Chapter 22
Behavior and Evolution: Crossed Glances

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Abstract Ethology was founded successively by the naturalist, psychological and neurophysiological trends. After the classic opposition between the environmentalist and the objectivist view on behavior, and then the constructivist currents of the naturalist ethology, a first synthesis was proposed by Tinberghen's four questions, integrating several scientific disciplines, and including the evolutionary question of ultimate causalities. In order to analyse what the theory of evolution brought to ethology and conversely, we collected and commented the opinions of several ethologists of different currents, in the context of the naturalist thought in ethology and the recent development of phylogenetics. Compared to the other data, the use of behavior in systematics raised some methodological problems concerning its ephemeral nature, the supposed difficulty to identify homology and the pretended lack of reliability of behavioral data compared to morphological and molecular ones. As a matter of fact, behavioral characters mapped on a tree or integrated into the phylogenetic data matrix have great potential, even though they remain controversial in systematics. As a source of heritable characters for phylogeny inference, behavior embodies both a product of evolution and one of the evolutionary factors. Hence behavioral studies can bring complementary explanations to evolutionary processes of speciation involving behavioral factors. A further and promising interest of the combined study of behavior and evolution concerns the epigenetic perspective of the influence of behavior on the rate of DNA methylation, which confirms that numerous behavioral adaptations appear before corresponding genetic modifications or mutations.

If animals and their behaviors have always fascinated human beings, as is shown by cave paintings and hieroglyphics (Galef 1996), it was not until the middle of the nineteenth century that ethology was given its current naming (*ethos*: habits) by Isidore Geoffroy Saint-Hilaire. This simple name covers a complex science, founded successively by naturalist, psychological and neurophysiological trends.

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These, far from opposing each other, built themselves collectively. For example, the contribution of Darwin (1859) is not limited to naturalist trends – for Darwin is also a co-founder of comparative psychology, proposing a continuity between human and animal which improves on the mechanistic Cartesian vision of psychology and neurophysiology (Campan and Scapini 2002). Following Darwin, studies about learning became clearer and attributed the leading role in the expression of behavior to imitation (Morgan 1894). At first purely philosophical, psychology became comparative by integrating evolutionist theories. Neurophysiology, stemming from Descartes's automaton model and from the reflexology of La Mettrie, joined with the rising field of comparative psychology thanks to the experiments of Thorndike on learning. These works proposed an idea under the name of the *law of the effect*, considering that positive or negative reinforcements[1] play a major role in the preservation of the connections between stimulus and response. This reflexologic vision of learning was introduced in the works of Watson (1913) in the USA and Pavlov (1927) in the Soviet Union. Enriched by these contributions, experimental comparative psychology evolved towards behaviorism – which influenced ethology in the beginning of the twentieth century. Behavior was then defined, according to Watson, as all the objectively observable adaptive reactions that a body, generally provided with a nervous system, executes in response to stimuli from the environment (Campan 1980). In opposition to this environmentalist vision of behavior (*tabula rasa*) which considers that bodies behave only in reaction to their environment, two important trends of modern ethology emerged some 20 years later. The first one constitutes the objectivist strain of naturalist ethology embodied by Lorenz (1935), who recycled, with the concept of instinct, certain ideas of Von Uexküll (1909) on "Umwelt" – the proper specific universe; he combined this with a sensible use of homology, a concept borrowed from compared anatomy and from Heinroth (1911), which allowed him to reconstitute the evolutionary history of ducks and geese (Anatidae) from their courtship displays and other behaviors (Lorenz 1941). According to Lorenz, behavior in general is innate and hereditary (but this author will amend this opinion later). The second trend is constructivist (Maier and Schneirla 1935). It proposed that instinct develops with the combined effect of maturation and experience – with the degree of inheritance or acquisition varying according to the phyletic level of the concerned organisms. A first synthesis of these two trends was proposed by Tinbergen[2] (1963) in the form of four questions corresponding to the main domains of investigation of ethology:

1. What are the immediate causes of the concerned behavior?
2. How does it develop during the life of the animal (ontogenesis)?
3. What is its function or its associated fitness?
4. What evolution did this behavior undergo during phylogenesis?

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[1] Phenomena connected to the expression of a behavior leading to an increase of its intensity or its frequency.

[2] The Nobel prize in Medicine was attributed in 1973 to Niko Tinbergen, Konrad Lorenz and Carl von Frisch (discoverer of the language of bees).

Behind each of these questions lies a trend of thought which expresses itself through scientific disciplines, and whose answers we can illustrate by means of an example: the behavior of the European roe deer in a situation of stress. When disturbed, the roe deer shows its anxiety by striking violently the ground with a foreleg.

1. The immediate cause of this behavior is the perception of a threatening stimulus (predator, rival, or observer) triggering a motor reaction.
2. The ontogenetic explanation of this motor action can be conceived of both in terms of sensori-motor links which formed during the development of the animal in the maturation of the nervous system, and the experience of the subject which has already expressed this behavior in a similar context (Guilhem 2000).
3. The function of this behavior can be interpreted as a pursuit deterrent signal sent to the predator or to the rival, indicating him that it is useless to approach because it has already been located (Danilkin and Hewison 1996; Reby et al. 1999).
4. If this behavior is expressed in a predictable and similar way by all the roe deer and by most of the Cervid species, it is likely that the ancestor of this ruminants family already demonstrated a homologous character (Cap et al. 2002).

The first two questions of Tinbergen were later classed as being relevant to proximate causalities and the two latter ones to ultimate causalities (Alcock 1993). This distinction led to another division of ethology into sub-disciplines such as cognitive science or behavioral ecology (Vancassel 1999). To further elaborate on this inventory of ethology, I asked several scientists in the study of behavior to locate themselves in the current ethological landscape, and then to answer the underlying question of this chapter which is to know what the theory of evolution brought to ethology and vice versa; here is what resulted from this inquiry.

1 Ethology: An Explosive Inventory

Describing the current state of ethology would be like commenting on a fireworks display since so much of this science seems to be quartered into diverse disciplines. The study of the internal and external causes which lead animals to act the way we observe them especially interests neurophysiology and cognitive science. Development (ontogenesis) is mainly of concern to psychology and embryology. Finally, the study of evolutionary causes (phylogenesis) and the functions of behavior concern phylogenetic systematics, genetics, and behavioral ecology. The confusion between them is such that certain disciplines want to either integrate or ignore the others. This is particularly the case with behavioral ecology (Krebs and Davies 1997).

