The Curious Incident of the Wasp in the Fig Fruit: Sex Allocation and the Extended Evolutionary Synthesis

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David M. Shuker

Abstract

How would we tell if we needed a new evolutionary synthesis? The rationale for the so-called Extended Evolutionary Synthesis (EES) is predicated on there being limitations, failings, or something missing from the current body of theory that evolutionary biologists use when seeking evolutionary explanations for the patterns of biodiversity we see around us. A number of topics have allegedly been neglected or obscured by evolutionary biologists, including the role of development in evolution ("evo-devo"), phenotypic plasticity, niche construction, behaviour, epigenetics, and trans-generational effects. These disparate topics more or less coalesce around two organising principles of EES thinking, that of organismal agency and non-genetic inheritance. In this chapter, I use the field of sex allocation to test the validity of the arguments that these topics have indeed been neglected. Sex allocation is a useful exemplar of evolutionary biology. Thanks to Fisher and Hamilton, it has a historically rich and well-understood theory base. Moreover, across more than five decades, there have been hundreds of empirical tests of components of that theory, across a huge diversity of organisms, such that sex allocation is one of the most successful and well-validated fields within evolutionary biology. If claims of the EES have credence, then the study of sex allocation should clearly highlight what we have missed or ignored. However, I show that all of the components put forward by proponents of the EES as needing to be added into evolutionary biology—with perhaps the exception of cultural evolution, as least outside of humans—have long been studied, implicitly and explicitly by those studying sex allocation. In many cases, the relevant concepts are there at the inception of the modern study of

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D. M. Shuker (✉)
School of Biology, University of St Andrews, St Andrews, UK
e-mail: david.shuker@st-andrews.ac.uk

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sex allocation, following Hamilton's ground-breaking paper in 1967. Having dispensed with the need for the EES, I finish by trying to understand why such a synthesis was ever called for in the first place.

Keywords

Evolution · Extended evolutionary synthesis · EES · Natural selection · Sex allocation · Sex ratios

29.1 Introduction

It is a truth, universally acknowledged, that an evolutionary biologist in possession of a new theory must be in want of a new evolutionary synthesis. Or at least, given the attempts to re-write evolutionary biology in recent years, it certainly sometimes feels like it (Welch 2017). Research fields and concepts such as evo-devo, niche construction, extended heredity, soft inheritance, epigenetics, phenotypic plasticity, and cultural evolution have been developed in the light of, or requisitioned in the hope of, providing a new over-arching framework for evolutionary biology, generally termed the Extended Evolutionary Synthesis (EES; Pigliucci 2007; Laland et al. 2014, 2015; Müller 2017; Uller and Laland 2019). Yet the proponents of the EES have so far failed to convince many evolutionary biologists that a major conceptual readjustment is necessary (Wray et al. 2014; Charlesworth et al. 2017; Futuyma 2017; Svensson 2020; other chapters in this volume). What is going on? Such a disagreement conveniently fits the narrative of an entrenched orthodoxy, gamely resisting attempts to undermine its intellectual integrity in the face of overwhelming and conflicting data, fighting off the oncoming paradigm shift for all it is worth. Moreover, as mortality has been suggested to be a primary driver of intellectual change (see Azoulay et al. 2019, following the famous quote by Max Planck), perhaps not enough ageing population geneticists are dead yet (see Charlesworth 2013 for a theoretical treatment of why they are not). Alternatively, perhaps the EES does not provide the novelty or newness needed for it to be a game-changing new paradigm after all?

As with any such emerging body of thought, however loosely defined, the EES no doubt means different things to different people. First, it is important to remember though that evolutionary biology—or any aspect of biology for that matter—has not stood still since the period, spanning the 1930s to the 1950s, when what we now term the "Modern Synthesis" (MS) emerged from the combining of Darwinian thinking and population genetics. The MS linked Mendelian genetics (however poorly understood and conceptualised "genes" themselves were during that period) with natural selection, adaptation, and ecological genetics at the population level, through to speciation, and patterns of macroevolution under the purview of palaeontologists (for a summary, see Mayr and Provine 1980). Importantly, the MS was not one "thing", but rather an emerging consensus, across sub-disciplines, that evolutionary change was fundamentally a population genetic process, even if one studied whole organisms or fossils, and went nowhere near a molecular laboratory to look at proteins, or eventually DNA. Behavioural ecology is a good example of a field that emerged and flourished in the years following the MS, using evolutionary principles—or at least natural selection—to explain the origin and maintenance of behaviour, despite being rather agnostic about genetic details (Krebs and Davies 1978; Grafen 1984; Davies et al. 2012).

This lack of standing still has meant that any evolutionary textbook published since the 1930s–50s is necessarily "extended" in its treatment of phenomena within the scope of evolutionary biology (a point often made, e.g., Wray et al. 2014; see also Rose and Oakley 2007 for examples of how simpler thinking, especially about genes and selection, during the MS has been superseded). This is most obviously true if we think of the ground-breaking work of Bill Hamilton for instance, such as his conceptualisation of inclusive fitness (Hamilton 1964; for his full contribution, see Hamilton 1997, 2001, 2005; Segerstrale 2013; Gardner, this volume). Or if instead we consider the realisation of the importance of neutral genetic variation, and thus genetic drift, in evolution, especially in terms of understanding evolution at the molecular level (Kimura 1983; the debates over the importance of drift versus adaptive evolution, for instance, at the genomic level, continue, but no-one doubts the ubiquity of genetic drift). Inclusive fitness and the neutral theory of evolution have provided two enormous theoretical contributions to evolutionary biology, extending its scope dramatically, including the range of phenomena we can explain. However, both were developed as part of, and remain situated within, the framework inherited from the MS and did not require a paradigm shift from the view of evolution as a population genetic process (see also Futuyma, this volume).

Likewise, little has stood still empirically either, although perhaps many of our most important findings have been to confirm, from phenotype to genotype, the action of evolution (from bacteria in the lab, to finches in the wild: Bell 2007; Grant and Grant 2010), and the genetic underpinnings of that evolution (Charlesworth and Charlesworth 2010). That said, many empirical findings have also shaped and extended our conceptual space, from the discovery of the near ubiquity of mate choice and post-copulatory sexual selection (Andersson 1994; Parker 1970; Eberhard 1996; Simmons 2001), to the murky world of genomic conflict, with its transposable elements, endosymbionts, driving chromosomes, and truly selfish genes (Burt and Trivers 2006). Therefore, many if not all evolutionary biologists surely agree on some form of "Extended Modern Synthesis", in which the foundational tenet of *evolution as genetic change* is used both to interpret and inform our observations, be they of fossils, feathers, or foraminifera. For the rest of the chapter, I will view evolution as genetic change occurring within populations across generations and call the population genetic view of evolution that has developed from the original Modern Synthesis, with all its subsequent theory and experiment, Standard Evolutionary Theory (SET). SET has not stood still in terms of its content, but its over-arching conceptual framework would be familiar to the architects of the original Modern Synthesis.

However, others have argued that we need a truly new, truly extended evolutionary synthesis that does more than tinker with the Modern Synthesis and the resulting

SET (Laland et al. 2015; Müller 2017). Despite the previous discovery of ground-breaking new theories and empirical observations such as those alluded to above (of which I have barely scratched the surface), it is only comparatively recently that this EES has been called for, one that replaces SET. There will, of course, be those who find themselves in between these positions (e.g. one reading of Bonduriansky and Day 2018 is to place those authors there, as they state they are not challenging SET but rather showing how trans-generational effects fit into SET), but in many cases it seems that the end-point of EES thinking is the *replacement* of SET, rather than its continued burnishing with new theory or data (EES proponents vary on the scale of change required, but the changes apparently needed by evolutionary biology are generally non-trivial: see summary in Lewens 2019). And that is what I wish to critique and to understand. In particular, I wish to explore the EES by reviewing one of the best studied phenotypes in all of evolutionary biology: sex allocation. Sex allocation benefits from an especially rich theoretical background, with its origins with Darwin and then Fisher—himself one of the key architects of the Modern Synthesis—and its development by Hamilton and others in that period following the Modern Synthesis. As such, we can perhaps view sex allocation as an archetypal SET trait—born of Fisher then developed and tested in his shadow ever since.

