The role of sensory ecology and cognition in social decisions: Costs of acquiring information matter

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Abstract

1. We generally assume that animals should maximize information acquisition about their environment to make prudent decisions. But this is a naïve assumption, as gaining information typically involves costs.

2. This is especially so in the social context, where interests between interacting partners usually diverge. The arms race involved in mutual assessment is characterized by the attempt to obtain revealing information from a partner while providing only as much information by oneself as is conducive to one's own intentions.

3. If obtaining information occasions costs in terms of time, energy and risk, animals should be selected to base their decisions on a cost–benefit ratio that takes account of the trade-off between the risk of making wrong choices and the costs involved in information acquisition, processing and use.

4. In addition, there may be physiological and/or environmental constraints limiting the ability to obtaining, processing and utilizing reliable information.

5. Here, we discuss recent empirical evidence for the proposition that social decisions are to an important extent based on the costs that result from acquiring, processing, evaluating and storing information. Using examples from different taxa and ecological contexts, we aim at drawing attention to the often neglected costs of information recipience, with emphasis on the potential role of sensory ecology and cognition in social decisions.

KEYWORDS

behaviour, constrains, costs, decisions, signals, sociality, trade-offs

1 | INTRODUCTION

Animals are constantly exposed to environmental challenges, and they are selected to take decisions based on information obtained from their environment. Thereby, the uncertainty inherent in environmental information should be minimized by obtaining sufficiently reliable cues. Collecting and using information is thus key to making prudent decisions (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005), which crucially affects an individual's fitness (Bradbury & Vehrencamp, 2000). While the current state of an animal's environment is important for effective decision-making, the situation can change, and hence environmental dynamics should be considered. This includes taking account of the range of options and their consequences, and the potential responses of the environment to any action an animal may take. Conditions are particularly complex in the social context (Dore et al., 2018; Patricelli & Hebets, 2016), because interaction partners are likely to respond to an individual's behaviour (Dawkins & Krebs, 1978; Patricelli, Krakauer, & Taff, 2016), which can markedly alter the situation. It is therefore assumed that animals should gather as much information as possible

from their social environment (Dall et al., 2005; Dall & Johnstone, 2002). However, information acquisition, processing, storage and retrieval involves costs (Dukas & Kamil, 2000; Laughlin & Mendl, 2004), so there is an essential trade-off between the urge to obtain sufficient reliable information from the environment on the one hand, and to save investing in uneconomic acquisition of information to instead make less informed but 'cheaper' decisions (Dall et al., 2005; Dunlap, Papaj, & Dornhaus, 2017; Stephens, 1989).

The contributions to this special feature on 'The role of sensory ecology and cognition in social decisions' use different model systems to scrutinize the ecology of decision-making in the social context. In this introductory chapter, we outline relevant concepts to provide a framework for the theme and the ensuing articles.

Individuals in social groups commonly experience interactions varying in strength, type and dynamics (Sueur & Mery, 2017; Székely, Moore, & Komdeur, 2010). Such interactions include various forms of competitive behaviours (e.g. aggression conducted to monopolize resources), cooperation (e.g. in defence, hunting or breeding) and displays (e.g. to affect social partners or to attract mates). Strategies will be selected that maximize inclusive fitness by adequate consideration of the costs and benefits involved in social decisions (Bourke, 2011).

While direct costs and benefits of social interactions have been quantified in several taxa, the costs and benefits associated with information acquisition serving to make prudent social decisions have received less attention. Social interactions usually involve an exchange of various cues and signals (Espmark, Amundsen, & Rosenqvist, 2000; Laidre & Johnstone, 2013). Animals may, for instance, display their resource-holding potential, signal their need for resources or help or advertise their quality to social partners (Bradbury & Vehrencamp, 2011). Competition for the attention of social partners (Wiley, 1994) and conflicts of interest between individuals (Johnstone, 1998) promotes the evolution of costly, conspicuous signals (Arak & Enquist, 1995; Polnaszek & Stephens, 2014). It seems obvious to assume that prospective receivers of such signals might attempt to gather as much information from them as possible (Bradbury & Vehrencamp, 2000). Here, we argue that this assumption may often not apply in nature because of the trade-off between the value of possessing perfect information and the costs involved in gathering, processing, keeping and retrieving this information. Our main focus is on the costs involved in information acquisition in a social setting, and on the trade-off between these costs and the costs of making wrong or suboptimal decisions.

