on the area with the greatest intensity of use, therefore producing a more realistic contour (Worton 1989). Isopleths or utilization distribution (UD) contours of 95 % and 50 % of the ranges calculated were generated using the command '*isopleth*' in GME. The 95 % UD is considered to be the representative range of the species within the study area while the 50 % UD is identified as the core area. As dolphins clearly do not use land, any landmasses included in the kernel estimation were eliminated using the '*erase*' function in ArcMap.

3 Results and Discussion

3.1 Habitat Characteristics

Water samples were collected on 257 occasions, of which 30 had dolphins present and 227 absent. The mean and standard deviation readings for all the parameters from 30 stations of dolphins' present category were as follows: temperature 30.42 ± 0.61 °C (mean ± SD), salinity 31.19 ± 2.26 PSU, pH 8.11 ± 0.19, depth 4.17 ± 2.40 m, distance to river mouth 3.74 ± 3.42 km and distance to land 1.76 ± 1.95 km. Kruskal-Wallis tests confirmed that the presence of Irrawaddy dol-

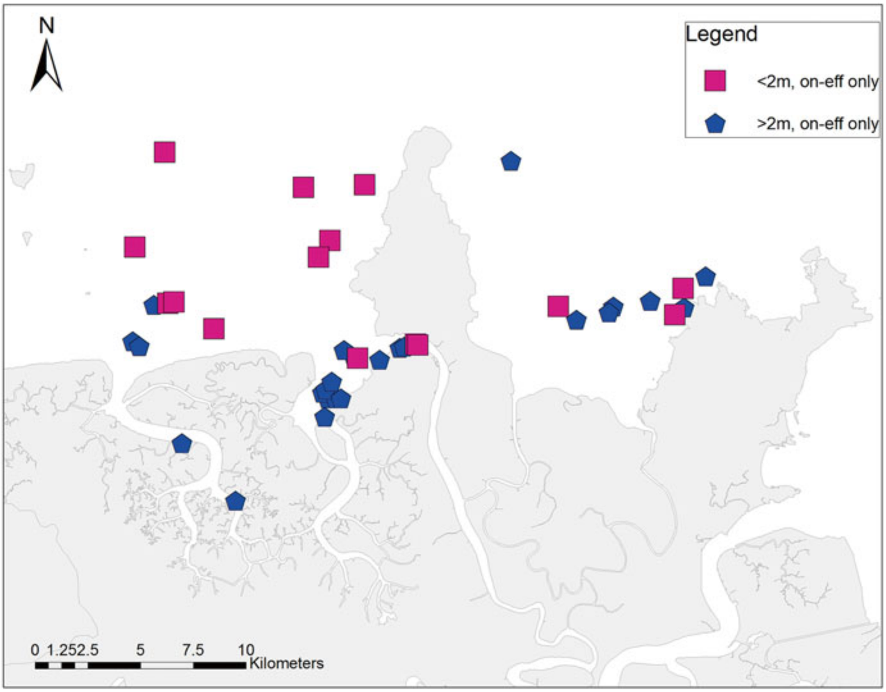

Fig. 2 On-effort sightings of Irrawaddy dolphins with in tidal states higher than 2.0 m vs. lower than 2.0 m. Note that this represents sightings made during 2009–2010

phins in Kuching Bay had statistically significant relationships to habitat parameters of salinity and distance to river-mouth, with chi-square = 4.694 and p-value = 0.03 (Table 1).

Conversely, Fisher's exact test on salinity revealed that the categories approached significance (p = 0.066) whereas for distance to river mouth there was a significant difference (p = 0.033). When distance to river mouth was re-stratified into two equal bins of 0–5.99 km and 6.00–14.39 km, Fisher's exact test yielded a significant result (p = 0.03), indicating that Irrawaddy dolphins are statistically more likely to be present in waters within a 6 km radius from river mouths than beyond that radius. Similarly, when salinity was restratified into two bins of 25–30.99 PSU and 31–35.99 PSU, the p-value of Fisher's exact test is 0.026.

There were 15 on-effort sightings of Irrawaddy dolphins made when the tide levels were 2.0 m or lower and 26 on-effort sightings at tide levels higher than 2.0 m (Fig. 2). In the Salak-Santubong bay, sightings that occurred in tidal states of less than 2.0 m were distributed predominantly in the nearshore areas and in the river mouth while sightings at tide level higher than 2.0 m occurred primarily in the river mouth and upriver. In the Bako-Buntal bay, sightings in both tidal states occurred almost exclusively near the Bako National Park except one sighting that occurred nearer to the tip of the Santubong peninsula. The on-effort sighting locations for tide level less than 2.0 m and more than 2.0 m were tested for normality using Shapiro-Wilks normality test. The test result indicated that the sighting locations were not normally distributed in relation to the tide levels. Hence the non-parametric Mann-Whitney *U* test was used to test whether the tide levels affect dolphin distribution. Irrawaddy dolphin distribution was found to be statistically significant between tide levels lower than 2.0 m and tide levels higher than 2.0 ($p = 3.153 \times 10^{-11}$).

The habitat characteristics selected by Irrawaddy dolphins in Kuching Bay reported here are similar to descriptions from other populations in the region that are known to occur in shallow waters of low salinity and high turbidity (Dolar et al. 1997; Smith et al. 2006, 2008). Whilst similar, this adds to the pool of knowledge specifically for this population of Irrawaddy dolphins in this particular region. The physical characteristic which appears to be the driving factor of the dolphins' habitat choice is distance to river mouth with 76 % of the dolphins' distribution occurring within 6 km of the river mouth and the 50 % core area delineated around the Salak river-mouth. Irrawaddy dolphins as well as other coastal cetaceans such as humpback dolphins (e.g., Lin et al. 2013), harbour porpoises (e.g., Embling et al. 2010; Booth et al. 2013) and common bottlenose dolphins (e.g., Mendes et al. 2002) are known to move in relation to tidal states. Tidal state also links the dolphins' distribution with their surroundings, as they seem to follow the interface between riverine and saline coastal waters, occurring inshore during high tides and further offshore during lower tides. This shows that the river mouth affiliation could be driven more by water flow and tidal currents and its possible effects on prey abundance than salinity or depth.

It is widely believed that prey availability is the main factor driving habitat choice of cetaceans (Baumgartner et al. 2001; Hastie et al. 2005). An ongoing study in Kuching Bay involving interviews with fishermen indicates that they prefer to set their nets on an outgoing tide to catch fish being swept out with the current. It is therefore possible that the dolphins, so often observed in association with this fishing effort, are using the same strategy. Irrawaddy dolphins in the mangrove forests of the Sundarbans and in the Mahakam River, Indonesia have an affinity for deep confluence areas as these areas have high fish abundance and the counter-currents from converging waters provide hydraulic refuge from fluvial and tidal currents (Kreb and Budiono 2005; Smith et al. 2006, 2008).

3.2 Range Pattern

Using kernel density estimation, the representative range (95 % UD) and core area (50 % UD) of Irrawaddy dolphins were estimated to be 246.42 and 37.22 km^2, respectively (Fig. 3). The core area was concentrated in the Salak-Santubong estuary (Fig. 3).

Only one previously published study provided information on ranging patterns of Irrawaddy dolphins using kernel density estimation (Sutaria 2009). The kernel density estimates of 246.62 and 37.22 km^2 in Kuching Bay are smaller than those

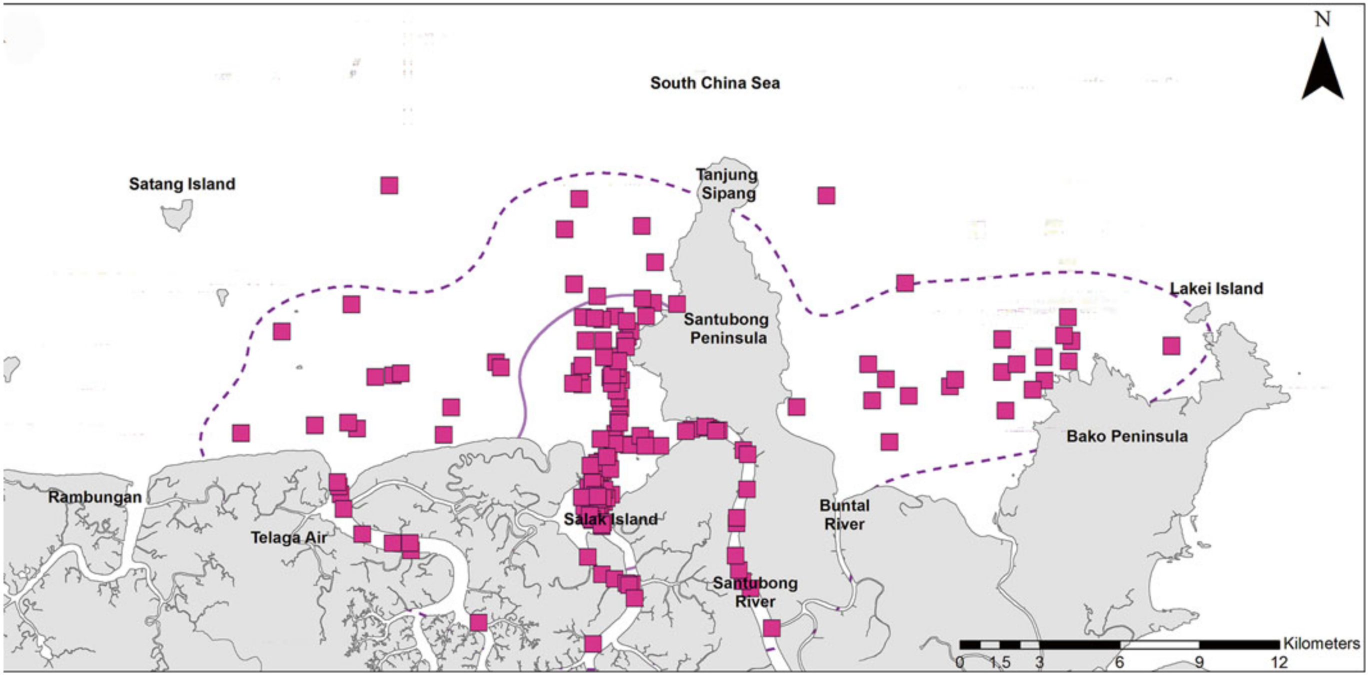

Fig. 3 Core areas (defined by *solid line*) and representative ranges (delineated by *broken line*) of Irrawaddy dolphins estimated using fixed kernel. Sighting data points represent the initial sighting location of dolphin groups representing on-effort sightings made between 2008 and 2012

reported in the Chilika Lagoon, India. Sutaria (2009) reported representative and core areas of 280 km^2 and 61 km^2, respectively, divided into two separate areas of the Outer Channel and South-Central Sector of Chilika Lagoon.

The representative range calculated in this study does not cover areas offshore from Tanjung Sipang (see Fig. 3). Movements of photographically identified Irrawaddy dolphins between the two bays of Salak-Santubong and Bako-Buntal are known to occur (Minton et al. 2013). As such, Irrawaddy dolphins would have to navigate either through the Santubong and Buntal rivers or around the point of the Santubong peninsula to move between the bays. However, since there were no records of sightings along Buntal River or Tanjung Sipang, further investigations are required to determine which route is actually more frequently used.

The association between river mouth distance, salinity, tidal height, critical areas and dolphins' distribution will help land use planners and developers as well as conservation managers to understand the types of habitats which need to be protected in order to conserve Irrawaddy dolphin populations in Sarawak. The habitat preference information is also critical for scientists as it will enable identification of potentially important Irrawaddy dolphin habitat in other parts of Sarawak that have not yet been surveyed and/or to inform Environmental Impact assessments in those areas.

3.3 Implications for Conservation

One of the major obstacles to wildlife conservation and management is the lack of adequate knowledge about species-habitat relationships. Most conservation strategies rely on protecting critical habitats from disturbances or threats to the target species (e.g., Saunders et al. 2002; Geldmann et al. 2013). As such, defining critical habitats, and understanding what role these habitats play in the species' survival is essential for conservation management.

The information presented here on the ranging patterns will help researchers and managers in assessing the target species' overlap with human activities. One of the biggest concerns is the location of the Irrawaddy dolphin core area. Located at the Salak river mouth, this area is also a targeted area for fishing, mostly using gillnets and trammel nets set from small fiberglass boats. Dolphin-watching also takes place in the Irrawaddy dolphin core area, offered by at least six tour operators (O'Connor et al. 2009) as well as a number of local fishers as an extra source of income. Therefore, these animals are at risk to entanglement in fishing gear and possible repeated noise pollution and disruption of feeding and resting activities from unregulated dolphin-watching (e.g., Bejder et al. 2006; Steckenreuter et al. 2012). An additional threat to the Irrawaddy dolphin population is the on-going construction of flood mitigation channel (Mah et al. 2012), designed to direct floodwater into the Salak River which is the core area of Irrawaddy dolphin habitat. Impacts associated with high input of fresh water into an estuarine system have been documented in Australia and New Zealand, these include higher rates of calf mortality

(Currey et al. 2009), incidence of skin disease (Rowe et al. 2010) and changes in habitat use (Fury and Harrison 2011). Without a management plan or mitigation measures in place, abrupt changes in salinity and turbidity might prove to be harmful to the population.