> We observe a tendency for ethology to be divided into poles of diverging interests: cognitive neurophysiology mainly studies humans, while behavioral ecology drifts towards population biology and genetics while integrating some behavioral parameters (symptomatically it is not called "environmental ethology"). We can try to resist such splitting by defending the preservation of a study of behavior itself as the center of interest: explaining behavioral

> phenomena within a frame of multiple and complementary approaches: phylogenetic, genetic, developmental, psychophysiological and environmental-social (Deleporte pers. comm.).[3]
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> If ethology takes evolution and systematics into consideration, the opposite is not true. The theory of evolution brought more weight to the study of interactions between genetics and behavior but also tipped the scales too much toward the search for ultimate causes, and particularly the functional causes magnified by behavioral ecology (Aulagnier pers. comm.).[4]

Notably inspired by game theory and it ideas on the costs and benefits of behavioral functions (Maynard-Smith 1974), behavioral ecology rests on the synthetic theory of evolution or neodarwinism to explain behavioral functions in terms of reproductive success (*fitness*) (Krebs and Davies 1981), a parameter difficult to quantify except under particular conditions of reproduction (Campan and Scapini 2002). This approach represents nevertheless three quarters of the publications in ethology and constitutes a full-grown discipline (Danchin et al. 2008). It also includes a sub-discipline which was strongly disputed in its early days: sociobiology (Wilson 1975). This approach explains social adaptation in functional and genetic terms, resting on the works of Hamilton (1964) concerning altruism and the genetic evolution of social behavior (*kin selection*). Applied to ethology, these theories encounter several problems.

> When we say "evolution" we mean a concept of the origin of species by natural selection. In that case, the most important thing would be the phylogenetic perspective regarding the transformation of behaviors from common ancestors into the variation we see in species today. This is beneficial because it helps put what we see in a larger context, and it helps us connect elements that may not be very similar now, but had a common origin long ago. However, this is generally NOT what the scientific community borrows from "evolution," rather most of the influence has been as much detrimental as beneficial. For example, people like very much to put modern variation into a sequence on a scale that they imagine represents "primitive – intermediate – advanced" or maybe "simple – intermediate – complex," a kind of scala naturae. They infer that the path of evolution is along the axis they have determined in the order in which they placed the different species. In general, any variation that is actually interesting is not in fact a linear sequence, but rather some kind of branching relationship, just like phylogenies are, and the "intermediate" values we observe today are not on their way to becoming the advanced or complex values by evolutionary force, rather the intermediate values are end points in their own rights. Often there is no evidence that the intermediate species are actually connected to both (or either) end point, but because Darwinians like to imagine lots of small steps, we put the intermediates in the middle and infer that evolution had to pass through there. This is bad because there is often no empirical evidence for that hypothesis, and indeed people don't even realize that it is an hypothesis, rather they think that they have demonstrated something. Another big problem is that people have ALWAYS felt that animals behave in a certain way for a reason (traditional folk tales are full of this kind of thinking) and a culture of adaptive thinking in a

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[3] Pierre Deleporte (Université Rennes 1, CNRS UMR 6552, Station biologique de Paimpont). Naturalist and evolutionary biologist, defends the maintenance of an ethology visible in all its dimensions.

[4] Stéphane Aulagnier (comportement et écologie de la faune sauvage, INRA, Castanet-Tolosan). As a naturalist trained in biometry, population genetics and biogeography, he is working on ecology, systematics and the conservation of mammals with dispersal as his central focus.

> Darwinian paradigm seems to reinforce that the animals are doing a certain thing in order to accomplish a goal that we identify ourselves. For example, perhaps we ask someone why the Furnariidae birds build big nests with mud, and then we will get a big adaptive explanation with a lot of selective context, and if the explanation is logical, we accept it with no questions. No one will ever say something modest, such as "well, there is plenty of mud around, and they started using it, and never had to stop." It may be that the big adaptive hypothesis has NO actual support at all, but we usually do not challenge it. Or, the observations that would refute the hypothesis are dismissed on an ad hoc basis to preserve the adaptive hypothesis because we believe that adaptation SHOULD explain the world around us. Of course, adaptive thinking is full of teleological errors, but because people are already inclined to find great functional reason in what animals do, I think animal behavior is especially full of bad hypotheses that are accepted because they tell a nice adaptive story (Wenzel pers. comm.).[5]
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> Since the awareness that behavior could be heritable and compared between species, ethology disappeared almost totally by fusing with behavioral ecology. Nevertheless, this contributed to limit the naivety of ecologists who consider functions and effects without taking into account the individual, plasticity and behavior in general (Grandcolas pers. comm.).[6]

In other words, phenotypes, characterized by behavior as well as by morphology, are considered in the same way as genes – that is to say, as the passive targets of natural selection (Dawkins 1976), which constitutes a drift in the interpretation of the theory of evolution.

> Some interpretations of the synthetic theory of evolution brought a singular way of considering behavior, inventing in some way the animal with computing genes, an automaton for estimating costs and benefits that allow it to choose the most effective behavior to take good position in an evolutionary race. Why are individual behavioral differences not limited to sex and age, while natural selection should have contributed to standardize so-called optimal behavior? We cannot explain this variability by saying that only the top of the pyramidal hierarchy of the attributes of life of a species or a population is preserved by a natural selection process which would privilege and improve the most efficient individuals by favoring their reproduction. It is rather the bottom of the pyramid that is "skimmed" of all the not viable individuals, or of those for which the interaction between genes and environment led to behavior not favoring reproduction in given environmental conditions (Gonzalez pers. comm.).[7]
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> Ethology brought numerous confirmations of the theory of evolution, but a big problem with behavioral ecology is to predict results by appealing only to reproductive success

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[5] John W. Wenzel (Carnegie Museum of Natural History, Pittsburgh): resolutely naturalist, who is secondarily interested by the links between behavioral ecology and phylogeny. According to him, ethology as a disciplinary field became established at first on these naturalists bases, with psychology and neurobiology coming later. If the contribution of these new approaches was very important (sociobiology, for example), none of these contributions is particularly useful without taking into account the animal and its natural universe such as it perceives it ("umwelt").

[6] Philippe Grandcolas (Origine, structure et évolution de la biodiversité, UMR 5202, CNRS, Muséum national d'histoire naturelle, Paris). Close to the disciplines (in decreasing order): systematics (comparative biology), evolutionary biology, ethology. See his chapter on "adaptation", Chap. 5, in this volume.

[7] Georges Gonzalez (comportement et écologie de la faune sauvage, INRA, Castanet-Tolosan). Naturalist trained in eco-ethology, which tries to understand with an enactivist view [See note 13] the role of personality in the functioning of groups of ungulates in nature or in captivity (deer, moufflon and isard).

> without really knowing proximal mechanisms which can influence behavioral plasticity. Conversely, without an evolutionary dimension, ethology has no great interest (Hewison pers. comm.).[8]
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> The theory of evolution set the study of behavior in a natural and historical frame, standing at the origin of comparative approaches like cognitive ecology – which joins behavioral ecology and enriches it. In return, ethology contributed by questioning some of the acquired principles of the Neo-Darwinian theory, by considering the pre-l and postnatal maternal influences on individual development, which explain the observation of some behaviors without any associated reproductive success (Bon pers. comm.).[9]

Beyond the question of reproductive success, which is under lasting debate for some field ethologists, the neodarwinian theory of evolution is not to be challenged and remains omnipresent in behavioral ecology. Thus, species would adapt to fluctuations in the environment through natural selection (Krebs and Davies 1981). According to this view, the lineages which go extinct would be the ones whose genetic variability would be too weak to allow them to adapt to the problems they confront (Van Valen 1973).

