



Review

Repetitive signals and mate choice: insights from contest theory

Sophie L. Mowles^{a,*}, Terry J. Ord^b^a School of Biosciences, University of Nottingham, Loughborough, U.K^b Evolution and Ecology Research Centre, and the School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW, Australia

ARTICLE INFO

Article history:

Received 20 October 2011

Initial acceptance 23 November 2011

Final acceptance 14 May 2012

Available online 28 June 2012

MS. number: 11-00846R

Keywords:

contest theory

courtship

decision rule

handicap principle

mate choice

ornament

repeated display

sexual selection

signal costs

signal function

Courtship displays are important in governing mate choice, ubiquitous throughout the animal kingdom and often spectacular in appearance. As such, they have received a long history of study that has greatly advanced our knowledge of intersexual selection. Yet despite this historical interest, critical gaps remain in our understanding of what aspects of courtship mates find attractive. In particular, the importance of signal repetition during courtship is beginning to become more apparent, but its functional significance in mate choice is still unclear. We outline how models of repeated displays, which have allowed us to make great strides in understanding agonistic contests, can also help us to understand mate choice. In fact, we contend that such models are essential for understanding the existence of repetitious courtship signals and the decision rules used by females when choosing among possible mates. Models of repeated displays offer an important, and currently unutilized, tool for the study of mate choice that we anticipate will provide new insights on intersexual selection. To facilitate this end, we present a practical guide of how researchers can implement a game theory approach in their studies of courtship displays and mate choice.

© 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Courtship and sexual behaviour have historically been an area of intense interest, with research focusing on the often spectacular displays used by animals to attract a mate. This interest has resulted in an extensive body of work on signal design and mate choice, from which we have discovered a great deal about intersexual selection. While we have amassed a large amount of knowledge on the design of ornaments and sexual displays, and what information these might contain (see Andersson 1994), this has only been partly successful in accounting for how receivers (typically females) choose among potential mates (typically males). There are still critical aspects about courtship that remain unstudied, and the traditional focus on the design of static signals such as ornaments has failed to explain fully female mate choice in a number of important systems (Table 1).

Indeed, even in the most iconic example of sexual selection, the courtship display of the peacock, *Pavo cristatus*, discrepancies exist in the parameters that females use when selecting a mate. Despite initial studies indicating that the appearance of the male's train is used in female choice (Darwin 1871; Petrie et al. 1991; Loyau et al.

2005), recent experimental tests have failed to support this idea (Takahashi et al. 2008; Dakin & Montgomerie 2011). For example, although a recent study by Dakin & Montgomerie (2011) demonstrated that manipulating train quality did result in a reduced female preference, this occurred only when train design was manipulated well outside of the limits of natural variation. Dakin & Montgomerie (2011) thus concluded that females must use some other, yet unknown, cue to choose between males.

Another area that has received much attention is the role of vocalizations in courtship, particularly song characteristics in birds. Some studies conclude that complexity is attractive (Hasselquist et al. 1996; Reid et al. 2004), while others suggest that achieving high call rates is key (Wilson & Mennill 2011). Where rate is important, one may conclude that intrinsic signal costs might advertise sender quality. For example, if the vocalization is an exhausting signal that can only be produced by males in good condition, females may favour high rates of repetition. This is true of the repeated roaring display of red deer, *Cervus elaphus*, where high roaring rates are preferred by females (McComb 1991), but are known to result in the exhaustion of males (Clutton-Brock & Albon 1979). However, vocalizations do not appear to be universally costly among species (Weary et al. 1991; Horn et al. 1995). For example, Horn et al. (1995) found that crowing by roosters, *Gallus gallus domesticus*, led to an increase in oxygen consumption, yet this level

* Correspondence: S. L. Mowles, Room C36, The Gateway Building, School of Biosciences, University of Nottingham, Sutton Bonington Campus, Loughborough, Leicestershire LE12 5RD, U.K.

E-mail address: sophie.mowles@nottingham.ac.uk (S. L. Mowles).

Table 1
Examples of species in which repeated displays of courtship may explain mate choice

| Species | Repeated signal | Key sources |
|--|---|---|
| Mammals | | |
| Brown hare, <i>Lepus europaeus</i> | Boxing | Holley & Greenwood 1984 |
| Neotropical singing mouse, <i>Scotinomys</i> spp. | Singing | Pasch et al. 2011a, b |
| Red deer, <i>Cervus elaphus</i> | Roaring | Clutton-Brock & Albon 1979; McComb 1991 |
| Birds | | |
| Peacock, <i>Pavo cristatus</i> | Wing shaking and train rattling | Petrie et al. 1991; Takahashi et al. 2008; Dakin & Montgomerie 2009 |
| Peacock pheasants, <i>Polyplectron</i> spp. | Lateral display | Davison 1983; Kimball et al. 2001 |
| Black grouse, <i>Tetrao tetrix</i> | Rookooing | Rintamaki et al. 2001 |
| Victoria's riflebird, <i>Ptiloris victoriae</i> | Alternate wing clap display | Frith & Cooper 1996 |
| Rooster, <i>Gallus gallus domesticus</i> | Crowing | Horn et al. 1995 |
| Manakins, <i>Manacus</i> spp. | Wing snapping and leaping | Schlinger et al. 2008 |
| Great tit, <i>Parus major</i> | Singing | Weary et al. 1991 |
| Reptiles | | |
| Anole, <i>Anolis</i> spp. | Headbobbing, dewlap extensions | Tokarz 2007 |
| Sagebrush lizard, <i>Sceloporus graciosus</i> | Headbobbing, shudders | Kelso & Martins 2008 |
| Veiled chameleon, <i>Chamaeleo calyptratus</i> | Head rolling, vibrating and chin rubbing | Kelso & Verrell 2002 |
| Greek tortoise, <i>Testudo graeca</i> | Ramming, biting and calling | Pellitteri-Rosa et al. 2011 |
| Amphibians | | |
| Túngara frog, <i>Engystomops pustulosus</i> | Calls | Ron 2008; Goutte et al. 2010 |
| Brazilian torrent frog, <i>Hylodes asper</i> | Foot flagging | Hartmann et al. 2005 |
| Panamanian golden frog, <i>Atelopus zeteki</i> | Calls and semaphoring | Lindquist & Hetherington 1998 |
| Allegheny Mountain dusky salamander, <i>Desmognathus ochrophaeus</i> | Tail undulation, leg waving and head rubbing | Vinnedge & Verrell 1998 |
| Fish | | |
| Three-spined stickleback, <i>Gasterosteus aculeatus</i> | Zigzag swimming display | Rowland 1995; Candolin 1999 |
| Green swordtail, <i>Xiphophorus helleri</i> | Back and forth swimming displays | Rosenthal et al. 1996 |
| Japanese medaka, <i>Oryzias latipes</i> | Round dances | Weir & Grant 2010 |
| Bicolor damselfish, <i>Stegastes partitus</i> | Vertical dives ('dips') | Knapp & Kovach 1991 |
| Pacific leaping blenny, <i>Alticus arnoldorum</i> | Headnodding | Ord & Hsieh 2011 |
| Gobies, Perciformes; Gobiidae | Vocalizations | Malavasi et al. 2008 |
| Lusitanian toadfish, <i>Halobatrachus didactylus</i> | Vocalizations | Amorim et al. 2010 |
| Electric fish, <i>Brienomyrus brachyistius</i> | Electric organ discharges | Wong & Hopkins 2007 |
| Invertebrates | | |
| Fiddler crab, <i>Uca</i> spp. | Claw waving | Matsumasa & Murai 2005; Murai & Backwell 2006 |
| Wolf spider, <i>Hygrolycosa rubrofasciata</i> | Drumming | Kotiaho et al. 1998; Parri et al. 2002 |
| Peacock spider, <i>Maratus volans</i> | Opisthosomal bobbing, leg waving and fan dances | Girard et al. 2011 |
| Cricket, Orthoptera; Gryllinae, Gryllidae | Stridulation | Hack 1998; Ketola & Kotiaho 2010 |
| Rice moth, <i>Corcyra cephalonica</i> | Wing fanning and ultrasonic pulses | Spangler 1987 |
| Parasitoid wasp, <i>Spalangia endius</i> | Wing fanning | King et al. 2005 |

of energetic expenditure was less than that necessary for performing low-level activities such as feeding and preening. This result directed Horn et al. to conclude that other costs, such as predation or social retaliation (Leonard & Horn 1995), may be more important in ensuring that crowing remains an honest signal. With such variation in the variety and level of costs incurred by signalling, the theory that signals must be costly to ensure their honesty ('the handicap principle', Zahavi 1975; Grafen 1990) is regularly challenged, with several papers suggesting signal costs are unnecessary to ensure honest information is transferred (e.g. Lachmann et al. 2001; Getty 2006; Számadó 2011; reviewed in Johnstone 1995).