2 | COSTLY SIGNALS

Cues and signals can be differentiated by their origin. It is widely accepted that signals are the product of selection (Laidre & Johnstone, 2013), whereas cues can be any biotic or abiotic attribute that may be used to make informed decisions (Maynard Smith & Harper, 2003). In order to be reliable and honest, signals are assumed to involve costs to the producer (Searcy & Nowicki, 2005). If signals are costly to produce, they may reflect the underlying quality of the

signaller, because high-quality signal producers can yield signals of greater intensity (handicap principle; Grafen, 1990; Zahavi, 1975, 1977). Perhaps the most renowned example is the peacock's tail, where males invest in elaborate ornaments to attract females, which makes them more vulnerable to predators. A male signals to females his ability to survive in spite of being handicapped, implying his high genetic quality (Zahavi, 1975). Nevertheless, dishonest signals about a sender's quality may be expected, if the costs to the receiver of a signal are high to reliably evaluating the signal (Mokkonen & Lindstedt, 2016). With increasing assessment costs of signals, receivers may be selected to opt for cheaper, less reliable information instead of fully assessing all potentially available information (Ręk, 2014), which may lead to 'conventional' rather than 'costly' signalling (Vehrencamp, 2000). As Dawkins and Guilford (1991) have aptly stated in their seminal paper on receiver psychology and the evolution of animal signals: 'If both the signaller and receiver pay costs, it will be their mutual advantage to reduce them wherever the value of the extra information contained in a costly signal is outweighed by the costs of giving and receiving the costly signal.'

3 | COSTS OF INFORMATION ACQUISITION

Trade-offs are a fundamental component of behavioural decisions, because resources such as time or energy are somewhat limited, and costly investments need to be balanced against each other. Thereby, sensory and cognitive processes play an important role (Caves, Brandley, & Johnsen, 2018; Del Guidice & Crespi, 2018; Endler, 2000), as collecting and using information may be difficult and typically involves costs (Elwood & Arnott, 2012; Guilford & Dawkins, 1991). Thus, prospective signal receivers should evaluate if collecting additional information is worth the effort, or if a certain level of uncertainty about a signal provider is acceptable because it would improve the receiver's cost/benefit ratio (Dawkins & Guilford, 1991; Waite, 2002). This would select for context-dependent receiver responses (Tibbetts, 2008). In the following sections, we shall discuss optimal assessment strategies in social interactions, with special emphasis on the costs involved in information acquisition.

4 | THE COSTS AND BENEFITS OF OPPONENT ASSESSMENT

If two competitors for resources meet, in principle they can use three different strategies to assess each other's resource-holding potential (RHP; that is, the ability to win an escalated contest; Parker, 1974) relative to that of their opponent: self-assessment, opponent-only assessment and mutual assessment (Arnott & Elwood, 2009). Mutual assessment may entail the cost of providing a potentially costly signal in order to elicit a signal from the opponent. For instance in territory contests of red deer *Cervus elaphus*, stags defend their harem by initially eliciting a low rate of roaring (Clutton-Brock & Albon, 1979), with the

opponent usually answering. Such roaring contests can escalate until exhaustion of one of the contestants, with high roaring rates reflecting a stag's quality. Thus, both the challenger and the defender may pay the costs of roaring at a high rate in order to receive honest information about the opponent's quality. Similarly, house crickets *Acheta domesticus* fight frequently for burrows, mates and other resources (Hack, 1997a; Loher & Dambach, 1989). Fights are costly in terms of energy and risk of injury (Hack, 1997b). Heavier males generally defeat their opponents (Hack, 1997a), which is why size asymmetry is the most important information to be gathered during assessment. Crickets use sequential mutual assessment to gain information about their opponents: each move is at the same time (energetically) costly and revealing information about the opponent (Hack, 1997a). Thus, assessment is not simply based on a passive process of receiving information, but it depends on the sequence of tactics each opponent performs. As each assessment step is costly, it may pay to refrain from trying to elicit responses from the opponent for obtaining the maximum quantity of information. In other words, trading of costly signals may imply that opponents will not always assess the full range of potentially available information, but instead opt for incomplete, yet cheaper information about the social partner.