In that case, what can sex allocation tell us about the EES? To do this, I will cast sex allocation in EES terms. By this I mean that I will take all the phenomena or conceptual spaces that EES proponents say are absent or poorly developed in SET and see how our study of sex allocation has fared under those terms. This will allow us to explore the overlap between the two explanatory frameworks, the SET and EES, in a *trait-focused* way. By doing so, I will critically scrutinise the claims of the EES with a well-studied phenotype in front of us. If SET has been unable to shed light on certain aspects of sex allocation, then bringing EES principles to sex allocation should make this obvious, consolidating the claims for such an extended view of evolution. However, if sex allocation theory and experiment has already pre-empted what is offered by the EES, then clearly the EES has less to offer than proponents might think. After all, why extend something that is already working, and already encompassing the apparent novelties of the EES? So, if the EES does represent something genuinely beyond the scope of SET, we might get a glimpse of just what that is when we have finished viewing sex allocation through the lens of the EES. My treatment of sex allocation will consider behaviour, phenotypic plasticity, niche construction, ontogeny, epigenetics, and trans-generational fitness effects and inheritance of multiple kinds, and so I will interrogate sex allocation fully in terms of what the EES claims to offer in terms of new evolutionary explanations and perspectives.

29.2 What Is Sex Allocation?

Sex allocation describes how sex and resources are allocated to offspring (Charnov 1982; West 2009). In terms of how sex is allocated, sex allocation is closely linked to, yet distinct from, sex determination (Bull 1983; Beukeboom and Perrin 2014).

For some systems, how sex is determined makes the mechanistic link to how sex is allocated (for instance, by the parent) fairly straightforward, at least at a phenomenological level. For example, in haplodiploid insects (such as bees and wasps), in which male offspring develop from unfertilised (haploid) eggs and female offspring develop from fertilised (diploid) eggs, mothers can determine the sex of their offspring by releasing sperm from their spermatheca to fertilise the passing eggs or not, immediately prior to oviposition (Cook 1993; Heimpel and De Boer 2008). Similarly, in species where the sex of offspring is determined by temperature during development (as in some reptiles), parents can determine sex of offspring by where eggs are placed or buried, or by the extent to which they bask prior to egg laying (Bull 1983; Janzen and Phillips 2006).

But sex allocation is also about how resources are allocated to the offspring of each sex, and indeed this is crucial for understanding the link between sex allocation and the sex ratio of offspring (either at birth/hatching, termed the primary sex ratio, or at some later ontogenetic point, such as offspring independence, termed the secondary sex ratio; West 2009). If each sex (i.e. male and female) costs different amounts to produce, then the fitness return per unit cost of producing sons or daughters may also differ (see below). Of course, each sex may cost the same in terms of energy and resources to produce (if that cost is just an egg, which either is or is not fertilised, for example). In these cases, the sex ratio of offspring will directly reflect sex allocation.

The theory of sex allocation has its origins with Darwin, Düsing, and Fisher, although the latter is usually credited with the key insights (Darwin 1871; Fisher 1930; Edwards 1998; West 2009). Fisher argued that selection on offspring sex ratios, and the sex allocation underlying sex ratios, will be shaped by frequency-dependent selection. This means that the selection acting on the parent (here we will consider the mother, for simplicity) in terms of her sex allocation depends in part on the sex allocation decisions made by other females in the population. The usual lecture-hall example is to assume that sons and daughters cost the same to produce, and then ask which sex is the best one for a mother to produce. In a male-biased population, clearly a mother would benefit from over-producing daughters, as they would find it easy to find mates, and the mother would maximise grand-offspring production. Producing sons would only add yet more males to the population, all competing for the limited number of females. Likewise, in a female-biased population, mothers would maximise their grand-offspring production by over-producing sons, who would again benefit from limited competition to find a mating partner. As a result, negative frequency-dependent selection, favouring production of the rarer sex, would lead to an equalisation of the population sex ratio, and unbiased sex ratios. (For completeness, note that at this population equilibrium, selection on sex ratios on a clutch-by-clutch basis is very weak; as the population sex ratio moves from equality, so the frequency dependence will again strengthen.)

Crucially though, Fisher realised that selection acted not on the sex ratio per se, but rather on sex allocation, including the energy required to produce a son or a daughter. So, all else being equal, at the sex allocation equilibrium the energy allocated to sons must equal the energy allocated to daughters. Here begins then our theoretical understanding of biased, unequal sex ratios, through the realisation that all else is often not equal when it comes to sons and daughters.

The next major theoretical step-forward was made by Hamilton (1967). In an astonishing paper, Hamilton showed how the fitness benefits of producing male or female offspring can differ, and that this can lead to unequal sex ratios (from here on, we will consider sex ratio as the proportion of offspring that are male). Perhaps the most famous scenario from this paper is what happens when related offspring—usually males—compete for mates. Hamilton showed that if offspring of a single female developed and then mated together, the mother would maximise grand-offspring by producing a very female-biased sex ratio (Hamilton 1967, 1979). This would reduce competition amongst her sons for mates, and also maximise the number of possible mates each male obtained (Taylor 1981). However, as more females contribute offspring to each localised breeding patch, then the optimal sex ratio is less female-biased, as the competition among related males (e.g. the brothers from a given mother) is reduced, even though those males are now competing with unrelated males. This means that a mother could get more fitness through sons that are able to mate with both unrelated females as well as their sisters. As more and more mothers contribute offspring to a patch, so Hamilton arrived at the classic Fisherian solution, where the overall fitness return of producing a son equalled the fitness return of producing a daughter and—all else being equal—a sex ratio of 0.5 was favoured. Hamilton termed this competition among related individuals for mates Local Mate Competition (LMC).

Hamilton was not only a brilliant theoretician, but he was also a brilliant natural historian (and the two things were probably not unrelated). Hamilton knew that species such as fig wasps and various parasitoid wasps laid eggs in localised groups, and that kin interacted and mated before mated females dispersed. Unsurprisingly then, it has been amongst fig wasps and parasitoids that numerous tests of LMC theory have been undertaken (Godfray 1994; West 2009; Figs. 29.1 and 29.2), as we will consider in more detail below.

The insight that interactions between relatives of one sex may alter the reproductive value of offspring of that sex applies more generally. In fact, LMC is just one form of Local Resource Competition (LRC; Clark 1978). If offspring of one sex compete for any kind of resource (which could include mates, but also any other necessary resource, such as food, territories, or nest sites), then the same logic applies, with localised competition amongst kin leading to a reduction in the production of the competing sex. When the resources are not mates, competition for resources often occurs between females (such as in a variety of primates, Clark 1978), and so competition amongst daughters is predicted to lead to a male-biased offspring sex ratio, and indeed it does (for a review of the evidence, see West 2009). Finally, interactions need not be competitive; if interactions among kin of one sex generate fitness advantages instead of costs, for instance, through helping parents to provision subsequent broods of offspring, then Local Resource Enhancement (LRE) can occur. Under LRE, biased sex ratios are predicted in the direction of the cooperatively interacting sex, and again evidence for LRE has come from a variety of species (including cooperatively breeding vertebrates, such as the Seychelles

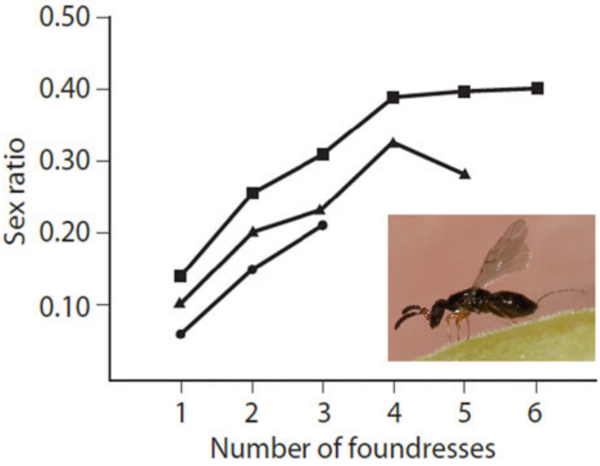

Fig. 29.1 Female fig wasps in the family Agaonidae allocate sex in line with predictions of Hamilton's theory of Local Mate Competition (LMC). Single foundresses lay extremely female-biased sex ratios, whilst as more foundresses lay eggs in the developing fig, so the number of males produced increases. Data re-drawn from Herre (1985). Sex ratio is the proportion of offspring that are male. Inset: a recently emerged female agaonid wasp, South Africa (Photo credit: Alan D Manson, CC-BY-4.0)

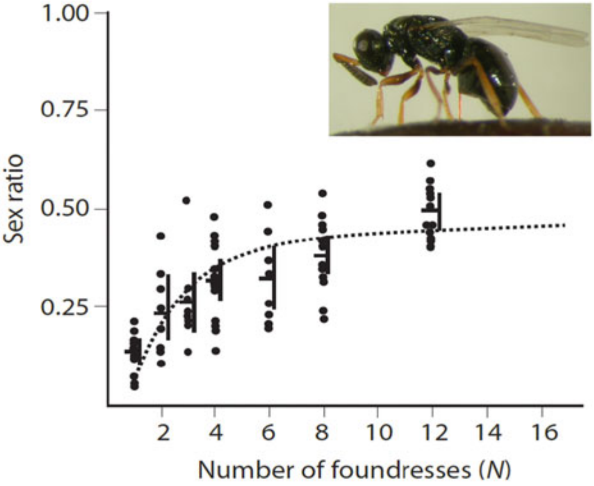

Fig. 29.2 Female *Nasonia vitripennis* parasitoid wasps facultatively allocate sex in line with LMC theory. Females respond plastically to the number of co-foundresses they lay eggs with. The dotted line is the predicted sex ratio under LMC for haplodiploids (Hamilton 1979). Data are re-drawn from Werren (1983). Insect: a female *Nasonia vitripennis* ovipositing on a blowfly pupa host (Photo credit: Dave Shuker and Stu West)

Warbler (*Acrocephalus sechellensis*), and primitively social bees: West 2009; Fig. 29.3). Importantly though, under LMC, LRC, and LRE, Fisherian negative frequency dependence is still acting, even if the optimum sex ratio is shifted from 0.5.