An often overlooked aspect of courtship is that signals are typically produced in bouts of repeated display. While repetition of some signals (e.g. attraction calls in crickets, Poulet & Hedwig 2005) may increase the detectability of the sender (Guilford & Dawkins 1991; Bradbury & Vehrencamp 1998), the significance of repetition during a courtship interaction remains unknown. We know from other social interactions (e.g. in aggression) that repeated signalling is often a reflection of the decision-making processes used by assessors (Clutton-Brock & Albon 1979; Enquist et al. 1990; Briffa et al. 1998). While aggressive displays also have static components that are assessed by competitors during contests, for

example weapons (Barki et al. 1997), ornamentation (Lailvaux et al. 2005; Vanhooydonck et al. 2005) or 'badges of status' (Rohwer 1977), it appears to be signal repetition that is most important in determining the outcome of extended aggressive interactions (Payne & Pagel 1996, 1997; Arnott & Elwood 2009). The production of demanding repeated displays during contests is intuitively linked to advertising fighting ability through demonstrations of stamina (e.g. Mowles et al. 2009, 2010), with each opponent attempting to 'prove its worth' and thereby avoid dangerous conflict. In contrast, it is similarly intuitive to consider the design of static ornaments used in courtship signals as important because they are so often spectacular in form and assumed to be 'attractive' to the opposite sex. Thus, it is not surprising that the focus lies on repetition for intrasexual selection, while for intersexual selection the focus is on ornamentation. However, recent studies (e.g. O'Loughlin & Rothstein 2010) have attempted to redress the balance by investigating female choice based on male motor performance (reviewed in Byers et al. 2010). Some studies have investigated the costs of repeated courtship displays (Kotiaho et al. 1998; Cady et al. 2011), but have not yet linked game theory models of repeated displays with courtship signal repetition. However, these models offer a successful paradigm for describing how the decision rules of an assessor dictate the repetition of signal production, and their

relevance to courtship was clearly evident to the early developers of game theory for agonistic contests (e.g. Payne & Pagel 1996).

RELEVANCE OF GAME THEORY TO REPETITIVE COURTSHIP DISPLAYS

While many sexual signals appear to be ornament derived, animals often perform repeated bouts of signals involving potentially costly behaviours. Consider, for example, the courtship display of male fiddler crabs, *Uca* spp., which is a well-known repeated motion display in which the male waves his enlarged major claw to attract females. Indeed, females have been shown to choose mates that wave more rapidly (Murai & Backwell 2006). Such repeated courtship signals are widespread in nature (see Fig. 1, Table 1). While game theory models of repeated displays have been used for describing contest behaviour, applying these models to sexual interactions can reveal key mechanisms driving female mate choice. For example, these models can help to identify the rules used by females to assess static ornaments presented during protracted courtship sequences (e.g. the ‘showing off’ of elaborate tail ornaments during the train-rattling display of peacocks or swimming display of male swordtails, *Xiphophorus helleri*; Table 1), male signal rates more generally, and the costs that might be incurred by performing mating signals. There are several game theory models of repeated displays that are relevant to courtship. Each model places a different amount of emphasis on the role of signal structure and on the role of costs (see Table 2). By evaluating each model in the context of a particular mating system, it is possible to identify the probable mechanisms or rules upon which females judge males. We introduce each of these models below and then discuss how two key attributes of male signalling, whether signals are escalated in the rate of production and the cost of signal production, can reveal how females choose among males and why.

Display Validation: Sending the Right Signals

When signals are passed between interacting animals, these often contain a small amount of error (either in production or reception). One function of signal repetition is thus to reduce this

error by allowing the information to be transmitted again. A model termed the ‘sequential assessment model’ (or SAM, Enquist & Leimar 1983; Enquist et al. 1990) explains this phenomenon in aggressive signalling. It assumes that information is gained throughout the course of signal production in a way analogous to statistical sampling (see Payne & Pagel 1997; Payne 1998). During courtship, the function of such repetition would thus be to increase the accuracy of the information about the male that is available to the female. The information and decision rules used by the female to assess male quality are therefore centred on the static characteristics of the signal, such as an ornament or another morphological feature being presented (e.g. body size), or the structure of the call or display itself. That is, females are evaluating males based on the qualities of the signal or cue, and the function of repetition is to allow females increased opportunities to assess the signal or cue. When signals are performed repeatedly for simple validation purposes, signal costs are not expected to be related to the rate of signalling, and the assessment of signal costs are therefore not part of the decision-making process. The diagnostic feature of the validation process is that the signal is produced at a constant rate (Fig. 2). Thus, if during courtship, a male signals repeatedly without escalation, then repetition is being used for signal validation.

Extrinsic Cost Thresholds: Devoting Time to the Cause

Aside from validation, another function of signal repetition may be to demonstrate some quality of the signaller to the receiver by demonstrating the signaller’s ability to withstand (or avoid) some costs associated with producing a signal repeatedly. These fall into two broad categories: extrinsic (i.e. ‘circumstantial’) and intrinsic costs. The function of signal repetition may be to allow the receiver to judge the quality of the signaller on its ability to produce a vigorous signal in the face of extrinsic costs such as reduced time away from other activities (e.g. foraging) and increased predation risk. For example, the courtship vocalizations of túngara frogs, *Engystomops pustulosus*, are open to exploitation by predatory bats, which capture significantly more frogs when frogs are calling (Tuttle & Ryan 1981), and courting wax moths, *Galleria mellonella*, are known to modify their signal rate when they detect the



Figure 1. Examples of species known to produce repeated displays during courtship. Top row: red deer, *Cervus elaphus*; Panamanian golden frog, *Atelopus zeteki*; fiddler crab, *Uca tangeri*. Bottom row: Pacific leaping blenny, *Alticus arnoldorum* (photo credit Georgina Cooke); African field cricket, *Gryllus bimaculatus*; Indian peafowl, *Pavo cristatus*.

Table 2
Key assumptions made under each function of repetitive signalling, as well as the criteria used by females to select mates

| Signal repetition function | Signal validation | Demonstrating extrinsic cost capacity | Demonstrating energetic cost capacity | Demonstrating inflicted cost capacity |
|----------------------------|--|--|--|---|
| Assumptions | Repetition provides additional information, analogous to statistical sampling | Repetition is a cumulative process, such that the signal is represented by the sum of the signaller's actions | Repetition is a cumulative process and results in the accumulation of energetic costs that limit the rate of performance | Repetition is a cumulative process, resulting in energetic costs that are augmented by direct costs inflicted by the receiver |
| Signal structure | Produced at a constant rate: escalation is absent | Escalation predicted | Escalation and/or de-escalation predicted | Escalation and/or de-escalation predicted |
| Signal costs | Costs do not contribute to decision making | Extrinsic costs such as exposure to predation, parasites and a reduction in foraging time | Energetic costs are related to the rate of signal production | Energetic costs are related to the rate of signal production, while additional costs are inflicted by the receiver |
| | Any costs are coincidental and a function of time spent in performance (time = energy) | Energetic costs are coincidental and a function of time spent in performance (time = energy) | | |
| Female decision rule | Assessment of a stimulus that is displayed repeatedly (e.g. the appearance of an ornament) | Assessment of the ability to produce a vigorous signal in the face of extrinsic costs (e.g. time away from other activities; increased predation risk) | Assessment of the ability to produce a vigorous signal despite its performance incurring significant energetic costs | Assessment of the ability to produce a vigorous signal in the face of energetic and inflicted costs |

ultrasonic calls of hunting bats (Jones et al. 2002). Furthermore, parasitoid flies are able to locate their field cricket, *Teleogryllus oceanicus*, hosts by homing in on their courtship calls, a process that has led to the evolution of silent morphs on the Hawaiian island of Kauai (Zuk et al. 2006; see also Bernal et al. 2006). The rate at which a signal is performed in the face of these dangers is important to a female in assessing male quality such that better quality males perform more obvious, higher intensity signals. This process is analogous to 'war of attrition' models developed for explaining displays in animal conflict, whereby the individual prepared to

devote the most time to signalling 'wins' the interaction (Maynard Smith 1974; Parker & Thompson 1980). In courtship, the signaller simply demonstrates this persistence quality to the receiver by performing a long, drawn-out display of repetitive signals. The receiver then chooses a mate from among observed signallers based on their ability to produce this extended repeated display. In this case, escalation is predicted in the rate of courtship signal production, but importantly, the costs are entirely extrinsic and any energetic expenditure incurred during signalling is simply a function of the time spent in display (time = energy, Fig. 2), and is not related to signal escalation specifically.