In light of the rapid coastal development taking place in the area, there is a need for continuous monitoring of the target species' distribution, habitat use and abundance. Long term monitoring is crucial to detect possible changes associated with the advent of the flood mitigation channel. This can be done with the already established and ongoing line-transect surveys and photo-identification studies as well as the use of passive acoustic monitoring (PAM). As larger datasets become available for line transect and photo-identification analyses, more robust estimates of abundance and ranging patterns as well as new parameters such as population trends, survival rates, individual ranging patterns and social structure can be obtained. Additionally, these data should also be tailored inform the IUCN Red List of Threatened Species criteria (IUCN 2012a, b) so that status assessment of Irrawaddy dolphin population in Kuching Bay could be performed.

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Economic Growth, Sustainable Development and Ecological Conservation in the Asian Developing Countries: The Way Forward

Choy Yee Keong

Abstract The Asian developing region, defined here for the purpose of analysis to include China, Malaysia, Thailand, Indonesia, the Philippines and Vietnam, is one of the most economically vibrant regions in the world. Acknowledging that rapid economic growth has had damaging environmental consequences, leaders in the region have made concerted efforts to strengthen the protection of the regional environment which is home to some of the richest and most biologically diverse habitats in the world. Each country has set up its environmental ministry or equivalent agency and enacted numerous laws to ensure stronger effort in biodiversity conservation and environmental protection. Despite these environmental protection initiatives, however, environmental degradation in the region remains a serious problem. Existing legislative efforts to halt extensive deforestation in the region have been hampered by various unsustainable resource use practices. In an attempt to make headway in an urgent task to contain this critical problem, this paper seeks to develop more adequate perspectives and concepts for an analysis of the complex process, which has led to the present conundrum, and to offer a way out of it. More specifically, in addressing the issues at hand, the paper examines the role of environmental ethics in fostering stronger environmental controlling actions based on the philosophical insights of Aldo Leopold's land ethics and empirical evidence drawn from field research on the indigenous environmental worldviews conducted between 2007 and 2011 in Malaysia. It is concluded that in halting further environmental decline in the region, it is necessary for the regional leaders to mark a higher level of ethical engagement with the natural environment.

1 Introduction

Sustainable development is defined in the Brundtland Report or "Our Common Future" as development that "meets the needs of the present without compromising the ability of future generations to meet their own needs" (WECD 1987). The

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Report which introduced a new growth model "that is forceful and at the same time socially and environmentally sustainable", places great emphasis on the needs to manage and use natural resources wisely so as to uphold the principle of intergenerational equity. More particularly, it calls for the need to achieve economic progress and social justice in ways that will not deplete the earth's finite resources.

Recognizing the growing importance of sustainable development, leaders in the Asian region, defined to include the world fastest developing country, China and the fast developing ASEAN economies, namely, Malaysia, Indonesia, Thailand, the Philippines and Vietnam (or the ASEAN-5), for the purpose of analysis, have expended much effort to sell to the public development policies that they believe would conform to the Brundtland's concepts of sustainable development.[1] In addition, with the growing awareness of the potential threats of environmental impairment caused by economic growth, all the countries in the region have ratified the United Nations Convention on Biological Diversity (CBD), a globally binding legal document on biodiversity conservation, as a sign of commitment to ensure that the regional rich biological diversity is conserved and sustainably managed towards enhancing social, economic and environmental well-being. Each country has also set up its environmental ministry or equivalent agency and enacted numerous laws to strengthen biodiversity conservation efforts.

Despite these environmental initiatives, however, the overall environmental conditions in the region have in fact worsened. Casual observation of what happens on the ground seems to indicate that national and regional environmental efforts have been unable to reverse the rapid loss of environmental resources and biodiversity in the region. Indeed, signs are evident that the regional environment is increasingly exposed to extensive and irreversible physical transformations as a result unrestraint pursuit of economic growth or material progress. One of the most disturbing environmental features in the region is the rapid and abrupt disappearance of species. This gravest environmental worry is reflected by the increasing number of the regional biological species being put under the purview of the IUCN Red List of Threatened Species (Hilton-Taylor et al. 2009; Wilson 2000; Carpenter and Peter 2009).[2]

In an attempt to make headway in an urgent task of containing these higher-order of environmental tragedies across the Asian region, this study seeks to develop more adequate perspectives and concepts for an analysis of the complex process, which has led to the present conundrum, and to offer a way out of it. Methodologically, it examines the dynamic implications of the link between economic growth and ecological sustainability under the spectrum of "Our Common Future". It further

[1] ASEAN comprises of ten countries of Southeast Asia, which include Singapore (developed nation state), Indonesia, Vietnam, Malaysia, Thailand, Cambodia, Laos, Brunei, Burma (Myanmar) and the Philippines (developing nations).

[2] IUCN (International Union for Conservation of Nature and Natural Resources) Red List is the world's most comprehensive information source on the global conservation status of biological species around the world. The IUCN

Categories of threat for the existing species include "near threatened", "vulnerable", and "critically endangered". The other two categories are "extinct" and "extinct in the wild" assesses the main driver behind the increasing incidence of the regional environmental paradox.

The assessment cogently demonstrates that the prevalence of the regional environmental issues partly lie in the lack of a philosophical basis for engagement with the natural environment when optimizing the economic use of nature. It is argued that the anthropocentric view of nature – the view which sees nature as serving human interests – still dominates the environmental regimes or society in the region to the extent that when environmental sustainability comes into conflict with economic growth or material progress, the former will be sidelined. To a large extent, environmental degradation in the region is human-induced; it is spurred by man's deeply entrenched exploitative behavior.

In addressing the above unsustainable anthropocentric value system, the study examines how human environmental attitudes and values help to influence individual behaviour and government policy concerning resource management and conservation practices based on the philosophical insights of Aldo Leopold's land ethics. The practical implications of Aldo Leopold's ethical argument in ecological conservation will be further examined based on field investigation of the indigenous environmental worldviews conducted in the state of Sarawak in Malaysia between 2007 and 2011. It is concluded that the environmental decline in the Asian region can possibly be addressed by altering man's actions founded on holistic environmental beliefs, ecological attitudes and values.

2 The State of Biodiversity in the Asian Region

It goes without saying that the Asian region as defined above is one of the most biologically rich and diverse environments in the world. Take the case of China, for instance, it is ranked third place behind Brazil and Colombia in terms of plant diversity (Lopez-Pujol et al. 2006, 2011). It has roughly 32,000 vascular plants, many of which are evolutionarily associated with ancient geological history. Also, more than half of these higher plants (17,300 species) are endemic (Huang et al. 2015; Ministry of Environmental Protection, China 2008). There are roughly 6347 species of vertebrates including 1244 species of birds and 3862 species of fish recorded in China. These account for about 14 % of the world's total vertebrate species (Ministry of Environmental Protection, China 2008). China is also listed as one of the world's 17 "megadiverse" countries.[3]

In the above connection, it may be revealed that the Three Gorges reservoir region located along the Yangtze River and with a total area of roughly 58,000 square kilometres (km^2), is one of most biologically diverse regions in China. It is

[3] Of the 170 countries in the world, a mere 17 countries which has less than 10 % of the global surface but lay claim to 70 % of the biological diversity on earth. The megadiversity concept was created to encourage and prioritize conservation efforts of biological resources around the world especially in these megadiverse countries (Conservational International 1998)

also one of the most fascinating ecological treasures in the world. It is home to over 6400 plant species (roughly 19 % of total number of species found in China) with 57 % of them categorized as endangered, 3400 insect species (8.5 % of China's total), more than 360 fish species, and more than 500 terrestrial vertebrate species (22 % of China's total) (Ministry of Agriculture, Beijing 1995; He and Xie 1995; Xie 2003; Wu et al. 2003; Tian et al. 2007; Zhang and Lou 2011). Twenty-seven percent of all the Chinese endangered freshwater fish are found in the Yangtze River which cut across by the Three Gorges dam, and of these roughly 177 species are classified as endemic (Yue and Chen 1998; Xie 2003; Fu et al. 2003; Zhang and Lou 2011).

Some of the most important and rare species found in the Three Gorges Dam area which are listed under the IUCN Red List as endangered are:

(i) The Chinese sturgeon, the hugest form of legendary fish species which has been swimming in the Yangtze waters for the past 140 million years. It would swim 3000 kilometres (km) upstream during spawning season (Evans 2007). The Chinese sturgeon is considered as a national treasure in China, and is now listed as Class I State protected species under the Chinese law (Hu et al. 2009).
(ii) The Chinese paddlefish or the "King of Yangtze", the world's longest freshwater fish. The species, which is placed under the China Species Red List, is protected under the Chinese state law.
(iii) The Yangtze River dolphin or Baiji, the world's rarest freshwater dolphin which has been thriving in the Yangtze River for the past 20 to 30 million years (Wu et al. 2003). The Baiji is classified as the First Category of National Key Protected Wildlife Species in China.
(iv) Other state protected or IUCN Red List species found in the Three Gorges dam area include the Yangtze finless porpoise, the Chinese tiger; the Chinese alligator; the Chinese giant salamander; the Siberian crane, and the giant panda.

The ASEAN-5 region is also one of the world's most biologically rich regions. Among the world's 17 megadiverse countries, three are located in the region, namely, Indonesia, Malaysia and the Philippines (Williams et al. 2001). Among these countries, Indonesia is the most diverse and biologically rich in the ASEAN region. It is also the third most biologically diverse country in the world. Occupying only 1.3 % of the earth's surface, it has 12 % of the world's mammal species (515 species with 36 % classified as endemic and first in the world in term of species richness). It ranks third for reptiles (with more than 600 species), fourth for birds (roughly 1519 species with 28 % classified as endemic) and fifth for amphibians (roughly 270 species) (UNEP 2010). There are 31,746 vascular plants recorded in Indonesia based on a taxonomic assessment conducted in 2007 (Hickey et al. 2004; Ministry of Environment, Indonesia 2005, 2009; Choy 2015). Also, new species continue to be discovered in the country on an annual basis (Yeager 2008). Indonesia is also a highly endemic region. The number of endemic fauna comprises 270 mammal species, 386 bird species, 328 reptile species, 204 amphibian species and 280 fish species (Ministry of Environment and Forestry of Indonesia 2014).

Malaysia ranks 14th out of the global-17 megabiodiverse list. Its rainforests contain roughly 306 species of mammals, 742 species of birds with high level of endemism, 242 species of amphibians, 567 species of reptiles, and 15,000 vascular plants, more than 449 species of freshwater fish, and more than 150,000 species of invertebrates (Ministry of Natural Resources and Environment, Malaysia 2014) The country is also ranked fourth in the Asian list in term of biological richness for amphibian (218 species) (IUCN 2009).

It may be of interest to note that out of the 13 states in Malaysia, the states of Sarawak and Sabah located in Borneo Island have important concentrations of threatened and highly endemic species (Hilton-Taylor et al. 2009; WWF 2010a, b).[4] Respectively, these two states contribute roughly two and four million hectares (ha) of their rainforests to the formation of the "Heart of Borneo" (HoB). The HoB is a tri-national and transboundary protected area made up of more than 23 million ha of biological rich dense tropical rainforests. It is located at the borders of West Kalimantan in Indonesia (share of HoB's contribution: roughly 16.8 million ha), the Malaysian states of Sarawak and Sabah, and Brunei (share of HoB's contribution: roughly 340,000 ha) (WWF 2010a).[5] It is the world's final tropical frontiers for scientific and biological research. Scientists have discovered more than 123 new species in this conservation zone for the past three years between 2007 and 2009 – an average of more than three new species per month (Thompson 2010). The rainforests in Sarawak alone are home to 185 animal species, 530 bird species, over 10,000 insect species, over 8000 plant species, more than 1000 species of orchid and with more new species continued to be discovered (Sarawak Forestry Corporation 2006). While in Sabah, its forests are home to roughly 6000 species of flowering plants, 2000 species of orchids, and 189 species of land mammals, out of which 42 are considered endemic to Borneo, 120 species of mammal, 300 species of bird, 72 species of reptile, 56 species of amphibian, and 37 species of fish (UNDP 2012; Sabah Forestry Department 2012).

The Philippines ranks 17th on the 17-global mega list. There are roughly 530 species of birds (some 185 species are endemic), at least 165 species of mammals (over 100 are endemic), about 235 species of reptiles (roughly 160 are endemic), nearly 90 species of amphibians (about 76 are endemic), and more than 9250 vascular plant species (about one-third is endemic), found in the country (Conservational International 2013). It also has among the highest rates of biological discovery in the world. For example, in the last 10 years, 36 new species of plants and animals have been discovered (Hance 2012a; see also, ACB 2010; Conservational International 2013). These include, for example, the Camiguin hawk owl, Cordillera shrew mouse, Zambales forest mouse, Sierra Madre mouse, and Southern Leyte frog (DENR-BMB 2014).

