Extended phenotypes as signals

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ABSTRACT

Animal signals may result from construction behaviour and can provide receivers with essential information in various contexts. Here we explore the potential benefits of extended phenotypes with a signalling function as compared to bodily ornaments and behavioural displays. Their independence of the body, their physical persistence and the morphological and cognitive conditions required for their construction allow unique communication possibilities. We classify various levels of information transfer by extended phenotype signals and explore the differences between secreted signals and signals resulting from collection and construction, which usually involve higher behavioural complexity. We examine evolutionary pathways of extended phenotypes with a signalling function with help of a comparative evaluation and conclude that often constructions first provide a direct fitness benefit, with a signalling function becoming more and more prominent during evolutionary progression. The abundance and variability of extended phenotypes as signals is impressive and provides unique possibilities for animal communication research.

Key words: non-bodily ornament, signalling value, mate choice, animal construction behaviour, sexual selection.

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I. INTRODUCTION

(1) General Introduction

The "selfish gene" concept (Dawkins, 1978) introduced an important aspect to evolutionary biology, as for centuries the animal's body was the main focus of zoological research. However, when genes are taken as important units of selection, potential effects of genes on the environment beyond an animal's body should be considered as well. The extended phenotype includes "all effects of a gene upon the world" (Dawkins, 1982). Each grain of sand a caddis fly larva (Trichoptera: Psychidae) includes in its armour and each single stick in a beaver's (*Castor fiber, C. canadensis*) dam are to some extent expressions of the individual's genotype, and therefore belong also to the phenotype of that organism (Dawkins, 1982). Likewise, parasite-induced changes of the host phenotype are part of the parasite's extended phenotype. For example, the shell of a snail that has been thickened due to a trematode infection (Cheng, 1973) is also part of the parasite's phenotype. If we wish to understand the evolution of extended phenotypes, we should focus on traits that influence the organism's fitness positively or negatively. Footprints for example, do usually not influence the fitness of the animal producing them and are therefore evolutionarily neutral.

The extended phenotype concept inspired several research fields: in physiology, the idea was adapted to describe hymenopteran colonies as "extended organisms" (Turner, 2000). In ecology, the fields of bioengineering (Sterelny, 2000) and niche construction (Laland, 2004) were significantly stimulated. In evolutionary and behavioural research, however, the peculiarities of extended phenotypes as compared to bodily traits largely have been ignored, perhaps because the extended phenotype concept has not been developed formally to provide testable predictions. Nevertheless, extended phenotypes show exclusive properties that are important for the understanding of behaviour and its evolution. Especially in the context of signalling, extended phenotypes provide unique opportunities to animals compared to bodily ornaments or behavioural displays.

Animal communication research in general may benefit from focusing on extended phenotype signals, because they provide good opportunities to unravel general principles due to their great susceptibility to experimental manipulation. Questions of general interest that may be investigated with extended phenotype examples include:

(1) Who are the intended and actual receivers of sexual signals, potential mates or competitors, and how can different signal functions be reconciled (Grether, 1996; Alonso-Alvarez, Doutrelant C. & Sorci G., 2004)? For example, satin (*Ptilonorhynchus violaceus*) and spotted bowerbirds (*Chlamydera maculata*) destroy each other's bowers that are aimed to attract females if they are too elaborate, i.e. if they do not match the builder's competitive ability (Madden, 2002; Wojcieszek, Nicholls & Goldizen, 2007).

(2) How does the acquisition of inadvertent social information alter the behaviour of eavesdroppers (Oliveira, McGregor & Latruffe, 1998b; Doligez, Danchin & Clobert, 2002)? Because signals and signal producers can easily be decoupled, extended phenotype signals are perfectly suited to test the effect of specific information on eavesdroppers' behaviour experimentally.

(3) What are the functions of multiple signalling (Candolin, 2003; Hebets & Papaj, 2005)? For instance, female satin bowerbirds use either observed male behaviour or bower quality for mate assessment, depending on their own age (Coleman, Patricelli & Borgia, 2004).

(4) Can receivers of signals judge the cognitive abilities of senders, and how? As corvids apparently adapt their caching behaviour to the pilfering probability of bystanders (Bugnyar *et al.*, 2007), such abilities might not be uncommon. If so, it may be easier for receivers to judge a signal or its producer when it persists for a prolonged period, which is the case with extended phenotypes (e.g. providing simultaneous signal assessment potential). Production of extended phenotype signals may be cognitively demanding and hence reveal the signaller's capabilities. Bowerbirds building more complex bowers have larger brains (Madden, 2001), which might hint in this direction.

(5) How do animals adjust signal transmission to different environmental conditions (Brumm & Todt, 2002; Ord *et al.*, 2007)? Bowers of golden (*Prionodura newtoniana*) and spotted bowerbirds differ substantially among populations, suggesting that either environmental differences or arbitrary changes in traits (i.e. cultural differences) may be responsible (Diamond, 1986).

(6) What is the importance of sensory biases in signal evolution (Basolo, 1990; Ryan, 1990)? Some signal characters of extended phenotypes may utilise pre-existing biases, such as preferences for colours of certain food items (Madden & Tanner, 2003). This might allow a better experimental test of the sensory trap hypothesis than using bodily ornaments, as any

manipulation of bodily ornaments may also change the behaviour of the displayer, whereas such influences can be avoided, at least partly, in extended phenotypes (Quader, 2005).

Below we discuss potential advantages and disadvantages of extended phenotype signals in comparison with bodily signals and behavioural displays. We describe and illustrate circumstances under which non-bodily ornaments are superior, discuss the evolution of extended phenotype signals and suggest directions for future research. We surveyed publications in the "ISI: Web of Science" database, searching for the following key words: extended phenotype*, extended-phenotype*, non-bodily ornament*, extra bodily ornament*, animal structure*, animal construction*, animal building* and animal decoration*. We consulted the resulting references and the citations therein. Several additional references were found independently of this search or were pointed out by colleagues.

(2) Definitions: what is an extended phenotype signal?

(a) Extended phenotype

The extended phenotype is the part of the phenotype expressed beyond the body. It includes any feature in the environment resulting from a manipulative action or construction behaviour of an individual. Since detailed investigations of the link between genes and behaviour are scarce, the extent to which the genotype determines the manipulative behaviour producing the extended phenotype and to which it is subject to environmental influences remains largely untested (but see Lijam *et al.*, 1997; Rushbrook, Dingemanse & Barber, 2008).

(b) Signals

Signals have been functionally defined as "structures or actions, which alter the behaviour of other organisms, which evolved because of this effect, and which are effective because the receiver's response has also evolved in response to the signal" (Maynard Smith & Harper, 2004). Use of this definition requires more information than is usually available. In addition, the last part of the definition precludes its use in the context of deceptive signals and mimicry. A more operational definition is that "signals are the vehicle that provides information from the sender to a receiver, who has different possibilities to respond" (Bradbury & Vehrencamp, 1998). This definition, however, hampers distinction between cues and signals, because it neglects the underlying evolutionary mechanisms. Therefore, we advocate here the short and perspicuous definition given by Bolhuis & Giraldeau, (2005): "a signal is something evolved to transmit information".

(c) Extended phenotype signal

We propose to restrict the term extended phenotype signal to cases where the extended phenotype comprises the complete signal or an indispensable element of a complex signal. Elements of complex signals are indispensable if they have a signalling character themselves that operates independently of the other signalling components. Therefore, we exclude any animal manipulation of the environment that just reinforces or accentuates a bodily ornament or a behavioural display; neither singing-burrows amplifying the court-song of crickets or barking geckos, nor display courts fabricated by magnificent birds of paradise (*Cicinnurus magnificus*) by clearing and picking leaves from surrounding vegetation to let light penetrate (Johnsgard, 1994) are hence extended phenotype signals.

In some cases an unambiguous classification of environmental manipulation as an extended phenotype with a signalling function is difficult, which applies particularly to chemical communication. For example, we do not consider a cloud of scent released in a medium as a manipulation of the environment in the sense of an extended phenotype signal. Although the environment's chemical composition has changed, the evolutionary function of pheromones is usually directly and immediately linked to the producer by serving to inform a particular receiver about a certain relation between the producer and its current location. This entails that the signal is not effective beyond the presence of the producer, which is usually an important property of the extended phenotype signal. By contrast, chemical marks deposited on the substratum, e.g. at the territory boundary, serve to inform conspecifics in particular in the producer's absence, therefore they should be considered as extended phenotype signals.

(d) Cues

Cues, in contrast to signals, are animate or inanimate features of the world that can be used by an animal as a guide to future action (Hasson, 1994). Thus, cues are by-products of the producer's actions that are not the result of selection to transfer information.

II. EXTENDED PHENOTYPE AS A SIGNAL

A signal provides reliable information to a receiver if its honesty is either guaranteed by common interests of signallers and receivers (Maynard Smith & Harper, 2004) or by costs involved in signal production (Zahavi, 1975). Costs include investment needed to ensure reliable signal transmission (efficacy costs: Guilford & Dawkins, 1991; Maynard Smith & Harper, 2004) and to ensure honesty (e.g. a handicap: Zahavi, 1975; Grafen, 1990). This applies also to extended phenotypes. It is not only costly to carry a peacock's tail, but also to build a bower and defend it against marauding neighbours (Borgia, 1985a), to collect and stick attractive algae to a nest (Barber, Nairn & Huntingford, 2001), or to move sand to erect craters for mate attraction (Östlund-Nilsson, 2001; Bucher, 2003; Schaedelin & Taborsky, 2006). Thus, the framework developed for the understanding of communication in animals by the means of bodily signals holds equally well for extended phenotypes with a signalling function.

In principle, information can be transmitted by signals at three different levels. First, there is the basic information

about the existence or presence of an organism, e.g. a conspecific or another competitor. An example of extended phenotypes as signals at this basic level are the walls of mudskippers, which surround the builder's territory to mark its claim. The second level includes signals transmitting information about specific characteristics of an individual, e.g. its size, sex, body condition, resource-holding potential, individual identity, group affiliation, relatedness or physiological and morphological state. Odour marks would be an example of extended phenotype signals here, because they can transfer information about the physiological status of the producer. At the third level, information is transferred about the physical and/or cognitive abilities of the producer via its behaviour. A signal will evolve when its production or enhancement is selected by the feedback of 'impressed' receivers. Formidable examples of extended phenotype signals at this level are the richly decorated bowers of many bowerbird species, which require complex behavioural processes such as choosing an optimal location, collecting appropriate construction material and decoration items, arranging them effectively and maintaining the bower over the breeding season by replacing perishable ornaments, as well as defending and mending the construction.

Alongside these three levels, there is another dimension of a signal: information about the motivation of the signaller, e.g. whether it is courting, displaying a defence disposition or ready to interact with social partners. Such motivational intention can be expressed on any of the above levels. Many extended phenotype structures produced to attract mates, such as cichlid sand craters or avian bowers serve this function, among others.

When comparing bodily ornaments, behavioural signals and extended phenotype signals, one important difference lies in the time component of these signals. While a behavioural display lasts only for as long as it is produced, bodily ornaments usually exist for prolonged periods, e.g. a breeding season, often even for the whole adult lifespan. Extended phenotype signals play an intermediate role: they persist longer than the behaviours involved, but usually for not as long as bodily signals. At the spatial level, extended phenotype signals differ in principle from behavioural signals and bodily ornaments, as they allow the signal to be decoupled in space from its producer. In the following, we present potential reasons why manipulating the environment may convey information more reliably or more efficiently than displaying behaviour or bodily ornaments.