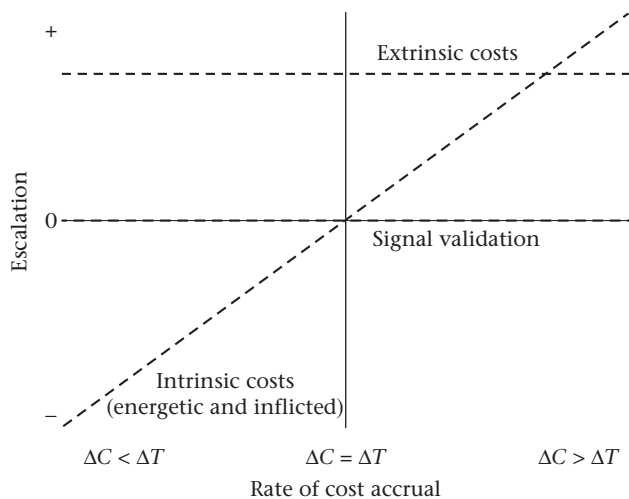


Figure 2. Predictions of the relationship between the rate of energetic cost accrual and the rate of signal escalation according to each function of signal repetition: (1) signal validation predicts no signal escalation (slope and intercept = 0); (2) extrinsic costs capacity predicts positive signal escalation (i.e. a display that may speed up or otherwise escalate in intensity; intercept = 0), but the rate of signal escalation is not related to the rate of cost accrual (ΔC ; which is instead related to the time spent in display, ΔT ; slope = 0); (3) intrinsic cost capacity (energetic and inflicted costs) predict both positive and negative signal escalation (i.e. signal rate increases or decreases as time progresses; intercept $\neq 0$) and that the rate of signal escalation is related to the rate of accumulation of energetic costs (i.e. high-intensity signals generate higher costs than predicted by time spent in display ($\Delta C > \Delta T$) and negatively escalating (decelerating) signals result in lower energetic performance costs than predicted by time spent in display ($\Delta C < \Delta T$; slope $\neq 0$)).

Energetic Cost Thresholds: Making the Effort

Some displays may incur significant energetic costs, such that they limit the rate of performance. In these cases, the function of repetition is to advertise the signaller's stamina, and thereby its quality, as the production of the signal is constrained to the rate that the signaller is capable of achieving. The energetic war of attrition model (E-WOA, Payne & Pagel 1996, 1997) was developed to describe this scenario in both contests and courtship. Signals of stamina in aggression have been supported by extensive studies demonstrating that the vigour of an agonistic display is correlated with the stamina of the sender (e.g. Brandt 2003) and with agonistic success (e.g. Clutton-Brock & Albon 1979; Briffa et al. 1998). Parallel studies are beginning to reveal that energetic costs are important in several courtship systems such as in wolf spiders, *Hygrolycosa rubrofasciata*, where the drumming courtship display is energetically costly and also correlated with the reproductive quality of the signalling male (Mappes et al. 1996; Kotiaho et al. 1998). If females are relying on this assessment of a male's intrinsic cost threshold to make decisions, then we would expect to see females choosing males that signal at a higher rate in the presence of energetic costs, and indeed female wolf spiders are known to prefer males that perform this signal at high rates (Parri et al. 1997; Shamble et al. 2009). However, an individual may not be able to maintain such energetic expenditure for a prolonged period, and thus, while signal escalation occurs in this scenario, de-escalation is also predicted to occur if males approach their exhaustion threshold and are unable to maintain high-intensity

signalling. Thus, in this system of signal repetition, both escalation and de-escalation in the rate of signal production are predicted and the rate of escalation/de-escalation is related to the rate of accrual of energetic costs.

Inflicted Cost Thresholds: Tough Love

In some courtship scenarios, the signaller may be expected to pay additional costs inflicted directly by the receiver. Payne (1998) modified the energetic war of attrition model to include these inflicted costs, which are likely to occur during aggression, and created the cumulative assessment model (CAM). This model is almost exclusively applicable to aggressive contests rather than to courtship, but there may be analogues where a signalling male is expected to bear costs inflicted by the female (e.g. potential injuries) or best them at a ‘testing’ process. For example, the ‘boxing’ behaviour of brown hares, *Lepus europaeus*, has been revealed to be a female fending off a courting male (Holley & Greenwood 1984). The ability of the male to box and similarly withstand blows from her paws is a test of his ability. If he is successful in boxing and can chase her down following the bout, she will usually solicit a mating. Thus, the ability of a male to respond physically, and best the female, demonstrates his quality as a potential mate.

The four functions of signal repetition described above make different predictions about the nature of information transmitted and the role of display costs in limiting performance. As each of the functions of signal repetition differs on the basis of signal escalation and costs, evaluating (1) whether signal escalation occurs and (2) whether any physiological costs are related to the rate of signal production is all that is required to distinguish which function of repetitious signalling is appropriate for a given species. Identifying the function of signal repetition will subsequently reveal how females discriminate between males and on what cues females base assessment. For example, following Fig. 3, if an observed courting male performs a series of signals, yet the accumulation of energetic costs is not related to the rate of signal production, then one would proceed down the left-hand side of the flow chart, leading to either (1) signal validation or (2) demonstrating the ability to withstand extrinsic costs as the function of repetition. These can then be differentiated by analysing the signal sequence for escalation. If the signal is maintained at a constant rate during

courtship, then the function is signal validation, whereas if the signal escalates, then the signaller is demonstrating its ability to bear extrinsic costs, similarly to Zahavi’s handicap principle (Zahavi 1975). (Validation is the only function that predicts that signals are produced at a constant rate and implies the cost of signal production is either absent in males or unimportant to females. In this sense, determining whether changes occur in the rate of signal production might appear to be the logical first step. However, clear insight into the evolutionary dynamics governing male and female behaviour during mating can only be obtained if an evaluation is made of whether males incur any cost during signal production. This is especially interesting because females are not using such costs to discriminate between males. Hence we recommend that the evaluation of signal costs be the first objective in distinguishing between the functions.) Alternatively, if the accumulation of energetic costs is related to the rate of signal production, then one would proceed down the right-hand side of the flow chart, with the demonstration of the ability to bear intrinsic costs being the function of signal repetition. Whether these costs are solely energetic or also inflicted will determine the nature of signal repetition. If the signalling male receives additional costs from the courted female, then demonstrating the ability to bear inflicted costs is the function for signal repetition, while in the absence of inflicted costs, the ability to bear energetic costs is appropriate.