To go alongside the effects of interactions amongst kin influencing the reproductive value of offspring to parents, there is a second major strand of sex allocation

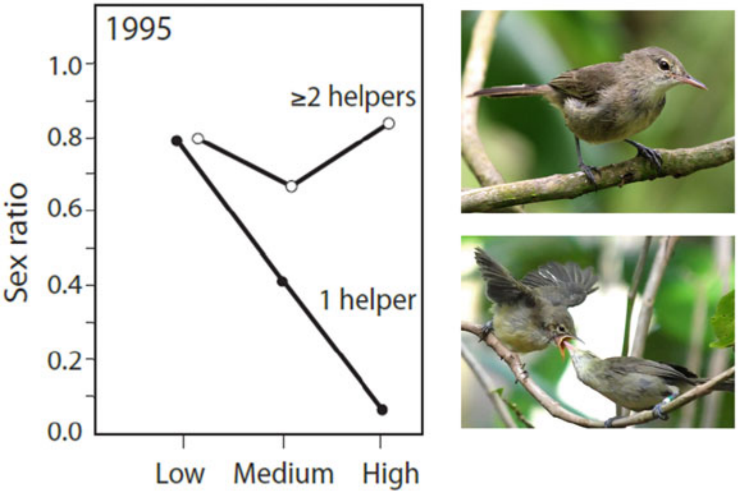

Fig. 29.3 The cooperatively breeding Seychelles Warbler (*Acrocephalus sechellensis*) allocates sex in line with predictions from Local Resource Enhancement theory. In this species, female young may remain at the next to help rear subsequent broods. In high quality territories, female offspring are favoured, in order to take advantage of the benefits of helpers at the nest. On low quality territories, there is insufficient food to support both new chicks and helpers, and so males are more likely to be produced. If more than two helpers are already present at the nest however, then the sex ratio is male-biased, regardless of territory quality. Data re-drawn from Komdeur et al. 1997. Insets: A Seychelles Warbler and feeding a fledgling (Photo credits: © Oscar Campbell; Charlie Davis). Sex ratio is proportion male

theory: condition-dependent sex allocation, also known as Trivers–Willard (TW) sex allocation (Trivers and Willard 1973; Charnov 1982; West 2009; for recent theoretical developments, see Veller et al. 2016). Under TW, the reproductive value of sons or daughters depends on the conditions under which those offspring develop. These conditions may be the extrinsic conditions of food availability, temperature, and so on, that brood experience from hatching or birth, through to adulthood. Alternatively, the conditions may be intrinsic to the parent (usually the mother), in terms of her condition and her ability to provide resources to the young (and, of course, both intrinsic and extrinsic factors may come into play).

The classic case of extrinsic condition-dependence involves sex allocation in solitary parasitoid wasps (Godfray 1994). Solitary parasitoids lay a single egg in or on an individual host (an egg, larva, or pupa of another insect, for example). The egg hatches, and the larva consumes the host, before pupating. Importantly, hosts are likely to vary in the resources they offer to a developing wasp larva. For instance, hosts may vary in size or stage of development, and thus vary in the amount or quality of food they represent. In insects, typically females benefit more in terms of fitness from a large body size than males do, as body size correlates more strongly with fecundity and hence fitness for females compared to how male body size influences fitness (for instance, through competition for mates). As such, a female

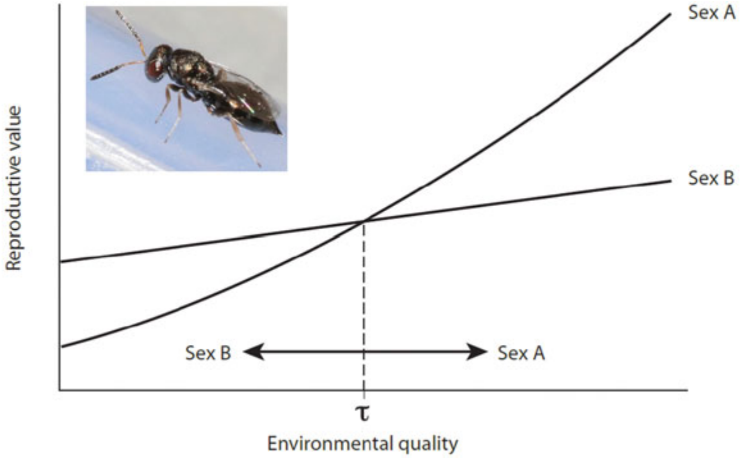

Fig. 29.4 Conditional sex allocation under the Trivers–Willard model. The reproductive value of an offspring of sex A or sex B varies with some component of environmental quality. At point τ, the fitness curves of the two sexes intersect. Below τ, production of sex B is favoured, and above τ the production of sex A is favoured. Inset: female *Anisopteromalus calandrae* places more male eggs on smaller hosts, and more female eggs on larger hosts, as predicted by T-W theory (Van Den Assem et al. 1983; Photo credit: ©James Bailey, BugGuide)

parasitoid is selected to place female offspring on large hosts, as large daughters offer the best route to fitness. However, sons still offer a route to fitness, and Fisherian frequency dependence still acts, so females are selected to produce sons when parasitizing smaller hosts. Put another way, male and female offspring have different fitness curves with relation to the size of host they develop in, and when those curves cross, offspring production should shift from sons to daughters (Fig. 29.4). This form of TW sex allocation was developed and tested by Charnov and colleagues back in the late 1970s (Charnov 1979; Charnov et al. 1981; Fig. 29.5), and since then the theory has been extensively tested and confirmed across dozens of species (Heinz 1998; West and Sheldon 2002; West 2009).

The classic case of Trivers–Willard sex allocation is associated with intrinsic condition however, in particular the condition of a mother during offspring development and the effect this has on the offspring's eventual fitness. If we consider a mammal such as a red deer, the condition of the mother influences embryonic development and size both at birth and as a yearling. Analogously to our solitary wasps, male and female deer benefit differentially from body size, only in this case large body size benefits males in terms of fitness disproportionately more than it does females. Large males are better competitors in the rut, better able to hold harems of females, leading to high reproductive skew amongst males. As such, a large son is an excellent way to produce a lot of grandchildren. Therefore, females in good condition should produce sons, whilst females in lesser condition should produce daughters (the evidence is broadly supportive in red deer, although appears ecologically context-dependent: Clutton-Brock et al. 1984, 1986; Kruuk et al.

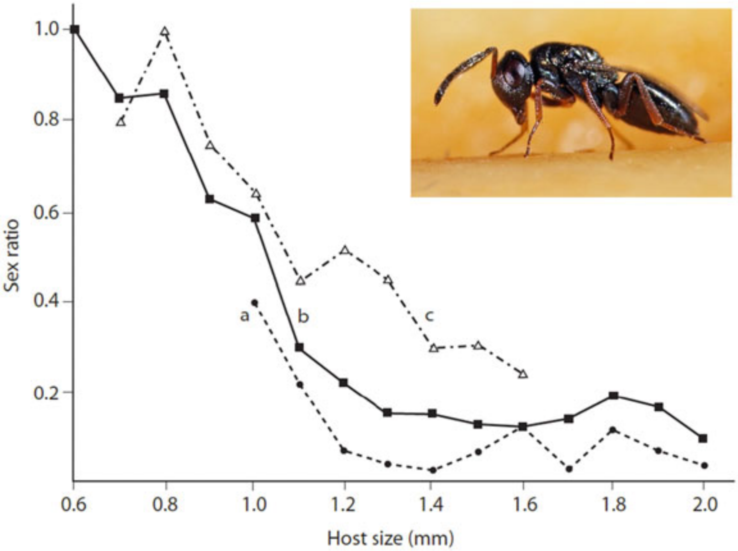

Fig. 29.5 Female *Lariophagus distinguendus* wasps vary their offspring sex ratios in line with Trivers–Willard conditional sex allocation. Males eggs are more likely to be placed on smaller hosts, and female eggs are more likely to be placed on larger hosts. The three lines (a, b, and c) represent three different protocols of presenting hosts of similar or different sizes to females and show that females take the relative size of hosts encountered into account (see Charnov et al. 1981 for details). Sex ratio is proportion male. Inset: a female *Lariophagus distinguendus* (© www.naturspaziergang.de/Andreas_Haselböck)

1999; Borowik and Jędrzejewska 2017; Fig. 29.6). Whilst more controversial in vertebrates (not least because of our poor understanding of how facultative sex allocation works in species with chromosomal sex determination, even though it clearly does: West et al. 2005), TW effects associated with maternal condition have been recorded in a number of species, and with intrinsic condition in other contexts in many more (Cameron 2004; Sheldon and West 2004). More generally, many aspects of sex allocation actually fall under the umbrella of condition-dependent sex allocation, including the evolution of sex-change in sequential hermaphrodites (Charnov 1982; West 2009), and it is probably only in a very few species that some form of condition-dependent effects are not present, however weakly, or however much they are dominated by Fisherian frequency dependence or interactions among kin. (It is worth noting that human primary sex ratios are not 0.5, but slightly male-biased, despite our chromosomal sex determination.)