(1) Potential advantages of non-bodily signals

(a) Signals persist in the absence of a signaller

Non-bodily ornaments maintain their signalling function even in the constructor's absence, while bodily ornaments and display behaviour require the physical presence of the signaller. In a mate choice context, for instance, a non-bodily ornament may allow a male to pursue other activities than just courting. Especially in lekking or lek-like mating systems, where male territories do not include food resources, this may result in prolonged territory tenure or increased courtship quality. In satin bowerbirds females visit

the bowers of potential mates and inspect them in the owner's absence (Coleman *et al.*, 2004). Bowers without bower owners provide females with multifaceted information about the male's construction skills, but probably no identity cue. Subsequently, females investigate only a subsample of males on these bowers according to their bower preferences. Territory defence is another context where a signal in the absence of the signaller may be useful. Tigers (*Panthera tigris*) leave claw-marks in the bark of trees as high up as possible (Thapar, 1986). These marks can inform intruders about the body size of the territory owner and thus the risk involved in trespassing. Likewise, chemical signals as territory markings may inform conspecifics about the markers' dominance, sex and reproductive status (Brown & MacDonald, 1985; Hurst, 1990*a*, *b*, *c*; Darden, Steffensen & Dabelsteen, 2008). The information conveyed to potential receivers by chemical marks can be complex and may even include identity (Hurst *et al.*, 2001), but marking does not require special behavioural skills that would be conveyed by the extended phenotype structure (Hurst & Beynon, 2004). Chemical marking frequently provokes counter-marking without encounter between opponents, which may also affect third parties. In the lekking blackbuck (*Antilope cervicapra*), for example, males mark their lek-territory with widely dispersed dung piles. Females seem to prefer territories with "clean" dung piles, i.e. males able to prevent others from marking on their piles (Kavita Isvaran, personal communication).

(b) Signals persist for prolonged periods

Extended phenotypes usually persist for prolonged periods, unlike behavioural displays. An extended phenotype may require high effort during construction, but once finished it may need only little investment to be maintained. Male ghost crabs (*Ocypode saratan*) build large sand pyramids near their burrows. Linsenmair (1967) suggested that these are a 'petrified display signal' for females, but experimental manipulations and mate choice observations are required to confirm this. By contrast, the "stotting" behaviour that many ungulates show to dissuade potential predators from attacking (Fitzgibbon & Fanshawe, 1988) needs to be performed repeatedly to be effective, which adds to its cost (Caro, 1986). Birds using a non-bodily signal by entwining snake exuviae or predator scat into their nests [e.g. *Myiarchus crinitus* (Bolles, 1890); *Ochetorhynchus certhioides* (Zyskowski & Prum, 1999); *Estrilda astrild* (Schuetz, 2004)] may deter predators for long periods without extra costs.

(c) Integrated information can be conveyed

Constructions may contain information about the builder's quality that has been integrated over a prolonged period, as is also the case for some bodily ornaments. By contrast, a behavioural display reflects primarily the individual's investment at the moment, which may vary with social circumstances (Green *et al.*, 1995) or environmental conditions (Gottlander, 1987). In the context of mate choice, females may need to sample repeatedly for a reliable assessment of mate quality (Sullivan, 1994). Therefore,

a structure requiring continuous investment during construction and maintenance is beneficial for mate assessment, as it provides information about the builder's performance throughout the existence of the extended phenotype. The sharp rim of sand craters built by some cichlid fish in the Great East African Lakes is constantly smoothed by water movements, impairing the quality of the crater considerably and deterring mate-searching females (Schaedelin, 2004; Schaedelin & Taborsky, 2006). Only continual maintenance keeps craters tidy. Additionally, crater diameter is an important attribute reflecting prolonged investment in sand transport (McKaye, Louda & Stauffer, 1990; McKaye, 1991; Kellog, Stauffer & McKaye, 2000; Schaedelin & Taborsky, 2006). Secreted extended phenotype signals, on the other hand, probably rather reflect the momentary condition of the animal. One might speculate that excretions could additionally transmit information about the infection history of an individual, and thus provide receivers with integrated information about the immuno-competence of the sender. However, to our knowledge this has not yet been tested. Some bodily ornaments may also involve long-term maintenance costs (Hamilton & Zuk, 1982). For example, nuptial coloration based on carotenoids can only be maintained if the signallers acquire enough carotenoids with their diet (Hill, 1992; Hill & Montgomerie, 1994). Mates responding to the intensity of such signals can thereby assess the overall foraging performance of the sender over a long period (Hill, 1990; Kodric-Brown, 1989; Milinski & Bakker, 1990).

(d) Effects from environmental quality and good genes can be separated

Bodily ornaments usually do not allow discrimination between direct effects of the environmental quality while the ornament was produced and the animal's ability to cope with this environment. A receiver assessing an ornament lacks information about whether its superior quality is due to the superb quality of the individual or to excellent environmental conditions persisting while the ornament developed. Such discrimination may be particularly difficult if ontogenetic and reproductive environments differ, when individuals are highly mobile or live in patchy habitats with high levels of variation in quality. Constructed, non-bodily ornaments provide potential receivers with more reliable comparative information about the relative quality of their constructors, since they were all produced in a similar environment. By inspecting the construction, signal receivers can deduce the relative behavioural abilities of the different signallers in a comparable environment. In addition, information about the environment in which the structure was built is usually available to receivers. Satin bowerbird males use decoration items that are scarce and females mate preferentially with owners of such exquisite bowers (Borgia, Kaatz & Condit, 1987). In crater-building cichlids assessment of the relative quality of a crater is reliable within a lek, whereas comparisons among leks at different depths might be devalued by divergent influence of water movements (Schaedelin & Taborsky, 2006). Yet, especially for complex signals involving a longer develop-

ment or learning period, an influence of divergent past environments cannot be excluded.

(e) Signals can be flexible

Extended phenotypes as signals have a great potential to express behavioural flexibility, similar to behavioural displays. In sticklebacks (*Gasterosteus aculeatus*), males build a nest from algae filaments glued together with kidney secretions and decorate the nest entrance using contrastingly coloured algae. Decorated nests are preferred by females (Östlund-Nilsson & Holmlund, 2003; Rushbrook *et al.*, 2008). Males were offered either green or reddish algae to construct a nest. After the nest construction was complete, the same and differently coloured algae were offered to the males. Males showed a flexible colour preference depending on their nest coloration and consistently chose the algae best contrasting with their nest to decorate the nest entrance. They will also use items never seen before, such as artificial glitter, and females seem to appreciate these novel artistic elements (Östlund-Nilsson & Holmlund, 2003). The petal or seed presentation of fairy wrens (*Malurus melanocephalus*) as part of male courtship illustrates another potential advantage of the flexibility of non-bodily ornaments: a non-bodily red element that can be instantaneously produced (Karubian & Alvarado, 2003) takes effect much quicker and is hence more efficient than a physiological change that would be required to intensify or enlarge the red back of the male, particularly if the colour itself is important and not its location on the body (Plenge, Curio & Witte, 2000). The immediate success and the relatively low costs of this supernormal stimulus probably favour petal presentation as a part of male courtship.

(f) Risky signals can be abandoned

Most extended phenotypes can be left behind immediately in an emergency, such as a predator attack. By contrast, morphological characters, like a long tail, can usually not be abandoned on demand. Consequently, the costs of a non-bodily ornament are primarily paid while producing it, whereas bodily ornaments are usually subject to antagonistic natural selection pressures for much longer periods, such as an entire breeding season or even beyond (Soler *et al.*, 1999). With bodily ornaments, a reduction of signalling costs can be achieved for example by covering bright plumage elements with duller feathers or developing conspicuous bodily signals only during a limited time of the year. Similar to covering a conspicuous bodily ornament, the possibility of abandoning a non-bodily ornament may reduce the costs of the signal to the producer and thereby also diminish the signal value to the receiver.

(g) Cognitive potential may be conveyed

Non-bodily ornaments may be highly suited to reveal cognitive abilities of their constructor. This applies probably exclusively to collected (and not excreted) extended phenotype signals that involve complex behavioural procedures. Bower construction requires cognitive skills such as good spatial memory, learning and the ability for innovation. Young males of satin bowerbirds take several years to

learn how to build an appropriate bower and do not build bowers until they are seven years old (Vellenga, 1986). Consequently, bowers may reliably indicate the cognitive abilities of the builder (Frith, Frith & Wieneke, 1994). Similar capabilities could be shown by complex display behaviour, but the persistent physical presence of an extended phenotype might facilitate assessment. More complex bowers might be built by species with larger brains in both males and females, the latter needing the capacity to assess bower quality (Madden, 2001). A recent comparative study indicates that bower building skills are mainly related to cerebellum size, while neither the whole brain, nor the telencephalon minus hippocampus, nor the hippocampus showed a correlation with bower complexity (Day, Westcott & Olster, 2005).

(h) Sensory biases can be exploited more effectively

Extended phenotype signals usually display conspicuous and showy characters, at least to the human observer. If such traits evolve on the basis of pre-existing biases (Madden & Tanner, 2003), their use as an extended phenotype signal allows for higher levels of exaggeration than in bodily ornaments. For example, the area available on the body of a male may be limited compared to the area that can be manipulated in the male's environment. In other words, it becomes possible for displaying individuals to provide a "supernormal stimulus" (Tinbergen, 1951).

(i) Maximum performance potential can be transmitted

Non-bodily ornaments can reveal the maximum effort an individual is able to achieve, particularly in relation to collected or constructed extended phenotypes. For example, black wheatear (*Oenanthe leucura*) males display their maximum working ability during stone-carrying behaviour. In piling up stones as a non-bodily ornament at the entrance of the breeding cavity the male reveals its condition and maximal muscle power. Females react to this post-mating signal with increased investment in the brood. Similar muscular power could otherwise be displayed by long flight distance, which is hard for observers to assess (Moreno *et al.*, 1994; Soler *et al.*, 1999), or by artistic flight manoeuvres. Some species show morphological adaptations to enable performance of elaborate courtship song flight (Hedenström & Møller, 1992). Similarly, morphological adaptations to stone-carrying behaviour in the black wheatear are known (Møller *et al.*, 1995).

(j) Signals may inform the signaller

Finally, the signaller itself may use a non-bodily signal as an information source. Apart from extended phenotype signals, orientation by echolocation and probably also using electric fields may serve a reflexive signalling function. Examples of extended phenotype signals include ant trails that help colony members move between a food source and the colony (Hölldobler & Wilson, 1990; Jackson & Ratnieks, 2006), and chemical cues marked around a burrow that help female shield bugs return home when provisioning

offspring (Hironaka *et al.*, 2007). Similarly, in mammals chemical marks may greatly facilitate orientation of the individuals that mark. In mice (*Mus domesticus*) territory markings which provide conspecifics with information on the marker's sex, dominance and reproductive status (Hurst, 1990*a,b,c*), additionally inform individuals about the territory in which they are located (Hurst *et al.*, 2001). Bumblebees (*Bombus* spp.) and honeybees (*Apis mellifera*) use con- and interspecific odour signals to improve the foraging efficiency of their colonies (Stout & Goulson, 2001), while the individually recognisable odour marks of the solitary bee *Anthophora plumipes* may provide more private information (Gilbert *et al.*, 2001). Reflexive chemical marks may also be useful in social assessment. Dwarf mongooses (*Helogale undulata*), for example, mark other group members with chemical secretions (Rasa, 1973). Their ability to recognise group members may be entirely based on their ability to recognise their own signal (Harper, 1991). Such reflexive use of extended phenotypes as signals may primarily apply to secreted signals. However, there are a few examples of constructed signals used by signallers. For example male fiddler crabs of the species *Uca terpsichores* relocate their burrows faster and from greater distance if they are adorned with hoods (Ribeiro *et al.*, 2006). A constructed signal that has been suggested to serve private use only is the stone ramparts of blackstarts (*Cercomela melanura*). Located at the nest cavity entrance, ramparts may function as an early warning system to breeding females (Leader & Yom-Tov, 1998) since predators cannot enter the cavity unperceived.

(2) Limitations of non-bodily ornaments

Despite the advantages set out above extended phenotype signals have also constraints. One potential disadvantage is that extended phenotype signals are usually spatially fixed. We can predict that individuals with greater resource holding potential will invest more in an extended phenotype. Spatial fixation may not be disadvantageous in the context of resource defence, since the signal is present where it is needed and does not impair the signaller under other circumstances. During mate choice, however, spatial fixation will mean that males can move only to a limited extent to display to females. In the mate choice context, we predict non-bodily ornaments to be more frequent in lekking species, where females visit stationary, clustered males and choose among them (e.g. McKaye, 1991; Schaedelin & Taborsky, 2006). Animals may compensate for spatial fixation by using additional traits to attract females, such as long-distance courtship calls or particularly conspicuous decorations in bowerbirds, or conspicuous courtship displays in crater-building cichlids.