When signals are mutually traded against each other, the costs for both social partners are similar, because each serve at the same time as signaller and receiver. Different assessment strategies may result in a more asymmetric distribution of costs between contestants. Animals may decide about a specific assessment strategy in dependence of their own body condition, which may determine whether to save energy or gaining information about the opponent is more important. Male red-winged damselflies *Mnesarete pudica*, for example, exhibit red-coloured wings that serve as cues for competitors during their energetically costly aerial contests (Guillermo-Ferreira, Gorb, Appel, Kovalev, & Bispo, 2015). Wing pigmentation correlates with fat reserves, and thus males with more opaque wings are more likely to win a contest (Contreras-Garduño, Canales-Lazcano, & Córdoba-Aguilar, 2006). The duration of aerial contests is positively correlated with the wing spot size of the loser, but not with that of the winner (Guillermo-Ferreira et al., 2015). As a fight is usually terminated by the loser surrendering to its competitor, this suggests that red-winged damselflies follow a self-assessment model, that is, that fight duration increases with a loser's enhanced physiological status (Elwood & Arnott, 2012). When wing spot size was experimentally manipulated, strong males changed their behaviour according to pigmentation of the opponent, while weaker males did not (Guillermo-Ferreira et al., 2015). Thus, strong individuals that may benefit from fights seem to adopt a mutual assessment strategy, whereas weak individuals save assessment costs and avoid long contests. This condition-dependent variation in male assessment strategies may illustrate the trade-off between paying the costs of assessment and taking the risk of unsuccessful or detrimental escalation due to limited information (Mesterton-Gibbons & Heap, 2013).

Status-dependent signal assessment was observed also in gelada baboons *Theropithecus gelada*. Harem males produce loud calls signalling their quality to deter challenges from bachelor males (Benítez, Pappano, Beehner, & Bergman, 2017). Receivers of these signals assess the calls in dependence of their own status and quality. Bachelor males respond stronger to low-quality calls, whereas harem-holders respond stronger to high-quality calls. By responding to low-quality calls only, bachelor males may benefit from avoiding confrontation with stronger competitors, whereas successful harem-holders often join other calling males of similar quality to benefit from a dilution effect against bachelors. Thus, bachelor and harem males use signals of divergent quality, and they respond differently to these signals in accordance with the costs entailed by their response to the received signals. Such specific signal assessment considering relative abilities of contestants may involve complex cognitive processing (Wilczynski & Ryan, 2010), but it can at the same time generate superior fitness payoffs (Elwood & Arnott, 2012).

Gathering information from a social partner may entail detrimental costs to the receiver if it is associated with exposure to external risks. Females often use duration, variety or persistence of a male's display as a criterion for choosing a mate (e.g. Burk, 1988). Thus, they spend considerable time close to a potential partner, which does not only impose costs in the form of the time spent for signal assessment (opportunity costs) but the vicinity to a signalling male may expose them also to increased predation risk, as predators are often attracted to signals (enhanced mortality risk; Hughes, Kelley, & Banks, 2012). Male decorated crickets *Gryllodes supplicans*, for example, call to attract females from burrows where they are protected from predators. Mediterranean house geckos *Hemidactylus turcicus* follow these calls and pre-date on the female crickets that respond phonotactically to the calling males (Sakaluk & Belwood, 1984). Thus, attending the calls for assessing male quality puts the female crickets at risk for being consumed by a 'satellite predator'. This should select females to adjust prudently if, where, and when to obtain signals for mate assessment (Hughes et al., 2012). Such an adaptive adjustment of the collection of social information is illustrated by adult great barred frogs *Mixophes fasciolatus*, which are highly attracted to odour cues of conspecifics, but respond less to these cues when a scent-hunting predator is present (the red-bellies black snake *Pseudechis porphyriacus*; Hamer, Lemckert, & Banks, 2011). Under predation risk, male frogs are however still attracted to unfamiliar conspecific scents, indicating that they adjust their behaviour to gather only new, important information when predators are present, while ignoring less informative cues from well-known individuals.