Although Thailand is not listed as one of the global-17 megadiverse countries, it is considered as one of the most biologically rich regions in the world. According to

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[4] Malaysia consists of 13 states with 11 states located in Peninsular or West Malaysia and 2 states, namely, Sarawak and Sabah located in East Malaysia, on the island of Borneo

[5] Currently, the Indonesian share of HoB's contribution is 12.6 million hectares while the proposed share is about 16.8 million. For Brunei, its share is roughly 576,000 ha (WWF 2010a). The 23.4 million hectares as stated above covered the proposed figure of Indonesia

the order of the World Conservation Monitoring Centre, Thailand is ranked 16th in term of biodiversity richness (Ministry of Natural Resources and Environment, Thailand 2014). Being connected to the Himalayan mountain range, Southern China, Peninsular Malaysia, Myanmar, Laos and Cambodia, the Thai forests provide excellent natural habitats for rich and diverse sources of biodiversity from three floristic elements, namely, Indo-Burmese, Indo-Chinese and Malaysia's elements. There are 4722 species of vertebrates comprising 336 species of mammals, 1010 species of birds, 394 species of reptiles, 157 species of amphibians, and 2825 species of fish found in Thailand. Of these, 555 species of vertebrates are classified as threatened. These include 118 species of mammals, 118 species of birds, 49 species of reptiles, 18 species of amphibians, and 202 species of fish (Ministry of Natural Resources and Environment, Thailand 2014; see also, Ministry of Natural Resources and Environment, Thailand 2009; ONEP 2009; Baimai 2010). Thailand also has about five percent (10,250 species) of all the vascular plants and gymnosperms in the world (Ministry of Natural Resources and Environment, Thailand 2014).

Vietnam is also considered as one of the world's most biologically diverse regions with very high rates of terrestrial endemism (Carew-Reid et al. 2010). There are roughly 310 species of mammals, 260 species of reptiles, 262 species of amphibian, 840 species of birds and 13,766 floral species found in the country (Ministry of Resource and Environment, Vietnam 2008; see also, Carew-Reid et al. 2010). Vietnam's global biodiversity significance was highlighted by the recent discovery of four large mammal species, namely, Saola (*Pseudoryx nghetinhensis*), Large-antlered Muntjac (*Megamuntiacus vuquangensis*), Annamite Muntjac (*Muntiacus truongsonensis*), and Khting Vor (*Pseudonovibos spiralis*), two new species of snake in the Annamite range of Truong Son and the central highlands (Warne and Phong 2002; Carew-Reid et al. 2010).

It is thus increasingly clear that the ecosystems in the Asian developing region are some of the earth's most distinctive biological treasures. Their exceptionally rich endowment of unique and highly endemic biota also makes it one of the most important priority conservation ecoregions in the world. Acknowledging that the rapid economic growth in the region has had damaging environmental consequences on these ecological treasures, regional leaders have established various institutional and legal frameworks to promote sustainable natural resource use and environmental protection. Despite these environmental protection initiatives, however, paradoxically, the overall regional environmental situations are becoming worse. In what follows is an attempt to examine this environmental paradox, and to suggest ways to mitigate the problems at hand.

3 The State of Economic Growth

Before entering into the core of the analysis, it is appropriate to provide a brief discussion on the economic growth trends in the Asian developing region as defined above. This enables us to see clearly the connection between economic growth and environmental sustainability in the region. Environmental sustainability may be loosely defined as the balance in sustaining the ecological health of the ecosystem while optimizing the instrumental use of nature to promote economic growth or satisfying human wants. It involves making responsible decisions and taking action to preserve the quality and capability of environment to support human life on a long-term basis. Environmental sustainability may be distinguished from ecological sustainability which is defined as the capacity of ecosystems to maintain and sustain their essential functions and processes, and biodiversity over time (see Holling's concept of resilience as discussed below). Also, it may be of passing interest to note the distinction between an environment and an ecosystem. While an environment refers to the sum total of surrounding things such as physical features or biological components, conditions and influences such as rainfall, temperature and thunderstorm, an ecosystem refers to an ecological unit in a specific area. The Heart of Borneo ecosystem as noted above is an example. As these terms are closely related, depending on circumstances of the case, they may be used interchangeably for analytical convenience.

To begin with, for decades, the Asian developing economies have joined the race to compete with one another to gain a competitive edge in the global economy. This dominant force of capitalist competition has changed the Asian economic order dramatically. Under the new economic order, the Asian economic dynamism continued to shape the global economic landscapes based on a new strategic economic impulse–the promotion of sustainable economic growth within the Brundtland's spectrum of sustainability.[6] The consensus among the Asian leaders is that the Brundtland model of sustainable development contributes to achieving not only economic growth and prosperity but also, environmental or ecological sustainability and intergenerational distributive justice. We shall have occasion here to examine whether the Asian model of sustainable growth conforms to the Brundtland's traits of sustainability.

To put issues into perspective, within one generation, the Asian region has been transformed into one of the most economically vibrant entities in the world today, having persistently achieved and sustained high economic growth for the past few decades based on the prescription of neoliberal economic policies (Choy 2014a). The priorities of neoliberal policies are to expand market forces, facilitate deregula-

[6]The term economic growth refers to the amount of goods and services produced in an economy. It may be expressed in term of an increase in GDP (gross domestic product), that is, quantitative growth. As distinct from economic growth, economic development is a wider concept. It is not only concerned with quantitative growth but also, qualitative expansion of an economy as a whole, that is, qualitative growth. Some of the important features associated with qualitative growth are: (i) modern economic transition from an agriculture or primary-product based economy to a manufacturing or industrial-based economy especially technologically advanced economy and, (ii) social improvement in the quality of life or standard of living of citizens. Sustainable development, as defined above may slightly be distinguished from economic development in term of the environmental emphasis it places on development process. That is, it is fundamentally concerned with prudent use of natural resources when promoting development so that future generations will not be worse off than the present generation

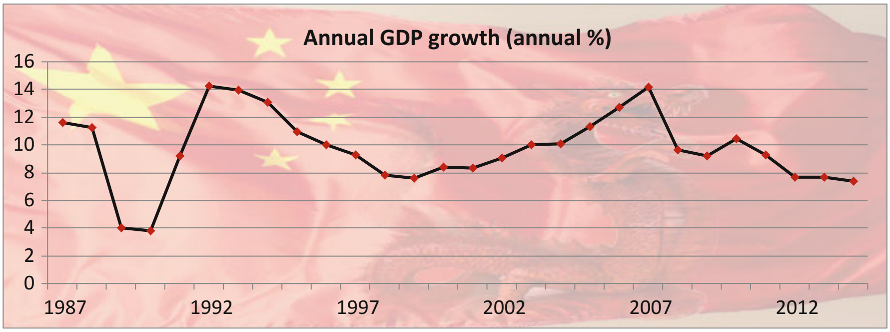

Fig. 1 Average GDP growth of China from 1987 to 2014 (Source: Countries and Economies, 2015, The World Bank, http://data.worldbank.org/country?display=default; World Economic Outlook, 2015, IMF 2015)

tions, promote free trade; privatization and global competitiveness, enhance mass production and consumption, attract foreign direct investment and maximize consumption (see, for example, FAO 2006; Chow 2012). The policies also place great emphasis on industrial expansion and the promotion of export-oriented growth (Haque 1999).

The rigor of the Asian economic dynamism is well illustrated by the rapid capitalist transformation in China since the adoption of its market reforms in 1978 under the leadership of Deng Xiaoping. Before the reform period, China's per capita GDP (gross domestic product) was lower than that of Malaysia, Indonesia and Thailand. In fact, China was one of the poorest countries in the world, with a GDP per capita of only US$165 (constant US$ 2000) (UNICEF 2014). However, since the commencement of market reforms, China has been achieving a remarkable GDP growth-far higher than the ASEAN-5 region. Over the past 28 years between 1987 and 2014, it has achieved an annual GDP growth of 9.7 % – three times the global average (Fig. 1).

Within a decade, China has been able to transform itself into a modern industrial state that many developing countries needed 100 years to achieve. It is also noteworthy that China has successfully achieved a 9.2 % GDP growth during the full-blown global recession in the year 2009. It is also the first of the major economies in the world, which was able to withstand the effects global recession (Zissis and Bajoria 2008; Xia and Wang 2012; Kong et al. 2012). China has also surpassed Japan as the world's second largest economy after the United States in 2010 —— a clear indication of its influence in changing the balance of power in the global economic order (Xia and Wang 2012; Yuan and Yu 2012).[7] Although China's GDP growth has slowed down to an average of 7.5 % between 2012 and 2014, it still remains a crucially influential world economic player.

[7] China's GDP in 2010 in figure was USD 5,878,629 while Japan's GDP was at USD 5,497,813 (World Bank 2011). The figures were increased to USD 8,227,103 for the former and USD 5,959,719 for the latter in 2011 (World Bank 2013a).

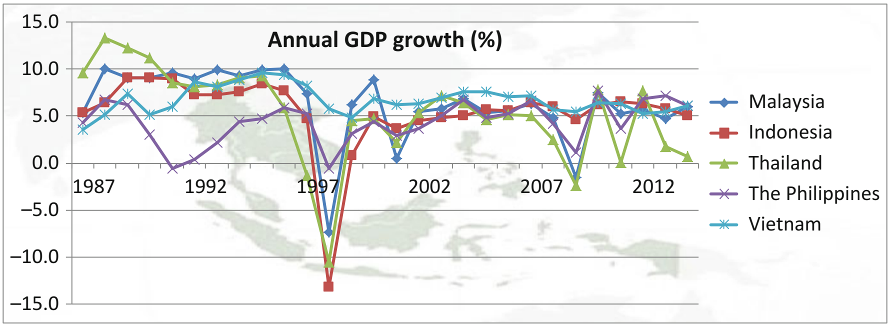

Fig. 2 Average GDP growth of ASEAN-5 from 1987 to 2014 (Source: Countries and Economies, 2015, The World Bank, http://data.worldbank.org/country?display=default; World Economic Outlook, 2015, IMF 2015)

If the ecological aspects of China's growth performances are to be appreciated fully, some discussions on the economic contribution of the Three Gorges dam project are warranted. In brief, the Three Gorges dam, which cuts across the Yangtze River (6300 km), is the largest in the world with a massive reservoir area measuring up to 58,000 km (Zhang and Lou 2011). It is also one of the most important economic pillars underpinning China's robust industrial development and socioeconomic progress. Indeed, the Three Gorges project has been crucial in sustaining the momentum of growth in China for the past few decades. Apart from generating electricity to power China's economic growth, the project has also led to the development of advanced inland shipping industry and heavy industrial development in the Yangtze economic zone.

To illustrate, shipping load along the Three Gorges waterway accounts for 80 % of the total shipping capacity of China's inland rivers. It was estimated that from 2003 to 2010, the amount of cargo load passed through the Three Gorges-Yangtze waterways exceeded 44 million tons, contributing to sustain robust growth of the Chinese economy (Yang 2011). For instance, the rapid industrialized provinces, namely, Jiangsu, Hube, Shanghai, Anhui, Hunan, Sichuan, Chongqing, Zhejiang, and Chongqing located around the Three Gorges region, contributed 41 % (US$ 3 trillion) to the overall Chinese GDP growth in 2011. The figure increased slightly to 42 % (US$ 3.55 trillion) in 2012 (Asia Times 2006; Zhang and Lou 2011; Gu 2012; Yao 2013).[8]

The ASEAN-5 economies have also attained an impressive record at an annual average of 5.5 % GDP growth in the same period (Fig. 2). Economic growth in the latter 1980s and early 1990s was so spectacular that it prompted the World Bank to label the region as an economic miracle (Intal et al. 2012). The promotion of export-led industries especially high value-added industries, which are associated with output

[8] Geographically, the Three Gorges region is located at the lower section on the upper reaches of the Yangtze River (6300 km) with a total area of 56,700 km^2

expansion and increased export and trading activities, has been the main driver for the impressive economic performances in the region (ASEAN 2007, 2008, 2012, 2014).

Malaysia, Thailand and Indonesia, termed as high performing developing economies (HPAEs), were together considered an important epicenter of growth in the Asian Pacific region. Take the case of Malaysia, for instance, it has attained a remarkable growth performance in the late 1980s and through the 1990s with an average annual growth rate of over eight percent based on a neoliberal shift from its primary product or agricultural-based economy to a manufacturing-based and export-oriented economy (Tik 2009). The manufacturing sector is an important economic pillar of the Malaysian economy, accounting for 25 % of GDP and more than 60 % of the country's total exports (Taborda 2013a; McGregor 2008; Lim 2009). The oil palm industry is also an important economic activity in Malaysia. Currently, Malaysia is the second largest producer of palm oil in the world (MPOB 2011). In view of its remarkable economic success, the World Bank has classified Malaysia as an upper-middle-income economy.