Utilizing established game theory models of repeated displays, and addressing how analogues of these are appropriate to courtship, is central to understanding the functions of signal repetition in courtship and exactly what aspects of male quality females are evaluating when assessing these repeated signals. For example, the inherent ability to manufacture a good-quality ornament may be important to a female, probably reflecting the genetic quality and overall health of the signalling male (Hamilton & Zuk 1982). On the other hand, the ability of the male to challenge predation risk and bear energetic production costs would be indicative of his fitness potential, as performance is associated with the ability to evade a predator (Leal 1999) or best a rival (Perry et al. 2004). If females are able to obtain all of the information that they need for deciding upon a potential mate within the first call or display, why do males of so many animals continue to repeat signals in long, drawn-out courtship sequences, especially considering that there is likely to be a time cost to both the signalling male and to the observing female? Game theory suggests the answer lies in the level of error

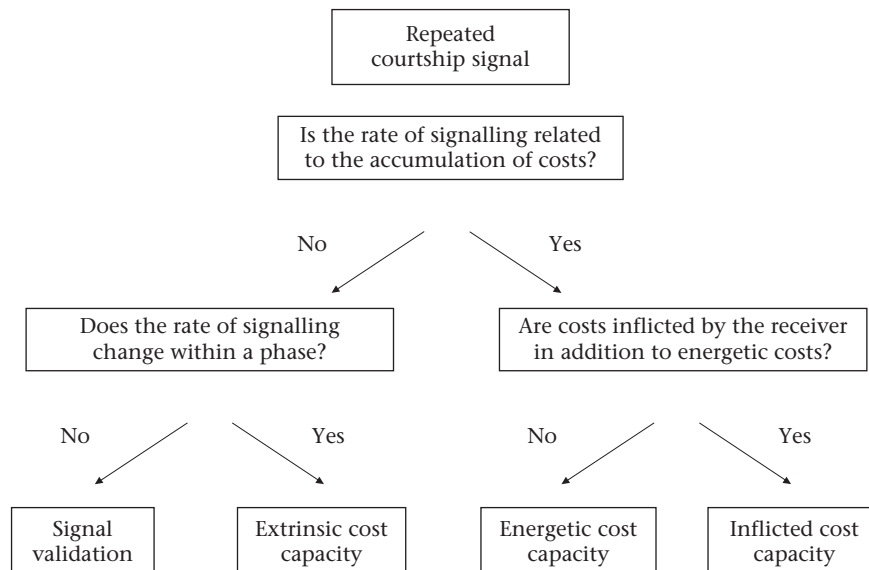


Figure 3. Key for identifying the functions of repeated displays based on the presence of costs and signal escalation.

in communication generally. Environmental noise (e.g. visual, acoustic or electrical) may make a single signal such as a colour, call or electrical discharge difficult to discern (van der Sluijs et al. 2011), necessitating a signal to be repeated.

The purpose of costs in signal production can also be explained by the four functions of repeated signals that we have outlined. Finding support for signal repetition as a means of demonstrating the ability to bear extrinsic costs implies that the performance of an elaborate and dangerous display, owing to the signaller's potential conspicuousness to predators, may provide valuable information to observing females via a handicap mechanism (Zahavi 1975; Grafen 1990). That is, those individuals that continue to signal in the face of predation threat presumably have the capacity to avoid predation, and would thus prove attractive as a mate, as they will sire offspring with a similarly high fitness potential (Weatherhead & Robertson 1979; Hamilton & Zuk 1982). Furthermore, identifying a physiologically costly repeated courtship display would confirm that the repetitive signals of interest incur intrinsic energetic costs, with the implication being that these costs inform females of the aerobic capacity and stamina of the displaying male. This capacity is likely to reflect qualities that would confer survivability in potential offspring, such as sprint speed in relation to predator avoidance. Physiologically costly displays can also serve to advertise the energetic reserves that the male has built up by being a successful forager, which can then sustain him while he provides parental care, leading to increased reproductive success (Knapp & Kovach 1991). By addressing repetitive courtship signals using this methodical approach, we can thus elucidate the qualities that females search for in potential mates, and, in turn, the qualities with which they are interested in provisioning their future offspring. Understanding the process of mate choice via repeated displays has the additional potential of demonstrating how sexual selection can shape display behaviours and lead to speciation.

Alternatively, when game theory does not account for male signal costs, it serves to highlight an evolutionary mismatch between female preferences and male signalling strategies. Both extrinsic (i.e. circumstantial) and intrinsic (i.e. energetic) costs are predicted to serve an important function in signal assessment; otherwise they would be selected against in males. If it is found that females are not making judgements based on signal costs (i.e. in signal validation), and yet males incur a nontrivial cost from signal production, then our focus should shift to discovering why males have not evolved an alternative, cheaper strategy for courtship. Perhaps costly male signals are a holdover from historically choosy females preferring expensive signals. Why this preference has been lost in females and not the associated signals in males could be investigated using a phylogenetic comparative approach (e.g. Ord et al. 2011). A comparative approach could also be used to test alternative hypotheses; for example, the costs associated with signal production are contemporary (e.g. the invasion of novel environments has led to new pressures from predation or parasites). Adaptation may therefore not have had enough time to occur or is inhibited in some way (e.g. because of physiological, morphological or genetic constraints). In many cases, without the application of a game theory approach to courtship, discovering the initial mismatch between female preferences and male costs would probably remain hidden.

SIGNAL ESCALATION AND COSTS: A METHODOLOGICAL APPROACH

Thus far we have established that there are four principal functions for the performance of repeated displays in courtship: (1) signal validation, (2) demonstrating the ability to bear extrinsic costs, (3) energetic costs and (4) inflicted costs. As we have

described, distinguishing between these involves analysing the temporal structure of the repeated signal, as well as how any costs associated with signal production are accrued (Figs 2, 3). Obtaining data of this kind is not trivial but, as we detail below, should be tractable for most study systems.

Identifying Signal Escalation

The initial problem faced when analysing repeated signalling is deciding what constitutes repetition: repetition of signal components (e.g. call notes, movements making up a display), repetition of whole signals or repetition of signal bouts (two or more signals strung together in a sequence, see Fig. 4). This will be dependent on the taxa being studied, and the main feature determining which approach to adopt will be the way in which signals are used during courtship. For example, a frog that produces a call made up of just one note uses a single-component signal system in which repetition can only occur in either the frequency of calls or bouts of calls. However, a frog that produces a call made up of several notes uses a multicomponent signal system and repetition can occur within the call itself (number of times notes are repeated within a call; e.g. túngara frogs: Ron 2008; Goutte et al. 2010; Ryan et al. 2010) in addition to the number of whole calls or bouts of calls (Fig. 5). The log-transformation protocol developed by Tolcamp & Kyriazakis (1999) and discussed in Ord & Evans (2003) provides a method for identifying whether a system is single- or multicomponent, and which type of repetition is likely to be the most salient to focus on.

The protocol involves measuring the duration of intervals between signal events, that is, all periods in which the animal is not signalling, and then log-transforming those intervals, which might occur between bouts, between signals within a bout and between components making up the signal itself. The frequency distribution of logged intervals will generate two peaks in a single-component system, representing the intersignal (short) and interbout (long) intervals. A multicomponent signalling system will result in three peaks corresponding to the intrasignal (very short), intersignal (short) and interbout (long) intervals (Fig. 5).

Once the system of signal repetition is identified, the best feature to use to measure signal escalation will be the extent to which intervals are consistent between signal events at each level. Determining the consistency of interval durations can be done by

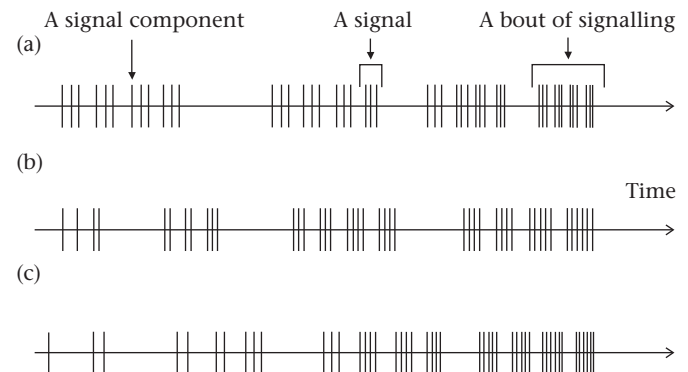


Figure 4. Timelines illustrating signal escalation in (a) the frequency of bouts or signals performed per unit time (reduction in intrasignal, intersignal and interbout intervals), (b) the frequency of components performed per signal and frequency of signals per bout (which results in prolonged signalling), and (c) a combination of escalation involving a shortening of the nonsignalling periods and an increase in signalling frequency. Escalation is thus identified by first measuring the level of variance in intrasignal, intersignal and interbout intervals (a) and then, if intervals are stereotyped, testing whether the frequency of signal production increases in increasingly lengthy bouts (b). However, both modes of escalation may also occur at the same time (c).