> Nevertheless the survival of a lineage and its evolution are not, for the main part, the result of an optimization by natural selection. The survival of a lineage is above all a question of viability, particularly when the environment changes. As for evolution, it is mainly the result of a drift within a set of viable phenotypes. The radiation of Darwin's finches supplies a good example. In the Galapagos archipelago, the common ancestor of the various species of finches met a gradient of seeds of various sizes, similar on all islands. The behavioral activity of this ancestor and his morphology (particularly the size of the beak) led it to attribute a taste for certain seeds, a behavior which happened to be viable and allowed it to multiply. Because of the small size of the resultant populations, the morphology of birds (size of beak, body, legs) derived in a random way in each island, and the size of seeds charged with taste varied accordingly because of the behavioral activity of birds. The islands being not perfectly isolated from one another, recolonization events took place. But the range of available seeds was narrower every time because a good part of them had been already consumed by other descendants from the same ancestor. Viable variations being more and more limited, the lineages stopped drifting. So, natural selection was not the mainspring of the evolution of Darwin's finches. On the contrary, it froze the system when the latter had been saturated in species in the course of recolonization. Its role was essentially conservative (Gerard pers. comm).[10]

The conservative role of natural selection on phenotypes is confirmed. The pending question thus concerns the appearance of new behavior, which cannot be explained any other way than by chance. On this point, the application of mutation/selection to

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[8] Mark Hewison (Comportement et écologie de la faune sauvage, INRA, Castanet-Tolosan). Trained in genetics, ecology and management of wild fauna, works on the behavioral ecology of ungulates in their natural environment, in particular the strategies of reproduction of the European roe deer.

[9] Richard Bon (Centre de recherche en cognition animale, UMR 5169, université Paul Sabatier Toulouse III). Teaching behavioral ecology and neurophysiology, member of the team collective behavior, ethology and modeling of CRCA, specialized in sexual segregation and collective behaviors.

[10] Jean François Gérard (Comportement et écologie de la faune sauvage, INRA, Castanet-Tolosan). Naturalist trained in eco-ethology and cognitive sciences, working on mechanisms generating individual behavior and collective phenomena, and on evolutionary consequences of these processes.

behavior remains problematic because it concerns epigenetic[11] phenomena whose determinism remains poorly known.

> How in an evolutionary perspective could social behavior appear from solitary ancestors? A hypothesis would be that subtle modifications of ways of signalling (hormonal or other) are sufficient to produce a large phenotypic diversity. Among the 40,000 spiders species, there are only thirty social species which appeared independently. It is certainly advisable to consider the environmental pressures on this evolutionary convergence, but also to consider if the solitary species have behavioral capacities for evolving towards more elaborate forms of social organization and the nature of the factors inducing their expression, by trying to isolate the basic rules and the necessary adds for producing more complex structures (Jeanson pers. comm).[12]

A last argument proposed by paleontologists concerns the preservation in numerous lineages of a surprisingly stable morphology despite the environmental modifications that occurred on Earth. This argument does not question the theory of evolution (at least not the strictly gradualist one), but it also does not agree that all species survive environmental fluctuations because of their capacity to evolve (Gould and Eldredge 1993). It would thus seem that species, and consequently individuals, do not attribute the same meaning to the changes arising in their environment (Vancassel 1990).

> Ethology can bring to the study of the evolution the opportunity to understand better the relations between organisms and their environment, for this relation shows itself through their behavior. The study of behavior teaches us above all what these organisms are sensitive to, what makes sense for them in what we qualify as "environment", because they come into relation with the environment through their behavior. For example, ultraviolet rays are not relevant for human beings because, contrary to insects which give sense them, we do not perceive them (Maublanc pers. comm.).[13]

This balancing of the neodarwinian hegemony in ethology was brought by the cognitive sciences, which appear successful in the study of proximal causes, notably due to the concept of auto-organization developed in *The tree of the knowledge* by Maturana and Varela. This conception considers that living systems, functionally closed, auto-build themselves, by generating their own organization. The environment is no more than a source of disturbance, constituting with the animal both sides of the same process, with object and subject specifying one another (Campan and Scapini 2002). This vision of life, stemming from thermodynamics and from chemical kinetics, even if it still remains vague, had the merit to propose

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[11] Changes of genetic expressions involved in the metabolism, the synaptic connections or the rates of transcriptions, which can be heritable without being attributable to transformations in DNA.

[12] Raphaël Jeanson (Centre de recherche en cognition animale, UMR 5169, université Paul Sabatier Toulouse III). Ethologist trained in neurosciences and in physiology, working particularly on the physiological bases of the evolution of social behavior through the links between individual and collective behavior.

[13] Marie-Line Maublanc (Comportement et écologie de la faune sauvage, INRA, Castanet-Tolosan). Naturalist trained in neurophysiology and eco-ethology, which defends a cognitive approach to ethology by studying the processes generating the organization and the dynamics of wild ungulate populations.

a new theoretical frame which was stimulated by the progress of modeling and artificial intelligence. Thus, the study of the mechanisms of collective behavior (with a methodology based on the practice of experimental ethology), brought collaborations with mathematicians for the modeling of simple mechanisms at individual levels that give rise to collective interactions.

> As the studied species are social, we meet with the same problems as physicists who study the coordination of shoals of fishes because they are well trained in the study of systems containing a large number of agents (Bon pers. comm.).

What is cognition, then? It is the productive action or the history of the structural coupling between body and environment that "enacts" a world (makes it emerge). How does it work? By means of a network of interconnected elements, which are capable of undergoing structural changes during a continuous history (Varela 1989). Here we see that ethology also fits in a historical perspective. As such, it is trivial to say that our representation of the animal kingdom has changed since our Palaeolithic ancestors. Implicitly, this change seems tightly bound to the present times.

> The tool formulates the problem; because without the progress of genetics, Neodarwinism would not have had such a development, and without computers cognitivism would certainly not have been born. In the same way, the ideas of an epoch shape the questioning and the views of scientists about the living world. Anybody can observe the convergence between the capitalist vision of the human world and the vision of evolution developed by behavioral ecology. The concepts of competition, fitness, investment, hierarchy, optimality, adaptation are strangely common to economy and to ecology. And very few scientists question this proximity. (Bideau pers. comm.).[14]

Overcoming the empty debate of innate versus experience, a synthesis of the four questions of Tinbergen was considered by various authors. All insisted both on the heredity of certain behavioral traits (while recognizing their variability) and on the importance of learning – which allows the organism to adapt itself to its environment (Eibl-Eibesfeldt 1984).

> Nevertheless, the history of ethology in France is particular because it was marked, in the past, by sectarian attitudes, particularly in the French Society for the Study of Animal Behavior (SFECA), where ecology, physiology and neurosciences were rejected. However ethology progressed and opened debates which in return fed the theory of evolution well before other disciplines – in particular molecular biology, which spent its time between the 50's and the 70's at working out techniques without having a central issue. For ethology it was exactly the opposite, it used rudimentary techniques (paper, pencil, chronometer) while implementing issues which brought considerable theoretical progress in the evolutionist reflexion. Ethology will have to work with molecular biology to understand for example how individual peculiarities of the maternal behavior of the female rat can influence its descent and induce hereditary modifications of maternal behavior of females in the following generations (Lassalle pers. comm.).[15]

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[14] Eric Bideau (Comportement et écologie de la faune sauvage, INRA, Castanet-Tolosan): Naturalist trained in eco-ethology, studying proximal mechanisms generating the social organization of wild ungulates. Having been a convinced neodarwinian, he began to see a tension between what was observed in ungulates in a natural environment and the explanatory mechanisms proposed by behavioral ecology.