Another drawback of an unattended non-bodily ornament might be its vulnerability to destruction. Destructive actions by conspecifics cannot be prevented while owners are absent (Borgia, 1985*b*). However, the effect of male-male interactions on the quality of the extended phenotype may best reflect the dominance status or quality of the owner and therefore guarantee an honest signal to conspecifics of both sexes (Madden, 2002). In satin bower-birds, the occurrence of feathers in bower decoration

depends strongly on the successful stealing behaviour of the male (Borgia & Gore, 1986). Furthermore, males destroy neighbouring bowers with massive negative impacts on bower quality (Borgia, 1985b). Thus, the non-bodily ornament offers a good index of social interactions without the need for constant eavesdropping of rare behaviour. Similar intrasexual competition was found for the bowers of regent bowerbirds (*Sericulus chrysocephalus*; Lenz, 1994), and its significance for spotted bowerbirds is debated (Borgia & Mueller, 1992; Madden, 2002).

Further, extended phenotypes might be prone to co-option, misuse or wrong assignment by conspecifics due to their independence from the body. Similar to acoustic communication, it may be difficult to assign information from an extended phenotype to the producer with sufficient certainty. Female black wheatears assess the building behaviour of males rather than judging the final stone pile (Soler *et al.*, 1996), perhaps to prevent wrong assignment. This limitation of extended phenotype signals will apply to these involving construction or collected items. It is likely that secreted extended phenotype signals are immune from identity theft. Occasional take-overs of bowers are observed in bowerbirds and they can easily be elicited in crater-building cichlids by experimental removal of the crater owner (Schaedelin & Taborsky, 2006). Although new crater owners start to court females immediately, the need for constant crater maintenance seems to limit crater theft. Also, a crater must apparently match the competitive ability of its owner. Even experimentally enlarged and hence supposedly more attractive craters are reconstructed to their owner's specific size within one day (Schaedelin & Taborsky, 2006), probably due to effects of male-male competition.

(3) Multiple signalling

Complex signalling is a major challenge for communication research and recent studies have raised a multitude of exciting questions (Candolin, 2003; Hebets & Papaj, 2005). In bowerbirds, for instance, multiple signals at the levels of bodily ornaments, behaviour and extended phenotypes act in concert. Male spotted bowerbirds exploit different signalling properties of decoration items by placing them at optimal places near their bower (Borgia, 1995a). White bones further away from the bowers may attract females from a further distance due to their conspicuousness, while the more hidden rarities placed in the bower enhance the female's willingness to mate (Borgia, 1995a). Distinct traits may provide information on different qualities of the sender (Johnstone, 1995a). In satin bowerbirds, bower quality correlates with plumage colouration, but only the latter provides females with specific information on blood parasite load (Doucet & Montgomerie, 2003). Females use different signal modalities depending on their age and probably on their experience (Coleman *et al.*, 2004); whereas younger females show a clear preference for opulently decorated bowers, older females rely on the courtship activity of bower owners.

Which combinations of signals involving extended phenotypes should be expected? We predict that if an extended phenotype signal conveys the current condition of its producer, it should be combined with a trait providing information about the individual's ontogenetic past. Immobile non-bodily ornaments should be supplemented by spatially more flexible courtship displays, as found for instance in many crater-building cichlids, where males may court a female some meters from their crater. Multiple signals may not only convey different information or supplement each other (Johnstone, 1995a); they may even be mutually dependent. The display behaviour of the spotted bowerbird may only work in connection with bowers (Borgia, 1995b). These unique bowers consist of semi-transparent straw walls, behind which the male performs a vigorous courtship display, including occasional attacks on females. It was shown experimentally that females prefer to assess the courting male through an intact straw wall, but then choose more vigorously courting mates, suggesting a threat-reducing function of these bowers (Borgia, 1995b). In satin bowerbirds greater bower quality reduces the threat of intense male displays to females (Patricelli, Uy & Borgia, 2003). To disentangle the effects of and interactions among multiple signals, experimental manipulation of signal components is required. Due to their suitability for experimental alteration, extended phenotype signals provide excellent research opportunities in this context.

III. DISTRIBUTION OF NON-BODILY ORNAMENTS ACROSS TAXA

Most non-bodily signals are features constructed or secreted by the signaller, although other types of extended phenotype signals can be imagined. One fascinating possibility is a parasite's manipulation of a feature of the host's body or beyond it (Thomas, Adamo & Moore, 2005). Recently it was shown, for example, that the malaria parasite *Plasmodium falciparum* manipulates the attractiveness of human odours to mosquitoes to maximise its transmission rate (Lacroix *et al.*, 2005).

Most constructed non-bodily ornaments are known from birds and fish, presumably due to the widespread evolution of nest and shelter construction skills in these groups. By contrast, secreted signals seem to prevail in mammals and insects, whereas web construction traits may serve as signals in spiders. Here we shall briefly outline examples from groups where extended phenotype signals have been studied; a more comprehensive collection of examples is provided in Table 1.

(1) Fish

Sticklebacks, which are among the best nest builders known in fishes, attach non-bodily ornaments to their nests to attract mates. In cichlids, mound-building behaviour of males to attract females has been described from at least a dozen species (Barlow, 2000). The convergent evolution of several species in two great African lakes, Lake Malawi and

Table 1. Summary of extended phenotypes and their potential to serve as a signal, based on currently available information. Family: an estimate of the number of species with a similar extended phenotype is given in parentheses. Source: S = self-secreted, C = collected/constructed. Behavioural level: B = basic (merely presence is signalled), Si = specific individual characteristic (different signal levels), Cx = information transfer by complex behaviour (signals convey high behavioural complexity). Signal: − probably no signalling function, +/− potential signalling function, + signalling function suggested, ++ signalling function shown. Reference: for well-studied taxa only representative references are cited.

Order	Family	Genus/species	Extended phenotype	Materials	Source	Function	Behavioural level	Signal	Reference
PHYLUM PROTISTA									
Class Aconoidasida									
Haemo-ida	Plasmodiidae	*Plasmodium falciparum* (malaria parasite)	Odour	Manipulation of human odour	S	Attraction of the mosquito as vector	B	++	Lacroix *et al.*, (2005)
PHYLUM ARTHROPODA									
Class Crustacea									
Decapoda	Maiidae	*Orgonia gracilis* (masking crab)	Body decoration	Algae and bryozoa	C	Protection of adults	B	−	Hansell, (1984)
	Ocypodidae	*Ocypode saratan* (ghost crab)	Sand pyramid	Sand	C	Mate attraction and dominance	Si	+	Linsenmair, (1967); Hansell, (1984)
	Ocypodidae	*Uca pugilator*	Burrow	Sand	C	Protection of adults	B	−	Hansell, (1984)
	Ocypodidae	*Uca beebi*	Burrow (pilars)	Sand	C	Protection of adults	B	−	Christy, (1988); DeRivera *et al.*, (2003)
	Ocypodidae	*Uca musica*	Burrow	Sand	C	Protection of adults	B	−	Christy *et al.*, (2001, 2002, 2003a, b)
	Ocypodidae	*Uca tangeri*	Burrow (mudballs)	Sand	C	Protection of adults	B	−	Oliveira *et al.*, (1998a); Oliveira & Custodio, (1998); Latruffe, McGregor & Oliveira, (1999); Burford, McGregor & Oliveira, (2001a, b)
Class Arachnida									
Araneae	Uloboridae (20)	*Uloborus, Zosis, Philoponella, Octanoba*	Web with stabilimenta (white silkband)	Silk	S	Prey attraction and predator deception	B	+/−	Herberstein *et al.*, (2000)
	Araneidae (52)		Web with stabilimenta (white silkband)	Silk	S	Prey attraction and predator deception	B	+/−	Herberstein *et al.*, (2000); Bruce *et al.*, (2001)
	Araneidae	e.g. *Agriope keyserlingi*	Web with stabilimenta (white silkband)	Zig-zac silk band or disc	S	Prey attraction	B	++	Herberstein *et al.*, (2000)
	Araneidae	e.g. *Gasteracantha*	Web with duller stabilimenta or debris and spider mimics	Silk	S	Prey attraction and predator deception	B	+	Hansell, (1984); Herberstein *et al.*, (2000)
	Araneidae	e.g. *Cyclosa confusa*	Web with duller stabilimenta or debris and spider mimics	Prey carcasses	C	Predator deception	B	+	Hansell, (1984); Herberstein *et al.*, (2000); Chou *et al.*, (2004)
	Araneidae	e.g. *Cyclosa conica*	Web and spider mimics	Prey carcasses	C	Prey attraction	B	+	Chou *et al.*, (2004)

Order/Class	Family	Species	Structure	Material		Function			Reference
	Tetragnathidae (6)	e.g. *Nephila madagascariensis*	Web with duller stabilimenta or debris	Debris or silk	C+S	Prey attraction and predator deception	B	+/−	Herberstein *et al.*, (2000)
	Tetragnathidae		Net	Silk	S	Prey attraction	B	+/−	von Frisch, (1974)
Acari	Tetranychidae	*Tetranychus urticae*	Network of threads	Silk	S	Mate location	B	+	Hansell, (1984)
Class Insecta Hymen-optera	Apidae	*Bombus* sp.(bumblebee)	Odour marks on flowers	Odour	S	Food gathering	B	++	Stout & Goulson, (2001)
	Apidae	*Apis mellifera* (honeybee)	Odour marks on flowers	Odour	S	Food gathering	B	++	Stout & Goulson, (2001)
	Apidae	*Anthophora plumipes*	Odour marks on flowers	Odour	S	Food gathering	B	++	Gilbert *et al.*, (2001)
Diptera	Empidinae	*Hilara sartor* (dance fly)	Balloon/nuptial gift	Anal gland secretion	S	Courtship display	Si	+/−	Hansell, (1984)
	Empidinae	*Empis snoddyi* (dance fly)	Balloon	Silk	S	Courtship display/species recognition	Si	+/−	Sadowski, Moore & Brodie, (1999)
	Empidinae	*Rhamphomyia sulcata* (dance fly)	Nuptial gift	Invertebrate and silk	S+C	Courtship display	Si	+?	LeBas *et al.*, (2004)
Orthoptera	Gryllotalpidae	*Gryllotalpa vineae* (mole cricket)	Burrow	Excavation in earth	C	Courtship display	B	+/−	Hansell, (1984)
	Oecanthidae	*Oecanthus burmeisteri* (tree cricket)	Leaf with a hole	Sculpting of leaf	C	Courtship display	B	+/−	Hansell, (1984)
PHYLUM VERTEBRATA Class Actinopterygii Gasterostei-formes	Gasterosteidae	*Gasterosteus aculeatus* (stickleback)	Nest	Kidney secretion and vegetation	S+C	Protection of young	Si →Cx	++	von Frisch, (1974); Hansell, (1984); Barber *et al.*, (2001) Östlund-Nilsson & Holmlund, (2003)
	Gasterosteidae	*Spinachia spinachia* (stickleback)	von Frisch, (1974)	Kidney secretion and vegetation	S+C	Protection of young	Si →Cx	++	Östlund-Nilsson, (2001)
	Gasterosteidae	*Pungitius pungitius* (stickleback)	Nest	Kidney secretion and vegetation	S+C	Protection of young	Si →Cx	++	Hansell, (1984)
Class Osteichthyes Perci-formes	Branchio stegidae	*Hoplolatilus geo* (deep-water sand tilefish)	Mound	Shell and coral pieces	C	Protection of adults	Si	+	Fricke & Kacher, (1982)
	Cichlidae	*Aulonocranus dewindti*	Crater	Sand	C	Courtship display	Si	+	Yanagisawa, Ochi & Gashagaza, (1997)
	Cichlidae	*Cyathopharynx furcifer*	Crater	Sand	C	Courtship display	Si	++	Schaedelin & Taborsky, (2006)
	Cichlidae	*Cyrtocara argyrosoma*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Cyrtocara atritaeniatus*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Copadichromis eucinostomus*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1983); McKaye *et al.*, (1990)
	Cichlidae	*Cyrtocara kirkii*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Cyrtocara kiwinge*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Cyrtocara labidodon*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Cyrtocara maginata*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Cyrtocara placodon*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)

Table 1. (*cont.*)