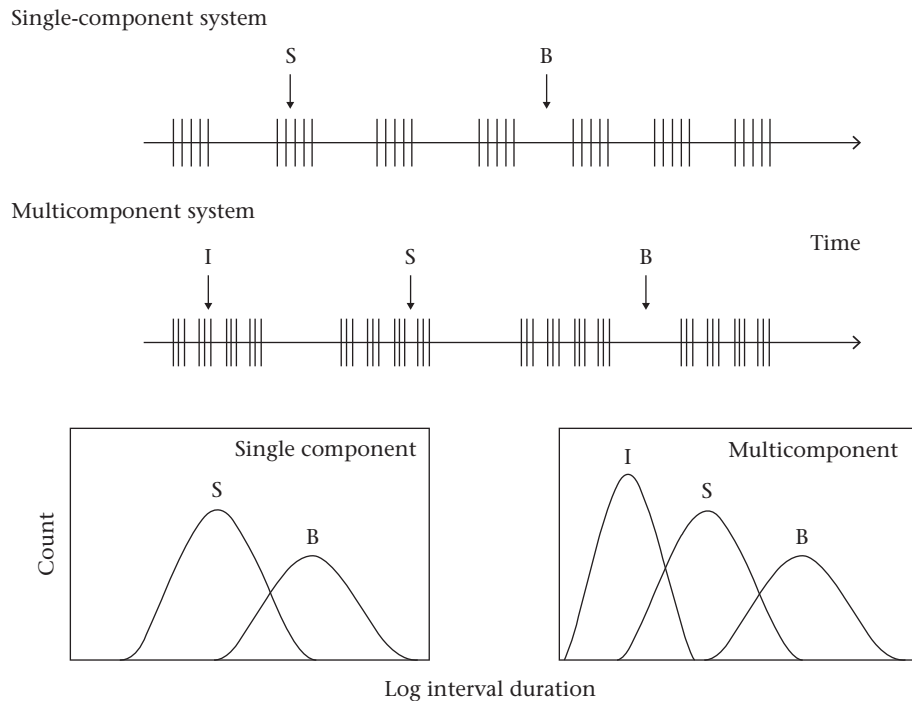


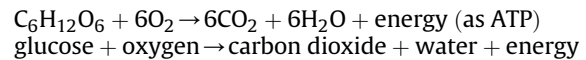
Figure 5. Timelines of signal production and frequency distributions of intersignal intervals performed by animals signalling in single-component and multicomponent systems: intrasignal intervals (I), intersignal intervals (S) and interbout intervals (B).

comparing the coefficient of variation (CV) of intrasignal, inter-signal and interbout intervals. The CV will be low for stereotyped aspects of courtship and high for less stereotyped aspects of courtship. For example, if intersignal and interbout intervals are found to be highly stereotyped, then either escalation is absent (i.e. in signal validation) or repetition is best examined in the number of components making up a signal (Fig. 4). If signal repetition is present and varies over time, then signal escalation (or de-escalation) is present. In this case, the function of signal repetition is either consistent with the demonstration of the ability to bear extrinsic costs (escalation only) or intrinsic costs (both escalation and de-escalation can occur). Distinguishing between these different demonstrations of ability requires estimating the probable costs associated with signal repetition.

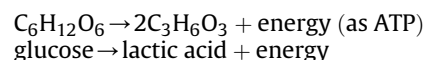
Analysing Signal Costs

Intrinsic, metabolic costs are incurred because of energetic expenditure and metabolism, whereby dynamic repeated displays act as 'behavioural indices' of quality (see Számadó 2011 for a review of mechanisms governing honest signalling). Energy reserves (e.g. fat or glycogen stores) and oxygen are needed to produce activity. As fat is a long-term store, any depletion is not likely to be noticeable during the timeframe of a discrete courtship interaction, although an animal may show a loss of condition over the long term (for example, male fallow deer, *Dama dama*, lose weight over the breeding season, Jennings et al. 2006). However, to identify whether costs are related to the vigour of a signal, more immediate mechanisms must be targeted.

To understand better how energetic costs are accrued, it is useful to consider the process of cellular respiration, the reaction that governs the production of energy and thus imposes the limits of performance on a displaying individual. In aerobic respiration, glucose (liberated from glycogen reserves) is metabolized in the presence of oxygen to produce energy, as well as carbon dioxide and water:



Thus the limiting factors to performing energetically costly behaviours are the mobilization of glucose and the ability to deliver oxygen to the tissues; hence indications of cellular respiration rate would be the rate of glucose mobilization and of oxygen consumption. If, however, an animal performs activity so demanding that it exceeds its aerobic capacity (the ability to provide adequate oxygen for aerobic respiration), then anaerobic respiration takes place, whereby glucose is metabolized to release energy in the absence of oxygen:



This process is extremely costly as a metabolic by-product, lactic acid (and especially the lactate ions formed from this), is particularly damaging to tissues. Furthermore, considerably less ATP is liberated from each molecule of glucose (Sadava et al. 2008) making anaerobic respiration much less efficient than aerobic respiration.

Until now, most studies investigating the energetic costs of courtship signals have focussed on gas exchange using either respirometry (Horn et al. 1995; Hack 1998) or the 'doubly labelled water' technique (Vehrencamp et al. 1989; Dearborn et al. 2005). Both of these procedures are invasive and potentially problematic as a result. To carry out respirometry, an animal must be placed within a metabolic chamber, which can only be done in captivity and with conditioned animals. The 'doubly labelled water' technique involves administering isotopically labelled water to the study organism, necessitating that the animal be repeatedly captured or otherwise repeatedly sampled in some way pre- and postcourtship, which might be possible for animals in captive settings or those with high site fidelity in nature (e.g. lekking species, Vehrencamp et al. 1989; Dearborn et al. 2005).

Studies involving assays of metabolites are comparatively rare, possibly because of the difficulty of safely transporting biological

material back from the field to the laboratory, or the discouragingly lengthy assays that must be carried out to analyse sugars (Raabo & Terkildsen 1960; Van Handel 1985) or lactate (Engel & Jones 1978). However, recent advances in portable blood testing kits for sports medicine now offer a sophisticated alternative for the behavioural sciences. These kits were initially designed for human blood testing but are also valid for nonhuman animals (e.g. invertebrates, Matsumasa & Murai 2005; Doake et al. 2010). They now make it possible to measure the immediate costs of signal production through the measurement of circulating glucose and lactate directly in the field. For example, one simple approach is to measure both glucose and lactate in signalling individuals and also in nonsignalling control individuals. Raised circulating glucose relative to controls would show that additional energy is needed to perform the activity and that it is being delivered to the tissues, whereas raised lactate would show that the animal has exceeded its aerobic capacity and has been respiring anaerobically. By comparing the concentration of circulating glucose and lactate between signalling individuals and controls, it is possible to ascertain quantitatively whether performing the courtship signal requires more energy than other nonsignalling activities.

Once the decision rule of the female has been identified based on a male's courtship behaviour, it can then be experimentally confirmed through playbacks to females or traditional mate choice trials using live males that differ naturally in their rate of repetition and signal escalation. Furthermore, incorporating these experimental procedures into a comparative study of closely related species that differ in their signalling behaviour may allow the possible evolutionary trajectory of signals to be revealed and thus provide insight into how repetitive courtship signals have evolved.

EVOLUTION OF REPEATED COURTSHIP SIGNALS

A rich history of studies into sexual selection has shown us how increasingly elaborate and costly signals are able to evolve because of female mating preferences for exaggerated traits. However, these investigations have largely focused on static courtship signals (ornaments). Given that signals are expected to start off simple and cheap and become progressively more elaborate and costly as females become choosy (e.g. Akre & Ryan 2011), it follows that preferences for repeated signalling may take a similar evolutionary trajectory, resulting in increased signal vigour and production costs, while natural selection should favour individuals that produce these costly signals more efficiently (see Getty 2006).