[15] Jean-Michel Lassalle (Centre de recherche en cognition animale, UMR 5169, université Paul Sabatier Toulouse III): Coming from psychology and neural physiology, he was influenced by

So, the future of ethology seems to orient itself toward a better understanding of the epigenetic phenomena at the origin of phenotype changes, without necessarily involving genetic mutations.[16] One of the major difficulties of the study of animal behavior thus comes from this tangle of disciplines which deal with temporally different causalities (immediate, ontogenetic and phylogenetic). Behavior shown by an animal at one moment and in a given place is immediately influenced by internal and environmental causes. This behavior is also bound to the proper experience of the individual, to its ontogenesis. In spite of this variability, it is undeniable that among all the behaviors expressed in a population, a species, a genus, a family, an order, some are specific to these taxa and can be similarly recognized as morphological or molecular characters.

> In the populations of finches of the Garonne valley in the South West of France, songs appeared as reliable markers of populations, accents differing according to biotopes within the same species, in geographically separate populations (metapopulations). This behavior allowed for the testing of hypotheses of metapopulations linked to landscape fragmentation (Joachim pers. comm.).[17]

The examples are numerous and illustrate the interest of behavior in evolution – particularly in phylogenetic systematics.

> The study of behavior should allows us to redraw the phylogenetic relationships between species by studying the transitions in the behavioral repertoires of each species. In halictine bees, certain behaviors regulating interactions between normally solitary individuals are present in primitively social species, where these behaviors govern the dominance interactions between the queen and the workers (Jeanson pers. comm.).

Despite its inter-disciplinary explosion and the recurring methodological criticisms against its use in systematics, the study of animal behavior can contribute to taxonomy – which names and classifies the organisms from the study of their relationships (phylogenies).

> Behavioral characters appear more and more as susceptible to contribute to the historical inference of phylogenies, confirming in a modern perspective what the early ethologists presented as the relevance of behaviors in taxonomic characters. Behavior often evolves a sufficiently slow and divergent way to allow for the reconstruction of the main lines of a plausible scenario at supra-specific level (Deleporte pers. comm.).

Thus, beyond the classificatory dimension, the use of behavior in systematics also allows us to elaborate evolutionary scenarios which enrich in return the theoretical study of evolutionary processes. These contributions of behavior to comparative biology date back to antiquity and constitute the essence of ethology: the naturalist thought.

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work in the genetics of behavior, neuro-anatomy and electrophysiology. Works presently on behavioral neurogenetics, which appears as a means for studying cognitive processes.

[16] Donaldson and Young (2008), Loison (2008), Robinson et al. (2008).

[17] Jean Joachim (Comportement et écologie de la faune sauvage, INRA, Castanet-Tolosan): Naturalist trained in the biogeographical theory of islands applied to the fragmentation of biotopes, works presently on the evolution of the biodiversity of birds according to environmental constraints.

2 Naturalist Thought in Ethology

The most ancient traces of the study of animal behavior date back to Aristotle (−345) who had already noticed that in all the species of Columbidae (pigeons and doves), males sit on the eggs in the daytime and females during the night (Lorenz 1950). Aristotle's *natural history* influenced the naturalist trends in the study of behavior until Lamarck (1809) and Darwin (1859) (through Buffon the encyclopaedist and Réaumur). The comparative study of behavior really began only with Leroy who for the first time distinguished instinct[18] from intelligence. Afterward two positions emerged in France concerning the study of biology and nature. On one side Cuvier, adept in studies within the laboratory, and on the other side Geoffroy Saint-Hilaire, who privileged the observation of animals in natural conditions. Nearly one century later, the famous entomologist Fabre, through his fascinating work conducted in a church that he transformed into a laboratory, demonstrated that it was possible to ally both methods. This revival of the naturalist current had begun in fact with Lamarck, who had advanced in his *Zoological Philosophy* (1809) several explanations for the evolution of nervous centers and intelligence that rested on the notion of heredity of acquired characters. When he published his *Origin of Species* (1859), Darwin recognized moreover that behavioral characters can be hereditary and thus reflect evolutionary affinities. Before him, works concerning the heredity of behavioral characters and their identification as characteristic of the phenotype were very rare. We can quote Saussure, who established the classification of Vespidae wasps from the compared analysis of their nests architecture. It was not until the beginning of the twentieth century that this kind of work reappeared with Whitman (1899) on Columbidae and Heinroth (1911) on Anatidae, each trying to establish relationships inside these families from behavioral characters. In opposition to comparative psychology and then behaviorism, this new naturalist trend did grow, its proponents refusing to admit that organisms developed from a *tabula rasa*, *i.e.* uniquely in reaction to their environment. Objectivist ethologists, conscious of the correctness of their observations, fought against the "environmentalists" who wanted to understand nothing except through the concepts of learning and stimulus-response. These two currents of Ethology spread apart progressively, and then a gap of ignorance settled down between the zoological knowledge of species and the recognition of individual variations. The objectivist current was first to undertake this naturalist development. Lorenz (1941), a pupil of Heinroth, was his follower in research on the homology of behavior in geese and ducks (Anatidae), and he empirically succeeded in establishing the first phylogeny based on behavioral characters. Numerous works from this period testify to a naturalist effervescence, both methodological (in regard to the criteria of behavioral homology (Remane 1952; Baerends 1958))[19] and practical (with the use of behavior for establishing

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[18] A definition of instinct, generally accepted in ethology, was given by Hebb in 1949: behavior with variable motor acts but with a final result predictable according to the belonging of the organism to a given species, without knowing its individual history.

[19] See Sect. 5.

relationships in diverse groups like spiders, insects, amphibians, birds and mammals). Tinbergen (1959) brought to light homologous courtship behaviors in gulls. He observed that certain postures remain almost identical in two species, while others differ by an exaggeration of the movements of the head. Tinbergen considered that such a "differential ritualization" would have allowed a process of sexual selection (Darwin 1871), where males exaggerating these postures would have more mating success with females responding to these signals; this would have ended in the separation of the two species when females finally answered only to one of the two extreme courtship postures (Campan and Scapini 2002).

The structuring of this "new" ethology current, being more interested in phylogenesis, is presently in progress – because it still turns out to be essentially limited to arthropods. Actually, the phylogenetic reliability of behavior is still under debate with vertebrates, where only a few studies were performed on teleostean fishes (McLennan et al. 1988; McLennan 1994), amphibians,[20] birds[21] and mammals.[22] There are two reasons for this reluctance for using behavior for vertebrate phylogenetic inference (Cap et al 2008): the application of the criterion of homology to behavior would be problematic, and behavior would be more sensitive to convergence than morphological or molecular characters (De Queiroz and Wimberger 1993). These critiques were strongly rejected by numerous biologists[23] who are pleading, on the contrary, in favor of the extensive use of behavior in systematics, which leads us now to examine the narrow links between ethology and phylogenetic systematics.