In this struggle for maximizing the information gain from social partners while minimizing the involved acquisition costs, it may pay to conceal information to a competitor. Moreover, it may even pay to conceal to a competitor one's information state in order to maintain an information advantage (Engqvist & Taborsky, 2017).

5 | THE COSTS OF PROCESSING, STORING AND RETRIEVING INFORMATION

To respond appropriately to the environment may pose a cognitively demanding challenge particularly with regard to the social

environment of an individual, due to the inherent dynamics and involved conflicts of interest (Varela, Teles, & Oliveira, 2020; Weitekamp & Hofmann, 2014). The first difficulties for desiring receivers of social cues and signals regard perception, detection and recognition of relevant signals. Not all information apparently available can be perceived by the central nervous system of an animal due to constraints of the receiving and processing apparatus (Caves et al., 2018; Römer, 2020). Moreover, the brain needs to interpret the information received by means of the sensory and neural systems. Perceptual salience filters and targeted attention help to sort the wheat from the chaff (Knudsen, 2007; Nityananda, 2016). The different steps in signal perception involve costs (Sartori, Granger, Lee, & Horowitz, 2014), both at the level of processing (e.g. material and energy demands; Maille & Schradin, 2017; Niven & Laughlin, 2008) and interpretation (e.g. discerning relevant from less significant information; Knudsen, 2018). If the costs for fully assessing a signal is high, receivers may be selected to settle for cheaper, but less reliable information instead (Dawkins & Guilford, 1991). Male corncrakes *Crex crex*, for example, perform quiet, low-frequency, amplitude-modulated 'soft calls' during territorial conflicts, which are physically difficult or costly to produce for small birds (Fletcher, 2007). Thus, reliability of information in the call is likely to be maintained by an inherent cost. The frequency spectrum of the call, being rather complex, is however also supposedly costly to assess for the receiver. Corncrakes respond preferably to signals that are cheaper regarding assessment, although they are less reliable (Rek, 2014). Animals respond indiscriminately to soft calls, although its fundamental frequency is a strong predictor of male size. They apparently ignore this cue, which might be expensive to assess, thus it seems not to act as signal under natural condition. Therefore, although corncrakes might gain additional information about their opponent by investing in assessment, they seem to resort to less reliable, but cheaper information instead. This strategy may be widespread when signal processing puts high demands on sensory and cognitive procedures. In addition, constraints on social memory may limit optimal behavioural responses, for example, the possibility to cooperate efficiently with social partners (cf. Furlong & Opfer, 2009; Milinski & Wedekind, 1998; Stevens, Volstorf, Schooler, & Rieskamp, 2011). This may select for the application of simpler response strategies (e.g. generalized reciprocity; Barta, McNamara, Huszár, & Taborsky, 2010; Gfrerer & Taborsky, 2017; Leimgruber et al., 2014; Pfeiffer, Rutte, Killingback, Taborsky, & Bonhoeffer, 2005; Rutte & Taborsky, 2007; Stanca, 2009; van Doorn & Taborsky, 2012).

status or RHP), and an 'efficacy' component, which concerns the transmission design of a signal (e.g. conspicuousness against background noise). The efficacy of a signal depends on its detectability (how easy it can be distinguished from the background), discriminability (how easy it can be distinguished from other stimuli) and memorability (how easy it can be memorized and retrieved).

Multiple communication channels and sensory systems may be involved in signal transmission, which can greatly affect signal efficacy (Partan & Marler, 2005). For instance, the addition of chemical signals to visual signals can play an important role during agonistic encounters in fish (Frommen, 2020), as shown in the cooperative cichlid *Neolamprologus pulcher*. In this species, chemical information transferred by urine bouts is crucial for controlling the level of escalation in territory conflicts, where the sole transmission of visual signals results in much higher aggression levels than when chemical information is available as well (Bayani, Taborsky, & Frommen, 2017). The ecological context can profoundly influence the processes by which animals perceive multisensory stimuli, especially with regard to environmental uncertainty (Munoz & Blumstein, 2012). To unravel the neuronal processes involved in the cross-modal association of social stimuli is a challenging target for future research (Moll & Nieder, 2015).