All the above theory and experiment were done *within the framework of SET*. I will shortly frame such examples of adaptive sex allocation in terms of the ideas and framework put forward by the EES though, to see how sex allocation fits with the EES perspective. Beforehand, I will outline the EES in a little more detail.

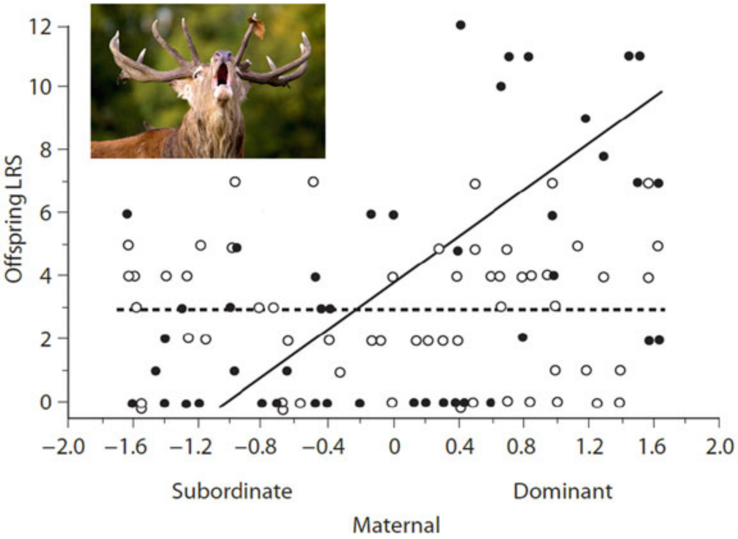

Fig. 29.6 Offspring lifetime reproductive success (LRS) varies for males (black circles, solid line) and females (white circles, dotted line) with respect to the social dominance of their mother. Dominant mothers in better condition produce the most successful sons. Data re-drawn from Clutton-Brock et al. (1984)

29.3 What Is the Extended Evolutionary Synthesis?

Briefly, the Extended Evolutionary Synthesis revolves around a set of ideas that have allegedly been (to a greater or lesser extent) excluded from, ignored by, or have only just become apparent to, the Standard Evolutionary Theory that we have inherited from the Modern Synthesis. In no particular order, these include developmental biology, phenotypic plasticity (both developmental, and at the organismal, behavioural, and/or life-history level), behaviour itself, niche construction, epigenetics, and trans-generational effects (which can be epigenetic in origin). In the interests of space, I will not pick apart the logic underlying these claims for each case, but rather I will try to distil out the essence of the claims made by the EES (e.g. Laland et al. 2014, 2015).

The EES seems to have two key components. First, there is an emphasis on *organismal agency*. This can be envisaged rather straightforwardly if we think of behaviour, as animals (and to some extent plants) can react moment-to-moment to facilitate necessary functions, such as feeding, copulating, or avoiding predators. More broadly, during development, the organism, at any or all levels of biological organisation, from the molecular through to the whole organism, can respond to internal and external stimuli, to release the next ontogenetic process or to maintain developmental homeostasis. The idea encapsulated by EES proponents when they mention phenotypic plasticity, niche construction or evo-devo say, is that organisms are not passive players in their own lives. Instead, they get involved, they do stuff. And what they do at time point x influences what happens at time point $x + 1$, and so organisms are the architects of their own futures, including the evolutionary consequences of those futures. Taken to its fullest extent, this organismal agency might lead one to change how one views causation in evolutionary biology, introducing, for example, the idea of *reciprocal causation* (Laland et al. 2011; see also Svensson 2018).

Second, there is an emphasis on *non-genetic inheritance*. This can take several forms, some of which are clearer than others. On the one hand, many organisms—including plants—influence the environment their offspring will face, and so in some sense offspring inherit aspects of their environment due to the actions of their parents (and indeed other organisms in the environment). A slightly more concrete form of non-genetic inheritance can arise if females place their offspring in environments that they themselves experienced as juveniles, so that young inherit the juvenile environment of their parent. This has been long-appreciated by entomologists however, and there is some evidence that host-plant specificity can arise in this way in phytophagous insects, leading to the formation of host races (Jaenike 1990; Feder et al. 1994; Powell et al. 2006). The mechanisms underlying these effects are less clear however (Barron 2001). The contribution of the parents to the offspring reaches its climax in the phenomenon that is so obvious as to be almost banal: parental care (the study of which is itself an active, long-standing, and non-trivial subset of evolutionary biology: Clutton-Brock 1991; Royle et al. 2012).

Another form of non-genetic inheritance within the EES is the inheritance of knowledge about the world, either from parents or other individuals in the population. Social learning is a form of between-individual knowledge transfer, and animals can "inherit" information in this way, including across generations, either through some form of teaching (a controversial concept outside of humans) or some other mechanism of social learning, such as copying or stimulus enhancement (Heyes 1994; Whiten 2019). Under some conditions, what we may think of as *culture* may arise (see below).

Finally, perhaps the most genetic-like form of non-genetic inheritance is that which occurs when epigenetic modifications to DNA (including histone modifications and DNA methylation) are inherited through the germline (reviewed by Bonduriansky and Day 2018). These epigenetic modifications do not change the DNA sequences themselves, but are chemical modifications to the DNA, in terms of ligands and associated proteins. There is growing evidence that within-individual epigenetic changes can persist via transmission through the germline (although it seems as though they are typically only *recreated* rather than directly *replicated*, as DNA itself is: Bonduriansky and Day 2018).

We will return to issues raised by these two key attributes of the EES below, but now we turn to sex allocation, viewed through the paradigmatic spectacles of the EES.

29.4 Sex Allocation in EES Terms

29.4.1 Sex Allocation as Behaviour (Organismal Agency)

From the theory and examples sketched above, sex allocation is very clearly an example of organisms having agency, and not being passive in the face of environmental conditions that influence their evolutionary fitness. Whether we think of fig wasp females varying their offspring sex ratios in the light of how many other females contribute eggs to the fig fruit (Fig. 29.1), parasitoid wasps such as *Nasonia vitripennis* varying their offspring sex ratios in response to the number of other females laying eggs on a host in order to reduce LMC among their sons (Fig. 29.2; see below), or birds such as Seychelles Warblers varying the sex ratio offspring in line with predictions from LRE theory (Fig. 29.3), we see potential interactions among kin shaping how parents allocate sex. They are definitely not passive actors.

Likewise, examples of Trivers–Willard sex allocation—from solitary parasitoid wasps such as *Anisopteromalus calandrae* and *Lariophagus distinguendus*, to vertebrates such as red deer (Figs. 29.4, 29.5 and 29.6)—show how sex-allocating females respond to prevailing environmental conditions, or indeed their own physiological condition, to allocate sex so as to try and maximise fitness. Given the development of much of the key theory in the late 1960s and early to mid-1970s, and a raft of empirical tests of that theory since the 1970s (West 2009), it is clear that at least in terms of sex allocation, evolutionary biologists (in the guise primarily of behavioural ecologists: Davies et al. 2012) have been hugely appreciative of the agency of organisms in shaping their reproductive success, the reproductive success of their offspring, and hence their inclusive fitness. Indeed, the whole of behavioural ecology—the study of the adaptive significance of behaviour—is, of course, *wholly focused* on the evolutionary consequences of behaviour. Behavioural ecologists study the way in which organisms respond, moment-to-moment, to environmental conditions, both intrinsic and extrinsic, biotic and abiotic, in order to influence their ability to pass on their genes. Sex allocation is a wonderful example, not least because of our ability to test predictions from theory both qualitatively *and* quantitatively (West and Sheldon 2002; West et al. 2002; West 2009), an ability largely unparalleled in other parts of behavioural and evolutionary ecology, thanks to the underlying simplicity of the trait and nature of the fundamental trade-off (son versus daughter). However, sex allocation is only one part of behavioural ecology, and only one part of how the knowledge of the importance of behaviour in shaping fitness, and thus evolution, has been with us for *many decades*. In terms of the evolutionary causes and consequences of organismal agency, the EES is playing catch-up, more than five decades after key theoretical advances made via SET, and multiple journals devoted to the subject. And all this without the idea of "reciprocal causation" as well, albeit with a nonetheless deep-seated, historical understanding of feedback loops in evolutionary biology (Fisher 1930; Bailey 2012).