3 Phylogenetics: A Science in Evolution

By definition, phylogenetics is the science studying relationships between living organisms that result from phylogenesis. If the sources of data used to infer these relationships diversified in time, this was also the case for the methods for inferring these relations. Historically, Aristotle (−327) made a first attempt at classifying living beings, but it was from Linnaeus on that the chaos of heterogeneous forms began to be put into some order. In his *Systema Naturae* (1758), Linné proposed the system of binominal nomenclature of living beings that is still used nowadays with some modifications (Malecot 2008), and which – when joined with the deposit of a type-specimen generally preserved in a natural history museum – allows a non ambiguous communication of the names of species. Although the typological

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[20] Cocroft and Ryan (1995), Ryan and Rand (1995), Robillard et al. (2006).

[21] Irwin (1996), McCracken and Sheldon (1997), Cicero and Johnson (1998), Zyskowski and Prum (1999).

[22] Kiley-Worthington (1984), Macedonia and Stranger (1994), Kurt and Hartl (1995), Cap et al. (2002, 2008).

[23] Brooks and McLennan (1991), Wenzel (1992), Miller and Wenzel (1995), Wimberger and De Queiroz (1996), Grandcolas et al. (2001), Peters (2002), Robillard et al. (2006).

species concept remains practical for identification, it has been completed by other more explicitly evolutionist concepts, particularly the "biological" species concept (Mayr 1969).[24] Species are then defined as groups of natural endogamic populations, isolated from a reproductive point of view from other sets of the same type. This species concept also relies on behavior as a precopulatory barrier to explain reproductive isolation (Mayr 1965). Curiously, it must be noted that his diagnoses practically never made reference to behavior, contrary to Buffon – who, by his popular approach, proposed more species descriptions that included specific behavior. As we see it, the comparative study of behavior began in fact with Leroy whose naturalist observations were pursued by Geoffroy Saint-Hilaire. The latter proposed as a criterion for the identification of homologue characters the principle of connections, borrowed from Owen under the term of homology, which stipulates that an organ is equivalent in two species if it has the same connections with the other organs (Darlu and Tassy 1993). Knowing the works of Geoffroy Saint-Hilaire, and inspired by its new teachings on the invertebrates whose name he created, Lamarck gave to systematics, until then strictly classificatory, an evolutionary dimension. In his *Zoological Philosophy* (1809), Lamarck spoke for the first time of the concept of phylogeny by proposing a schematic representation of the filiation of animals, while keeping a classic representation of genealogical type, from top to bottom. Beyond this major progress for systematics, behavior appears as a motor of transformation. The first explanatory theory of evolution thus has behavior for a unique process. The repeated usage of some limb strengthens it, its non-usage weakens it and tends to remove it at the end of several generations. These ideas on evolution were totally rejected by the fixist Cuvier, for whom the anatomy of Vertebrates had no secrets. After Lamarck, Darwin turned the debate in favor of transformism; and if we consider *pangenesis*, it is not one but two theories of evolution that were proposed by Darwin in his Origin of Species (1859) and then in his Variation of Animals and Plants (1868). Only the former will reach our times, after being screened by "Weismannian" selection. This theory of gradual evolution of species (*Natura not facit saltum*) is based on natural selection, of which there are three fundamental principles (Campan and Scapini 2002; Danchin et al. 2008): variation explains that the members of a species differ in their characteristics; heredity makes it so that parents pass their distinctive characteristics on to their descendants; differential reproduction means that, under the effect of natural selection, some individuals produce more descendants than others because of their inherited characteristics.

For Darwin, a natural classification had to reflect the relationships between living organisms according to the model of descent with modification. To make this message well understood, the only illustration of *The Origin of Species* is a phylogeny that Darwin defined later in terms of the genealogical lineages of all organized beings. Haeckel followed him closely, proposing for the first time the term "phylogeny" and the first phylogenetic tree of living beings. Being inspired by the last chapters of *The Origin of Species*, he also formulated the biogenetic law of recapitulation, according to which ontogenesis recapitulates phylogenesis.

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[24] See Sarah Samadi chapter on "species", in the present work.

After Lamarck, Darwin (1859, 1868) also developed a theory of acquired characters (pangenesis), which would be refuted by Weismann. The discovery of the three laws of heredity[25] by Mendel in 1865, and later by Hugo de Vries, as well as the contribution of Hardy and Weinberg in statistics applied to population genetics (Plutynski 2008), participated in the implementation of the synthetic theory of evolution. The latter will be based on variation/selection (random mutation and natural selection), and will dominate from the 1940s until the present, revolving around several theoreticians the most influential of which were Mayr (who established the biological species concept (Mayr 1965, 1969, 1981)), Dobzhansky (a geneticist for whom nothing makes sense in Biology except in the light of evolution (Dobzhansky 1966, 1977)), and Simpson (a paleontologist of the Chicago school, and a supporter like Cuvier of big biodiversity crises (Simpson 1951)). Besides the neutralist theory of Kimura on the preservation of genes that are not necessarily advantageous, and the theory of the selfish gene of Dawkins (1976) taking the place of the individual as the unit of selection, the only notable event in neodarwinism was the work of Gould which questioned the gradualist dimension of evolution with his theory of punctuated equilibriums (Gould and Eldredge 1993), borrowing the ideas of Cuvier on long evolutionary stasis without change, and those of Mayr who had already recognized that the isolation of small peripheral populations accelerated the evolutionary process. Other works of Gould on heterochrony of development and on exaptation[26] will complete the concepts of current neodarwinism. Finally, a methodological evolution occurred in the 1960s. Three schools of thought emerged in systematics according to their concept of similarity (Darlu and Tassy 1993):(i) phenetics, which makes no distinction between homology and analogy, and which claims that similarity between taxa is expressed by calculations of global resemblance (Sneath and Sokal 1973); (ii) evolutionary systematics, which rejects analogies and considers only homologous characters without distinguishing the derived states from the primitive ones (Simpson 1961; Mayr 1969); (iii) phylogenetic systematics (Hennig 1966) or cladistics, which suggests classifying the living only on the basis of phylogenetic relationships, which are established only from the sharing of homologous derived characters (synapomorphies).

The evolution of systematic concepts came along with a qualitative and quantitative evolution of the data used for phylogeny inference. They were at first morphological characters before other sources of data came to complete this field of investigation. Thanks to technological progress, molecular phylogenetics knew a certain success by resolving several evolutionary “puzzles” like *e.g.* that of Cetartiodactyla gathering Artiodactyls and Cetaceans, the latter being more closely related to hippopotamus (Milinkovitch 2003). Comparative Biology thus diversified by integrating data relative to the genotype (genetics) and the phenotype of the living (cytology, physiology, morphology, ecology and ethology). Behavior is any expression of an animal observed at a given moment and place (Campan and Scapini 2002). It is a part of the phenotype of an individual or of a

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[25] Dominance, segregation and independent assortment of characters (See Plutynski 2008).