Despite the potential for multicomponent stimuli to reduce uncertainty relative to single-component cues, animals may not necessarily utilize all components of multisensory information, depending on underlying costs and benefits of perception and information processing. Rainbow trout *Oncorhynchus mykiss*, for instance, settle their social hierarchy through visual and olfactory cues released by dominant individuals (Höjesjö, Axelsson, Dahy, Gustavsson, & Johnsson, 2015). However, subordinates react to the combination of both cues similarly as to visual exposure alone, suggesting that visual cues are more important than chemical cues for recognition and response decisions. Subordinate fish move closer to the dominant, likely as a type of inspection behaviour (Dugatkin & Godin, 1992). As the extra information provided when adding chemical cues does not change the behaviour or physiological response of subordinates, multimodal signal transmission seems to be redundant in this system. Visual information has been suggested to be more accurate, direct and reliable, while chemical cues may be more diffuse, for example, due to mixing with chemicals originating from different individuals. Olfactory cues may function, however, as a first cue alerting receivers to the presence of a second, visual cue, which may increase the probability of detection and recognition by the receiver (cf. Smith & Belk, 2001).

6 | SIGNAL COMPLEXITY

Information should be effectively transmitted in order to affect the behaviour of the receiver. While the environment itself plays an important role in the transmissibility of a signal, the receivers 'psychological landscape' is crucial as well (Guilford & Dawkins, 1991). Signal design contains two components: A 'strategy' component, which reflects signal construction by natural selection to adequately convey the desired information (e.g. competitors or potential mates displaying their health

7 | EVOLUTIONARY ECOLOGY OF SOCIAL DECISIONS IN THE LIGHT OF SENSORY AND NEURAL MACHINERY

The role of sensory ecology and cognition in social decisions was the theme of a recent workshop we have organized at Arolla in the Swiss Alps. It seemed timely to discuss the state of the art and future directions of this emerging and highly topical research field. Several keynote speakers of this workshop were glad to provide

insight into their personal views and approaches through contributions to this special feature of *Functional Ecology*, and other experts were joining on the way of compiling this volume. Its primary aim is to provide the reader with insights, opinions and examples from a field that is highly integrative by its very nature. This makes it utterly impossible to be comprehensive, or even approximately representative. Rather, these contributions can provide a brief glimpse of aims, concepts and empirical research in this developing branch of evolutionary ecology.

In their article, Susana Varela, Magda Teles and Rui Oliveira (Varela, Teles, & Oliveira, 2020) draw a firm line between social cognition and social competence, the former being viewed as a by-product of natural selection on the latter. Their conceptual framework highlights that selection directly acts on functional performance traits such as choosing mates, raising offspring and forming social bonds, while lower ranking traits such as social and non-social cognition constitute correlated, secondary targets of selection. They propose that enhanced social cognitive abilities should evolve if selection favours social competence, which will in turn affect the significance of social learning in the ecology of a species.

Rachel Page and Ximena Bernal relate selection on sensory strategies to detect prey to the ecology of predator–prey dynamics, focusing on bats in a comparative framework (Page & Bernal, 2020). Predation is an important force selecting potential prey to be cryptic, which prompts predators to adjust their sensory strategy appropriately in order to detect prey. To this end, predators may use both private and social information. Using a comparative framework, this article illustrates that bats often use cues, signals or behaviours of other individuals to gather information during foraging. Each of these strategies comes with its own set of costs and benefits, depending on the particular environment of the species. The successful integration of public and private information and the trade-offs involved in information acquisition are core questions in this field of research.