29.4.2 Sex Allocation as Phenotypic Plasticity

From the above examples, it is also abundantly clear that the ability to respond to the environment when allocating sex is a superb example of phenotypic plasticity. Indeed, it is *nothing but* phenotypic plasticity. To be more formal for a moment, phenotypic plasticity is the ability of a given genotype to produce multiple phenotypes across a range of environments (e.g. Schlichting and Pigliucci 1998). Classic lecture-hall examples of phenotypic plasticity include the variation in growth rates of clones of plants across a range of nutrient availabilities, ambient temperatures, or light regimes. Indeed, when we think of plants, the ubiquity of phenotypic plasticity is clear, even banal. Likewise, since all the different behaviours an animal exhibits can be considered different phenotypes (even if lumped into big classes, such as foraging, searching for mates, avoiding predators, finding shelter), then behaviour is itself avowedly phenotypically plastic. Indeed, it is the job of behaviour to be plastic, its whole point. Phenotypic plasticity is everywhere, and sex allocation is no exception, with Figs. 29.1, 29.2, 29.3, and 29.5 showing these plastic responses—or *reaction norms*—very clearly. Moreover, sequential hermaphroditism is sex allocation as phenotypic plasticity *par excellence*. Sequential hermaphrodites, including sex-changers such as *Amphiprion* clown fish, for example, produce different sexes across their lives, which is nothing if not developmental plasticity. Species can go from male to female (protandrous sex-changers) or female to male (protogynous sex-changers), or even—in a few extraordinary examples—make *two* changes during their lives (West 2009).

One of the benefits of our theoretical and empirical understanding of sex allocation is that we have been able in some cases to tease apart the basis of this phenotypic plasticity, for instance, in terms of the information females use when making more or less subtle sex ratio shifts. Take the gregarious parasitoid wasp *Nasonia vitripennis*. Females of this species parasitise blowfly pupae, laying multiple eggs per host. Males are short-winged (brachypterous), and so mating primarily takes place on the fly puparium when adult males and females emerge following eclosion inside. If only one female lays eggs on a given host, then her sons and daughters will mate with each other, which is exactly the scenario Hamilton envisaged for LMC to occur. *Nasonia* has not unsurprisingly been a well-studied model organism for how LMC shapes sex allocation, beginning with the pioneering work of Werren (1980, 1983). We know now that ovipositing female *Nasonia vitripennis* facultatively (i.e. plasticly) change their sex allocation in response to the presence and number of other females (termed *foundresses*) that also contribute eggs to a host or patch of hosts (Werren 1983; Shuker and West 2004; Burton-Chellew et al. 2008; Fig. 29.2), the size and hence fecundity of other foundresses (Flanagan et al. 1998), the number of eggs already on a host (Werren 1980; Cook et al. 2016), the presence of eggs on other hosts in the patch (Shuker et al. 2005, 2006), the number of other parasitized hosts on the patch (Shuker et al. 2006), the size of the overall patch (which influences how offspring from different broods interact: Shuker et al. 2007), as well as the timing of when other eggs were laid on the patch (Shuker et al. 2006). Just as importantly, we also know that female *N. vitripennis* do not respond to some environmental conditions that theory would lead us to expect them to (i.e. they are not perfectly adapted). For instance, they do not take into account the relatedness of the male they mate with (Shuker et al. 2004a), the females they oviposit with (Reece et al. 2004; Shuker et al. 2004b), or even the difference between con- and heterospecifics (Ivens et al. 1998). As such, we know quite a lot about what sorts of information female *Nasonia* use when facultatively allocating sex under LMC, i.e. how they are phenotypically plastic in the face of changing predictors of the level of LMC their sons will face.

Similarly, we have been able to address some questions as to the mechanistic basis of sex allocation and hence phenotypic plasticity in *Nasonia*. Briefly, in terms of genetics, data from Orzack and colleagues in the 1980s and 1990s showed that variation in sex allocation in *Nasonia* has a heritable component (albeit not a terribly large one; as might be expected for a trait so plastic and dependent on specific environmental conditions, the environmental component of sex ratio is large: e.g. Orzack and Parker 1986, 1990; Orzack 1990; Orzack and Gladstone 1994; Pannebakker et al. 2011). More recently, there have been studies of the mutational heritability of sex ratio (Pannebakker et al. 2008), and the first quantitative trait loci (QTL) for sex allocation in *Nasonia* have been identified (Pannebakker et al. 2011). The latest work suggests that sex allocation is highly polygenic however, with many genes influencing variation in sex allocation (Pannebakker et al. 2020).

The study of the mechanistic basis of phenotypic plasticity has been boosted in recent years by the growing availability of gene expression (transcriptomic) studies in non-model organisms, opening up the opportunity to study what genes and gene networks underlie the changes in phenotype visualised in reaction norms (e.g. Aubin-Horth and Renn 2009; Oppenheim et al. 2015; Lafuente and Beldade 2019). The study of sex allocation in *Nasonia* has been no different. However, interestingly, the extremely plastic and nuanced responses to LMC cues are *not* associated with changes in gene expression (*at all*: Cook et al. 2015a, 2018). Instead, the very impressive and rapidly responding patterns of sex allocation in this wasp seem to be products of the underlying neural architecture constructed prior to adulthood. Indeed, patterns of adaptive sex allocation have recently been experimentally disrupted by exposure to sub-lethal doses of neurotoxic neonicotinoid pesticides, which disrupt acetylcholinesterase receptors (Whitehorn et al. 2015; Cook et al. 2016). The phenotypic plasticity of *Nasonia* therefore seems to be largely hard-wired in.

In summary, sex allocation should be considered a canonical form of phenotypic plasticity, spanning behavioural and developmental plasticity. And so, for those interested in the genetics and mechanistic underpinnings of reaction norms or wanting to quantify the evolutionary consequences of plasticity—an avowed aim of the EES—then sex allocation should be a great place to start. And yet sex allocation is often absent from discussions of phenotypic plasticity. However, perhaps one of the problems for EES proponents, especially for those outside of the animal behaviour or behavioural ecology communities, is that the day-to-day, in-your-face obviousness of phenotypic plasticity means that it is not even mentioned in many cases. My own work on sex allocation summarised above has rarely if ever included the term in the abstract or keywords of my publications; moreover, a Web of Science search reveals 2157 papers with the search term “sex allocation” (Web of Science Core Collection: 2/08/2021, search by DMS), but only 92 that include both “sex allocation” AND “phenotypic plasticity” (i.e. 4.3%). To truly understand how evolutionary biologists have appreciated and studied phenotypic plasticity requires more than just the easy scholarship of the search engine, but also a deeper understanding of the traits we study and how we study them.

29.4.3 Sex Allocation as Niche Construction

Niche construction is a concept that describes the effects organisms have on their environments (Odling-Smee et al. 2003). Taken at its broadest, as organisms continually interact with their environments and necessarily change them moment-to-moment, it just describes the fact that organisms interact with their abiotic and biotic environments; in other words, it is synonymous with many definitions of ecology. In these broad terms then, there is not really such a thing as niche construction theory (NCT), in the same way that there is not really a “theory of ecology”. Rather, ecology is a “thing” about which we have many theories. A slightly looser, more manageable view of niche construction, and hence NCT, is to focus on the effects organisms have on themselves and other organisms via their behaviours and so forth, including their extended phenotypes such as nests. The overlap with the preceding discussion about behavioural agency will already be clear to many readers, but here I briefly put sex allocation in niche construction terms.