Order	Family	Genus/species	Extended phenotype	Materials	Source	Function	Behavioural level	Signal	Reference
	Cichlidae	*Enantiopus* sp.	Shallow nest or sand patches	Sand	C	Species recognition	Si?	−	Barlow, (2000); F.Schaedelin, personal observations
	Cichlidae	*Lestradea perspicax*	Crater	Sand	C	Courtship display	Si	+	Yanagisawa *et al.,* (1997)
	Cichlidae	*Lethrinops aurita*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Lethrinops furcicauda*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Lethrinops furcifer*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Lethrinops parvidens*	Crater	Sand	C	Courtship display	Si	+	Kellog *et al.,* (2000)
	Cichlidae	*Limnotilapia dardennii*	Sand slope	Sand	C	Courtship display	Si	+	Yanagisawa *et al.,* (1997); F. Schaedelin, personal observations
	Cichlidae	*Ophthalmotilapia nasuta*	Crater	Sand	C	Courtship display	Si	+	Yanagisawa *et al.,* (1997)
	Cichlidae	*Ophthalmotilapia ventralis*	Sand patch on stone	Sand	C	Courtship display	B	−	F. Schaedelin, personal observations
	Cichlidae	*Oreochromis saka*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Oreochromis squamipinnis*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Cichlidae	*Trematocranus microstoma*	Crater	Sand	C	Courtship display	Si	+	McKaye, (1991)
	Gobidae	*Boleophthalmus boddarti* (mudskipper)	Burrow and rampart; wall around territory	Excavation and building with mud	C	Protection of adults	B	+/−	Hansell, (1984); Clayton, (1987)
	Gobidae	*Pomatoschistus microps* (common gobby)	Nest	Plant material	C	Protection of young	Si	+	Jones & Reynolds, (1999)
	Labridae	*Crenilabrus melops* (corkming wrasse)	Nest	Plant material	C	Protection of young	B	+/−	Hansell (1984)
	Labridae	*Crenilabrus ocellatus* (ocellated wrasse)	Nest	Plant material	C	Protection of young	B	+/−	von Frisch, (1974)
Class Aves **Apodi-formes**	Apodidae	*Collocalia* (swiftlet)	Nest	Saliva and other natural light material	S+C	Protection of young	B	+/−	von Frisch, (1974)
Passeri-formes	Corvidae	*Pica pica* (Eurasian magpie)	Nest	Plant material	C	Used by Clamator glandarius (great spotted cuckoo) for protection of young	Si	+/−	Soler *et al.,* (1995)
	Aegithalidae	*Aegithalos caudatus* (long-tailed tit)	Nest	Moss, plant fibres, spider silk	C	Protection of young; maybe courtship display	Si	+	Hansell, (1984)
	Paridae	*Remiz pendulinus* (penduline tit)	Nest	Plant material, feathers	C	Protection of young	Si	+/−	von Frisch, (1974); Hoi & Valera, (1994)

Family	Species	Structure	Material		Function			Reference
Maluridae	*Malurus melanocephalus* (red-backed fairy wren)	Petal presentation	Flower petals	C	Courtship display	Si	+	Karubian & Alvarado, (2003)
Hirundinidae	*Hirundo rustica* (barn swallow)	Nest	Mud and straw	C	Protection of young	Si	++	Soler *et al.*, (1998*a*)
Alaudidae	*Ammomanes deserti* (desert lark)	Nest	Plant material	C		B	?	Meinertzhagen, (1949)
Laniidae	*Lanius excubitor* (northern shrike)	Nest	Plant material and prey	C	Courtship display	Si	+	Yosef & Pinshow, (1989)
Muscicapidae	*Oenanthe leucura* (black wheatear)	Piles at entrance of nest cavity	Pebbles	C	Courtship display	Si	++	Moreno *et al.*, (1994); Soler *et al.*, (1996, 1998*b*)
Muscicapidae	*Cercomela melanura* (blackstart)	Ramparts at entrance of nest cavity	Pebbles	C	Protection of adults	B	++	Leader & Yom-Tov, (1998)
Paradisaeidae	*Cincinnurus* (magnificent bird of paradise)	Light channel to light the "stage"	Removing leaves	C	Courtship display	B	+	Hansell, (1984)
Passeridae	*Euplectes jacksoni* (Jackson's widowbird)	Court area	Plant material	C	Courtship display	Si	+	Andersson, (1991)
Ploceidae	*Malimbus cassini* (black-throated malimbe)	Nest	Plant material, feathers	C	Protection of young	B	+/−	von Frisch, (1974)
Ploceidae	*Philetairus socius* (social weaver)	Communal nest	Plant material	C	Protection of young and adults	B	+/−	Hansell, (1984)
Ploceidae	*Hyphantornis capensis* (Cape weaver)	Nest	Plant material	C		B	+/−	Skead, (1947)
Ploceidae	*Ploceus velatus* (masked weaver)	Nest	Plant material	C		B	−	Howman & Begg (1983)
Ptilono rhynchidae	*Amblyornis flavifrons* (yellow-fronted gardener bowerbird)	Bower	Twigs and berries	C	Courtship display	Cx	++	Diamond, (1982*b*); Hansell, (1984)
Ptilono rhynchidae	*Amblyornis inornatus* (vogelkop gardener bowerbird)	Bower	Twigs, leaves, flowers and berries	C	Courtship display	Cx	++	Hansell, (1984); Diamond, (1986, 1988)
Ptilono rhynchidae	*Amblyornis macgregoriae* (Macgregor's bowerbird)	Bower	Twigs and leaves	C	Courtship display	Cx	++	Hansell, (1984)
Ptilono rhynchidae	*Amblyornis subalaris* (streaked bowerbird)	Bower	Twigs, leaves and berries	C	Courtship display	Cx	++	von Frisch, (1974); Hansell, (1984)
Ptilono rhynchidae	*Archboldia papuensis* (Archbold's bowerbird)	Bower	Ferns, bamboo leaves, beetle elytra and snail shells	C	Courtship display	Cx	++	Hansell, (1984); Frith & Frith, (1990)
Ptilono rhynchidae	*Chlamydera nuchalis* (great bowerbird)	Bower	Twigs and white items	C	Courtship display	Cx	++	von Frisch, (1974)
Ptilono rhynchidae	*Chlamydera lauterbachi* (yellow-breasted bowerbird)	Bower	Twigs, leaves, flowers and berries	C	Courtship display	Cx	++	von Frisch, (1974)
Ptilono rhynchidae	*Ptilontyrhynchus violaceus* (satin bowerbird)	Bower	Twigs, leaves, flowers, fruits, shells and blue plastic items	C	Courtship display	Cx	++	von Frisch, (1974); (Borgia, (1985*b*); Borgia *et al.*, (1985, 1987)

Table 1. (*cont.*)

Order	Family	Genus/species	Extended phenotype	Materials	Source	Function	Behavioural level	Signal	Reference
	Pilono rhynchidae	*Sericulus chrysocephalus* (regent bowerbird)	Bower	Twigs, leaves, flowers, berries and other blue items	C	Courtship display	Cx	++	Lenz, (1994)
	Pilono rhynchidae	*Chlamydera maculata* (spotted bowerbird)	Bower	Twigs, berries, pods, glass, snail shells	C	Courtship display	Cx	++	Madden, (2003)
	Pilono rhynchidae	*Prionodura newtoniana* (golden bowerbird)	Bower	Sticks, lichens, seeds and flowers	C	Courtship display	Cx	+?	Frith & Frith, (1998)
	Orthonychidae	*Orthonyx spaldingii* (chowchilla)	Nest	Twigs, plant pieces, fern and rootlets	C	Courtship display	Cx	+/−	Frith, Frith & Jansen, (1997)
	Passeridae	*Ploceus cucullatus* (village weaver)	Multiple nests	Multiple nests	C	Courtship display	B	+	Collias & Collias, (1984); Hansell, (1984)
	Passeridae	*Ploceus philippinus* (baya weaver)	Multiple nests	Multiple nests	C	Courtship display	B	−	Quader, (2005)
	Passeridae	*Ploceus benghalensis* (blackthroated weaver bird)	Multiple nests	Multiple nests	C	Courtship display	B	+/−	Alis & Ripley, (1987)
	Passeridae	*Ploceus manyar* (Indian streaked weaver bird)	Multiple nests	Multiple nests	C	Courtship display	B	+/−	Alis & Ripley, (1987)
	Passeridae	*Estrilda astrild* (waxbill)	Nest supplement	Scat	S	Protection of young and adults	B	+/−	Schuetz, (2004)
	Troglotydae	*Campylorhynchus brunneicapillus* (cactus wren)	Nest		C	Protection of young	B	+	von Frisch, (1974)
	Troglotydae	*Troglodytes troglodytes* (wren)	Nest	Moss and leaves	C	Protection of young	B	+	von Frisch, (1974); Hansell, (1984)
	Tyrannidae	*Legatus leucophaius* (piratic flycatcher)	Nest stealing		C	Protection of young	B	−	von Frisch, (1974)
	Tyrannidae	*Myiarchus crinitus* (great crested flycatcher)	Nest supplement	Snake exuviae	C	Protection of young and adults	B	+	Bolles, (1890)
	Furnariidae	*Furnarius* and many more (ovenbirds)	Nest	Clay and plant material	C	Protection of young and adults	B	+/−	Zyskowski & Prum, (1999)
	Furnariidae	*Ochetorhynchus certhioides* (Chaco earthcreeper)	Nest supplement	Snake exuviae or cellophane	C	Protection of young and adults	B	+/−	Zyskowski & Prum, (1999)
Pelecani-formes	Sulidae	*Sula dactylatra* (masked booby)	Vestigal nest	Vegetation fragments	C	Pair bonding	B	−	Nelson, (1967); Hansell, (1984)
Class Mammalia									
Artio-dactyla	Bovidae	*Antilope cervicapra* (blackbuck)	Dung piles	Dung	S	Courtship display	Si	+	K. Isvaran (personal communication)
	Bovidae	*Ourebia ourebi* (dwarf antelope)	Marks	Scant markings	S	Territory defence	B	+	Brashares & Arcese, (1999)
Carnivora	Felidae	*Panthera tigris* (tiger)	Marks	Claw marks on trees	S/C	Territory defence	Si	+	Thapar, (1986)

Order	Family	Species	Structure	Material	Function				Reference
Chiro-ptera	Peropodidae	*Cynopterus sphinx* (tent-roost bats)	Tent out of leaves	Leaf	Protection of young and adults	C	B	+/−	Balasingh *et al.*, (1995)
Rodentia	Muridae	*Neotoma cinerea* (bushy tailed woodrat)	Nest	Arms the heap of twigs with cactus spines	Protection of young and adults	C	B	+/−	von Frisch, (1974)
	Muridae	*Mus spicilegus* (mound-building mouse)	Mound	Heaps of wheat	Food storage and thermoregulation	C	B	+/−	M. Hoelzel (personal communication)
	Chinchillidae	*Lagostomus maximus* (plain vizcacha)	Mound	Earth mound, garbage added	Burrow entrance	C	B	−	Hudson, (1872)
	Muridae	*Mus domesticus* (house mouse)	Marks	Urine markings	Territory defence, orientation	S	Si	+ +	Hurst, (1990*a, b, c*)
	Herpestidae	*Helogale undulata* (mongoose)	Marks	Urine markings	Group recognition	S	Si	+	Rasa, (1973)
	Muridae	*Pseudomys chapmani* (pebble mound mouse)	Mound	Pebbles	Thermoregulation	C	B	−	Kitchener, (1983)

Lake Tanganyika, suggests that in the presence of the required construction skills, non-bodily ornaments are likely to evolve. Future research is needed to confirm the signalling value of sand and particle structures in many fish species. For example, the mounds built by the deep-water sand tilefish *Hoplolatilus geo* (Fricke & Kacher, 1982) appear to have a signalling function, they consist of tens of thousands of pieces of broken shells and corals and are much larger than expected if they function only as shelters from predators or for sleeping. These mounds might serve as territory markers or to attract females, but a signal function of these mounds has not yet been shown. In general, non-bodily ornaments may be much more common in fish than is currently thought, due to observer bias (Amundsen, 2003).

(2) Birds

Birds have evolved often intricate nest-building abilities (Hansell, 2005), such as weaving skills of many weaverbirds. The direct functionality of nests makes it difficult to assess whether nest characteristics have a signalling function. Yet, nest characteristics may easily acquire a signalling significance in addition to direct functional benefits, for instance early in the construction phase (Grubbauer & Hoi, 1996). Particularly convincing examples of this are nest-like structures that are not used as nests, or features added to the nest as decorations. Flowers are attached to uncompleted nests by some weavers (*Ploceus benghalensis, P. manyar*: Alis & Ripley, 1987), and European starlings (*Sturnus vulgaris*) adorn their nest with green plant material before egg laying (Gwinner, 1997). However, nest adornment of blue tits with aromatic herbs probably serves to reduce parasite infection (Petit *et al.*, 2002). Whether inclusion of aromatic herbs serves another function such as mate attraction remains to be clarified.