In the 1980s, Thailand embarked on a neoliberal shift of development paradigm from an agrarian and resource-based economy to a manufacturing and export-oriented economy. During the early 1990s, the export-based manufacturing industries in the country had been playing an important role in sustaining its double-digit annual growth (Islam and Chowdhury 1997). In the late 1980s, it was able to edge over the rest of the Southeast Asian developing countries to become one of the fastest growing economies in the world (Muscat 1994; Taborda 2013b). Rubber cultivation remains an important commercial agricultural activity in the Thai economy while coffee plantation, tea and cacao commercial cropping are increasingly becoming important (Ministry of Resources and Environment, Thailand 2006). Thailand is ranked as an upper-middle-income economy by the World Bank. Although the political instability between November 2013 and May 2014, which culminating in a military takeover of the government in May, has drastically slowed its economic growth to 0.7 % in 2014, GDP growth is projected to improve to 3.6 % in 2015 and 4.1 % in 2016 due to a relatively calm political environment and increased public fixed investment (ADP 2015).

Compared to Malaysia and Thailand, Indonesia's economy is less export-oriented. Since the Suharto's dictatorial regime, its economic policy has always been a mix of state intervention and free-market forces (Wijaya 2009). However, despite its half-hearted shift towards more market-intensive policies, the neoliberal force of structural transformation seems to have delivered strong exports and FDI performance in the Indonesian economy between 2007 and 2008 (Prasetio 2009). Currently, Indonesia is the largest economy in ASEAN and the 17th largest in the world. Industry is the most important growth engine in the Indonesian economy, making up roughly 46.5 % of total GDP (Taborda 2013c). Indonesia continued to post significant economic growth with its GDP expanding to six percent in the first quarter of 2013 although growth in the year was expected to slow down due to decreasing private consumption and physical investment, and a contraction in mining services (Taborda 2013c). Similar to Malaysia, the palm oil industry is one of the most important economic pillars of the Indonesian economy (Budidarsono et al.

2013). In fact, the country is the largest exporter of palm oil in the world (MPOB 2011). Although GDP growth slowed to five percent in 2014, political transition to the new government led by President Joko Widodo in Indonesia in October 2014 is expected to improve investment climate and spur greater economic growth. It is projected that GDP growth will increase to 5.5 % in 2015 and six percent in 2016, respectively (ADP 2015).

Although the Philippines is classified as a lower-middle income economy by the World Bank, it has been achieving an annual GDP growth at five percent since 2002, significantly higher than the previous two decades. Also, amid global uncertainties, it was able to achieve 6.8 % GDP growth in 2012 (Fig. 2). In the first quarter of 2013, driven mainly by robust domestic consumption and government spending, its economy further expanded to 7.8 %, up from 7.1 % in the previous quarter, making it the fastest growing economy in Asia (Taborda 2013d). Robust private consumption, investment, and exports continued to drive Philippines' strong GDP growth to 6.1 % in 2014. GDP growth is projected to increase to 6.4 % in 2015 and 6.3 % in 2016, respectively (ADP 2015). It may be of passing interest to note that the Philippines' economy is one of the most consumer-driven economies in the Asian region, with its domestic consumption contributing to the largest expenditure component of GDP (Colombo 2013). Private consumption grew by 5.6 % in 2013 and contributed more than half of the increase in GDP (ADP 2014). The Philippines' economy continues to depend on remittances from its overseas workers, which account for about 10 % of GDP growth (Lester and Yap 2013). Indeed, remittances are the force behind powerful consumption growth as well as real estate expansions in the country (Banyan 2010).

Interestingly, among the ASEAN-5 economies, the economic performance of Vietnam is the most impressive. It has been achieving an annual average GDP growth of 6.6 % for more than a decade since it implemented the new open door policy called *Doi Moi* (Renovation) in 1986 (Fig. 2). Its persistent high rate of economic growth has made it one of the fastest growing economies in the world (Intal et al. 2012). Roughly 73 % of the wealth creation in Vietnam derives from the economic use of natural capital including cropland, pasture, timber and minerals. Approximately 55 % of the wealth comes from the agricultural sector. Some of the major agricultural activities include the production of rice, black pepper, coffee, tea and rubber (World Bank 2008; Trading Economics 2014). Rising foreign direct investment helped to sustain a strong economic growth of six percent in 2014. GDP growth is projected to increase to 6.1 % and 6.2 % in 2015 and 2016, respectively. Compared to 2013, industry in Vietnam had increased by 7.1 % in 2014 (ADP 2015). Recently, manufacturing, information technology and high-tech industries are becoming increasingly important in the Vietnamese economy (Trading Economics 2014).

In summary, as shown in Table 1, the economic growth of China and ASEAN-5 over the past few decades at an annual average of 9.7 % and 5.5 %, respectively, have been extraordinary compared to the advanced OECD countries or the upper-middle income Latin American, Caribbean or African economies. The high economic performances have also led to a dramatic change in socio-economic structure by creating new middle class or affluent industrialized societies in the region (Kahn 1996; Robison 1996; Hewison 1996; Hill 1999).

Table 1 Economic growth of the Asian developing economies: a comparative view

	Country	Annual average GDP growth between 1987 and 2014
East Asian fast developing economy (world's fastest growing economy)	**China**	**9.7%**
ASEAN-5 (Southeast Asian fast developing economies)	**Vietnam**	**6.6%**
	Malaysia	6.2%
	Thailand	5.2%
	Indonesia	5.4%
	The Philippines	4.3%
	ASEAN-5 average	**5.5%**
OECD (selected countries)	Japan	1.6%
	Korea	5.8%
	U.S.A	2.6%
	UK	2.2%
	France	1.8%
	Australia	3.2%
	OECD average	**2.9%**
Upper middle-income Latin American and Caribbean region (selected countries)	Argentina	3.2%
	Brazil	2.5%
	Mexico	2.8%
	Peru	2.5%
	Venezuela	2.5%
	Ecuador	3.3%
	Latin American/Caribbean average	**2.8%**
Upper middle-income South Africa (largest economy in Africa)	**South African average**	**2.5%**

In the next section, the discussion will consider the interface between economic growth and environmental sustainability.

4 Economic Growth and Environmental Sustainability: The Asian Way

Acknowledging the threat of environmental degradation caused by rapid economic growth and increasing material consumption, the Asian leaders have reaffirmed their commitment to achieving the sustainability goals of "Our Common Future" by putting greater weight to integrate environmental concerns into development discourse

Table 2 Environmental protection laws in the Asian countries

World's fastest growing developing economies	ASEAN-5 (fast developing economies in Southeast Asia)				
China	Malaysia	Thailand	Indonesia	The Philippines	Vietnam
Environmental Protection Law (1979, amended in 1989)	National Policy on Biological Diversity (1998)	The Forest Act (1941, amended in 1948, 1982 and 1989)	Environmental Management Act (1997, revised 1982, 1990)	Executive Order 578 (2006): a decree which seeks to "protect, conserve, and sustainably use biological diversity to ensure and secure the wellbeing of the present and future generations of Filipinos"	Forest Protection and Development Law (1991, amended 2004)
Wildlife Protection Law (1988)	National Forestry Policy (1978, revised 1993)	Wildlife Reservations and Protection Act (1960, amended in 1992)	Forestry Law (1999)	Presidential Decree 1151 or The Philippine Environmental Policy (1977): a decree which seeks to promote a harmonious relationship with nature, sustainable resource use and the principle of intergenerational equity	Land Use Law (1993, amended 1998, 2003)

(continued)

Table 2 (continued)

World's fastest growing developing economies	ASEAN-5 (fast developing economies in Southeast Asia)				
China	Malaysia	Thailand	Indonesia	The Philippines	Vietnam
Fisheries Law 1986 (amended in 2000 and 2004)	Environmental Protection Enactment, Sabah (2002, amended 2004)	National Park Act (1961)	Conservation Law (1990)	Presidential Decree 1152 of the Philippine Environment Code (1977) (mandates the Department of Environment and Natural Resources to establish a system of national resource exploitation and wildlife conservation)	Environmental Protection law (1993, amended 2005)
Water Pollution Prevention Law (1984, revised 1996)	Sabah Forestry Policy (2005)	National Forest Reserve Act (1964)	Environmental Protection Law (2009)	Presidential Decree 705 or the Revised Forestry Code of the Philippines (1975) (primary legal instrument guiding the use and management of forest resources and biodiversity conservation)	Law on Fisheries (2003)

Solid Waste Pollution Prevention Law (1995)	Natural Resources and Environment Ordinance, Sarawak (1993, amended 1997, 2001)	Reforestation Act (1992)	Cultivation Law (1992)	Republic Act 7586 or the National Integrated Protected Area System Act, 1992	Ordinance on Plant Varieties (2004)
Protection of Terrestrial Wildlife Law (1992)	Wild Life Protection Ordinance, Sarawak (1998)	Tambol Council and Tambol Administration Organization Act (1994) (aims to strengthen the role of local government in sustainable natural resource use and management)	Plantation Law (2004)	Sustainable Forest Management Act (2005, 2009)	Biodiversity Law (2008)
Regulation on the Protection of Aquatic Wild Animals (1993)	National Parks and Nature Reserves Ordinance, Sarawak (1998)	Thailand Constitution (2007) (seeks to promote systematic management and use of natural resources for the benefit of the public)	Ministry of Agriculture Regulation (2007)	Republic Act 9147 or the Wildlife Resources Conservation and Protection Act (2001)	Decree 32 on the Management of Endangered, Precious, and Rare Species of Wild Plants and Animals (2006)

in order to protect the regional environment and natural resources. At the same time, regional leaders have also put in place comprehensive environmental institutions and legal systems to strengthen efforts for natural resource management, genetic resource conservation, and environmental protection (Table 2).

To elaborate, in the case of China, for example, apart from the enactment of various environmental laws as shown in Table 2, it had also set up the State Environmental Protection Commission in 1984. In 1998, it was elevated to the status of State Environmental Protection Administration and finally became the Ministry of Environmental Protection (MEP) in 2008. Its main function is to formulate environmental protection guidelines, policies and laws in order to ensure sustainable development. It goes without saying that environmental protection was among the most heavily legislated sectors of public policy in China during the post-Mao period (Ross and Silk 1987).

In the post-Mao era, the Bruntdland Report also provided a remarkable conceptual framework and impetus for shaping policies based on the integration of environmental concerns into development policy. In the wake of the Earth Summit held in 1992, China ratified the United Nations CBD. This was followed by the formulation and adoption of the National Biodiversity Action Plan in 1994 which was aimed at halting the loss of biodiversity by 2020. In the same year, it also adopted its local Agenda 21, also known as the White Paper on China's population, environment, and development in the twenty-first century. China's Agenda 21 sought to reinforce its commitment to environmental preservation and sustainable resource use while pursuing economic growth and social development. Indeed, China was one of the first few countries in Asia to propose and implement sustainable development strategies, and to publish its first, second and third national sustainable development reports in 1997, 2002 and 2012, respectively (NDRC 2012). Under the umbrella of the Scientific Outlook on Development (SOD), China formulated and implemented the 11th Five-Year Plan (2006–2010) and the 12th Five-Year Plan (2011–2015) to promote sustainable development (Hu 2014).

In the ASEAN-5 region, in the wake of *Our Common Future*, the regional leaders also ratified various international agreements as a sign of commitment to sustainable development. At the national level, in an attempt to ensure stronger effort in biodiversity conservation and environmental protection in line with the United Nations CBD, each country has strengthened its environmental controlling framework based on the establishment of formal institutions such as the Ministry of Natural Resources and the Environment in Malaysia, in Thailand and in Vietnam; the Department of Environment and Natural Resources in the Philippines; and the Directorate General of Forest Protection and Nature Conservation in Indonesia. To demonstrate further commitment to promoting sustainable development, each country has also created its local Agenda 21 in order to execute full integration of sustainable development principles and environmental concerns of Agenda 21. Environmental protection is also being reinforced based on the enactment of a wide range of environmental laws as shown in Table 2.

Table 3 ASEAN environmental protection declarations and accords

1	Manila Declaration on the ASEAN Environment (1981)
2	ASEAN Declaration on Heritage Parks and Reserves (1984)
3	Bangkok Declaration on the ASEAN Environment (1984)
4	ASEAN Agreement on the Conservation of Nature and Natural Resources (1985)
5	Jakarta Resolution on Sustainable Development (1987)
6	Manila Declaration of 1987
7	Kuala Lumpur Accord on the Environment and Development (1990)
8	Singapore Resolution on Environment and Development (1992)
9	Bandar Seri Begawan Resolution on Environment and Development (1994)
10	ASEAN Vision 2020 (1997)
11	Jakarta Declaration on Environment and Development (1997)
12	Kota Kinabalu Resolution on the Environment (2000)
13	Yangon Resolution on Sustainable Development (2003)
14	Cebu Resolution on Sustainable Development (2006)
15	ASEAN Declaration on Environmental Sustainability (2007)
16	ASEAN Charter (2008)
17	Cha-am Hua Hin Declaration on the Roadmap for an ASEAN Community 2009–2015 (2009)
18	ASEAN Socio-Cultural Community (ASCC) Blueprint 2009–2015 (2009)
19	Joint Declaration on the Attainment of the Millennium Development Goals in ASEAN 2009
20	Statement by the ASEAN Environmental Ministers for the eleventh meeting of the conference of the parties to the Convention on Biological Biodiversity 2012
21	New Delhi ASEAN -India Ministerial Statement on Biodiversity (2012)

At the regional level, each ASEAN-5 member country has endorsed a series of environmental agreements and declarations in order to strengthen regional cooperation for the conservation and sustainable use of biodiversity (ASEAN 1997, Table 3). The most important document adopted by the regional leaders is the ASEAN Agreement on the Conservation of Nature and Natural Resources (1985), a legally binding agreement which serves to guide effective implementation of regional action plans or programmes for the promotion of green economy by balancing the three pillars of sustainable development, namely, the economic, social and environmental dimensions. The ASEAN Agreement provides some of the most holistic guidelines for the design of environmental protection and sustainable resource management framework to ensure that the regional rich biological diversity is conserved and sustainably managed in line with the Brundtland concept of sustainability and the United Nations CBD (Choy 2015). It is worth noting that Article 1 of the ASEAN Agreement explicitly requires each member country to undertake and adopt measures in accordance with its national laws to ensure sustainable use of natural resources.