[26] See chapter by Philippe Grandcolas on the notion of adaptation, Chap. 5, this volume.

taxon (species, genus, family…) the same way as the other sources of characters,[27] and it is undeniable that most behaviors have an instinctive component according to the acceptation of Hebb (1949) [See Note 18]. Despite all of these links which unite ethology and systematics, numerous methodological problems persist even today. These misunderstandings, often stemming from ignorance, did not prevent several syntheses from emerging.

4 Behavioral Characters in Phylogenetics

The use of behavior in systematics raises some methodological problems. Among the main arguments advanced by its detractors, behavior is too unstable to indicate relationships (Baroni Urbani 1989). This ephemeral nature of behavioral characters and the apparent easiness with which animals can modify their behavior could support this opinion – thus making behavior a phenotypical trait that is difficult to characterize because of its particular instability (Aronson 1981). This erroneous vision can be explained by a confusion between various aspects of behavior (proximal and ultimate causes). However, it is easy to avoid such errors if we attentively observe a high number of species – and fairly closely related species at that (De Queiroz and Wimberger 1993). This is the reason why ethologists, conscious of the relevance of their observations on the whole behavioral repertoire of numerous species, were the only ones to use behavior in phylogenetic studies – despite the theoretical and methodological objections which we will consider below.

4.1 The Criteria for Behavioral Homology

Another critique against the use of behavior in systematics would be the difficulty in identifying homologous behavioral characters (Atz 1970; Aronson 1981). Generally, we consider the structures of the phenotype as homologous if they owe their resemblance to a common origin. If homology seems *a priori* more evident in morphology, it is essentially because we understand direct genetic relation through common origin – which is not always the case for behavior, particularly in groups such as birds or mammals where the part of learning by imitation is important for the acquisition of certain behaviors. What is aimed at by such criticisms is precisely the “homology of tradition” – like human languages, certain aspects of songs of passerine birds (Joachim and Lauga 1996), or for example the washing of food in salt water by Japanese macaques – which nevertheless constitute relevant characters for relating populations or species.

What is thus the nature of the homology of behavior? Beyond the fact that it seems more complex than morphology, it remains nevertheless that behavioral

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[27] See Chapter by Véronique Barriel on the notion of character, Chap. 7, this volume.

characters can be inherited[28] and thus reflect evolutionary affinities. This problem concerning the nature of homology is not specific to behavior, because it is also met in studies using other sources of data (Wimberger and De Queiroz 1996). Behavioral homologues are defined above all else by the fact that they find their origin and similarity in the same exclusive ancestor (Wenzel 1992). Even if two behaviors satisfy diverse homology criteria, they are not homologous if they were derived independently from various ancestors. We then speak of analogous behaviors in unrelated animals who share a similar position in trophic networks[29] (scavengers, carnivores) – like the quarry behavior in both the European vultures (Falconiforms) and the Americans ones (Ciconiiforms); or the same biotopes for gliding flight in the forest expressed by flying phalangers (Marsupials), the flying lemur (Dermoptera), or flying squirrels (Rodents). If this phenomenon of convergence is well known in behavior, it is also the case in morphology. For example, dental characters seem wrongly homologous in various unrelated mammals; their resemblance being caused, particularly in Artiodactyls, by a similar, more or less abrasive diet, leading to a low height of molar crowns (brachyodonty) in Cervids and Moschids or a high one (hypsodonty) in Antilocaprids, Bovids and Camels (Scott and Janis 1993). The plasticity of behavioral development also has its equivalent in morphology, with morphological ecotypes bound to the ecophysiology of development. A striking example is that of turbos (marine gastropods), where the same species, *Turbo cornutus* presents thorny or smooth shells according to the conditions of the sea currents. On the other hand, the older and the more divergent the evolution within a group, as is the case with the controversial Afrotherian mammals (where a taxon is supported only by molecular studies (Waddell et al. 1999)), the more it turns out to be difficult to establish homologies between structures that often disappear in present forms. This is when taxonomists become strongly dependent on fossil discoveries. In this respect, we can stress that the lack of fossil data does not affect only behavior but also molecular data beyond some 1,000 years, and that nobody tries to criticize molecularists for this problem. We can simply emphasize the interest of fossil data as a desirable supplement to other data. Difficulties for establishing homologies also exist for molecular markers because of alignment problems. At the molecular level, the term "orthology" replaces that of homology and opposes that of "paralogy," which is a resemblance due to the duplication of genes independent of any speciation event. These distinctions make molecular analysis collide with a specific problem similar to that of the plasticity of development – because even if DNA hardly "develops" during the life of the individual, it can undergo mutations in certain cells (without mentioning recombining meiotically).

These problems with homology were largely debated in systematics, particularly concerning behavior.[30] The classic homology criteria for behavior were proposed a long time ago by Baerends (1958), transposing the criteria of Remane (1952)

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[28] Hoy and Paul (1973), Hoy (1990), Kimura et al. (2005).

[29] Related to the diet.

[30] Baerends (1958), Lauder (1986), Wenzel (1992), Deleporte (1993), Hall (1994), Martins and Hansen (1996), Robillard and Desutter-Grandcolas (2004).

devised for anatomy. The criterion of position or similar topography (Baerends 1958) is established by the similarity found in the emergence of a behavior. Tinbergen (1959) suggested considering the place of the behavior in a stereotypical sequence as the "criterion of position". The quality criterion (special quality) is the most difficult to define because it requires that movements or complex vocalizations appear in the same context and be explainable in terms of motivation and function. The criterion of connection by intermediates implies the use of long behavioral sequences and postulates (for example, a connection between intermediate ritualized movements and highly ritualized movements (Wenzel 1992)). The latter criterion is problematic when a species shows both forms successively. In morphology certain homologies built following this criterion may be rejected by Patterson's Conjunction Test (1982), but this is not of great utility for problems raised by behavior (Wenzel 1992). With the development of cladistic methods in morphology (Hennig 1966), these criteria evolved a little. For cladistics, homology is a hypothesis of ancestry (Lewin 1987). So we speak of primary homology when we first propose the homology between characters, because of their resemblance, which is an initial guess (De Pinna 1991). When the tree of phylogenetic relationships is built from these supposedly similar characters, the distribution of the characters on the tree allows for the establishment of the so called secondary homology for every character – that is, similarity resulting effectively from a common ancestor. The result is very often that certain supposedly homologous characters are in fact homoplasies (convergences or reversions), possibly linked to a similar environment or development. Thus, they were acquired independently and direct heredity has nothing to do with it. Homology is inheritance from a common ancestor, while homoplasy (convergence, reversion) is a resemblance which is not (Simpson 1961). Presently, in morphology, three criteria allow us to identify homology without knowing the phylogeny *a priori* (Patterson 1982). The criterion of resemblance relies on the principle of connections: an organ is equivalent in several species if, under some shape or function, it has the same connections with the other organs. This criterion must be completed by identifying the primitive (plesiomorphic) and derived (apomorphic) states of the homologous characters by using outgroup characters which polarize the direction of transformations of the characters by rooting the topology. The criterion of non-coexistence allows us to distinguish true homology from serial homology (or homonomy): two homologous characters cannot coexist in the same organism, and this problem arises when comparisons are made between serial organs like the mandibles and ambulacres of crustaceans. Finally, the criterion of congruence allows us to build trees from various characters. Truly homologous characters are congruent – that is, they allow us to build the same phylogenetic tree – which characterizes secondary homology (De Pinna 1991).[31] Congruence is the most severe test of homology (Patterson 1988): it is based on the principle of parsimony, which favors the least possible homoplasy (that is, the shortest tree in terms of the number of transformation steps).