The stone piles around chinstrap penguin (*Pygoscelis antarctica*) nests are another example where an extended phenotype serves a direct function (they reduce the flooding risk), but it is unclear whether they are also used as signals in pre-mating sexual selection (Fargallo, De Leon & Potti, 2001). Both parents closely monitor the quantitiy of stones at the nest and react to changes in their stone piles (Moreno, Moreno & De Leon, 1999).

(3) Mammals

Mammals rarely build elaborate nests, with the notable exception of rodents. This may partly explain why mammals are not known to have elaborated extended phenotypes that serve as visual non-bodily ornaments. However, there are a few exceptions. It has been proposed that some characteristics of tent-roosts of bats (e.g. *Cynopterus sphinx*) might play a role in harem formation (Balasingh, Koilraj & Kunz, 1995), since females join the male in its roost only after he has completed the palm-leaf roost-tent. A conspicuous extended phenotype construction among mammals is the pebble mound of the mouse *Pseudomys chapmani* (pebble mound mouse; Anstee, Roberts &

Oshea, 1997). Yet, the extreme persistence of pebble mounds that are continued over generations suggests a direct benefit rather than a signalling function. In contrast to visual signals, olfactory non-bodily ornaments are probably very common in mammals. Many species use scent to inform conspecifics about the producer's presence, strength, reproductive status, or quality (Brown & MacDonald, 1985; Rich & Hurst, 1998; Sliwa & Richardson, 1998; Rozhnov & Rozhnov, 2003).

(4) Insects

Arthropods are among the most impressive builders of nests, especially taking into account their small body size. Despite the enormous diversity of arthropods and the extraordinary building abilities of Isoptera, Lepidoptera and Hymenoptera (Hansell, 2005), few examples of extended phenotype signals have been reported in insects. Again an investigation bias may be partly responsible. Nevertheless, certain insect groups (e.g. Hymenoptera, Isoptera) are well studied and build complex structures. The apparent absence of a signalling component to these constructions may be due to the dominating importance of chemical rather than visual cues in arthropod communication. Chemical non-bodily signals are probably widespread in arthropods, such as the trail marks of ants and pheromone marks in some stingless bees (Carthy, 1951; Jackson *et al.*, 2006; Jackson & Ratnieks, 2006) but few species mark territory boundaries in the way that vertebrates do (Hölldobler & Wilson, 1990). An exception is African weaver ants (*Oecophylla longinoda*), which mark territory boundaries with colony-specific pheromones in faecal material. Hölldobler & Wilson (1990) showed that in contests between two colonies the outcome depends on the previous colony-specific markings in the arena. In addition, anal-drop deposition in these ants serves to localise a food source and to help foragers return to the nest (Dejean & Beugnon, 1991).

(5) Spiders

Some extended phenotypes of arthropods may have evolved to deceive receivers. It was suggested that stabilimenta, linear, cruciate or spiral patterns of densely woven silk bands in spider webs (Fig. 1), mimic floral structures to attract insect prey (Herberstein *et al.*, 2000). Alternatively, it has been suggested that stabilimenta make the web less recognisable to prey (Herberstein *et al.*, 2000). Empirical evidence is controversial, but at least in some species webs with stabilimenta do attract more prey than webs without silk bands (Bruce, Herberstein & Elgar, 2001). Other elements of the spider's web might also have a signalling function. For example, mesh size is used as an indicator of the owner's body size by females of *Nephilengys cruentata* trying to usurp a net (Schuck-Paim, 2000). Yet, the mesh size is probably a mere by-product of the body size of the constructor and would hence classify as cue and not as signal.
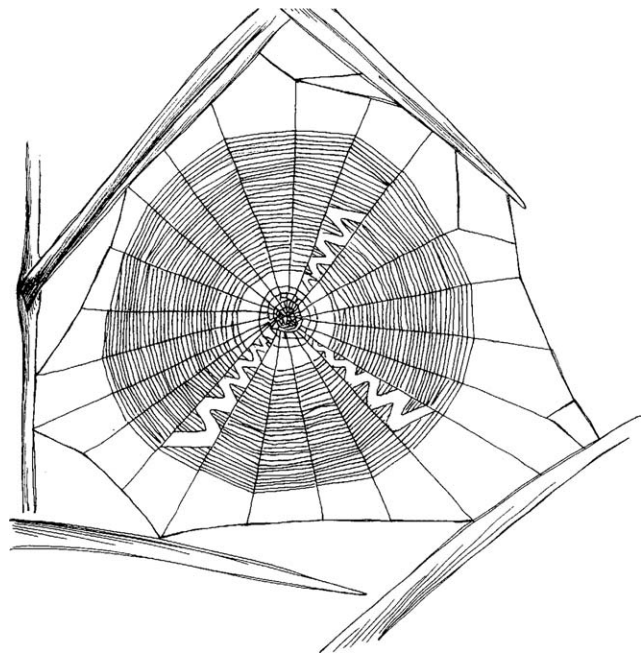

Fig. 1. Sketch of an orb-web spider net with an uncompleted cruciate stabilimentum.

(6) Crustaceans

It can be difficult to differentiate between extended phenotypes evolved to transmit information, i.e. signals, from cues where information is transferred merely as a secondary effect (see Maynard Smith & Harper, 2004). In several species of fiddler crabs, the male builds sand structures around his burrow that attract females [*Uca beebi* (Christy, 1988), *Uca tangeri* (Oliveira *et al.*, 1998a), *Uca musica* (Christy *et al.*, 2002)]. However, in *U. musica* once the female entered the burrow, she was equally likely to mate in burrows with and without sand hoods (Christy, Backwell & Goshima, 2001; Christy, Baum & Backwell, 2003b). Females hiding behind these sand constructions may reduce their predation risk, similar to the use of other structures available on exposed sandy beaches. Even though both partners profit from sand mounds, they might not transfer information and hence are not signals.

It may be that, when tested properly, some apparent examples of an extended phenotype with a signalling function turn out to provide solely a direct benefit to the producer or receiver, whereas in other cases a hidden signalling component of a structure has been overlooked (Soler *et al.*, 1998a; Östlund-Nilsson & Holmlund, 2003). Detecting a signalling function of a structure that also serves other purposes, or disentangling experimentally a signalling function from direct functions can be difficult. Therefore, an apparent scarcity of extended phenotype signals in any taxon may result primarily from observation bias, with the limitations of the human sensory system of particular importance. For example, chemical signals are apparently widespread among mammals, but due to technical detection problems they are rarely investigated.

A true limitation to the use of extended phenotype signals in any taxon might be that their production may be constrained by the exacting requirements to produce or recognise them. Functional constraints and limited resources may reduce the observable variation in a construction to such an extent that sufficient information transfer is difficult. Anatomical requirements for elaborate constructions and advanced cognitive capabilities may be a precondition to arrange and judge some complex extended phenotypes, such as the vogelkop gardener bowerbird's (*Amblyornis inornatus*) bowers (Diamond, 1986).

Considering the examples provided in Table 1, it appears that self-secreted extended phenotype signals are usually basic signals of absence or presence (eight cases versus four cases with more complex information), whereas collected or constructed extended phenotype signals usually reveal more complex information about the individual characteristics of the signaller (31 cases versus eight cases with basic information). We do not interpret these differences further at this stage, as a proper comparative analysis accounting for phylogenetic contrasts would be required to infer significant patterns. It is puzzling why there are so few cases known in which secreted extended phenotype signals serve to reveal complex information about individual characteristics, but this may result from an information bias caused by methodological difficulties. Alternatively, secreted extended phenotypes may be less suitable to convey multilayered information since they are not based on complex behaviour.

IV. THE EVOLUTION OF NON-BODILY SIGNALS

An evolutionary transition from a bodily ornament to a non-bodily ornament has been suggested for bowerbirds (Gilliard, 1969); this was supported for one branch of bowerbirds, the avenue builders (Kusmierski *et al.*, 1997). One possible scenario for the evolutionary transition from bodily to non-bodily ornaments would be as follows: increased plumage ornamentation caused by sexual selection presumably carried on increased predation risk [Endler *et al.* (2005), but see also Borgia, Coyle & Zwiers, (2007) and Endler, (2007)]. Consequently, exaggeration of conspicuous and thereby costly signals may have shifted from bodily to non-bodily ornaments, thereby increasing the signal efficacy (Gilliard, 1969; Diamond, 1982a; Borgia, Pruett-Jones & Pruett-Jones, 1985), whereas plumage coloration retained a species recognition function (Endler *et al.*, 2005). Increased signalling efficacy can be achieved using display courts (Johnsgard, 1994), by selection of decoration items and bower location (Endler *et al.*, 2005), or by structures that allow males to court more vigorously without increasing threats to females [Borgia & Presgraves, (1998), but see Humphries & Ruxton, (1999) and Madden, (2006)].

Alternatively, extended phenotypes serving a direct function can also evolve a signalling component (Wagner & Balshine-Earn, 1999; Borgia & Coleman, 2000; LotemBorgia, 2006). Amending the environment bears costs and is often condition dependent and therefore revealing. Crater building or piling up stones is costly due to investments in time, energy (Bucher, 2003), or required muscular power (Møller *et al.*, 1995). In the black wheatear, for instance, stone-carrying display was shown to reflect male health status (Soler *et al.*, 1999). Long-term costs of extended phenotype signals are more difficult to demonstrate, due to the potential involvement of various life-history trade-offs that may be concealed by variation in individual quality or of display traits with time (Stearns, 1992; Kokko, 1997; Borgia, 2006). For example, there was no correlation between male satin bowerbird display costs and male mortality or successive display in following years (Borgia, 1993).

It is generally expected that individuals of high quality produce more costly traits and hence also would create more expensive structures, regardless of whether individual variation exists mainly in physical or in cognitive abilities, hence these traits may serve as honest signals (Grafen, 1990; Johnstone, 1995b). Soler, Møller & Soler (1998b) suggested that individual variation in nest-building activity of birds and consequently in nest size could serve as a condition-dependent signal to mates. They attributed size differences between nests built by a pair or by single birds to sexual selection. However, a more parsimonious explanation cannot be excluded: nest size may merely reflect the number of building individuals without any significant role of sexual selection.

Nest-inspection behaviour is frequently observed in female birds. Male barn swallows (*Hirunda rustica*) seem to raise attractiveness by increasing nest size and thus nest cup volume, but not nest mass (Soler *et al.*, 1998a). This suggests that females may assess nest size but not nest mass, even though larger nests built with the same amount of nesting material might not be as stable as smaller ones. In the village weaver (*Ploceus cucullatus*), males usually build several nests; females choose the best (Collias & Collias, 1984). However, in the Baya weaver (*Ploceus philippinus*) nest location rather than the manufacturing of the nest is a key determinant in female choice (Quader, 2005). Female wrens (*Troglodytes troglodytes*) only lay eggs after careful inspection of several nests (Evans & Burn, 1995). As in other examples, the benefits of nest choice to females could be direct, e.g. through nest stability or nest size, or indirect, if only males of high quality are able to build (several) neat or large nests. These alternatives are not exclusive.

Female penduline tits (*Remiz pendulinus*) inspect nests at a very early stage of male nest building and prefer larger loop constructions, which are the basis of larger nests with better insulation (Hoi & Valera, 1994; Grubbauer & Hoi, 1996; Hoi, Schleicher & Valera, 1996). Using correlates of nest size early in the nest-building phase saves time, but may carry a greater risk of mistakes. This may explain the high female nest desertion frequency in penduline tits (Hoi & Valera, 1994; Hoi *et al.*, 1996). In widow birds of the genus *Euplectes,* there may be an inverse relationship between male investment in nest building and complexity of their court display (Johnsgard, 1994), even through display courts and the associated behaviour may have originated from male nest-initiation and female nest inspection (Andersson, 1991). Females of three species inspect rapidly produced

structures made of loose grass blades, even though few or none of these are subsequently used for nesting (Andersson, 1991). As an extreme, females of the Jackson's widow bird (*Euplectes jacksoni*) inspect a male-built court area, which is not used as a nest at all (Andersson, 1991).