Based on the ASEAN regional environmental protection framework, various environmental protection programmes have been initiated and implemented. These include the ASEAN Heritage Parks Programme, ASEAN-Wildlife Enforcement Network and the tri-country Heart of Borneo Initiative (HoBI), which involves Indonesia, Malaysia and Brunei. The HoBI concerns the protection of about 23 million hectares of ecologically connected and biologically diverse forest straddling Indonesia (Kalimantan), Malaysia (Sarawak and Sabah) and Brunei (Choy 2015).

5 Environmental Protection Initiatives and Ecological Sustainability: The Reality

5.1 The Chinese State of Environment

Despite the above far-reaching environmental protection initiatives, however, mere casual observation of what has been happening on the ground reveals that rapid economic growth accompanied by increased resource consumption in the region has caused a steady and alarming deterioration of its environment. In China, for instance, up to 70 % of its rivers and lakes are seriously polluted, and ecological degradation is widespread (Morton 2006; WWF 2012). It may well be noted that of the world's 20 most polluted rivers, 16 are in China (McBeath and Leng 2006). The dumping of untreated waste water and animal wastes into the rivers by industries is widespread (Turner and Ellis 2007). For example, petrol chemical plants and factories located by the bank of the Yangtze River release large amounts of industrial wastes including toxic materials, heavy metals (cadmium, mercury, lead, and arsenic), chemical effluents and organic matters, into the river every year. The amount of discharge increased at an alarming rate from 15 billion tons in the 1980s to 33.9 billion tons in 2010, causing unprecedented destructive impacts on the Yangtze aquatic ecosystem (WWF 2007; Wong et al. 2007; Ting 2011; Mo 2011). Not surprisingly, the Yangtze River is now one of the most polluted and endangered rivers in the world (WWF 2007).

Also, it is estimated that 5850 tons of organic pollutants are released into Chinese waters everyday compared to 2750 tons in the United States, 1700 tons in Japan, 1150 tons in Germany, 1600 tons in India, and 300 tons in South Africa (Refkin and Cray 2013). The construction of the Three Gorges dam in the Yangtze River system also resulted in massive loss of natural habitats, exerting immense pressure on the regional biodiversity and threatening the long-term survival of the Siberian crane, Chinese tiger, giant panda and red panda (WWF 2004). All these species are classified as endangered either by the IUCN, U.S. Fish and Wildlife Service or the World Wildlife Fund. They are also totally protected by the Chinese national laws such as the Environmental Protection Law or the Wildlife Protection Act as noted above. It may also be noted that the "living fossil", the ancient *Cathaya argyrophylla* trees and dawn redwood trees which date back to millions of year have been irreversibly extirpated due to uncontrolled human economic activities. The continued existence of 47 plant species which are unique to the Three Gorges region are also being threatened due to extensive habitat fragmentation (Lopez-Pujol et al. 2006).

Other adverse ecological impact of the Three Gorges architectural monument is the blockage of the migratory paths of certain fish species to their spawning grounds in the upriver (Gao et al. 2009a; Gleick 2009). For example, taking 2002 as a pre-dam baseline, from 2003 to 2005, the commercial harvests of four important commercial species of carp, namely, grass carp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitrix*), black carp (*Mylopharyngodon piceus*) and bighead carp (*Aristichthys nobilis*), were found to be 50–70 % below the pre-dam levels due the disturbances of their migratory routes during spawning seasons (Xie et al. 2007; Zhang et al. 2012). In addition, since 1998, only three to ten adults have been found below the dam annually (Berra 2007).

A myriad of factors caused by unsustainable human activities such as increased shipping traffic, blockage of fish's migratory routes, uncontrolled river pollution and extensive habitat degradation coupled with illegal and unsustainable bycatch by fishermen by rolling hook long-line fishing, gill nets, electrocution and dynamite or other banned destructive fishing methods have resulted in the extinction of the world's most critically endangered and rare cetacean, the Yangtze River dolphin (Baiji or goddess of the Yangtze) (Ding et al. 2006; Turvey et al. 2007). The evolutionarily distinct Baiji had been thriving in the Yangtze River for the past 20–30 million years. In the past, the relic species was commonly hunted in the local fisheries for meat, oil and leather. Its population dropped drastically from a healthy number of 6000 in the 1950s to only 1 individual in 2004. It was declared extinct in 2006; making it the first dolphin that mankind directly drove to extinction. This happened despite having in place various ecological protection programs and legal instruments to protect its continued survival.

The continued deterioration of the Yangtze ecosystem is also evidenced in the decline or extinction of many notable aquatic species that used to thrive in the river. The endemic Chinese paddlefish which dates back to 70 million years ago, for instance, may have become extinct in 2003 as none have been sighted in the wild since then (Bourton 2009; Gao et al. 2009b). In addition, with the population declined drastically from 2000 in 2006 to about 1000 in 2012, the state protected Yangtze finless porpoises are also increasingly facing the threat of ecological extinction as a result of various unsustainable human economic activities (Lovgren 2007; Wang et al. 2010; Qiu 2012; Hance 2012b, 2013a).

Illegal wildlife trade in China also contributes to endangering the continued survival of many of its rare and endangered species. China is a top consumer country for illegal wildlife products and one of the world's hotspots for illegal trade in wildlife and wildlife parts (Felbab-Brown 2011). Furthermore, compared to the average global rate of biological loss of 10 %, the rate of biodiversity loss in China is about 15–20 % (McBeath and Leng 2006) The China Red List indicates that 40 % of mammals, seven percent of birds, 28 % of reptiles, 40 % of amphibians and three percent of fish are vulnerable to ecological extirpation (McBeath et al. 2014).

In summary, the disappearance of Baiji in the wild is a stark indication of how unrestrained pursuit of economic growth and socioeconomic progress is changing irreparably the country's natural environment. It also symbolizes the loss of harmony of human beings with nature. This is excruciatingly clear particularly since the Baiji had long been recognized as the rarest and most critically threatened mammal species on earth, and despite China having expressed serious commitment to its ecological conservation by legally categorizing it as the First Category of National Key Protected Wildlife Species.

5.2 *The ASEAN-5's State of Environment*

Similarly, in ASEAN-5, despite having in place comprehensive environmental protection institutions and legal frameworks, and the adoption of various regional declarations and conventions to safeguard the ecological integrity of the environment and to promote sustainable resource use, environmental degradation remains a serious problem confronting the region today. Existing legislative efforts and regional cooperation to halt extensive deforestation in the region have been hampered by uncontrolled and illegal logging activities, large-scale monoculture expansion and dam construction, among others.

5.2.1 Indonesia

As a case in point, in Indonesia, between 1985 and 2008/9, it lost 49 % (12.5 million ha) of its 1985's original natural forest cover (25.3 million ha) due to unsustainable pulp and paper industrial development, uncontrolled oil palm plantation expansions and illegal logging activities. This accounts for almost 50 % loss in 23 years with forest cleared at an annual average of 542,000 ha per year. By 2008/9, the nation has only 12.8 million ha of its natural forest cover left (WWF 2010a). This has made Indonesia the most significant contributor to the loss of forests in Southeast Asia (Stibig et al. 2007; ESCAP 2011). In 2012, Indonesia further lost another 800,000 ha of forest due to various economic activities. This is extensive compared to Brazil which lost about 460,000 ha in the same year (Margon et al. 2014).

Oil palm plantation development is the biggest cause of deforestation in Indonesia today. To cite a specific example, between 2009 and 2011, Indonesia had converted 300,000 ha of forest into oil palm plantations (Butler 2013a). Even the highland forests found in steep hills and mountains, such as those in Sumatra, Sulawesi, and Halmahera, were cleared for short-term economic gains. Indeed, time and again, the Indonesian rainforests are left to be invaded by loggers, poachers, and miners because of poor or non-enforcement of laws (Felbab-Brown 2013). Behind the scene of this unsustainable resource use, it is noteworthy that natural resources in the country have long been regarded as cheap and undervalued commodities (National Development Planning Agency 2003). This tends to give rise to disincentive for environmental conservation when optimizing the economic use of nature.

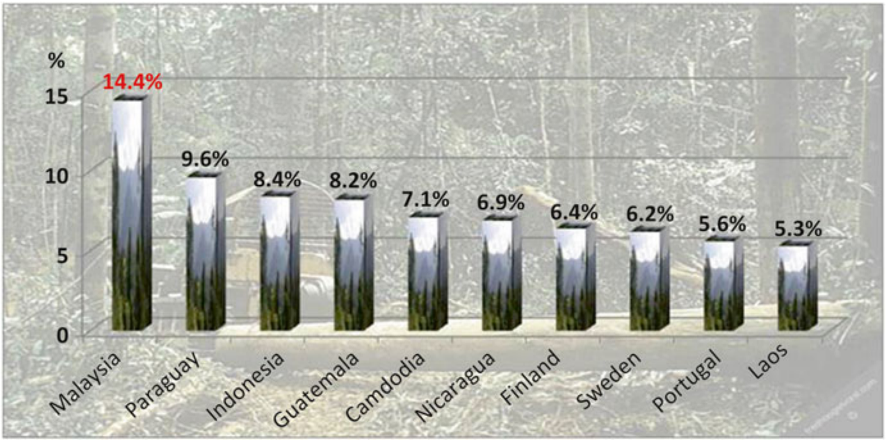

Fig. 3 Rate of deforestation in Malaysia between 2000 and 2012: a global comparison

Unmistakably, such a massive scale of deforestation, and hence habitat fragmentation and destruction is detrimental to the continued survival of some of the world's iconic and endangered species such as the Bali, Javan and Sumatran tigers, the Sumatran elephant, the Javan rhinoceros and the orangutan (Brown and Jacobson 2005; WWF 2010b). The loss of habitat due to commercial agricultural development and illegal hunting has led to the extinction of the Bali and Javan tiger in the country (Brown and Jacobson 2005). Illegal hunting and pollution such as soil erosion caused by deforestation also contribute to aggravate the ecological status quo. Indonesia is now rated as one of the top ten countries in the world with the most threatened species, and a global hotpot of great conservation concern (Hickey et al. 2004; Yeager 2008; ACB 2010).[9] Indonesia is also the world's third largest source of greenhouse emissions due to deforestation and land degradation and conversion, contributing significantly to climate change (PEACE 2007).

5.2.2 Malaysia

Between 2000 and 2012, Malaysia lost 4.7 million ha of forest, an area larger than the size of Denmark or the state of Virginia. This made Malaysia's rate of deforestation the highest in the world at 14.4 %, compared to Indonesia at 8.4 % during the same period (Butler 2013b, Fig. 3). Unrestrained logging activities, physical conversion of natural forests into mega-dam infrastructures, oil palm and rubber-wood plantations are some of the most important drivers of deforestation in Malaysia (Litta 2012; Butler 2013b; Choy 2015). To cite an example, between 1990 and

[9] For a region to qualify as a hotspot, two strict criteria must be met, that is (i) it must contain at least 1500 species of vascular (higher order) plants (>0.5 % of the world's total) as endemics, and (ii) it has to have lost at least 70 % of its original habitat

2005, one million ha of forest were cleared for oil palm plantation development in the country (Subramanian et al. 2011).

The construction of the Bakun and Murum dams in the state of Sarawak has also aggravated the environmental situations. These two dam projects have necessitated an irreversible destruction of roughly 94,000 ha of some of the world's most biologically diverse rainforests (Choy 2005). The unsustainable resource use practice in Malaysia is also well reflected by the degazettement of the Bikam Permanent Forest Reserve for monoculture development in the state of Perak located in West Malaysia. In 2003, roughly 400 ha of the forest reserves were clearcut for oil palm plantation development. For the past few years since 2009, over 9000 ha of the permanent forest reserves in the state have been degazetted for timber production and other commercial activities (Hance 2013b).