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[31] On primary and secondary homology, See chapter by Véronique Barriel on the notion of character, Chap. 7, this volume.

The current ascendancy of the congruence criterion appears as symptomatic of the difficulty to assess homology among characters. As for behavior, this criterion taken from morphology became essential in determining homology both for reconstructing phylogenies (Lauder 1986; McLennan et al. 1988), and to understand the evolution of behavioral characters by analyzing their distribution (mapping) on trees built from other data – or by integrating them directly into the matrix of phylogenetic characters.[32] So, if the theoretical problems and the practices of the use of behavior in systematics were characterized for a long time by a certain methodological vagueness concerning homology criteria, it seems today that this gap has been filled. This methodological evolution owes its maturation to some major contributions – among which is the work of Wenzel (1992) on the homology criteria applied to various behavioral categories. However, in spite of all of these efforts to legitimize the use of behavior in systematics, ethological characters are generally considered as being "inferior" to morphological ones as indicators of phylogenetic relationships (De Queiroz and Wimberger 1993). The reasons for such a conception are due as much to the absence of knowledge about the work on behavioral phylogenies as to the absence of recognition of the proper limits of the other sources of data concerning the problems of homology and sensitivity to homoplasy.

4.2 Supposed Weakness of Behavior Compared with Other Data in Systematics

Schematically, the previously evoked criticisms suggest that a phylogenetic analysis undertaken with behavioral characters would produce more homoplasies (convergences or reversions) than with morphological characters (Wimberger and De Queiroz 1996). Deprived of any scientific foundation, this opinion persists presently. The morphological method would remain the basis of the natural system, particularly because it is the only one applicable to fossil material. However, if it is true that behavior cannot be fossilized, which allows comparison only between current species, certain fossil evidence can nevertheless supply information about the behavior of extinct species. For example, the remains of collective nests of Dinosaurs inform us about their sociability; or how the tracks of sediment eaters show us the evolution of grazing techniques between the Cambrian and the Devonian (Seilacher 1967). This other critique against the lability of behavior thus appears acceptable, to some extent, as regards all the extrapolations made from the products of past animal activities. However, concerning the extant species, blaming behavior for its ephemeral and emergent nature appears as intellectual dishonesty given the important technological progress (video recordings and acoustics) that facilitated the collection and the preservation of behavioral data

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[32] Coddington (1988, 1990), Carpenter (1989), Deleporte (1993)

(Altmann 1974). In fact, besides the ancient works which remain largely ignored, more recent studies have supplied good phylogenetic estimations – which, as already indicated by Wenzel (1992), strongly invalidates these criticisms. Moreover, measuring the respective rates of homoplasy[33] in behavioral and morphological character sets underlined the fact that behavioral characters were no more and no less sensible to homoplasy than morphological ones, and that they constituted a source of data as reliable as other ones to infer the evolutionary history of any animal group (See De Queiroz and Wimberger 1993; Cap 2006).

5 Behavior Mapped on a Tree or Integrated into the Matrix

All work using behavior in systematics can be clustered in two approaches: the first one, occasionally called "mapping", consists in arranging on a tree already built from other data one or several behavioral characters, privileging in this way the phylogenetic topology of a molecular or morphological tree.[34] An interest of "mapping" consists in testing hypotheses concerning the evolution of certain behavioral categories on an already built tree, *e.g.* sociality. In wasps, arranging on a morphological consensus tree various attributes such as solitary, monogyne or polygyne[35] (characterizing colony foundation types) allowed Carpenter (1989) to test different hypotheses about the evolution of sociality in this taxonomic group. However, mapping behavioral characters on a tree that is already built from other data however indicates that we have doubts about the primary homology of those behavioral traits (Deleporte 1993); thus, we should logically not make use of phylogenetic inference for these behaviors, not even for optimizing scenarios, because this supposes some confidence in the homology of the considered traits. To be coherent, it would thus be necessary to perform the analysis by integrating these characters into the data matrix of phylogenetic characters (Grandcolas et al. 2001; Lecointre and Deleporte 2005).

Accordingly, the second approach for using behavior in phylogenetics consists in putting the behavioral characters directly in the matrix from which the relationships will be established. Numerous studies follow this approach by using modern techniques of phylogeny reconstruction and applying them to a vast range of zoological groups such as arachnids (Coddington 1990), insects (Desutter-Grandcolas and Robillard 2003; Legendre et al. 2008a, b), teleostean fishes (McLennan et al. 1988; McLennan 1994), amphibians (Robillard et al. 2006), birds ((Irwin 1996) – where Lorenz's phylogeny of anatids was validated by cladistic methods applied also to morphology (Prum 1990)), and certain mammal groups like bovids (Kurt and Hartl 1995; Lundrigan 1996) or cervids (Cap et al. 2002, 2008). Behavior being

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[33] Characters which seem convergent on the tree of the relationships and the measure of which is made by indications of coherence and retention index (CI and RI).

[34] Coddington (1988, 1990), Carpenter (1989), Mattern and McLennan (2000), Lusseau (2003).

[35] Colony founded by one queen (monogyne) or several (polygyne).

integrated into the matrix or not, one of the main objectives of the use of behavior in systematics is to establish evolutionary scenarios which include the "ancestral ethotypes" inferred at the nodes of the phylogenetic tree (Cap et al. 2002). Only the criterion of secondary homology (De Pinna 1991) allows us to infer homology by common ancestry. Optimal evolutionary scenarios allow us to test or simply to suggest hypotheses about evolutionary processes (Deleporte 2002). The analysis of Cervids showed a likely influence on sexual selection exercised by females on males to explain the descent of the larynx during the rutting call, as a means for rutting stags to "sound" more impressive toward other males and females (Charlton et al. 2007; Cap et al. 2008). This new field of investigation brought to systematics by the study of behavior has great potential, but it can be effective only by recognizing the limits of this particular data constituted by behavioral characters.