The females of some genera have already been shown to exhibit latent preferences for signal repetition. For example, in the classic case of the túngara frog, males produce a 'whine', which is important in mate recognition (Ryan et al. 2010). However, some males produce calls with 'chucks' appended to the whine. These more complex calls, incorporating repetitions of chucks, are preferred by females. The innovation of this novel signalling component may have arisen as the chuck appears to make the signalling male easier for females to localize (Ryan et al. 2010), with the consequence that the chuck also makes the signalling male more conspicuous to predators (Tuttle & Ryan 1981; Ryan et al. 1982). Thus, the elaborated call incurs a signalling cost because of increased predation risk, while calls with higher repetition (more chucks) are also preferred by females (Goutte et al. 2010; to an extent, see Akre et al. 2011).

Similarly, in swordtails, signal elaboration can illustrate the evolution of a dynamic repeated display from a 'cheap' signal that evolved by exploiting a female preference for larger body sizes (Ryan & Wagner 1987) and ornamentation (Ryan & Rand 1993). Female swordtails are known to discriminate between males, preferring males with longer swords (Basolo 1990). There is also

evidence showing that the sword effectively exploits a pre-existing female preference for large body size in males (Rosenthal & Evans 1998). The sword therefore seems to have initially evolved as a cheap way for males to appear large. However, this fails to explain why males would present the sword in a repeated courtship display. Importantly for an honest signal of quality, the sword incurs a cost because of increased energetic expenditure from drag during swimming (Basolo & Alcaraz 2003). Of special relevance is that the sword is incorporated into repeated motion displays (Basolo & Alcaraz 2003), and males that present the sword to females using these courting displays are preferred over non-displaying males (Rosenthal et al. 1996; Cummings & Gelineau-Kattner 2009; Wong et al. 2011). The display involving the sword incurs energetic costs (Cummings & Gelineau-Kattner 2009), and, thus, a costly repeated display has evolved, originating from a latent female preference for an ornamental trait.

The importance of female preference for repeated courtship displays may be further illustrated in situations in which sexually selected ornaments have been lost (Wiens 2001), but apparently associated motion displays remain. For example, in peacock pheasants, *Polyplectron* spp., the majority of the males bear eyespots similar to those of modern peafowl. However, two species are much less ornamented than the others in the genus, and recent genetic data have shown that these drab phenotypes are derived, with the presence of eyespots being a trait ancestral to the peacock-pheasants and the peafowl. However, all of these species still exhibit dynamic repeated displays in courtship, with peacock-pheasants performing lateral displays (Kimball et al. 2001) in which the head and tail are swung back and forth and the wing furthest from the female is flapped vigorously (Davison 1983). Thus, although the visual ornament is no longer present, the repeated courting behaviour itself is still informative.

FUTURE DIRECTIONS

We have illustrated the prevalence and importance of signal repetition in courtship behaviour, and how analogues of game theory models of repeated displays developed for use in aggression can help to explain the function and evolution of these repeated signals in courtship. The four discrete functions for signal repetition discussed should be applicable to a whole suite of mating systems centred on various signal modalities including acoustic, movement, electric and seismic signals, all of which are produced in bouts of repeated signalling. In such systems in which repetition is a given, the identification of these functions can elucidate how females make mate choice decisions. Further research into how female preferences for male signal sequences have evolved may reveal an evolutionary trajectory from cheap infrequent signal repetition to those of high cost, elaboration and extensive repetition. The four functions we present here imply that such a sequence of increasing signal vigour and increasing production costs (validation → extrinsic costs → energetic costs/inflicted costs) might have been important for some communication systems. We might therefore expect that one decision rule in females could lead to the subsequent evolution of another as females become increasingly more choosy. This hypothesis remains open to investigation.

Acknowledgments

We thank Mark Briffa, Mike Kasumovic and Devi Stuart-Fox for discussions of key concepts. We are also grateful to Ana Sendova-Franks and four anonymous referees for useful comments on the manuscript. S.L.M. was supported by a UNSW Writing Fellowship and a University of Nottingham Anne McLaren Fellowship.