Similarly, a shift from an original, direct benefit to a pure signal function of an extended phenotype has apparently occurred in the dance flies *Empidae* spp. (Hansell, 1984; Kessel, 2004). Males of some species show nuptial feeding of prey items to females. In other species the prey item is wrapped into a silk balloon and in several of these the male removes the body fluid of its gift before donating it, reducing its value greatly (Hansell, 1984). Finally, in *Hilara sartor* males offer the female a completely empty silk balloon (Hansell, 1984; Kessel, 2004) and in *Rhamphomyia sulcata* males seem to trick females with unprofitable but impressive gifts (LeBas, Hockham & Ritchie, 2004). The initial nutritional benefit for the female might turn into an indirect benefit of increased attractiveness of her sons if they also produce bigger and more attractive, but presumably cheaper silk balloons.

When comparing a species producing extended phenotype signals with closely related species, a gradual change is sometimes apparent from the original beneficial utilisation of the extended phenotype to a mere signal function. Intermediate forms of extended phenotype signals have been described in birds building courts, cichlids building craters, dance flies producing nuptial gifts, spiders producing stabilimenta and sticklebacks constructing nests (see above). In Baya weavers (Quader, 2005) males build an excess of nests (up to seven) that are apparently judged by females; subsequently only visited nests are completed for breeding. However, nest location rather than nest architecture seems to be the main choice criterion for females (Quader, 2005). In many other birds nests may provide information about the constructor in addition to their function as a safe environment for developing offspring (Hoi & Valera, 1994; Soler, Møller & Soler, 1998b; Hansell, 2000). One might speculate that such gradual evolutionary change from a functional use of a trait to a pure signalling function in extended phenotype signals may be different from the evolution of exaggerated morphological bodily traits, where female preference evolved indirectly due to their genetic correlation with male traits under direct selection (Ryan, 1998). This might be worth testing with an appropriate comparative analysis.

processes may provide multilayered information on the constructor's abilities.

(4) Non-bodily ornaments can reliably indicate body condition integrated over a longer period of time and persist for prolonged periods without causing permanent costs, signalling even in the absence of the signal producer.

(5) Due to their behavioural origin non-bodily ornaments have high flexibility and can be abandoned in emergencies.

(6) Extended phenotype signals occupy an intermediate position in the time span a signal is effective: they persist for longer than signalling behaviours, but are usually less permanent than bodily signals.

(7) Extended phenotypes are especially suited to reveal cognitive abilities or maximum performance potential.

(8) Non-bodily ornaments have the extraordinary potential to serve as reflexive signals.

(9) Extended phenotypes as signals are used predominantly in a sexual context, either to attract mates or to reveal dominance. However, they can also serve to convey information across species barriers and provide great potential in the context of multiple signalling.

(10) Extended phenotypes as signals are widely distributed among animal taxa and comparative evidence suggests that often extended phenotypes serve a direct benefit in the first phase (e.g. bird nests), with a signalling function gaining importance at a later stage of evolution.

(11) Extended phenotype signals can be easily manipulated in controlled experiments and therefore provide unique research opportunities for questions of general interest in studies of animal communication.

(12) For both theoretical and methodological reasons the study of extended phenotypes as a signal should be an important aim to further our understanding of signal evolution. Future research should clarify their genetic basis and, in many cases where this is unclear, their functional significance.

VII. ACKNOWLEDGMENTS

V. CONCLUSIONS

(1) Non-bodily ornaments provide diverse advantages compared to behavioural displays or bodily ornaments.

(2) They allow discrimination between the effects of the environment and an individual's ability to cope with it.

(3) Extended phenotype signals can convey a wide range of information. Secreted signals probably inform receivers mainly about physiological parameters and individual identity, whereas signals resulting from complex behavioural

VIII. REFERENCES

ALIS, S. & RIPLEY, S. D. (1987). *Handbook of the birds of India and Pakistan*, Bombay, Oxford: Oxford University Press.

ALONSO-ALVAREZ, C., DOUTRELANT C. & SORCI G. (2004). Ultraviolet reflectance affects male-male interactions in the blue tit (*Parus caeruleus ultramarinus*). *Behavioral Ecology* **15**, 805–809.

AMUNDSEN, T. (2003). Fishes as models of sexual selection and parental care. *Journal of Fish Biology* **63**, 17–52.

ANDERSSON, S. (1991). Bowers on the Savannah: display courts and mate choice in a lekking widowbird. *Behavioural Ecology* **2**, 210–218.

ANSTEE, S. D., ROBERTS, J. D. & OSHEA, J. F. (1997). Social structure and patterns of movement of the western pebble-mound mouse, *Pseudomys chapmani*, Western Australia. *Wildlife Research* **24**, 295–305.

BALASINGH, J., KOILRAJ, J. & KUNZ, T. H. (1995). Tent construction by the short-nosed fruit bat *Cynopterus sphinx* (Chiroptera: Pteropodidae) in Southern India. *Ethology* **100**, 210–229.

BARBER, I., NAIRN, D. & HUNTINGFORD, F. A. (2001). Nests as ornaments: revealing construction by male sticklebacks. *Behavioural Ecology* **12**, 390–396.

BARLOW, G. W. (2000). *The cichlid fishes: nature's grand experiment in evolution*, Cambridge, Massachusetts: Perseus Publishing.

BASOLO, A. L. (1990). Female preference predates the evolution of the sword in swordtail fish. *Science* **250**, 808–810.

BOLHUIS, J. & GIRALDEAU, L. A. (2005). *The Behaviour of Animals: Mechanisms, Function and Evolution*, Oxford: Blackwell Publishing.

BOLLES, F. (1890). Snake skins in the nests of *Myiarchus crinitus*. *Auk* **7**, 288.

BORGIA, G. (1985a). Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus violaceus*). *Behavioral Ecology and Sociobiology* **18**, 91–100.

BORGIA, G. (1985b). Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour* **33**, 266–271.

BORGIA, G. (1993). The cost of display in the non-resource-based mating system of the satin bowerbird. *American Naturalist* **141**, 729–743.

BORGIA, G. (1995a). Complex male display and female choice in the spotted bowerbird - specialized functions for different bower decorations. *Animal Behaviour* **49**, 1291–1301.

BORGIA, G. (1995b). Threat reduction as a cause of differences in bower architecture, bower decoration and male display in two closely-related bowerbirds *Chlamydera nuchalis* and *C. maculata*. *Emu* **95**, 1–12.

BORGIA, G. (2006). Preexisting male traits are important in the evolution of elaborated male sexual display. *Advances in the study of behaviour* **36**, 249–302.

BORGIA, G. & COLEMAN, S. W. (2000). Co-option of male courtship signals from aggressive display in bowerbirds. *Proceedings of the Royal Society of London Series B - Biological Sciences* **267**, 1735–1740.

BORGIA, G., COYLE, B. & ZWIERS, R. (2007). Evolution of colorful display. *Evolution* **61**, 708–712.

BORGIA, G. & GORE, M. A. (1986). Feather stealing in the satin bowerbird (*Ptilonorhynchus violaceus*): male competition and the quality of display. *Animal Behaviour* **34**, 727–738.

BORGIA, G., KAATZ, I. M. & CONDIT, R. (1987). Flower choice and bower decoration in the satin bowerbird *Philonorhynchus violaceus* - A test of hypotheses for the evolution of male display. *Animal Behaviour* **35**, 1129–1139.

BORGIA, G. & MUELLER, U. (1992). Bower destruction, decoration stealing and female choice in the spotted bowerbird *Chlamydera maculata*. *Emu* **92**, 11–18.

BORGIA, G. & PRESGRAVES, D. C. (1998). Coevolution of elaborated male display traits in the spotted bowerbird: an experimental test of the threat reduction hypothesis. *Animal Behaviour* **56**, 1121–1128.

BORGIA, G., PRUETT-JONES, S. G. & PRUETT-JONES, M. A. (1985). The evolution of bower-building and the assessment of male quality. *Ethology* **67**, 225–236.

BRADBURY, J. W. & VEHRENCAMP, S. L. (1998). *Principles of animal communication*, Sunderland, Massachusetts: Sinauer Associates.

BRASHARES, J. S. & ARCESE, P. (1999). Scent marking in a territorial African antelope: I. The maintenance of borders between male oribi. *Animal Behaviour* **57**, 1–10.

BROWN, R. E. & MACDONALD, D. W. (1985). *Social odours in mammals*, Oxford: Clarendon Press.

BRUCE, M. J., HERBERSTEIN, M. E. & ELGAR, M. A. (2001). Signalling conflict between prey and predator attraction. *Journal of Evolutionary Biology* **14**, 786–794.

BRUMM, H. & TODT, D. (2002). Noise-dependent song amplitude regulation in a territorial songbird. *Animal Behaviour* **63**, 891–897.

BUCHER, M. (2003). The costs of a non-bodily ornament: crater building in the cichlid fish, *Cyathopharynx furcifer*. 1–27: University of Bern.

BUGNYAR, T., SCHWAB, C., SCHLOEGL, C., KOTRSCHAL, K. & HEINRICH, B. (2007). Ravens judge competitors through experience with play caching. *Current biology* **17**, 1804–1808.

BURFORD, F. R. L., MCGREGOR, P. K. & OLIVEIRA, R. F. (2001a). Male-like mudballing behavior of some female fiddler crabs (*Uca tangeri*). *Journal of Ethology* **19**, 97–103.

BURFORD, F. R. L., MCGREGOR, P. K. & OLIVEIRA, R. F. (2001b). Mudballing revisited: Further investigations into the construction behaviour of male *Uca tangeri*. *Behaviour* **138**, 221–234.

CANDOLIN, U. (2003). The use of multiple cues in mate choice. *Biological Reviews* **78**, 575–595.

CARO, T. M. (1986). The function of stotting - a review of the hypotheses. *Animal Behaviour* **34**, 649–662.

CARTHY, J. D. (1951). The orientation of two allied species of British ant. 2. odour trail laying and following in *Acanthomyops-(lasius)-fuliginosus*. *Behaviour* **3**, 304–318.

CHENG, T. C. (1973). *General Parasitology*, New York: Academic Press.

CHOU, I.-C., SHEN, P.-S., WANG, P.-H. & TSO, I.-M. (2004). A test of prey-attracting and predator defence functions of prey carcass decorations built by *Cyclosa* spiders. *Animal Behaviour* **69**, 1055–1061.

CHRISTY, J. H. (1988). Pillar function in the fiddler crab *Uca beebei* (I): Effects on male spacing and aggression. *Ethology* **78**, 53–71.

CHRISTY, J. H., BACKWELL, P. & SCHONER, U. (2003a). Interspecific attractiveness of structures built by courting fiddler crabs: experimental evidence of a sensory trap. *Behavioral Ecology and Sociobiology* **53**, 84–91.

CHRISTY, J. H., BACKWELL, P. R. Y. & GOSHIMA, S. (2001). The design and production of a sexual signal: Hoods and hood building by male fiddler crabs *Uca musica*. *Behaviour* **138**, 1065–1083.

CHRISTY, J. H., BACKWELL, P. R. Y., GOSHIMA, S. & KREUTER, T. (2002). Sexual selection for structure building by courting male fiddler crabs: an experimental study of behavioral mechanisms. *Behavioural Ecology* **13**, 366–374.

CHRISTY, J. H., BAUM, J. K. & BACKWELL, P. R. Y. (2003b). Attractiveness of sand hoods built by courting male fiddler crabs, *Uca musica*: a test of a sensory trap hypothesis. *Animal Behaviour* **66**, 89–94.

CLAYTON, D. A. (1987). Why mudskippers build walls. *Behaviour*, 185–195.

COLEMAN, S. W., PATRICELLI, G. L. & BORGIA, G. (2004). Variable female preferences drive complex male displays. *Nature* **428**, 742–745.

COLLIAS, N. E. & COLLIAS, E. C. (1984). *Nest building and bird behaviour*, Princeton: Princeton University Press.

DARDEN, S. K., STEFFENSEN, L. K. & DABELSTEEN, T. (2008). Information transfer among widely spaced individuals: latrines as a basis for communication networks in the swift fox? *Animal Behaviour* **75**, 425–432.

DAWKINS, R. (1978). Replicator selection and extended phenotype. *Zeitschrift für Tierpsychologie - Journal of Comparative Ethology* **47**, 61–76.