6 Limits and Perspectives of the Use of Behavior in Systematics

Despite all these encouraging results, behavioral data remains controversial in systematics, because it must be acknowledged that the absence of observation of a behavioral feature does not always mean its certain absence; and even if this limit refers to intraspecific variability, which is not specific to behavior, it constitutes nevertheless a handicap in regard to other types of data. However, the problems connected to observation bias, like the cyclical absence of expression of certain behaviors, could be corrected by the contribution of additional observations which stem from bibliography – hence the interest of creating on-line accessible behavioral data banks, like there are for molecular studies with GenBank. The other critique, which consists in believing that it would be more difficult to identify homologous behavioral characters, had been widely fantasized, as Wenzel (1992) demonstrated; it is ironic to notice that the same criticism concerning the difficulty of establishing homology between characters emanates today from molecularists against morphologists (Scotland et al. 2003), the latter experiencing the same attacks that they formerly imposed on behaviorists. Such attitudes, particularly concerning teaching, could threaten to erase disciplines in ethology and in morphology (Jenner 2004). Generally, any data set is able to correctly define clades in most of the taxonomic groups, but it is more difficult to establish the relationships between these groups (Gatesy and Arctander 1999). This observation has nothing imaginary within it and owes its explanation to several phenomena. The first one would be homoplasy, which can confuse the issue of phylogenetic reconstruction because of a similar evolution for taxa in identical environmental conditions. Another cause would come from the difference of evolution speed between characters – qualified as mosaic evolution by De Beer (1954), and then as heterobathmy of characters by Hennig (1966). This is the case with the posterior hind legs of mammals that evolved faster than the forelegs (loss of fingers). Concerning behavior, certain ancestral characters can also persist without any apparent functional reason. Such a behavioral relic, like the threatening sideways display of the canine teeth,[36] is present in Moschids or musk deer (Flerov 1952; Green 1985) as well as in most Cervids. In the latter, the superior canine regressed or completely disappeared (Cap 2006). Finally, the use of cladograms relying on a model of diversifying and strictly dichotomous evolution sometimes turns out to be difficult to apply at the specific or generic levels – given the possible natural hybridization between different species. In fact, this phenomenon is recognized in the eighteenth century in plants (Buican 1972); and even if cases of hybridization remain rather unusual in animals (Holliday 2004), there are several famous examples where hybridization created fertile descendants between species of the same genus (wolf and coyote, white-tailed deer and mule deer, common hare and boreal hare, gelada baboon and those of the savannas), and between different genera (Herzog and Harrington 1991) – as was shown for the Pere's David deer, *Elaphurus davidianus*, whose natural hybrid origin is now asserted (Pitra et al. 2004). These examples should bring systematicians to take account of tokogenetic relations (which is a secondary branch of the systematics developed by Mayr (1969)), whose representation of relationships, both dichotomous and overlapping (in networks with branch crossings), is probably closer to reality when we consider the interior of species. Given that species are only a taxonomic convention, certain crossings called intergeneric, like that between the roach and the toxostome (Lecointre pers. comm.), question in return the outlining of species; because if we consider that they are in fact two subspecies, there is no more hybridization and thus no more problem of representation. Hybridization can also have an influence on the evolution of a group. The influence of interbreeding on the birth of a lineage that will become a long-lasting one particularly concerns the advantage of heterozygotes or the Boesiger effect (1974) – which was demonstrated both in terms of reproductive success in flies (Campan 1980), and of the resolution of problems in mice (Lassalle et al. 1979).[37] In the case of interspecific crossings observed in Cervids, the crossing of the red deer, *Cervus elaphus,* with the sika, *Cervus nippon*, produces descendants with intermediary mating calls (Long et al. 1998; Cap et al. 2008). Hybridization can thus be a cause of disturbance for the phylogenetic signal, because the dichotomous branches of a classic tree cannot account for such events which can generate a number of species as important as the parents species. The study of pre-copulatory barriers, of which hybridization embodies a crossing over, can constitute a promising field of study in systematics, bringing it an improved legibility – because this science still remains obscure for biologists and even more for the public (Cap and Desutter-Grandcolas 2010) due to the obscure anatomical or genetic terms used. As Darwin (1859, 1871 [2000]) had planned it, sexual behavior turns out to be of great interest as evolutionary markers for most of the zoological groups (Cap 2006). There are also particularities in vocalizations and other sounds,[38] as well as specific

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[36] Posture of approach towards a fellow, a rival or a predator, superior lip rolled up, letting the superior canine appear (Cap 2006).

[37] The effects of heterosis or hybrid vigour which show themselves at the level of F1 are not permanent and dissolve partially from F2 on (Lassalle pers. comm.)

[38] Reby and McComb (2003), Poole et al. (2005), Robillard et al. (2006), Cap et al. (2008)

movements such as immobile flight in the kestrel hawk, or walking with an oscillating tail in all wagtails. An interesting perspective would be to compile these "ethotypes" for every zoological group and to establish a behavioral classification – as was already tempted in bovids (Walther 1974).

7 Conclusion

The relationships between ethology and systematics seem today to reunite, because behavior embodies at the same time a product of evolution (phylogenesis) and something which participates in it: behavioral data can bring complementary explanations to evolutionary processes by their acting in speciation by interrupting the genic flow between populations (Campan and Scapini 2002); however, as a factor of preservation of interspecific barriers, it is one of the active factors of evolution and a source of heritable characters for phylogeny reconstruction. Beyond the classificatory perspectives that are useful for systematicians and for environment managers (UICN), a last question that is hardly evoked in this chapter concerns the appearance of new behaviors. These innovations lead us back to mutations. A legitimate question would be to know if these appear accidentally and if they are necessary for the appearance of new behaviors. Because if the genetic origin of certain behaviors is demonstrated (*e.g.* Kimura et al. 2005), genes do not directly specify the behavior but code for molecules which build and govern the functioning of the brain and the general nervous system, thereby allowing for behavioral expression. Thus, information perceived by the individual in its environment (social context and habitat) can alter the expression of genes in the brain and consequently of behavior (Robinson et al. 2008). Moreover, the type or intensity of social stimuli can have various epigenetic effects – such as a change in metabolism, in synaptic connections or in the rates of transcription in the genome. Most surprisingly, these modifications in genetic expression are heritable without being attributable to mutations in the DNA sequence. This phenomenon was already brought to light in rats with the transmission of the maternal styles of breeding (Champagne et al. 2008). Young rats bred by caring mothers (which is measured in terms of the frequency of grooming contacts) will have descendants less sensitive to stress and who will take better care of their young, while those brought up by less caring mothers will be more sensitive to stress and, in turn, will take lesser better care of their own young. Researchers noticed that the high rates of grooming by the mothers allowed to limit DNA methylation[39] in descendants, which entailed a limitation in the response to stress in the latter. Other results showed that the expression of the genes of receptors sensitive to oxytocin could be correlated with social bounding in two species of voles. In the monogamous species, contacts between partners and paternal care are more important than in the polygamous species. The latter can become monogamous by being injected (by viral vector), with a sequence which will increase the receiver's rate of

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[39] Epigenetic phenomenon modifying the expression of certain genes (CH3 fixed to the DNA).

oxytocin receptors, mimicking in some way the effect of bonding in monogamous species (Donaldson and Young 2008). These experiences confirm that numerous behavioral adaptations can appear in a lineage before any genetic modification, as was already shown by Waddington (1975) for morphological characters. In humans, this phenomenon is largely emphasized given that our cultural epigenetic evolution overrode our genetic evolution (Butovskaya 1999).

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