References

- Akre, K. L. & Ryan, M. J. 2011. Female túngara frogs elicit more complex mating signals from males. *Behavioral Ecology*, **22**, 846–853.
- Akre, K. L., Farris, H. E., Lea, A. M., Page, R. A. & Ryan, M. J. 2011. Signal perception in frogs and bats and the evolution of mating signals. *Science*, **333**, 751–752.
- Amorim, M. C. P., Simoes, J. M., Mendonca, N., Bandarra, N. M., Almada, V. C. & Fonseca, P. J. 2010. Lusitanian toadfish song reflects male quality. *Journal of Experimental Biology*, **213**, 2997–3004.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Arnott, G. & Elwood, R. W. 2009. Assessment of fighting ability in animal contests. *Animal Behaviour*, **77**, 991–1004.
- Barki, A., Harpaz, S. & Karplus, I. 1997. Contradictory asymmetries in body and weapon size, and assessment in fighting male prawns, *Macrobrachium rosenbergii*. *Aggressive Behavior*, **23**, 81–91.
- Basolo, A. 1990. Female preference for male sword length in the green swordtail, *Xiphophorus helleri* (Pisces, Poeciliidae). *Animal Behaviour*, **40**, 339–349.
- Basolo, A. L. & Alcaraz, G. 2003. The turn of the sword: length increases male swimming costs in swordtails. *Proceedings of the Royal Society B*, **270**, 1631–1636.
- Bernal, X. E., Rand, A. S. & Ryan, M. J. 2006. Acoustic preferences and localization performance of blood-sucking flies (*Corethrella* Coquillett) to túngara frog calls. *Behavioral Ecology*, **17**, 709–715.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Brandt, Y. 2003. Lizard throat display handicaps endurance. *Proceedings of the Royal Society B*, **270**, 1061–1068.
- Briffa, M., Elwood, R. W. & Dick, J. T. A. 1998. Analysis of repeated signals during shell fights in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B*, **265**, 1467–1474.
- Byers, J., Hebets, E. & Podos, J. 2010. Female mate choice based upon male motor performance. *Animal Behaviour*, **79**, 771–778.
- Cady, A. B., Delaney, K. J. & Uetz, G. W. 2011. Contrasting energetic costs of courtship signaling in two wolf spiders having divergent courtship behaviors. *Journal of Arachnology*, **39**, 161–165.
- Candolin, U. 1999. The relationship between signal quality and physical condition: is sexual signalling honest in the three-spined stickleback? *Animal Behaviour*, **58**, 1261–1267.
- Clutton-Brock, T. H. & Albon, S. D. 1979. Roaring of red deer and the evolution of honest advertisement. *Behaviour*, **69**, 145–170.
- Cummings, M. E. & Gelineau-Kattner, R. 2009. The energetic costs of alternative male reproductive strategies in *Xiphophorus nigrensis*. *Journal of Comparative Physiology A: Neuroethology Sensory Neural and Behavioral Physiology*, **195**, 935–946.
- Dakin, R. & Montgomerie, R. 2009. Peacocks orient their courtship displays towards the sun. *Behavioral Ecology and Sociobiology*, **63**, 825–834.
- Dakin, R. & Montgomerie, R. 2011. Peahens prefer peacocks displaying more eyespots, but rarely. *Animal Behaviour*, **82**, 21–28.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- Davison, G. W. H. 1983. The eyes have it: ocelli in a rainforest pheasant. *Animal Behaviour*, **31**, 1037–1042.
- Dearborn, D. C., Anders, A. D. & Williams, J. B. 2005. Courtship display by great frigatebirds, *Fregata minor*: an energetically costly handicap signal? *Behavioral Ecology and Sociobiology*, **58**, 397–406.
- Doake, S., Scantlebury, M. & Elwood, R. W. 2010. The costs of bearing arms and armour in the hermit crab *Pagurus bernhardus*. *Animal Behaviour*, **80**, 637–642.
- Engel, P. C. & Jones, J. B. 1978. Causes and elimination of erratic blanks in enzymatic metabolite assays involving the use of NAD⁺ in alkaline hydrazine buffers: improved conditions for the assay of L-glutamate, L-lactate, and other metabolites. *Analytical Biochemistry*, **88**, 475–484.
- Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387–410.
- Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y. & Segerdahl, N. 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, **40**, 1–14.
- Frith, C. B. & Cooper, W. T. 1996. Courtship display and mating of Victoria's riflebird *Ptiloris victoriae* with notes on the courtship displays of congeneric species. *Emu*, **96**, 102–113.
- Getty, T. 2006. Sexually selected signals are not similar to sports handicaps. *Trends in Ecology & Evolution*, **21**, 83–88.
- Girard, M. B., Kasumovic, M. M. & Elias, D. O. 2011. Multi-modal courtship in the peacock spider, *Maratus volans* (O. P.-Cambridge, 1874). *Plos ONE*, **6**, e25390. <http://dx.doi.org/10.1371/journal.pone.0025390>.
- Goutte, S., Kime, N. M., Argo, T. F. & Ryan, M. J. 2010. Calling strategies of male túngara frogs in response to dynamic playback. *Behaviour*, **147**, 65–83.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.
- Guilford, T. & Dawkins, M. S. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour*, **42**, 1–14.
- Hack, M. A. 1998. The energetics of male mating strategies in field crickets (Orthoptera: Gryllinae: Gryllidae). *Journal of Insect Behavior*, **11**, 853–867.
- Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites. *Science*, **218**, 384–387.
- Hartmann, M. T., Giasson, L. O. M., Hartmann, P. A. & Haddad, C. F. B. 2005. Visual communication in Brazilian species of anurans from the Atlantic forest. *Journal of Natural History*, **39**, 1675–1685.
- Hasselquist, D., Bensch, S. & von Schantz, T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature*, **381**, 229–232.
- Holley, A. J. F. & Greenwood, P. J. 1984. The myth of the mad March hare. *Nature*, **309**, 549–550.
- Horn, A. G., Leonard, M. L. & Weary, D. M. 1995. Oxygen-consumption during crowing by roosters: talk is cheap. *Animal Behaviour*, **50**, 1171–1175.
- Jennings, D. J., Gammell, M. P., Carlin, C. M. & Hayden, T. J. 2006. Is difference in body weight, antler length, age or dominance rank related to the number of fights between fallow deer (*Dama dama*)? *Ethology*, **112**, 258–269.
- Johnstone, R. A. 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biological Reviews*, **70**, 1–65.
- Jones, G., Barabas, A., Elliott, W. & Parsons, S. 2002. Female greater wax moths reduce sexual display behavior in relation to the potential risk of predation by echolocating bats. *Behavioral Ecology*, **13**, 375–380.
- Kelso, E. C. & Martins, E. P. 2008. Effects of two courtship display components on female reproductive behaviour and physiology in the sagebrush lizard. *Animal Behaviour*, **75**, 639–646.
- Kelso, E. C. & Verrell, P. A. 2002. Do male veiled chameleons, *Chamaeleo calyptratus*, adjust their courtship displays in response to female reproductive status? *Ethology*, **108**, 495–512.
- Ketola, T. & Kotiaho, J. S. 2010. Inbreeding, energy use and sexual signaling. *Evolutionary Ecology*, **24**, 761–772.
- Kimball, R. T., Braun, E. L., Ligon, J. D., Lucchini, V. & Randi, E. 2001. A molecular phylogeny of the peacock-pheasants (Galliformes: *Polyplectron* spp.) indicates loss and reduction of ornamental traits and display behaviours. *Biological Journal of the Linnean Society*, **73**, 187–198.
- King, B. H., Saporito, K. B., Ellison, J. H. & Bratzke, R. M. 2005. Unattractiveness of mated females to males in the parasitoid wasp *Spalangia endius*. *Behavioral Ecology and Sociobiology*, **57**, 350–356.
- Knapp, R. A. & Kovach, J. T. 1991. Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes-partitus*. *Behavioral Ecology*, **2**, 295–300.
- Kotiaho, J. S., Alatalo, R. V., Mappes, J., Nielsen, M. G., Parri, S. & Rivero, A. 1998. Energetic costs of size and sexual signalling in a wolf spider. *Proceedings of the Royal Society B*, **265**, 2203–2209.
- Lachmann, M., Számadó, S. & Bergstrom, C. T. 2001. Cost and conflict in animal signals and human language. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 13189–13194.
- Lailvaux, S. P., Hathway, J., Pomfret, J. & Knell, R. J. 2005. Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). *Functional Ecology*, **19**, 632–639.
- Leal, M. 1999. Honest signalling during prey-predator interactions in the lizard *Anolis cristatellus*. *Animal Behaviour*, **58**, 521–526.
- Leonard, M. L. & Horn, A. G. 1995. Crowing in relation to status in roosters. *Animal Behaviour*, **49**, 1283–1290.
- Lindquist, E. D. & Hetherington, T. E. 1998. Semaphoring in an earless frog: the origin of a novel visual signal. *Animal Cognition*, **1**, 83–87.
- Loyau, A., Jalme, M. S. & Sorci, G. 2005. Intra- and intersexual selection for multiple traits in the peacock (*Pavo cristatus*). *Ethology*, **111**, 810–820.
- McComb, K. E. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour*, **41**, 79–88.
- Malavasi, S., Collatuzzo, S. & Torricelli, P. 2008. Interspecific variation of acoustic signals in Mediterranean gobies (Perciformes, Gobiidae): comparative analysis and evolutionary outlook. *Biological Journal of the Linnean Society*, **93**, 763–778.
- Mappes, J., Alatalo, R. V., Kotiaho, J. & Parri, S. 1996. Viability costs of condition-dependent sexual male display in a drumming wolf spider. *Proceedings of the Royal Society B*, **263**, 785–789.
- Matsumasa, M. & Murai, M. 2005. Changes in blood glucose and lactate levels of male fiddler crabs: effects of aggression and claw waving. *Animal Behaviour*, **69**, 569–577.
- Maynard Smith, J. 1974. Theory of games and evolution of animal conflicts. *Journal of Theoretical Biology*, **47**, 209–221.
- Mowles, S. L., Cotton, P. A. & Briffa, M. 2009. Aerobic capacity influences giving-up decisions in fighting hermit crabs: does stamina constrain contests? *Animal Behaviour*, **78**, 735–740.
- Mowles, S. L., Cotton, P. A. & Briffa, M. 2010. Whole-organism performance capacity predicts resource-holding potential in the hermit crab *Pagurus bernhardus*. *Animal Behaviour*, **80**, 277–282.
- Murai, M. & Backwell, P. R. Y. 2006. A conspicuous courtship signal in the fiddler crab *Uca perplexa*: female choice based on display structure. *Behavioral Ecology and Sociobiology*, **60**, 736–741.
- O'Loughlin, A. L. & Rothstein, S. I. 2010. It's not just the song: male visual displays enhance female sexual responses to song in brown-headed cowbirds. *Condor*, **112**, 615–621.
- Ord, T. J. & Evans, C. S. 2003. Display rate and opponent assessment in the Jacky dragon (*Amphibolurus muricatus*): an experimental analysis. *Behaviour*, **140**, 1495–1508.
- Ord, T. J. & Hsieh, T. H. 2011. A highly social, land-dwelling fish defends territories in a constantly fluctuating environment. *Ethology*, **117**, 918–927.
- Ord, T. J., Charles, G. K. & Hoffer, R. K. 2011. The evolution of alternative adaptive strategies for effective communication in noisy environments. *American Naturalist*, **177**, 54–64.