Put simply, sex allocation is a *perfect* example of niche construction. An organism does something—allocate sex—that constructs the niche for that offspring, i.e., the ecological consequences of being male or female, influencing the fitness of that offspring, and hence the inclusive fitness of the sex-allocating parent. More concretely, let us consider some examples. First, let us take fig wasps, such as the so-called pollinating fig wasps in the family Agaonidae. Adult females visit a developing fig (called the syconium), and lay eggs within the syconium, collecting pollen from the flowers within the fig as they do so. Females will visit multiple syconia, laying eggs and collecting and depositing pollen, and so providing pollinator services for the fig plant. The eggs are laid in the flowers and form gall-like structures, and male and female fig wasps develop by consuming the gall. Adult males are wingless and spend their whole lives inside the fig, competing for freshly-eclosed adult females to mate with. As such, fig wasps provide another case-study for local mate competition, with foundress females varying their offspring sex ratios depending on how many females contribute eggs to the fig, as predicted by LMC theory (Fig. 29.1; Frank 1985; Herre 1985; for further details Herre et al. 1997; for sex allocation in non-pollinating fig wasps, see Fellowes et al. 1999).

But there is also lots of niche construction here, from the females placing the eggs inside the developing fig (constructing the natal niche), the gall that forms around each egg and developing larva (constructing the larval niche), through to the mating dynamics of the males and females (constructing the mating system niche), which all will be shaped by the oviposition and sex allocation decisions of the foundress females. Similarly, as we have already seen, gregarious parasitoids such as *Nasonia* likewise influence the interactions amongst their offspring—constructing their mating system niche—by influencing the sex ratio (and also, of course, clutch size, but we will focus on sex allocation). In both fig wasps and parasitoids then, mothers construct the mating niche of their offspring, taking into account the number of other foundresses laying eggs, plus a number of other more or less subtle determinants of local mate competition (see above).

Second, it is not only in terms of LMC that females construct the niches of their offspring. Under Trivers–Willard sex allocation, females may determine the niche of their offspring in a sex-dependent way. In the rather startling "zombie cockroach killer" wasp (better known as *Ampulex compressa*), females put a fertilised egg destined to develop into a female on a large cockroach host, and an unfertilised egg on a smaller cockroach host (Arvidson et al. 2018). Whilst this is niche construction—the food availability and hence the developmental trajectory of the male or female offspring is determined by the mother—*A. compressa* is rightly infamous for another bit of niche construction (well, invasive neuroscience really). Females inject venom containing neuropeptides into the brain of the cockroach host, which ablate its escape response, allowing the wasp to lead the "zombie" cockroach by the antenna to a burrow, where the wasp will then lay an egg on the immobilised, but not dead, cockroach (Haspel et al. 2003; Gal and Libersat 2008).

Third, a variety of organisms determine sex via experience of local environmental cues, for instance, during gestation or development within an egg. Perhaps the best-known form of environmental sex determination (ESD) is temperature-dependent sex determination (TSD), which occurs across a range of reptiles (see above). TSD does not preclude adaptive sex allocation however. Instead, mothers may manipulate the sex of their offspring by determining where the eggs develop, for example, how shallow or deep they are placed in a natal pit, dug in sand or soil. At different depths, the temperature will subtly change, influencing the resulting sex ratio of the brood. This is clearly niche construction: the mother *literally* digs a pit, of a given depth, and places eggs into it in such a way that the developmental trajectories are manipulated to give a certain sex ratio. As should be clear by now, the fitness of the resulting offspring will be influenced by the mother's decisions, and hence by her niche construction.

It is worth emphasising though that the theoretical and empirical studies reviewed in this section were conceived and conducted without the need for (nor indeed, without the formal conception of) niche construction as a concept; niche construction is merely one conceptualisation of things evolutionary ecologists have been doing for decades (a point also made by Keller 2003; Brodie 2005; Scott-Phillips et al. 2014; Gupta et al. 2017). Nonetheless, sex allocation is niche construction, and again we might think that it should be firmly under the aegis of the EES.

29.4.4 Sex Allocation as Ontogeny

Part of the EES manifesto is that development has been down-played or ignored by evolutionary biologists and was effectively absent from the Modern Synthesis (Laland et al. 2015). Whilst one may argue whether that is actually true, certainly the field of "evo-devo" has flourished over the last couple of decades, particularly on the back of our increased ability to scrutinise and manipulate DNA sequences. Indeed, in many ways evo-devo is largely the study of developmental genetics (see Diogo 2016, 2018 for a critique of evo-devo, and the absence of "evo"). However, here we are interested in evo-devo in terms of how ontogeny shapes, and is in turn shaped by, evolution. As will be increasingly apparent, the interconnectedness of aspects of the EES means that I begin to risk repeating myself. As such, I will be brief. Ontogenetic processes are clearly part and parcel of sex allocation in many cases. For instance, as we have seen above, the developmental consequences of a given environment or food resource for embryonic/larval development can differ between male and female offspring. Those sex-specific developmental trajectories influence the evolution of sex allocation—such as when to switch between producing male and female offspring—and are themselves subject to selection.

There are subtle interactions too between sex allocation and development. When the gregarious larvae of parasitoid wasps develop on the same host, the larvae will compete for resources, for instance, by scramble competition for food, with fast developing offspring perhaps benefiting. If development is sex-specific, and in many cases it is, with males being smaller and developing more rapidly than their larger sisters, then this competition may be asymmetric with respect to sex (asymmetric larval competition: Godfray 1986; Sykes et al. 2007). Again, for any given species, the developmental profiles of males and females will have been influenced by various aspects of natural and sexual selection (fecundity, mate finding, and so on) that influence how large and with what resources an offspring reaches adulthood. These developmental differences may shape how kin compete for resources, and thus again shape the reproductive value to a parent of producing a son or daughter. In the gregarious parasitoid wasp *Nasonia vitripennis* discussed above, the effect of asymmetric larval competition on sex allocation is small when compared to that caused by LMC (Sykes et al. 2007), but in other species competition between the sexes for resources arising from different patterns of development can be more striking (such as in the rather remarkable polyembryonic wasps: Grbić et al. 1992).

A lovely example of the sometimes very intimate relationship between development and sex allocation comes from sex-changing sequential hermaphrodites (Charnov 1982; West 2009). Sex-changing organisms switch between male and female sexual function over their lives, going in either direction (or even changing twice), depending on the shape and steepness of the male and female fitness functions with respect to age, size, or some other aspect of developmental state. This means that sex allocation—the decision to be male or female—is closely tied to the moment-to-moment development and growth of the organism, and what that means for its fitness. Thus, the important evo-devo links between (a) development and the phenotype, and (b) phenotype and stage-specific fitness, such that fitness effects loop back to shape developmental trajectories and hence phenotypic trajectories, are clearly all present in these species, with the study of them decades old (Charnov 1982). In fact, one could argue that sequential hermaphrodites should be a research priority, or key set of model systems, for understanding how development, phenotypes, and fitness interact. What is more, as with the whole field of sex allocation, we have a robust theoretical framework which we can adorn with mechanistic details and empirical tests. And as all these examples show, sex allocation provides many clear exemplars of the ways in which organismal development influences phenotype and hence fitness. And again, sex allocation should therefore be a strong component of arguments promoting the EES. Unfortunately, SET got there first.

29.4.5 Sex Allocation as Epigenetics

When we turn to the role of epigenetics and sex allocation, here at last we come to a relatively newer component of the study of sex allocation, one which is more or less contemporaneous with the EES movement. First, I should clarify again that sex allocation is not synonymous with sex determination, and the role of epigenetics in sex determination, for instance, through DNA methylation being involved in the regulation of sex determination, is being increasingly well recognised (even if many mechanistic details are lacking). For instance, in sea bass (*Dicentrarchus labrax*) and the mixed-mating system Mangrove Rivulus fish *Kryptolebias marmoratus*, epigenetics have been implicated with sex determination (Ellison et al. 2015, see also Consuegra and Rodríguez López 2016 for discussion); there are also some associations between epigenetic modification and sex or mating type in plants (Harkess and Leebens-Mack 2017; and epigenetics may underlie *terroir* in our wine, but that is another story: Xie et al. 2017).

In *Nasonia vitripennis*, sex determination has been convincingly shown to involve some non-genetic trans-generational effect (i.e. there are neither sex chromosomes in this haplodiploid insect, nor single- nor multi-locus complementary sex determination: Verhulst et al. 2010; Beukeboom and Van De Zande 2010). Following extensive study, it is now clear that sex is determined by the presence (in diploid, fertilised embryos) or absence (in haploid, unfertilised embryos) of a paternally inherited copy of a gene (with the excellent name of *wasp over-ruler of masculinization*, or *wom*: Zou et al. 2020). The maternally inherited copy is epigenetically silenced, leading to male sex determination in unfertilised embryos. However, when it comes to sex allocation in *Nasonia*, there is now indirect evidence for a role of epigenetics too, and in particular DNA methylation, in terms of regulating sex allocation and thus sex ratio in this species (Cook et al. 2015b, 2019a, b).

The motivation for the study of Cook et al. (2015b) came from theory developed by Wild and West (2009), exploring the role of genomic conflict in sex allocation. In particular, they explored how genomic imprinting could influence sex allocation, across a range of scenarios, including facultative sex allocation under LMC.