DAWKINS, R. (1982). *The extended phenotype: the long reach of the gene*, Oxford: Oxford University Press.

DAY, L. B., WESTCOTT, D. A. & OLSTER, D. H. (2005). Evolution of bower complexity and cerebellum size in bowerbirds. *Brain behavior and evolution* **66**, 62–72.

DEJEAN, A. & BEUGNON, G. (1991). Persistent intercolonial trunkroute-marking in the African weaver ant *Oecophylla latreille* (Hymenoptera, Formicidae) - Tom-thumb versus Ariadne orienting strategies. *Ethology* **88**, 89–98.

DERIVERA, C. E., BACKWELL, P. R. Y., CHRISTY, J. H. & VEHRENCAMP, S. L. (2003). Density affects female and male mate searching in the fiddler crab, *Uca beebei. Behavioral Ecology and Sociobiology* **53**, 72–83.

DIAMOND, J. (1982a). Evolution of bowerbirds' bowers: animal origins of the aesthetic sense. *Nature* **297**, 99–102.

DIAMOND, J. (1982b). Rediscovery of the yellow-fronted gardener bowerbird. *Science* **216**, 431–434.

DIAMOND, J. (1986). Animal art - Variation in bower decorating style among male bowerbirds *Amblyornis inornatus. Proceedings of the National Academy of Sciences of the USA* **83**, 3042–3046.

DIAMOND, J. (1988). The experimental study of bower decoration by the bowerbird *Amblyornis inornatus*, using colored poker chips. *The American Naturalist* **131**, 631–653.

DOLIGEZ, B., DANCHIN, E. & CLOBERT, J. (2002). Public information and breeding habitat selection in a wild bird population. *Science* **297**, 1168–1170.

DOUCET, S. M. & MONTGOMERIE, R. (2003). Bower location and orientation in Satin Bowerbirds: optimising the conspicuousness of male display? *Emu* **103**, 105–109.

ENDLER, J. A., WESTCOTT, D. A., MADDEN, J. R. & ROBSON, T. (2005). Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution* **59**, 1795–1818.

ENDLER, J. (2007). Colorful thoughts about colorful displays. *Evolution* **61**, 713–715.

EVANS, M. R. & BURN, J. L. (1995). An experimental analysis of mate choice in the wren: a monomorphic, polygynous passerine. *Behavioural Ecology* **7**, 101–108.

FARGALLO, J. A., DE LEON, A. & POTTI, J. (2001). Nest-maintenance effort and health status in chinstrap penguins, *Pygoscelis antarctica*: the functional significance of stone-provisioning behaviour. *Behavioral Ecology and Sociobiology* **50**, 141–150.

FITZGIBBON, C. D. & FANSHAWE, J. H. (1988). Stotting in Thomson gazelles - An honest signal of condition. *Behavioral Ecology and Sociobiology* **23**, 69–74.

FRICKE, H. & KACHER, H. (1982). A mound-building deep water sand tilefish of the Red Sea: *Hoplolatilus geo* n. sp. (Perciformes: Branchiostegidae). Observations from a Research submersible. *Senckenbergiana maritima* **14**, 245–259.

FRITH, C. B. & FRITH, D. W. (1990). Archbolds Bowerbird *Archboldia papuensis* (Ptilonorhynchidae) uses plumes from king of saxony bird of paradise *Pteridophora alberti* (Paradisaeidae) as bower decoration. *Emu* **90**, 136–137.

FRITH, C. B. & FRITH, D. W. (1998). Nesting biology of the Golden Bowerbird *Prionodura newtoniana* endemic to Australian upland tropical rainforest. *Emu* **98**, 245–268.

FRITH, C. B., FRITH, D. W. & JANSEN, A. (1997). The nesting biology of the Chowchilla, *Orthonyx spaldingii* (Orchonychidae). *Emu* **97**, 18–30.

FRITH, C. B., FRITH, D. W. & WIENEKE, J. (1994). An exceptionally elaborate bower structure of great bowerbird *Chlamydera nuchalis* (Ptilonorhynchidae). *Australian Bird Watcher* **15**, 314–319.

GILBERT, F., AZMEH, S., BARNARD, C., BEHNKE, J., COLLINS, S. A., HURST, J. L. & SHUKER, D. (2001). Individually recognizable scent marks on flowers made by a solitary bee. *Animal Behaviour* **61**, 217–229.

GILLIARD, E. T. (1969). *Birds of paradise and bower birds*, Garden City, New York: The Natural History Press.

GOTTLANDER, K. (1987). Variation in the song rate of the male pied flycatcher *Ficedula hypoleuca* - causes and consequences. *Animal Behaviour* **35**, 1037–1043.

GRAFEN, A. (1990). Biological signals as handicaps. *Journal of theoretical Biology* **144**, 517–546.

GREEN, D. J., COCKBURN, A., HALL, M. L., OSMOND, H. & DUNN, P. O. (1995). Increased opportunity for cuckoldry may be why dominant male fairy-wrens tolerate helpers. *Proceedings of the Royal Society of London Series B - Biological Sciences* **262**, 297–303.

GRETHER, G. F. (1996). Sexual selection and survival selection on wing coloration and body size in the rubyspot damselfly *Hetaerina americana. Evolution* **50**, 1939–1948.

GRUBBAUER, P. & HOI, H. (1996). Female penduline tits (*Remiz pendulinus*) choosing high quality nests benefit by decreased incubation effort and increased hatching success. *Ecoscience* **3**, 274–279.

GUILFORD, T. & DAWKINS, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour* **42**, 1–14.

GWINNER, H. (1997). The function of green plants in nests of European starlings (*Sturnus vulgaris*). *Behaviour* **134**, 337–351.

HAMILTON, W. D. & ZUK, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

HANSELL, M. H. (1984). *Animal architecture and building behaviour*, London and New York: Longman Group Limited.

HANSELL, M. H. (2000). *Birds nest and construction behaviour*, Cambridge, MA: Cambridge University Press.

HANSELL, M. H. (2005). *Animal Architecture*, Oxford: Oxford university press.

HARPER, D. G. C. (1991). Communication. In *Behavioural Ecology* (eds. J. R. Krebs & N. B. Davies), pp. 374–397. Oxford: Blackwell.

HASSON, O. (1994). Cheating signals. *Journal of theoretical Biology* **167**, 223–238.

HEBETS, E. A. & PAPAJ, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* **57**, 197–214.

HEDENSTRÖM, A. & MØLLER, A. P. (1992). Morphological adaptions to songflight in passerine birds: a comparative study. *Proceedings of the Royal Society of London Series B - Biological Sciences* **247**, 183–187.

HERBERSTEIN, M. E., CRAIG, C. L., CODDINGTON, J. A. & ELGAR, M. A. (2000). The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biological Reviews* **75**, 649–669.

HILL, G. E. (1990). Female house finches prefer colorful males - sexual selection for a condition-dependent trait. *Animal Behaviour* **40**, 563–572.

HILL, G. E. (1992). Proximate basis of variation in carotinoid pigmentation in male house finches. *Auk* **109**, U1–12.

HILL, G. E. & MONTGOMERIE, R. (1994). Plumage colour signals nutritional condition in the house finch. *Proceedings of the Royal Society of London Series B - Biological Sciences* **258**, 47–52.

HIRONAKA, M., FILIPPI, L., NOMAKUCHI, S., HORIGUCHI, H. & HARIYAMA, T. (2007). Hierarchical use of chemical marking and path integration in the homing trip of a subsocial shield bug. *Animal Behaviour* **73**, 739–745.

Hoi, H., Schleicher, B. & Valera, F. (1996). Nest size variation and its importance for mate choice in penduline tits, *Remiz pendulinus*. *Animal Behaviour* **51**, 464–466.

Hoi, H. & Valera, F. (1994). Female mate choice and nest desertion in penduline tits, *Remiz pendulinus*: the importance of nest quality. *Animal Behaviour* **48**, 743–746.

Howman, H. R. G. & Begg, G. W. (1983). Nest building and nest destruction by the masked weaver, *Ploceus velatus*. *South African Journal of Zoology* **18**, 37–44.

Hölldobler, B. & Wilson, E. O. (1990). *The Ants*, Heidelberg, Berlin: Springerverlag.

Hudson W. H. (1872). On the habits of the Vizcacha (*Lagostomus trichodactylus*). *Proceedings of the Zoological Society of London*, 822–833.

Humphries, S. & Ruxton, G. D. (1999). Bower-building: coevolution of display traits in response to the costs of female choice? *Ecology Letters* **2**, 404–413.

Hurst, J. L. (1990a). Urine marking in populations of wild house mice *Mus domesticus* Rutty. I. Communication between males. *Animal Behaviour* **40**, 209–222.

Hurst, J. L. (1990b). Urine marking in populations of wild house mice *Mus domesticus* Rutty. II. Communication between females. *Animal Behaviour* **40**, 223–232.

Hurst, J. L. (1990c). Urine marking in populations of wild house mice *Mus domesticus* Rutty. III.Communication between sexes. *Animal Behaviour* **40**, 233–243.

Hurst, J. L. & Beynon, R. J. (2004). Scent wars: the chemobiology of competitive signalling in mice. *Bioessays* **26**, 1288–1298.

Hurst, J. L., Payne, C. E., Nevison, C. M., Marie, A. D., Humphries, R. E., Robertson, D. H. L., Cavaggioni, A. & Beynon, R. J. (2001). Individual recognition in mice mediated by major urinary proteins. *Nature* **414**, 631–634.

Jackson, D. E., Martin, S. J., Holcombe, M. & Ratnieks, F. L. W. (2006). Longevity and detection of persistent foraging trails in Pharaoh's ants, *Monomorium pharaonis* (L.). *Animal Behaviour* **71**, 351–359.

Jackson, D. E. & Ratnieks, F. L. W. (2006). Communication in ants. *Current biology* **16**, R570–R574.

Johnsgard, P. A. (1994). *Arena Birds: Sexual Selection and Behavior*, Washington and London: Smithsonian Institution Press.

Johnstone, R. A. (1995a). Honest advertisement of multiple qualities using multiple signals. *Journal of theoretical Biology* **177**, 87–94.

Johnstone, R. A. (1995b). Sexual selection, honest advertisement and the handicap principle - reviewing the evidence. *Biological Reviews of the Cambridge Philosophical Society* **70**, 1–65.

Jones, J. C. & Reynolds, J. D. (1999). The influence of oxygen stress on female choice for male nest structure in the common goby. *Animal Behaviour* **57**, 189–196.

Karubian, J. & Alvarado, A. (2003). Testing the function of petal-carrying in the Red-backed fairy-wren *(Malurus melanocephalus)*. *Emu* **103**, 87–92.

Kellog, K. A., Stauffer, J. R. JR. & McKaye, K. R. (2000). Characteristics that influence male reproductive success on a lek of *Lethrinops* c.f. *parvidens* (Teleostei: Cichlidae). *Behavioral Ecology and Sociobiology* **47**, 164–170.

Kessel, E. L. (2004). Mating activities of balloon flies. *Systematic Zoology* **4**, 97–104.

Kitchener, D. J. (1983). Pebble-mound mouse. In *Complete book of Australian Mammals* (ed. Ronald Strahn), pp. 416–417: Sydney: Augus & Robertson.

Kodric-Brown, A. (1989). Dietary carotenoids and male mating success in the guppy: an environmental component to female choice. *Behavioral Ecology and Sociobiology* **25**, 393–401.

Kokko, H. (1997). Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology* **41**, 99–107.

Kusmierski, R., Borgia, G., Uy, J. A. C. & Crozier, R. H. (1997). Labile evolution of display traits in bowerbirds indicates reduced effects of phylogenetic constraint. *Proceedings of the Royal Society of London Series B - Biological Sciences* **264**, 37–313.

Lacroix, R., Mukabana, W. R., Gouagna, L. C. & Koella, J. C. (2005). Malaria infection increases attractiveness of humans to mosquitoes. *PLOS* **3**, 1–4.

Laland, K. N. (2004). Extending the extended phenotype. *Biology & Philosophy* **19**, 313–325.

Latruffe, C., McGregor, P. K. & Oliveira, R. F. (1999). Visual signalling and sexual selection in male fiddler crabs, *Uca tangeri*. *Marine Ecology Prog.Ser.* **189**, 233–240.