The extensive development-induced habitat fragmentation or destruction has led to the extinction of the Javan Rhinoceros in Peninsular Malaysia, and the extinction of Sumatran Rhinoceros in the state of Sarawak (Greenpeace 2004). In 2015, the Sumatran rhinoceros has been declared extinct in the wild in Malaysia (Zorthian 2015). Habitat destructions caused by human's economic activities also threatens the continued survival of a wide range of key forest-dependent and endangered mega-fauna such as tiger, Pygmy elephant, Orangutan, and Clouded leopard. On the whole, about 14 % of the mammals in Malaysia are listed under the IUCN Red List as endangered, and 47 out of the 218 species of amphibian in the country are threatened with extinction (Hilton-Taylor et al. 2009).[10] Other species whose ecological survival is critically threatened due to human activities are the Black shrew, Malayan Tapir, and Mouse deer. Malaysia is also classified as one of the global hotspots of conservation priority.

The irreversible destruction of the Bikam Permanent Forest Reserve as noted above also resulted in the extinction of keruing paya (*Dipterocarpus coriaceus*). Keruing paya is a large hardwood tree listed as Critically Endangered on the IUCN Red List (Hance 2013). The degazettement of the permanent forest reserves in the state of Perak as discussed above could possibly lead to the extinction of the last stand of keruing padi (*Dipterocarpus semivestitus*) found in the region. It also increasingly threatening the continued survival of a range of protected species including leopard, Malayan tapir, siamangs, and the great Argus pheasant thriving in the region (Hance 2013b).

It may be remarked in light of the above that despite enacting the National Forestry Policy and the National Wildlife Act which empower the government to demarcate forests of high conservation values as totally protected areas, they have not been ecologically effective or environmentally meaningful. This is because to a greater extent, forests are legally classified in the "production" category meant for sustaining long-term timber production rather than environmental protection (Nagle 2009). To give a specific example, for instance, under the Statement of Forest Policy

[10] The IUCN Red List is the world's most comprehensive information source on the global conservation status of biological species. The Red List's categories of threat for the existing species include "near threatened", "vulnerable", and "critically endangered". The other two categories are "extinct" and "extinct in the wild"

(1954) or the Forest Ordinance (1958, revised in 1977) as enacted in the state of Sarawak, sustainable forestry management is mostly being interpreted as continuous flow of forest products and benefits rather than the promotion of environmental protection or sustainable resource use. Indeed, the practice of commercial exploitation remains a key component of Malaysia's approach to biodiversity management (Nagle 2009).

5.2.3 The Philippines

In the Philippines, years of unmitigated and uncontrolled forest destruction caused by commercial logging and agricultural conversion have contributed to tremendous loss of its original natural forests. In 1934, it was estimated that about 17 million ha of the country's land area were covered with forest (Carandang 2005). However, between 1934 and 1988, forest had been cleared at an average of roughly 198,000 ha per year. The total forest loss within this period was 10.72 million ha (Fig. 4). Out of the total area of the forest lost, roughly 95 % were converted to various economic uses such as agricultural expansions, while 0.52 % was damaged by logging activities (Rebugio et al. 2007).

Between 1990 and 2000, Philippine further lost more than 800,000 ha of forests mainly due to agricultural expansion, illegal logging and widespread timber harvesting despite government's timber harvesting bans. In fact, timber harvesting increased by nearly 30 % from 2008 to 2013 (Panela 2014). The alarming rate of forest destruction has left the country with only seven percent of its original lowland forests (PRB 2006; Mongabay 2011). Besides, the country also has lowest forest cover in the ASEAN region (World Bank 2013b, Table 4).

Out of the remaining forest habitat in the Philippines, it seems that only four percent of the area is suitable for a large number of endemic species. These include 6000 plant species and 1196 known species of amphibians, birds, mammals and reptiles (Isaacson 2011). Furthermore, according to the Philippines' Department of

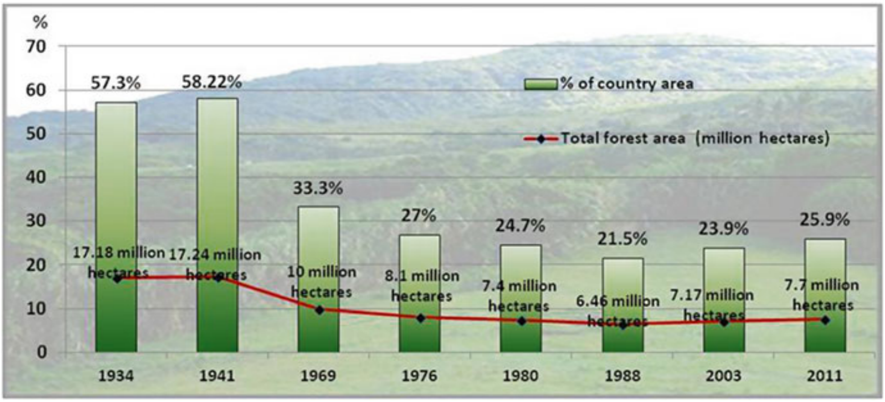

Fig. 4 Deforestation in the Philippines

Table 4 The Philippines' forest cover in 2011: a comparative view (Source: World Development Indicators: Rural environment and land use, 2013, The World Bank, http://wdi.worldbank.org/table/3.1#)

Country	Forest cover (million hectares)	Forest area (% of land area)
Indonesia	93.7	51.7
Myanmar	31.4	48.2
Malaysia	20.4	62
Thailand	19	37.2
Lao	15.7	67.9
Vietnam	14	45
Brunei Darussalam	12.7	71.8
Cambodia	10	56.5
Philippines	7.7	25.9

Environment and Natural Resources, in view of massive change in the environmental conditions, the rate of species extinction in the country is 1000 times the natural rate (Isaacson 2011). Indisputably, despite the imposition of logging ban on old-growth forests and the enactment of various legal environmental conservation instruments, the country is still losing its remaining forest at an alarming rate. Manifestly, various factors such as the abuses of logging concessions, illegal harvesting, and unsustainable use of forestry resources have worked to frustrate the objectives and effectiveness of the national environmental laws and natural resource management policies (GEF 2009; Guiang 2001).

Some of the important species which are increasingly exposed to the threat of extinction due to massive environmental change include the Philippines eagle, Philippine tarsier, tamaraw, kagwang, the Philippine tube-nosed bat, the Philippine spotted deer, Calamian deer and the Philippines forest turtle, among others (Maala 2001; Duckworth et al. 2012; Conservational International 2011). Species which were unable to withstand the human force of economic destruction such as the Cebu warty pig, Panay flying fox, and Chapman's fruit bat have become extinct (Alave 2011). In view of serious habitat destruction, the Philippines supports more severely threatened endemic species than any other countries in the world (Oliver 2006; ACB 2010; Duckworth et al. 2012). It is one of the few countries that is in its entirety, both a hotspot and a mega-diverse region (Conservational International 2013). Also, the country is now classified as ten of the world's most threatened forest hotspots, and one of the top global conservation priority areas (ACB 2010; Conservational International 2011).

5.2.4 Thailand

In Thailand, biodiversity loss is mostly due to the following economic activities:

(i). Excessive logging of forests
(ii) Commercial exploitation of rare plant species
(iii) Poaching of tigers, bears, turtles, and seahorse

(iv) Overhunting of wildlife
(v) Disturbance of natural habitats caused by the clearance of mangroves for shrimp farming, conversion of peat swamps into cropland
(vi) Irreversible destruction of virgin forest for dam building and road construction
(vii) Expansion of rubber, coffee, tea and cacao plantations, among others (Delang 2005; Ministry of Resources and Environment, Thailand 2006; Stibig et al. 2007; Trisurat et al. 2011; Trisurat and Duengkae 2011).

Overall, Thailand has lost roughly 70 % of its original forest cover (Corlett 2009; Trisurat and Duengkae 2011). Since 1980, Thailand lost 43 % of its 1973's forest cover (WWF 2013). Worth noting is the stunning rate of forest loss in the Greater Mekong Sub-region which covers Myanmar, Thailand, Cambodia, Laos, Vietnam, and Yunnan and Guangxi in China. Between 1973 and 2009, the sub-region excluding China lost just under a third of its forest cover. Thailand and Vietnam experienced the highest rates of loss at 43 % each compared to 22 % in Cambodia, 24 % in Laos and Myanmar (WWF 2013). Incontrovertibly, the imposition of logging ban in 1989 and the formulation of various environmental policies such as the Forest Protection Act (1913), First National Economic and Social Development Plan (NESDP); National Forest Policy (1985), and the 7th NESDP (1992–1996) in Thailand, have not been able to contribute effectively in addressing its decades-old problem of illegal logging and upland encroachment (Lakanavichian 2001).

The extensive disruption of natural habitat has substantially increased the number of threatened mammal species in Thailand from 38 species in 2004 to 57 in 2012 (Baillie et al. 2004; World Bank 2013c). This made Thailand as having one of the highest threatened mammal species in the world. Extensive habitat disruption also affects the continued existence of range of species thriving in the region. These include 45 species of birds, 23 species of reptile and 72 species of fish (ESCAP 2011). Some of the critically endangered species which have not been able to withstand the force of human-induced ecological disturbances such as the Schomburgk's deer, Eld's deer, Kouprey, the Javan and Sumatran rhinoceros have become extinct in the country (Nabhitabhata and Chan-ard 2005).

5.2.5 Vietnam

Similar to Thailand, Vietnam has also lost 43 % of its 1973's natural forest cover (WWF 2013). Deforestation in the country is mainly caused by the expansion of coffee plantation, timber harvesting for the furniture industry, illegal logging, and infrastructure development especially dam construction (Carew-Reid et al. 2010; Drollette 2013a; OECD 2014). These economic activities impacted heavily on the ecological integrity of the country's natural forests, which are either degraded, poorly stocked or badly fragmented (WWF 1998). In 2010, its biodiversity-rich primary forest coverage dropped below one percent compared to 12 % in 2005 due to unrestrained forest exploitations (Hance 2011;

ESCAP 2011). This poses massive ecological threat of extinction of roughly 700 species of plants and 300 species of animals found in the region (Carew-Reid et al. 2010; PARC Project 2006).

The rapid disappearance of closed-canopy forest has resulted in the wild extinction of nine rare animal and plant species. These include four forest animal species, namely, the two-horn rhino, kouprey, tapir and otter civet (Ministry of Resource and Environment, Vietnam 2008; Vietnam Net 2013). According to Vietnam Red Book 2007, the total number of endangered wildlife species has increased by 161 species to 882 species. These include 418 animal species and 464 plant species (Ministry of Resource and Environment, Vietnam 2008). Particularly, the banting, the Javan rhinoceros, tiger, the Asian elephant, and the saola are increasingly exposed to the threat of extinction (CNRES 2000; Tordoff et al. 2012; Drollette 2013b). The 2007 Red Book revelation indicates a worrying situation about the reduction of Vietnamese flora and fauna resources. Indeed, Vietnam is now regarded as one of the world's most endangered terrestrial ecoregions as well as a top global conservation hotspot (World Bank 2005; Sterling et al. 2006; Hilton-Taylor et al. 2009). It is increasingly clear that the enactment of one of its most comprehensive environmental protection laws, the Biodiversity Law (2008) has not been effective to address its exploitative mode of resource utilization and biodiversity destruction (Nagle 2009).

It is also relevant to note that in all the ASEAN-5 countries, poaching and illegal wildlife trading also exarcebate the ecological quagmire in the region (Sodhi et al. 2004, ASEAN undated). The alarming scale of illegal wildlife trade in the region has resulted in the drastic decline of the number of high commercial value species such as the tiger, elephant, rhino, pangolin, and wild orchids and rare plants in Indonesia and Vietnam (ACB undated). If left unchecked, illegal wildlife trade will lead to massive and irrevocable loss of many of the world's unique and rare species endemic to the region (Nayar 2009; Inciong 2013). It is noteworthy that Malaysia, Indonesia, the Philippines and Vietnam share the dubious reputation of being among the world's top ten wildlife smuggling hubs (Felbab-Brown 2011; Gooch 2011).

6 Environmental Laws and Ecological Conservation-the Paradox

It is manifestly clear from the above discussions that the well-entrenched institutional and legal frameworks have not been effective in addressing the environmental problems in the region. In fact, the overall regional environment has worsened and new environmental threats and challenges continue to emerge. Indeed, the above quantitative environmental and ecological investigation provides ample evidence of growing level of environmental degradation across the region. This strongly suggests that decisions on "sustainable resource use" in the region were mostly guided by self-interest and economic maximization motive so much so that the well-established legal and institutional instruments were ineffective in containing environmentally destructive resource use practices under the guise of "sustainable development".

Viewed from the Asian perspective, sustainable development is often taken to mean growth that lasts for an indefinite period of time, and the meaning of sustainability is to a large extent, referred to sustaining economic growth and consumption rather than sustaining the ecological health of the natural environment. Thus the Asian concept of "sustainable development" has in practice contributed to exposing the regional environment to heightened risks of over-exploitation and ecological destruction.

The Asian environmental paradox bespeaks the fact that institutional capacity building and legislative enactment alone cannot offer an adequate tool for containing the massive biodiversity disruptions across the region. As it turned out, the regional environmental issues or ecological problems are not due to the deficiency of environmental laws but basically owing to the lack of an ethical commitment to environmental protection and sustainable resource use. Put it bluntly, the Asian environmental problem is a behavioral problem -a moral failure that led to collective stewardship collapse. To bring the regional environment in closer accord with the Brundtland's trait of sustainability, substantial changes in human responses to the environment based on the ethical principles of natural resource use is a *condicio sine qua non*. This will be examined in the ensuing section.