Genomic imprinting, or the passing on of parent-of-origin information (i.e. whether a chromosome has been maternally or paternally inherited), is necessary for maternally or paternally inherited alleles to influence the phenotype—and hence the fitness consequences—of an offspring. The classic example is conflict between maternally and paternally inherited alleles in developing embryos in utero in mammals; theory suggests that paternally inherited alleles should try and extract more resources from the mother during development than maternally inherited alleles (Moore and Haig 1991; Haig 2000). Remarkably, data from a number of mammals suggest that such a conflict actually occurs. Importantly though, alleles need to "know" (very much in inverted commas) whether they have been maternally or paternally inherited, i.e. the parent-of-origin information is crucial, and so some form of genomic imprinting is necessary, to pass this non-genetic information across generations.

Cook et al. (2015b) tested the ideas of Wild and West (2009) in *Nasonia vitripennis*, using the demethylating chemical 5-aza-dC to disrupt patterns of DNA methylation across the genome (see Ellers et al. 2019 and Cook et al. 2019a, b for a discussion of the efficacy of this technique). The authors found that there was a small but significant shift in sex allocation in response to the DNA methylation manipulation, with sex ratios going up (i.e. becoming less female-biased). In terms of the predictions of Wild & West, this would suggest that unmanipulated sex ratios in *N. vitripennis* are closer to a maternally inherited allele optimum than a paternally inherited allele optimum, and disrupting DNA methylation shifts things upward (although again, we reiterate the effect is small, as predicted by Wild and West 2009). Importantly, Cook et al. (2015b) showed that the shape of the reaction norm—the pattern of facultative sex allocation with respect to foundress number—was unaffected by the chemical treatment. Thus, the facultative or phenotypically plastic aspect of sex allocation was not disrupted, rather sex ratios across the range of foundress numbers tested were higher for treated mothers than for controls.

Much remains to be explored here. More recently, Cook et al. (2019b) have shown that 5-aza-dC causes widespread changes in DNA methylation across the genome, and so candidate causal CpGs will be difficult to identify. Moreover, it has so far not been possible to show the parent-of-origin effects at the epigenomics level in *Nasonia vitripennis* required (Wang et al. 2016; Olney et al. 2021; but see Zou et al. 2020). Nonetheless, these data suggest a role for epigenetics in sex allocation, through an effect not just on sex determination mechanisms, but on the control of sex allocation itself. How widespread the role for epigenetic mechanisms will prove to be is as yet unknown, but theory such as that provided by Wild and West (2009) offer places to start to look.

Importantly for the overall message of this chapter though, it must be remembered that the theory of Wild and West (2009) was developed very much in the tradition of Standard Evolutionary Theory. In other words, they were interested in genetic evolution, and how genomic conflicts could evolve and influence *genetic transmission* across generations, through phenotypes influenced by non-genetic inheritance of epigenetic information. Likewise, one of the key originators of genomic imprinting and genomic conflict theory—David Haig—places his theory very much in the population genetic terms of SET (Haig 2000, 2007, 2014). This again poses the same problem for proponents of the EES. If SET can foster and engender ideas and theory—in this case about the evolutionary development and consequentiality of genomic imprinting, and the non-genetic transmission inherent to genomic imprinting—then why are epigenetic effects put forward as evidence for the need of an extended synthesis? Hasn't SET again got there already?

29.4.6 Sex Allocation and Trans-Generational Effects

As should be obvious from the examples and discussion above, sex allocation is *all about* trans-generational effects, both in terms of how one generation (the parents) influences the phenotypes of another (the offspring), but also in terms of how those phenotypes then influence the fitness of the offspring, and hence the inclusive fitness of the parents. Indeed, we have basically been talking about nothing else apart from trans-generational effects, with parents shaping the environments, the phenotypes, and the fitness of their offspring. (As an aside, I note that this is of course true for other well-studied aspects of behavioural ecology, such as the evolution of parental care; the idea that the theory of the evolution of parental care was stunted under the SET is obviously a non-starter: Clutton-Brock 1991; Royle et al. 2012.) As such, it should be uncontroversial that sex allocation is all about trans-generational effects that go far beyond just the inheritance of genes, and so again it is hard to argue that the importance of trans-generational fitness effects has been absent from SET until very recently. Perhaps more importantly, nor do such effects over-turn or invalidate SET. Quite the opposite. We have been able to understand those effects for more than 50 years *because of* Standard Evolutionary Theory.

However, I will finish this section with just one further example, which again highlights theory developed multiple decades ago, which argues against a one-eyed view of the SET as comprising genes-only trans-generational effects, and within-generation only fitness effects. The so-called haystacks models of sex allocation are in effect extensions of Hamilton's LMC models. The name comes from an early model of Maynard Smith (1964), describing an idealised mouse species that colonises and lives within a haystack for several generations before dispersing. Already one can see that multiple generations living in the same localised resource will likely engender trans-generational effects, including the "inheritance" of a given habitat state, and of course niche construction. Bulmer and Taylor (1980) developed the first models of sex allocation in haystacks, with the main difference to predictions from LMC models coming from the extent to which mating can occur between individuals after dispersal, which can then interact with the number of generations spent in the haystack prior to dispersal to influence sex allocation (for a review of the theory, including later developments, see West 2009). The notion that SET comprises "unilinear" effects (for example, Müller 2017) belies the ecological realities, the *actual biology*, that the SET has been employed to explain, in many cases overwhelmingly successfully. Instead, sex allocation shows that SET not only can deal with interacting fitness effects, but it can also help *identify* and *predict* them through its predictive framework.

29.4.7 Sex Allocation as Culture

This last section addresses culture and the possible role of cultural evolution in patterns of sex allocation. To begin with, a sketch of relevant terminology will be useful, as definitions can vary. In terms of the biology of culture, I will consider that organisms may have traits that together provide the *capacity for culture*. These are more or less straightforward biological traits, with genetic underpinnings like any other biological trait, that allow organisms to be cultural. These traits include learning, and especially social learning, among-individual communication, the ability to perceive and to attend to relevant social cues and/or signals, and sufficient among-individual social interactions, including across generations, for cultural phenotypes to be transmitted. Many social organisms will have some or all of these traits to some extent, although culture is not a given outcome (for reviews of social learning and culture in animals, see, for instance, Whiten et al. 2011; Hoppitt and Laland 2013; Aplin 2018; Whiten 2019, 2021).

I will define *culture* itself as a set of one or more shared behavioural phenotypes, and any physical products thereof (such as artefacts), that are originated, learned, and transmitted within- and across-generations. Culture is thus an *emergent phenotypic property* of biological organisms, such that the nature and extent of the cultural phenotype is not itself genetic in origin, even though all the underlying machinery, and variation in expression of that machinery across individuals in the population, will have a genetic component. Cultural phenotypes may influence the fitness of individuals, and so we expect gene-culture coevolution to influence the evolution of underlying cultural capacities (Feldman and Laland 1996) and indeed what cultural products populations express. Cultural phenotypes, by their very nature, may be somewhat ephemeral and hard to pin down though. Whether instantiated only by behaviour or alongside physical artefacts, the cognitive basis of culture (as a learned "thing"), means that culture is neurally encoded, forming part of an organism's mental landscape, explicitly or otherwise.

What possible links are there between culture and sex allocation? First, for non-human animals, potentially rather few. This is not because of a dearth of culture: far from it. Over the last two decades or so, there has been a great flourishing of research into animal cultures, and we now know that cultural transmission of behaviours can occur not just in humans or other primates, but across cetaceans, birds, and indeed insects (Whiten 2021). It is likely that many more examples of culture and cultural transmission will be uncovered the more we look. However, it perhaps not immediately clear how, or under what circumstances, cultural preferences for sex allocation could evolve in non-human animals. One possible route would be if a cultural preference for a certain sex or sex ratio emerged by chance in a species in which there was selection for a different sex ratio, but no underlying genetic variation in sex allocation or sex determination. For example, if male offspring were rare, and that rarity led to greater attention by a parent due to an underlying attraction to novel stimuli, then through imitation or local enhancement, this could lead to greater attention being paid by other parents towards male offspring in other litters, and the greater likelihood of death of the increasingly ignored female young. This would mean there was a culturally transmitted trait (parenting effort) that biased offspring survival towards males.