Leader, N. & Yom-Tov, Y. (1998). The possible function of stone ramparts at the nest entrance of the blackstart. *Animal Behaviour* **56**, 207–217.

LeBas, N. R., Hockham, L. R. & Ritchie, M. G. (2004). Sexual selection in the gift-giving dance fly, *Rhamphomyia sulcata*, favours small males carrying small gifts. *Evolution* **58**, 1763–1772.

Lenz, N. (1994). Mating behaviour and sexual competition in the regent bowerbird *Sericulus chrysocephalus*. *Emu* **94**, 263–272.

Lijam, N., Paylor, R., McDonald, M., Crawley, J. N., Deng, C., Herrup, K., Stevens, K. E., Maccaferri, G., McBain, C. J., Sussman, D. J. & Wynshaw-Boris, A. (1997). Social interaction and sensorimotor gating abnormalities in mice lacking Dvl1. *Cell* **90**, 895–905.

Linsenmair, K. E. (1967). Konstruktion und Signalfunktion der Sandpyramide der Reiterkrabbe *Ocypode saratan* Forsk. (Decapoda Brachyura Ocypodidae). *Zeitschrift fur Tierpsychologie - Journal of Comparative Ethology*, 403–456.

Lotem, A., Wagner, R. H. & Balshine-Earn, S. (1999). The overlooked signaling component of nonsignaling behavior. *Behavioral Ecology* **10**, 209–212.

Madden, J. R. (2001). Sex, bowers and brains. *Proceedings of the Royal Society of London Series B - Biological Sciences* **268**, 833–838.

Madden, J. R. (2002). Bower decorations attract females but provoke other male spotted bowerbirds: bower owners resolve this trade-off. *Proceedings of the Royal Society of London Series B - Biological Sciences* **269**, 1347–1351.

Madden, J. R. (2003). Male spotted bowerbirds preferentially choose, arrange and proffer objects that are good predictors of mating success. *Behavioral Ecology and Sociobiology* **53**, 263–268.

Madden, J. R. (2006). Interpopulation differences exhibited by Spotted Bowerbirds *Chlamydera maculata* across a suite of male traits and females preferences. *Ibis* **148**, 425–435.

Madden, J. R. & Tanner, K. (2003). Preferences for coloured bower decorations can be explained in a non sexual context. *Animal Behaviour* **65**, 1077–1083.

Maynard Smith, J. & Harper, D. (2004). *Animal Signals*, Oxford: Oxford University Press.

McKaye, K. R. (1983). Ecology and breeding behaviour of a cichlid fish, *Cyatocara eucinostemus*, on a large lek in Lake Malawi, Africa. *Environmental Biology of Fishes* **8**, 81–96.

McKaye, K. R. (1991). Sexual Selection and the evolution of the cichlid fishes of Lake Malawi, Africa. In *Cichlid fishes: Behaviour, Ecology and Evolution* (ed. Keenleyside M.H.A.), pp. 241–257. New York: Chapman and Hull.

McKaye, K. R., Louda, S. M. & Stauffer, J. R. (1990). Bower size and male reproductive success in a cichlid fish lek. *American Naturalist* **135**, 597–613.

MEINERTZHAGEN, C. R. (1949). Notes on Saudi Arabian birds. *Ibis* **91**, 465–482.

MILINSKI, M. & BAKKER, T. C. M. (1990). Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* **344**, 330–333.

MORENO, J., SOLER, M., MØLLER, A. P. & LINDEN, M. (1994). The function of stone carrying in the black wheatear, *Oneanthe leucura*. *Animal Behaviour* **47**, 1297–1309.

MORENO, S., MORENO, J. & DE LEON, A. (1999). The effect of nest size on stone-gathering behaviour in the chinstrap penguin. *Polar Biology* **22**, 90–92.

MØLLER, A. P., LINDEN, M., SOLER, J. J., SOLER, M. & MORENO, J. (1995). Morphological adaptations to an extreme sexual display, stone-carrying in the black wheatear, *Oenanthe leucura*. *Behavioural Ecology* **6**, 368–375.

NELSON, J. B. (1967). The breeding behaviour of the white booby *Sula dactylatra*. *Ibis* **109**, 194–231.

OLIVEIRA, R. F. & CUSTODIO, M. R. (1998). Claw size, waving display and female choice in the European fiddler crab, *Uca tangeri*. *Ethology, Ecology & Evolution* **10**, 241–251.

OLIVEIRA, R. F., MCGREGOR, P. K., BURFORD, F. R. L., CUSTODIO, M. R. & LATRUFFE, C. (1998a). Functions of mudballing behaviour in the European fiddler crab *Uca tangeri*. *Animal Behaviour* **55**, 1299–1309.

OLIVEIRA, R. F., MCGREGOR, P. K. & LATRUFFE, C. (1998b). Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proceedings of the Royal Society of London Series B - Biological Sciences* **265**, 1045–1049.

ORD, T. J., PETERS, R. A., CLUCAS, B. & STAMPS, J. A. (2007). Lizards speed up visual displays in noisy motion habitats. *Proceedings of the Royal Society of London Series B - Biological Sciences* **274**, 1057–1062.

ÖSTLUND-NILSSON, S. (2001). Fifteen-spined stickelback (*Spinachia spinachia*) females prefer males with more secretional threads in their nests: an honest-condition display by males. *Behavioral Ecology and Sociobiology* **50**, 263–269.

ÖSTLUND-NILSSON, S. & HOLMLUND, M. (2003). The artistic three-spined stickelback *(Gasterosteus aculeatus)*. *Behavioral Ecology and Sociobiology* **53**, 214–220.

PATRICELLI, G. L., UY, J. A. C. & BORGIA, G. (2003). Multiple male traits interact: attractive bower decorations facilitate attractive behavioural displays in satin bowerbirds. *Proceedings of the Royal Society of London Series B - Biological Sciences* **270**, 2389–2395.

PETIT, C., HOUSSAERT-MCKAYE, M., PERRET, P., BLONDEL, J. & LAMBRECHTS, M. M. (2002). Blue tits use selected plants and olfaction to maintain an aromatic environment for nestlings. *Ecology Letters* **5**, 585–589.

PLENGE, M., CURIO, E. & WITTE, K. (2000). Sexual imprinting supports the evolution of novel male traits by transference of a preference for the colour red. *Behaviour* **137**, 741–758.

QUADER, S. (2005). Elaborate nests in a weaverbird: A role for female choice? *Ethology* **111**, 1073–1088.

RASA, O. A. E. (1973). Marking behaviour and its social significance in the African dwarf mongoose, *Helogale undulata rufula*. *Zeitschrift für Tierpsychologie - Journal of Comparative Ethology* **32**, 293–318.

RIBEIRO, P. D., CHRISTY, J. H., RISSANEN, R. J. & KIM, T. W. (2006). Males are attracted by their own courtship signals. *Behavioral Ecology and Sociobiology* **61**, 81–89.

RICH, T. J. & HURST, J. L. (1998). Scent marks as reliable signals of the competitive ability of mates. *Animal Behaviour* **56**, 727–735.

ROZHNOV, V. V. & ROZHNOV, YU. V. (2003). Roles of different types of excretions in mediated communication by scent marks of the common palm civet, *Paradoxurus hermaphroditus* Pallas 1777 (Mammalia, Carnivora). *Zoology* **30**, 584–590.

RUSHBROOK, B. J., DINGEMANSE, N. J. & BARBER, I. (2008). Repeatability in nest construction by male three-spined sticklebacks. *Animal Behaviour* **75**, 547–553.

RYAN, M. J. (1990). Sexual selection and mate choice. *Oxford Surveys in Evolutionary Biology* **7**, 157–195.

RYAN, M. J. (1998). Sexual selection, receiver biases, and the evolution of sex differences. *Science* **281**, 1999–2003.

SADOWSKI, J. A., MOORE, A. J. & BRODIE, E. D. (1999). The evolution of empty nuptial gifts in a dance fly, *Empis snoddyi* (Diptera:Empididae): bigger isn't always better. *Behavioral Ecology and Sociobiology* **45**, 161–166.

SCHAEDELIN, F. C. & TABORSKY, M. (2006). Mating crater of *Cyathopharynx furcifer* (Cichlidae) are individually characteristic extended phenotypes. *Animal Behaviour* **72**, 753–761.

SCHAEDELIN, F. C. (2004). The signalling value of an extended phenotype: construction of sexy craters in *Cyathopharynx furcifer*. Universität Bern.

SCHUCK-PAIM, C. (2000). Orb-webs as extended-phenotypes: web design and size assessment in contests between *Nephilengys crustata* females (Araneae, Tetragnathidae). *Behaviour* **137**, 1331–1347.

SCHUETZ, J. G. (2004). Common waxbills use carnivore scat to reduce the risk of nest predation. *Behavioral Ecology* **16**, 133–137.

SKEAD, C. J. (1947). A study of the cape weaver. *The Ostrich* **18**, 1–42.

SLIWA, A. & RICHARDSON, P. R. K. (1998). Responses of aardwolves, *Proteles cristatus*, Sparrman 1783, to translocated scent marks. *Animal Behaviour* **56**, 137–146.

SOLER, J. J., CUERVO, J. J., MØLLER, A. P. & DE LOPE, F. (1998a). Nest building is a sexually selected behaviour in the barn swallow. *Animal Behaviour* **56**, 1435–1442.

SOLER, J. J., MØLLER, A. P. & SOLER, M. (1998b). Nest building, sexual selection and parental investment. *Evolutionary Ecology* **12**, 427–441.

SOLER, J. J., SOLER, M., MØLLER, A. P. & MARTINEZ, J. G. (1995). Does the great spotted cuckoo choose magpie hosts according to their parenting ability? *Behavioral Ecology and Sociobiology* **36**, 201–206.

SOLER, M., MARTIN-VIVALDI, M., MARIN, J. M. & MØLLER, A. P. (1999). Weight lifting and health status in the black wheatear. *Behavioural Ecology* **10**, 281–286.

SOLER, M., SOLER, J. J., MØLLER, A. P., MORENO, J. & LINDEN, M. (1996). The functional significance of sexual display: Stone carrying in the black wheatear. *Animal Behaviour* **51**, 247–254.

STEARNS, S. C. (1992). *The evolution of life histories*, Oxford, New York, Tokyo: Oxford University Press.

STERENLY, K. (2000). The "genetic program" program: a commentary on Maynard Smith on information in biology. *Philosophy of Science* **67**, 195–201.

STOUT, J. C. & GOULSON, D. (2001). The use of conspecific and interspecific scent marks by foraging bumblebees and honeybees. *Animal Behaviour* **62**, 183–189.

SULLIVAN, M. S. (1994). Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. *Animal Behaviour* **47**, 141–151.

THAPAR, V. (1986). *TIGER: Portrait of a predator*, London: Collins.

THOMAS, F., ADAMO, S. & MOORE, J. (2005). Parasitic manipulation: where are we and where should we go? *Behavioural Processes* **68**, 185–199.

TINBERGEN, N. (1951). *The study of instinct*, Oxford, London, New York: Oxford University Press.

TURNER, J. S. (2000). *The extended organism: The physiology of animal-built structures*, Cambridge: Harvard University Press.

VELLENGA, R. (1986). Bower-building behaviour of immature satin bowerbirds *Ptilonorhynchus violaceus*. *Australian Bird Watcher* **11**, 166–167.

VON FRISCH, K. (1974). *Animal Architecture*, New York: Harcourt Brace Jovanovich.

WOJCIESZEK, J. M., NICHOLLS, J. A. & GOLDIZEN, A. W. (2007). Stealing behaviour and the maintenance of a visual display in the satin bowerbird. *Behavioral Ecology* **18**, 689–695.

YANAGISAWA, Y., OCHI, H. & GASHAGAZA, M. M. (1997). Fish Communities in Lake Tanganyika, Kyoto: Kyoto University press.

YOSEF, R. & PINSHOW, B. (1989). Cache size in shrikes influences female mate choice and reproductive success. *The Auk* **106**, 418–421.

ZAHAVI, A. (1975). Mate selection - a selection for a handicap. *Journal of theoretical Biology* **53**, 205–214.

ZYSKOWSKI, K. & PRUM, R. O. (1999). Phylogenetic analysis of the nest architecture of neotropical ovenbirds (Furnariidae). *The Auk* **116**, 891–911.