7 Environmental Ethics: The Key to Ecological Sustainability

The Asian environmental protection initiatives have failed to bring an environmentally sustainable mode of development in the region because the regional policy makers were too preoccupied with the self-interested aims of catching up with the industrial West in term of higher economic growth and material progress. Natural resource use ethics in the region were and are still fundamentally governed by economic motives, entailing little environmental protection obligations. Thus, despite having comprehensive environmental protection frameworks in place, conservation still proceeds at a snail's pace. The remedy here is to find ways to change the self-interested and exploitative mode of environmental behaviour when optimizing the economic use of nature.

To wit, no important change in environmental behaviour or natural resource use ethics was ever accomplished without improving our relationship with the natural environment. However, we can be ethical only if we see ourselves as a part of the natural world. In this regard, a proper understanding of the ethical connection between humanity and the natural environment is appropriate. To wit, nature provides various ecosystem services through biological, chemical, and physical interactions between biotic (living) components such as plants, animals and other living organisms, and abiotic (non-living) components such as air, water, soil and sunlight.

Some of the critical services provide by the ecosystems to sustain human wellbeing and continued existence include climate change regulation, drought and flood mitigation, detoxification and decomposition of toxic or industrial wastes, and air and water purification, among others. It is no exaggeration to say that man's continued existence and long-term socio-economic prosperity hinges on maintaining the ecological health of the ecosystems, that is, the capacity of ecosystems to deliver a continued flow of regulating functions, services and control mechanisms over time. Undoubtedly, as it is made clear above, sustainable use and management of ecosystems constitutes one of the major challenges facing the Asian region today.

It may thus be remarked that humans, being an interdependent part of nature, owe a moral responsibility to preserve the health of the ecosystem out of ecological necessity and ethical imperative for protecting the welfare of not only the present but also, the future generations. These ecological and ethical responsibilities are some of the most defining mental representations of our relationship with nature. Indeed, these beliefs have a central place in the foundation of environmental ethics. Environmental ethics may be defined as a set of moral principles that guides certain forms of right conduct toward non-human natural entities. According to Aldo Leopold, who is universally hailed as the father of contemporary environmental ethics, a conduct is right "when it tends to preserve the integrity, stability, and beauty of the biotic community and "is wrong if it tends otherwise" (Leopold 1949:224–225). Biotic community includes "soils, waters, plants and animals" or collectively, land (ecosystem) (1949:204).

Leopold explicitly asserts that an ethical relationship with nature is based on "love, respect, admiration and a high regard for its value" (1949:223). By value, Leopold means intrinsic value, that is, value in the "philosophical sense" (1949:223). More specifically, intrinsic value refers to value that something has for its own sake regardless of its value to humanity, for itself or as an end in itself, not just a means to another end. The source of value for intrinsically valued objects is not their use, but rather the value they have beyond their use, or in spite of their usefulness. Intrinsic value may be conferred by a valuer on an object. In this case, we may say that the object has value for its own sake. Intrinsic value of an object may also arise independently of the valuation of valuers. In such a case, we may say that the object is valuable both in and for itself.

Intrinsic value may be contrasted to instrumental value. Something is said to be instrumentally valuable if it is valuable as a means to an end (Ouderkirk and Hill 2002). Instrumental value is always a function of an object's usefulness. In other words, the value of an object lies not in the object itself but in its usefulness in serving as a means or instrument to attain something else of value. Under an instrumental worldview, human beings are intrinsically valuable and all non-human entities including natural beings and objects, are valuable only as means or instruments which serve human interests (Callicot 1989). Instrumental value is often associated with money, commodities or materialism. Considering the natural environment such as forest or wilderness as a resource base is to treat it as having instrumental value. Implicitly, many environmental problems arise out of the instrumental value human beings overly placed on nature (Des Jardins 2013). More specifically, one of the main causes of environmental problems in the Asian economies is their strong tendency to prioritize economic growth or human consumption over sustainability concerns, which is, in turn, attributed to the lack of ethical considerations for the environment on the part of the stakeholders when optimizing the instrumental or economic use of nature.

When human beings continue to exhibit a strong inclination to treat the natural world as having mere instrumental value, it will tend to lead to serious threats of unrestrained exploitation of natural resources, biotic despoliation or environmental destruction. This is because mere human interests on the instrumental worth of nature do not point to the general ethical desirability for preserving the integrity, stability, and beauty of the biotic community. Under the instrumentally dictated resource use system, nature is a means, not an end in itself and thus, the name of the game is to optimize the economic use of nature for achieving the highest material gains possible. Thus, it is a lack of love, respect and moral concern for non-human entities that induces humans' abusive use of nature.

Precisely, as what Leopold has conceded, we abuse the use of nature because we regard it as a commodity belonging to us. Nonetheless, if we were to see nature as a community to which we belong, that is, seeing ourselves as a part of it, we will feel obliged to undertake the "obligations over and above self-interest" to preserve its integrity and continuous existence (1949:209). The metaphor, "community" denotes the interconnectedness or interdependence between human beings and the natural world (Rolston 2000). Here, apart from human beings, the non-human entities are also considered as intrinsically valuable. Wild-flowers and songbirds are such examples. As Leopold declared, wildflowers and songbirds, many of which cannot put into "economic use" are entitled to continuance as members of the biotic community because they are intrinsically valuable (1949:210). Humans, being a part of nature are obliged to show appropriate concern for and duties to protect the intrinsic value of these natural beings or other non-human entities, which made up the biotic community.

These duties may be discharged through the "extension of the social conscience from people to land" and "a limitation on freedom of action in the struggle for existence", collectively called here the ecological conscience (Leopold 1949:223; 202). In other words, human beings should exercise restraint when optimizing the economic or instrumental use of nature so as to avoid exerting undue influence on the intrinsically valuable biotic community. The development of the ecological conscience based on the integration of environmental values and the change of environmental attitudes, rather than simply from the imposition of environmental laws, represent one of the most effective means in protecting the integrity, stability, and beauty of the biotic community. From a practical point of view, such ethical and environmental attitudes would not only encourage us to maintain a state of harmony with nature but also, to induce us to undertake the obligations to protect its ecological integrity and continued existence for the benefits of future generations (Callicott 1989).

However, it may be noted that the extension of Leopold's ecological conscience to nature does not necessarily call upon us to completely withhold any form of ecological disturbances to the natural environment. Rather, it requires us to undertake certain forms of moral obligation to protect the integrity and stability of the environment when harnessing its instrumental use. This is well reflected in Leopold's assertion that, "conservation means harmony between men and land" (1999:207). That is to say, it is a "positive exercise of skill and insight" to keep "the resource in working order, as well as preventing overuse" (1999:164). In other words, when optimizing the economic use of nature, there is a need to observe its ecological health so as to preserve the intrinsic value of the non-human entities. Leopold defines ecological health as the "capacity for self-renewal in biota" (1999:164).

In above connection, it may be of interest to note that Leopold's ecological health concept found a correspondence with the ecological sustainability concepts eloquently examined by Crawford Stanley Holling, an ecologist who is often acclaimed as the founding father of resilience theory for his pioneering work on ecosystem dynamics and ecological resilience. From an ecological perspective, Leopold's "capacity for self-renewal in biota" may be interpreted as ecological resilience of the ecosystem. Resilience or more specifically Holling's resilience, is defined as "the ability of a system to maintain its structure and patterns of behavior in the face of disturbance" (Holling 1986:296). Put differently, Holling's resilience is a measure of the ability of a system to absorb changes in the face of disturbances (Holling 1973). An ecosystem or an integrated system of human beings and natural resources ("biotic community" in Leopold) is said to be resilient if it is able to withstand external pressure when disturbed and retain its domain of attraction (Holling and Walker 2003).

In summary, environmental ethics plays an important role in influencing human beings to make ecologically sustainable decisions when optimizing the economic use of nature (Choy 2014b). It also helps us to be more aware of and concern for the risk of causing irreversible damage to natural landscapes to the detriment of future generations. More particularly, environmental ethics is a moving force of behaviour which encourages us to be more ecologically minded in affirming the virtue that human beings are a part of nature, that is, members of the biotic community, and that the ecological health of the natural environment should be protected as a matter of biotic right irrespective of the presence or absence of economic values. This will draw us nearer to admitting our obligation over and above economic self-interest in our dealing with nature, and refrain from acting in a manner that causes extensive and irreversible destruction to the natural environment. In what follows is an empirical study to show how the admission of our ecological conscience to nature could be brought to bear upon questions of sustainable resource use and management in a real world system.

Fig. 5 Geographical indication of the targeted areas of study

Table 5 Targeted areas of study in Sarawak, East Malaysia

Year	Month	Name of longhouse/tribe	Location
2007	May	Mudung Ambun (Kenyah)	Bintulu
	May	Terbila Tubau (Kenyah)	Bintulu
2008	February	Ado Bilong (Penan)	Bintulu
	May	Long Bala (Kenyah)	Bintulu
	May	Long Apok (Penan)	Bintulu
	May	Rumah Anthony Lerang (Kenyah)	Bintulu
	August	Rumah Bagong (Iban)	Bintulu
	August	Rumah Jalong (Kenyah)	Bintulu
	August	Long Biak (Kenyah)	Bintulu
	August	Kampong Gumbang (Bidayuh)	Kuching
	August	Tanah Mawang (Iban)	Kuching
	August	Nanga Entawai (Iban)	Sibu (Song)
	August	Kulleh Village (Iban)	Sibu (Song)
	October	Rumah Amit (Iban)	Bintulu
	October	Rumah Mulie (Iban)	Bintulu
	October	Rumah Kiri (Iban)	Bintulu
	October	Uma Sambop (Kenyah)	Bintulu
	November	Rumah Akeh	Miri
2009	January	Long Lawen (Kenyah)	Bintulu
	January	Long Wat (Penan)	Bintulu
	January	Long Pelutan (Penan)	Bintulu
	January	Long Peran (Penan)	Bintulu
	January	Long Jek (Penan)	Bintulu
	July	Long Koyan (Kenyah)	Bintulu

(continued)

Table 5 (continued)

Year	Month	Name of longhouse/tribe	Location
	October	Rumah Sekapan Pitt (Kenyah)	Bintulu
	October	Long Dungun (Kenyah)	Bintulu
	October	Sekapang Panjang (Kenyah)	Bintulu
	October	Rumah Aging Long (Penan)	Bintulu
	November	Kampong Sg. Entulang (Iban)	Miri
	November	Kampong Sg. Buri (Iban)	Miri
	November	Long Laput (Kayan)	Miri
	November	Long Tutoh (Kenyah)	Miri
	November	Long Ikang (Kenyah)	Miri
	November	Long Banyok (Kenyah)	Miri
	December	Long Miri (Kenyah)	Miri
	December	Long Na'ah (Kayan)	Miri
	December	Long Pillah (Kayan)	Miri
	December	Long Kesih (Kayan)	Miri
2010	February	Arur Dalan (Kelapit)	Miri (Bario Highland)
	February	Bario Asal (Kelapit)	Miri (Bario Highland)
	February	Ulung Palang (Kelapit)	Miri (Bario Highland)
	August	Rumah Busang (Iban)	Miri
	November	Rumah Ranggong, Sungai Sah (Iban)	Miri (Niah district)
	November	Rumah Umpur (Iban)	Miri (Niah district)
	November	Rumah Ampan (Iban)	Miri (Niah district)
	November	Rumah Usek (Iban)	Miri (Niah district)
	November	Rumah Tinggang (Iban)	Miri (Niah district)
2011	February	Batu Bungan (Penan)	Mulu (near Miri)
	February	Long Iman (Penan)	Mulu (near Miri)
	February	Long Terawan (Berawan)	Mulu (near Miri)

8 Environmental Ethics: An Empirical Assessment

This section is an attempt to reinforce the argument that the existence of ecological conscience tends to encourage a conviction of individual responsibility for preserving "the integrity, stability and beauty" of the biotic community based on a field study conducted in the state of Sarawak in Malaysia. The fieldwork, which was conducted between 2007 and 2011, covered 50 indigenous settlements located mostly in the forest interiors in the state (see Fig. 5; Table 5). One of the main aims of the fieldwork was to assess the relationship between environmental ethics and environmental conservation. More specifically, it evaluates the contributions of the local people's environmental worldviews and moral environmental sentiments to preserving "the integrity, stability and beauty" of the biotic community in the local region.