In humans, on the other hand, there is all too much evidence that post-conception sex ratios are manipulated due to culturally inherited preferences for one sex of offspring over another. In a number of human societies, female offspring have been or are valued less than males, leading to sex-specific infanticide or neglect (for a variety of perspectives across historical and contemporary cultures, see, for instance, Sen 1990; Hesketh and Xing 2006; Lynch 2011; Klasen and Wink 2002; Mitra 2014; Barman and Sahoo 2021; Beltrán Tapia and Raftakis 2021; for a theoretical gene-culture treatment, see Kumm et al. 1994). In these cases, the value of sons versus daughters may be associated with a whole raft of cultural traits that define the societal norms in which the individuals live, including how resources—such as land, money, and so on—are inherited within or among families across generations. These highly multi-layered cultural components of human societies are unequalled in other animals, and so the role for culture to play such a strong role in biological evolution, including in such fundamental traits such as sex allocation, is much more limited. That said, sex-specific infanticide is known in non-human animals, in organisms as diverse as ants, hamsters, and *Eclectus* parrots (Bourke and Franks 1995; Beery and Zucker 2012; Heinsohn et al. 2011). However, the role of cultural evolution in this infanticide is as yet unexplored.

29.5 Discussion

There are many aspects of sex allocation I have not been able to include here. This is true in terms of the sophisticated theoretical machinery that has already been developed, and the rich diversity of empirical examples across animals and plants (and of course protists: malaria parasites provide a wonderful example of sex allocation under LMC: Reece et al. 2008). Nonetheless, I have clearly shown that the study of sex allocation—very active for more than four decades, with a history dating back to the origins of the Modern Synthesis itself—has historically embraced, and continues to embrace, the aspects of biology emphasised by the Extended Evolutionary Synthesis, but that have supposedly been ignored by evolutionary biologists.

As such, sex allocation is the dog that did not bark in the night, curious by its absence from discussions of the EES. If the EES is predicated on the idea that evolutionary biologists working with the inherited Modern Synthesis framework—Standard Evolutionary Theory as I have framed it here—have missed, or ignored, or been unable to accommodate new findings in their SET paradigm, then sex allocation presents a considerable challenge to the EES. Why are not fig wasps a poster-child for an EES? Their extraordinary behaviour, its plasticity, and its evolutionary consequentiality born of trans-generational fitness effects, should all be grist to the mill of the EES. The key concepts of the EES—organismal agency through adaptive plasticity and trans-generational effects—are what sex allocation is fundamentally all about. The problem is though that the theory that underpins all these responses, including the role of epigenetics in mediating genomic conflicts in a very EES sort of way, exists profoundly within the SET framework. Fundamentally, *no new way of doing theory was required*. Instead, sex allocation has been modelled in all sorts of way within SET, from very explicit population genetics models, through to the increasingly implicit genetics that lie at the heart of evolutionary game theory (West 2009). Sex allocation shows how SET can deal with all of the kinds of phenotypes the EES proponents say are problems or that require “a new perspective”.

One might argue that sex allocation is small beer, only a fraction of the edifice that is evolutionary biology under SET; one could say that the EES is “bigger than sex allocation”, for instance. Whilst it is true that sex allocation is only a part of modern evolutionary biology, it has an important standing because—as mentioned at the beginning—it has been a branch of evolutionary biology where some of the most explicit tests of SET have been attempted. But is sex allocation mainstream evolutionary biology? It is always open to debate as to how important or mainstream any one field is, but it would be hard to argue that sex allocation is just a niche interest for those who—like me—like little black wasps. Hamilton’s foundational 1967 paper has been cited 2490 times (Web of Science Core Collection: 2/8/2021, search by DMS), and those papers themselves have been cited a total of 116,283 times (amusingly this means that Hamilton 1967 has its own *h*-score of 147!). Sex allocation theory is clearly mainstream evolutionary biology, and has been described as a touchstone for SET, as one of the most successful bodies of predictive theory in evolutionary biology (Frank 2002). Yet I hope that this review exhaustively shows that sex allocation also exhibits all of the main categories of “neglected” or “unappreciated” aspects of the world that the EES claims to bring to the party, including organismal agency, trans-generational effects, and the importance of developmental conditions shaping selection.

I suggest that arguments for the EES, and by extension for a rejection or a replacement of Standard Evolutionary Theory, have to emphasise or create the impression of a lack, a neglect, a “something missing”, from SET and its outlook in order to look credible. Whilst it might be argued that all the EES is arguing for is an embellishment or two of SET, in line with the empirical and theoretical accretions discussed in the Introduction, many of the arguments made in favour of the EES seem to demand a more deep-seated change (see Introduction). However, the need for such change fits uneasily when one of the most successful areas of evolutionary biology, that has been developed and tested under the umbrella of the SET for decades, has so many of the apparent components of the EES deep in its warp and weft. Researchers have diligently explored how different evolutionary and ecological factors—including behavioural constraints—have shaped the evolution of sex allocation for decades, prefiguring most if not all of the “missing aspects” of evolutionary biology. Sex allocation is full to brimming of all the things the proponents of the EES say are missing or have been underplayed. Put another way, sex allocation is very much the offspring of SET, thanks to Hamilton, Trivers, and many others, and yet it fits remarkably well with what the EES claims to bring. Fundamentally, I suggest that the successful development of sex allocation theory demolishes arguments for the EES as having any necessary role to play and exposes the fallacy of narratives of "neglect" in mainstream evolutionary biology (see also Gupta et al. 2017).

In conclusion, we have then the curious case of the wasp in the fig fruit. All along, the study of sex allocation has been utilising what EES proponents have argued has been ignored by evolutionary biologists, which should not be the case if SET presents this insurmountable barrier to properly understanding how phenotypes evolve. To emphasise this contradiction, I have presented a lot of biology in the preceding pages, but I make no excuses for that. Any successful call for some kind of new synthesis cannot just be in opinion pieces and philosophical reviews. It has to deal with the nuts and bolts of actual biology, and the biology that evolutionary biologists have done and continue to do. And in terms of that biology, if sex allocation has been hiding in plain sight, how many other sub-disciplines of evolutionary biology have also been studying their phenotypes of choice through a similar, multi-faceted kaleidoscope, even if they have not been avowedly "developmental", or have not used the term "niche construction", "phenotypic plasticity", or "trans-generational"? The truth is probably most, if not all of them. Which means that the EES has little to offer. So why the EES at all?

Philosophers of science have recently argued that maybe one issue is that the two frameworks are seeking different kinds of explanations for evolutionary phenomena, or have different explanatory "standards", even if it is not yet clear what those differences might be (Lewens 2019; Baedke et al. 2020). However, thanks to Tinbergen (1963), we have long known that there are many different kinds of questions that biologists ask about traits, spanning mechanism, ontogeny, function, and phylogeny. Yes, biologists can easily talk past each other, especially if careers are to be made, but I think the disconnect between the SET and EES (which is clearly real) is less about questions, and ironically not even necessarily that much about evolution at all. After all, why ignore adaptive sex allocation in pro-EES arguments? No, I suggest that the truth is that the EES is actually all about freeing organisms from evolution itself.

The focus of the EES is clearly the phenotype. Organismal agency and allowing organisms to change across generations independently of genetic inheritance is what the EES is all about. This breaking of the links between genotypes and phenotypes, to allow phenotypes to be free *from* evolution, or at least from free from evolution as genetic change, is what is at its core. The EES is much more about a theory of phenotype than it is a theory of evolution. And I think this key aspect of the EES needs to be understood. All of its components are about emphasising *how organisms are made*, with the bolt-on comment that we need to understand that phenotypic construction when studying evolution. The problem is that we already know very well that both organismal agency and trans-generational effects are both outcomes of, and contributors to, natural selection, as so clearly evidenced in the review of sex allocation presented here. These are not some new weird facts of biology either; we have known of examples of both (for example, for organismal agency read behaviour, for trans-generational effects read parental care), in terms of ecological context and evolutionary consequentiality, for many decades. As such, I do not think that the EES can contribute to evolutionary biology, because fundamentally it wants to extend *away from* evolutionary biology. It wants organisms with some other kind of agency, phenotypes that are built and changed some other way, independently of natural selection. You might not read that many places, but how else to explain the implicit "something-else-ness" of the EES, and the slippery slope that maybe phenotypic change over time is evolution too, and that we can dispense with genetic change. Whether it is explicitly stated or not, clearly evolution as genetic change is the target of the EES. But phenotypic change without genetic change is not evolution as evolutionary biologists think of it and indeed is deeply problematic. This is perhaps Darwin's key insight, alongside the mechanism of natural selection itself (and not just in Darwin 1859, but even more so in Darwin 1868). Darwin ended up knowing full well that the biological diversity we see today cannot be explained by phenotypic variation alone: phenotypic variation is cheap, thanks to the ubiquity of phenotypic plasticity. Heredity was, and is, crucial. If you want to explain biological diversity, and traits such as sex allocation, then evolution needs to be framed in population genetic terms. And on these terms, the Extended Evolutionary Synthesis has no tenable argument to make, nothing *new* to offer, in the face of Standard Evolutionary Theory.

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