- Parker, G. A. & Thompson, E. A. 1980. Dung fly struggles: a test of the war of attrition. *Behavioral Ecology and Sociobiology*, **7**, 37–44.
- Parri, S., Alatalo, R. V., Kotiaho, J. & Mappes, J. 1997. Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata*. *Animal Behaviour*, **53**, 305–312.
- Parri, S., Alatalo, R. V., Kotiaho, J. S., Mappes, J. & Rivero, A. 2002. Sexual selection in the wolf spider *Hygrolycosa rubrofasciata*: female preference for drum duration and pulse rate. *Behavioral Ecology*, **13**, 615–621.
- Pasch, B., George, A. S., Campbell, P. & Phelps, S. M. 2011a. Androgen-dependent male vocal performance influences female preference in Neotropical singing mice. *Animal Behaviour*, **82**, 177–183.
- Pasch, B., George, A. S., Hamlin, H. J., Guillette, L. J. & Phelps, S. M. 2011b. Androgens modulate song effort and aggression in Neotropical singing mice. *Hormones and Behavior*, **59**, 90–97.
- Payne, R. J. H. 1998. Gradually escalating fights and displays: the cumulative assessment model. *Animal Behaviour*, **56**, 651–662.
- Payne, R. J. H. & Pagel, M. 1996. Escalation and time costs in displays of endurance. *Journal of Theoretical Biology*, **183**, 185–193.
- Payne, R. J. H. & Pagel, M. 1997. Why do animals repeat displays? *Animal Behaviour*, **54**, 109–119.
- Pellitteri-Rosa, D., Sacchi, R., Galeotti, P., Marchesi, M. & Fasola, M. 2011. Courtship displays are condition-dependent signals that reliably reflect male quality in Greek tortoises, *Testudo graeca*. *Chelonian Conservation and Biology*, **10**, 10–17.
- Perry, G., Levering, K., Girard, I. & Garland, T. J. 2004. Locomotor performance and social dominance in male *Anolis cristatellus*. *Animal Behaviour*, **67**, 37–47.
- Petrie, M., Halliday, T. & Sanders, C. 1991. Peahens prefer peacocks with elaborate trains. *Animal Behaviour*, **41**, 323–331.
- Poulet, J. F. A. & Hedwig, B. 2005. Auditory orientation in crickets: pattern recognition controls reactive steering. *Proceedings of the National Academy of Sciences, U.S.A.*, **102**, 15665–15669.
- Raabo, E. & Terkildsen, T. C. 1960. On the enzymatic determination of blood glucose. *Scandinavian Journal of Clinical & Laboratory Investigation*, **12**, 402–407.
- Reid, J. M., Arcese, P., Cassidy, A., Hiebert, S. M., Smith, J. N. M., Stoddard, P. K., Marr, A. B. & Keller, L. F. 2004. Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia*. *Animal Behaviour*, **68**, 1055–1063.
- Rintamäki, P. T., Hoglund, J., Alatalo, R. V. & Lundberg, A. 2001. Correlates of male mating success on black grouse (*Tetrao tetrix* L.). *Annales Zoologici Fennici*, **38**, 99–109.
- Rohwer, S. 1977. Status signaling in Harris sparrows: some experiments in deception. *Behaviour*, **61**, 107–129.
- Ron, S. R. 2008. The evolution of female mate choice for complex calls in túngara frogs. *Animal Behaviour*, **76**, 1783–1794.
- Rosenthal, G. G. & Evans, C. S. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proceedings of the National Academy of Sciences, U.S.A.*, **95**, 4431–4436.
- Rosenthal, G. G., Evans, C. S. & Miller, W. L. 1996. Female preference for dynamic traits in the green swordtail. *Animal Behaviour*, **51**, 811–820.
- Rowland, W. J. 1995. Do female stickleback care about male courtship vigour? Manipulation of display tempo using video playback. *Behaviour*, **132**, 951–961.
- Ryan, M. J. & Rand, A. S. 1993. Species recognition and sexual selection as a unitary problem in animal communication. *Evolution*, **47**, 647–657.
- Ryan, M. J. & Wagner, W. E. 1987. Asymmetries in mating preferences between species: female swordtails prefer heterospecific males. *Science*, **236**, 595–597.
- Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982. Bat predation and sexual advertisement in a Neotropical anuran. *American Naturalist*, **119**, 136–139.
- Ryan, M. J., Bernal, X. E. & Rand, A. S. 2010. Female mate choice and the potential for ornament evolution in túngara frogs *Physalaemus pustulosus*. *Current Zoology*, **56**, 343–357.
- Sadava, D., Heller, H. C., Orians, G. H., Purves, W. K. & Hillis, D. M. 2008. *Life, the Science of Biology*. 8th edn. Sunderland, Massachusetts: Sinauer.
- Schlinger, B. A., Day, L. B. & Fusani, L. 2008. Behavior, natural history and neuroendocrinology of a tropical bird. *General and Comparative Endocrinology*, **157**, 254–258.
- Shamble, P. S., Wilgers, D. J., Swoboda, K. A. & Hebets, E. A. 2009. Courtship effort is a better predictor of mating success than ornamentation for male wolf spiders. *Behavioral Ecology*, **20**, 1242–1251.
- van der Sluijs, I., Gray, S. M., Amorim, M. C. P., Barber, I., Candolin, U., Hendry, A. P., Krahe, R., Maan, M. E., Utne-Palm, A. C., Wagner, H.-J. & Wong, B. B. M. 2011. Communication in troubled waters: responses of fish communication systems to changing environments. *Evolutionary Ecology*, **25**, 623–640.
- Spangler, H. G. 1987. Ultrasonic communication in *Coryra cephalonica* (Stainton) (Lepidoptera: Pyralidae). *Journal of Stored Products Research*, **23**, 203–211.
- Számadó, S. 2011. The cost of honesty and the fallacy of the handicap principle. *Animal Behaviour*, **81**, 3–10.
- Takahashi, M., Arita, H., Hiraiwa-Hasegawa, M. & Hasegawa, T. 2008. Peahens do not prefer peacocks with more elaborate trains. *Animal Behaviour*, **75**, 1209–1219.
- Tokarz, R. R. 2007. Changes in the intensity of male courtship behavior following physical exposure of males to previously unfamiliar females in brown anoles (*Anolis sagrei*). *Journal of Herpetology*, **41**, 501–505.
- Tolkamp, B. J. & Kyriazakis, I. 1999. To split behaviour into bouts, log-transform the intervals. *Animal Behaviour*, **57**, 807–817.
- Tuttle, M. D. & Ryan, M. J. 1981. Bat predation and the evolution of frog vocalizations in the neotropics. *Science*, **214**, 677–678.
- Van Handel, E. 1985. Rapid determination of glycogen and sugars in mosquitoes. *Journal of the American Mosquito Control Association*, **1**, 299–301.
- Vanhooydonck, B., Herrel, A. Y., Van Damme, R. & Irschick, D. J. 2005. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Functional Ecology*, **19**, 38–42.
- Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M. 1989. The energetic cost of display in male sage grouse. *Animal Behaviour*, **38**, 885–896.
- Vinnedge, B. & Verrell, P. 1998. Variance in male mating success and female choice for persuasive courtship displays. *Animal Behaviour*, **56**, 443–448.
- Weary, D. M., Lambrechts, M. M. & Krebs, J. R. 1991. Does singing exhaust male great tits. *Animal Behaviour*, **41**, 540–542.
- Weatherhead, P. J. & Robertson, R. J. 1979. Offspring quality and the polygyny threshold: 'the sexy son hypothesis'. *American Naturalist*, **113**, 201–208.
- Weir, L. K. & Grant, J. W. A. 2010. Courtship rate signals fertility in an externally fertilizing fish. *Biology Letters*, **6**, 727–731.
- Wiens, J. J. 2001. Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends in Ecology & Evolution*, **16**, 517–523.
- Wilson, D. R. & Mennill, D. J. 2011. Duty cycle, not signal structure, explains conspecific and heterospecific responses to the calls of black-capped chickadees (*Poecile atricapillus*). *Behavioral Ecology*, **22**, 784–790.
- Wong, R. Y. & Hopkins, C. D. 2007. Electrical and behavioral courtship displays in the mormyrid fish *Brienomyrus brachyistius*. *Journal of Experimental Biology*, **210**, 2244–2252.
- Wong, R. Y., So, P. & Cummings, M. E. 2011. How female size and male displays influence mate preference in a swordtail. *Animal Behaviour*, **82**, 691–697.
- Zahavi, A. 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.
- Zuk, M., Rotenberry, J. T. & Tinghitella, R. M. 2006. Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biology Letters*, **2**, 521–524.