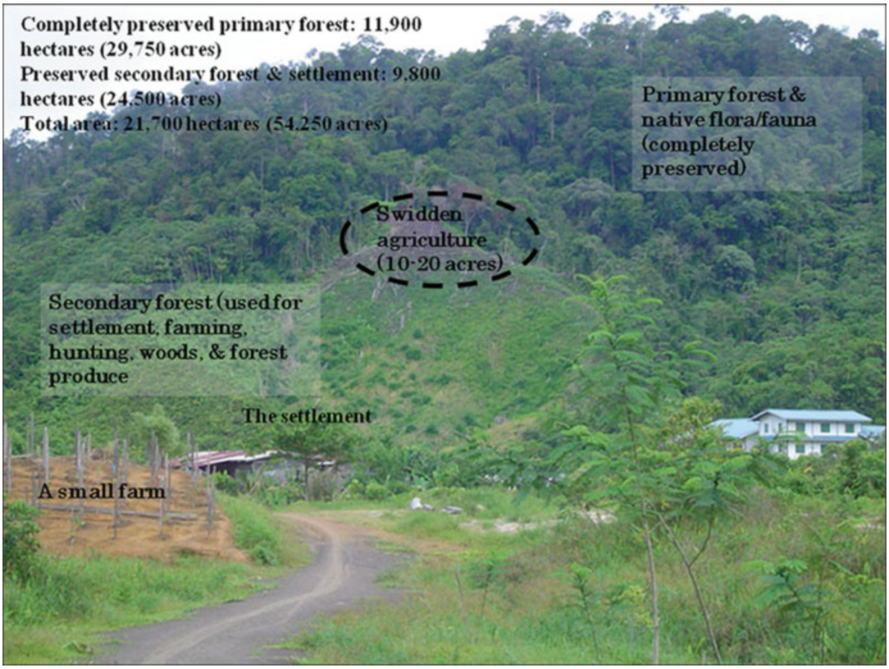

Fig. 6 Indigenous land use patterns (a diagrammatic representation)

Fieldwork and interviews were conducted with the indigenous people, including village headmen and old and young men and women through random house visits and field encounters. Interviews were primarily conducted in the Malay language and all the translations are mine. On average, 10–15 households from each longhouse were interviewed. Unless otherwise indicated, the names of the interviewees are withheld in order to protect their privacy, as agreed with them.

To start, when asked about his views on his community's environmental perceptions during an interview conducted in 2009 in Long Lawen, the community's chief, Gara Jalong, replied:

> *Lands and forests are our Datuk Nenek Moyang Temuda* (*ancestral domain*). *They are a* '*green bank*' *for our cultural identity and socioeconomic survival. Our community possess 21,700 hectares of forests and out of these, 11,900 hectares are marked as completely preserved areas. These are our communal forests and we are bounded by our* adat (*custom*) *to protect them from degradation so that they could be passed down to our future generations in good state*…. (Fig. 6).

He further added that:

> *In order to use our land resources sustainably, each household, depending on the size of its family, uses about 10 to 20 acres of the secondary forests for shifting cultivation. The same piece of land is used over and over again after it is allowed to replenish. In this way, we are able to manage our lands and forest in a sustainable way*… (Fig. 6).

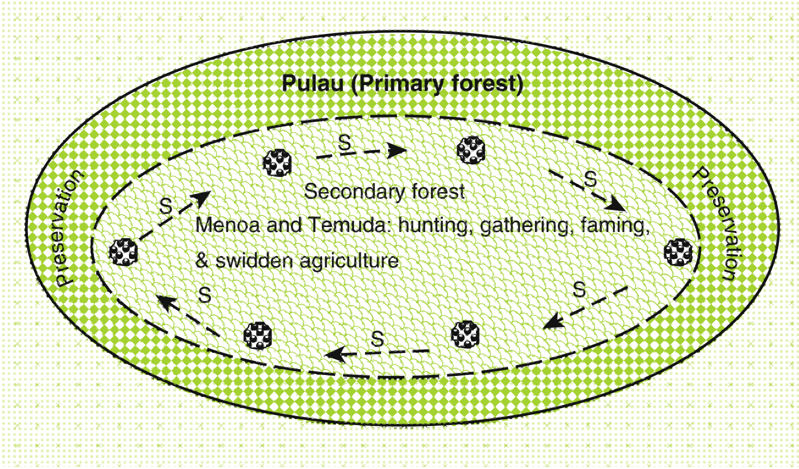

Fig. 7 Indigenous land use patterns in Long Lawen, Sarawak, Malaysia (Source: Choy 2004)

Basically, the local communities' land use system may be categorized into three distinctive patterns as follows:

(i) Hunting and gathering in the forested region, known as *pemakai menoa*,
(ii) Farming on agricultural land located in the vicinity of the tribal longhouses, called *temuda*, and
(iii) Preservation of old-growth forest, termed *pulau*. The *pulau* preservation initiative aims to protect catchment areas and the medical plants and fruit trees found in these areas. Taken together, *pemakai menoa*, *temuda*, and *pulau* constitute the ancestral domains of the indigenous communities (see Figs. 6 and 7).

Datuk Nenek Moyang Temuda or ancestral domain refers to lands on which the indigenous people have lived since time immemorial. Historically, it contributes to defining the cultural identity and spiritual attachment of the communities to their traditional lands. Furthermore, the term "*adat*" (custom or moral codes) refers to the oral traditions, cultural beliefs, rights and responsibilities, and customary practices that were created, nurtured, and preserved by previous generations based on their daily interactions with nature. These normative unwritten rules have been inherited wholly or partially and further developed by successive generations over the past few centuries (Colchester 1993). *Adat*, which is obligatory rather than cohesive, not only governs the social behaviors of the local communities but also, prescribes certain ethical norms in the use of the natural environments in such a way as to avoid massive and irreversible destruction to the natural surroundings.

It is particularly noteworthy that during a farm encounter, Unit Liah, in her mid-30s, was asked whether she would give up her land resources for, say, one million Malaysian ringgit (roughly US$267,000 as of June 12, 2015), which would allow her to buy anything she wanted (such as a big, modern house, a car, and other luxurious items). Her reply was:

> *Of course not*! *Land resources are the most important things to us. They are not meant for sale. What is money without land*? *The dense-forested place here also gives our people pleasant and comfortable living conditions compared to town area.…although we are not rich*, *we are happy and satisfied living here…Our adat also requires us to protect the land for the benefits of our children…* (2009).

We conducted further interviews with other local inhabitants in the same year, including Juk Nyok Along, Loong Lian, Siting Selong, Suti Lawa, Nyanting Anyie, Julit, Sam, and Chu from *Long Lawen* and Engkong Muang, Mamay, Uluk Impung, and Yaos, among others, from *Long Anau*, a subsidiary settlement of the Long Lawen communities located near the logging camp.[11] All similarly reported that they feel psychologically comfortable, spiritually satisfied, and economically stable living in the forests. They also conceded that they were bound by their *adat* to use the land in a sustainable way by practicing shifting cultivation in order protect the interests of their future generations.

In order to furnish a large sampling and a qualitative index of the overall studies, field research was also carried out in other areas of the forest interiors in the following settlements. Similarly, the communities were surveyed about their environmental morality, cultural beliefs, and ways of life as noted above. A few selected revelations from the interview processes are worth noting:

1. Long Peran (Penan community) – The chief of the longhouse affirmed that the local people are bonded by their *adat* "*to use the natural resources sustainably and to protect them from degrading for the benefits of our future generations… and we feel happy roaming around in the forested areas and listening to the birds*' *sound…*" (2009)
2. Rumah Aging (Penan community) – The chief of the longhouse contended that, "*We show a lot of respect and love to our surrounding areas including the trees planted by our Datuk Nenek Moyang* (*ancestors*)*…when we see the fruit trees they planted bearing fruits*, *we feel joyful and grateful to them…*" He further disclosed that, "*Sometimes we feel a sense of emptiness in our heart when we see some of the forests surrounding our areas have been felled for plantation development…we also feel sad when some of the wild birds which used to rest or fly around in our areas disappeared because of this…*" (2009)

   (i) Interviews were conducted with the local communities from other longhouses including Mudung Abun (Kenyah community), Terbila Tubau (Kenyah community), Uma Sambop (Kenyah community), Long Bala (Kenyah community), Long Apok (Penan community), Rumah Anthony (Kenyah community), Long Pelutan (Penan community), Long Wat (Penan community), Long Jek (Penan community), Long Koyan (Kenyah community), Rumah Sekapan Pitt (Kenyah community), Rumah Sekapan Panjang

[11] The establishment of the subsidiary settlement near the logging camp is to enable the local communities to market their agricultural products.

(Kenyah community), and Long Dungun (Kenyah community), among others. Villagers in all of these communities also share common ethical and moral orientations toward their land resources. For instance, in a revealing statement, the longhouse's chief from Uma Sambop had the following to say: "*An indigenous individual who has lost his ancestral lands is just like a ship without a captain…*" (2008).

The moral and environmental trends of the local communities as revealed from the above interviews may be simply summarized as follows:

(i) All unanimously concurred that traditionally they owe a moral responsibility to use their land resources sustainably and to protect them from alienation for the benefit of their future generations.
(ii) All show due respect and passion toward their surrounding areas, including the trees planted by their ancestors. This harmonious human-nature relationship is harnessed through the local people's daily interaction with nature.
(iii) All those who have travelled to town areas feel that they are happier living in the forests than in the town because forests give them a sense of belonging.

9 Indigenous Land Use Philosophy: Some Remarks

The above revelations uncovered some of the salient features of the ethical and moral orientations of the local communities toward the natural environment. To start, despite the diversity among indigenous groups, tribal languages, and geographic locations, all respondents in the forest interiors consistently recognize the cultural and spiritual importance of the forest landscapes that were once the dwellings of their remote ancestors. To the local communities, the forest landscapes are apparently reverential in the sense that they are imbued with an array of sentimental qualities such as cultural values, social morality, passion, and spiritual and psychological significance, among others.

Essentially, the indigenous centuries-old adat (culture) command the local communities to use their forest resources sustainably so as to protect "the integrity, stability and beauty" of the natural environment for the benefit of their future generation. To the local communities, the natural environment is not only instrumentally valuable but also intrinsically regarded for its non-economic or non-use values such as cultural, aesthetic, spiritual, and psychological values. The indigenous belief in environmental value pluralism induced certain psychological attributes of land resources, such as the belief in moral duty or fiduciary responsibility to protect the natural environment from degradation for the benefit of future generations.

More specifically, indigenous perception on nature is based on a matrix of the spiritual, ecological, ethical, social, aesthetic, and psychological affection or satisfaction they derive from their interactions with the biotic community. This simply means that to the local communities, land resources are to a great extent intrinsically valuable (Choy 2014b). These environmental dispositions serve to guide the local communities in determining how much of their ancestrally defined forest landscape they should preserve, how much culturally modified landscape they should demarcate, and in what ways the land should be modified in order to foster mutually enhancing human-nature relations that are in accord with their *adat* (Choy 2014b). An important lesson that may be drawn from these observations is that if a person acts in accordance to the above environmental perceptions, moral obligations, or ethical duties when optimizing the economic use of nature, this tends to result in more prudent resource use patterns.

What may further be remarked is that sustainable resource use and environmental conservation cannot be decoupled from the ethical principle of environmental sustainability. It is also explicitly comprehensible that if decision-making on natural resource use were predominantly dictated by economic motive, there will be little hope that the growing ecological impairment in the region can be contained effectively based on legislations or environmental policies alone. Indeed, all strategies for environmental control or ecological conservation are not just solely concerned with legislative requirements. This is made clear from the failure of the Asian ways in containing widespread environmental disruptions in the region based on authoritative rules and regulations. Besides, ethical or ecological values cannot be legislated or decreed based on environmental laws. It can only be inculcated based on education. Upon this account, it is fair to say that the unsustainable nature of the Asian course of development is unlikely to be mitigated let alone halted, so long as the ethical percepts for sustainable resource use does not find an unequivocal expression in economic reasoning or the legislative order.

10 Concluding Remarks

The policy objective of rigorous economic growth has been paramount in the political agendas of the Asian region. Typically, rapid economic growth in the region is achieved with more attention paid to economic benefits than to costs, in particular ecological costs. This is reflected by the mushrooming of a wide range of dominant economic activities in the region such as timber extraction, commercial-scale monoculture conversion, and mega dam or large-scale infrastructure development, all seek to optimize the highest level of economic advantage possible out of nature. That is to say, the environment is viewed instrumentally as a resource base to satisfy the needs of economic growth and human material consumptions. This is in stark contrast to the indigenous people in the tropical rainforests in Sarawak who take the view that the environment is not only instrumentally valuable but also, intrinsically worth.

There is thus something profoundly incoherent in the regional dominant growth models despite having being shown to be receptive to the natural environment by putting in place a wide range of environmental legislations to regulate the destructive force of the economic growth processes. It may well be that by and large; the current ecological predicaments in the region are an attitudinal issue and implementation problem rather than a product of legislative deficiencies. Put otherwise, the root of the problem mainly lie in the lack of intrinsic moral standing on the part of policy makers or economic agents when optimize the economic use of nature.

It should be clear by now that whether policy makers or economic agents would choose to get unhooked from ecologically damaging economic activities ultimately depend on how they embrace nature. That said, the ecologically destructive transformation of natural environment in the Asian region will neither be reduced nor halted if the ethical concerns of environmental sustainability failed to find an unequivocal expression in their economic systems or legislative orders. We have to conclude that the Asian natural environment would not be what it is today had the regional policy makers or economic agents embraced the ethical philosophy of sustainable resource use in the real sense of the meaning.

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