Using acoustic communication in insects as an example, Heiner Römer draws our attention to the limitations complex environments can pose on the transmission of signals, and on the design of the sensory and neural system of receivers. To understand the design of insect sensory systems, laboratory studies elucidating the neurological pathways of signal transfer and processing must be complemented by studies of the ecology of target species to unravel the role of complex environments in the transfer of information. Here, the specific focus is on spatial and temporal partitioning in the signalling of species in multispecies assemblages, which serves to reduce acoustic masking interference.

Joachim Frommen (Frommen, 2020) focusses on the specific conditions characterizing the aquatic medium when intentions are communicated among social partners. Most studies of the sensory modalities involved in aggressive encounters have so far focussed on terrestrial animals using visual and acoustic information. Here we learn how aquatic organisms signal aggressive potential, and how information delivered and obtained can reduce the costs and risk of injury in agonistic encounters.

Knörnschild, Fernandez, and Nagy (2020) compare the complexity of calls, and the role of complex social environments for intraspecific communication between different species of bats. Bat calls encode information on individual identity, sex and relatedness, which receivers can use to make decisions about mate choice, territorial defence, resource allocation and cooperation. Vocal complexity is hypothesized to increase with social complexity, which is tested using a comparative approach based on phylogenetically independent contrasts. As predicted, the complexity of vocalizations increases with social group size, highlighting the importance of making use of complex information in a social context.

In our introductory chapter to this special feature we have aimed at drawing attention to the inevitable costs involved in the acquisition of conducive environmental information in the social context. These costs vary depending on whether receivers choose to pay for full assessment or to settle for a less informative situation involving less heavy burden (Dawkins & Guilford, 1991). Since Zahavi (1975, 1977) drew our attention to the significance of costs involved in signal production in order to convey a reliable message, the research focus has largely been on the costs of producing rather than on the costs of receiving a signal. However, as we have outlined above, for understanding the evolutionary ecology of social decisions we need to study also the manifold costs involved in gathering, assessing and storing information. Thus, the popular idea that animals should gather as much information as possible in order to opt for the best decision may not be realistic in the natural world. Instead, individuals should trade-off costs that are caused by acquiring additional information against the risk of taking wrong decisions (e.g. Bradbury & Vehrencamp, 2000; Enquist & Leimar, 1983; Koops, 2004). Abandoning expensive assessment contests may pay under certain circumstances even at the expense of being less well informed as a consequence (e.g. in red deer and house cricket), especially if self-assessment has revealed a relatively low RHP (e.g. in red-winged damselflies). The ecological context is of crucial importance when deciding about the optimal investment in obtaining social information, such as predation risk (e.g. in decorated crickets and great barred frogs) or the availability of alternative opportunities (e.g. in galagos). Hence, our message is that the role of sensory ecology and cognition in social decisions must be viewed in an ecological context when aiming to unveil the evolution of animal communication and social structure.

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REFERENCES

Arak, A., & Enquist, M. (1995). Conflict, receiver bias and the evolution of signal form. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *349*(1330), 337–344.

Arnott, G., & Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal Behaviour*, *77*(5), 991–1004. https://doi.org/10.1016/j.anbehav.2009.02.010

Barta, Z., McNamara, J. M., Huszár, D. B., & Taborsky, M. (2010). Cooperation among non-relatives evolves by state-dependent

generalized reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1707), 843–848.

Bayani, D. M., Taborsky, M., & Frommen, J. G. (2017). To pee or not to pee: Urine signals mediate aggressive interactions in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behavioral Ecology and Sociobiology*, *71*(2), 37. https://doi.org/10.1007/s00265-016-2260-6

Benítez, M. E., Pappano, D. J., Beehner, J. C., & Bergman, T. J. (2017). Evidence for mutual assessment in a wild primate. *Scientific Reports*, *7*(1), 2952. https://doi.org/10.1038/s41598-017-02903-w

Bourke, A. F. (2011). *Principles of social evolution*. Oxford, UK: Oxford University Press.

Bradbury, J. W., & Vehrencamp, S. L. (2000). Economic models of animal communication. *Animal Behaviour*, *59*, 259–268. https://doi.org/10.1006/anbe.1999.1330

Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer Associates.

Burk, T. (1988). Acoustic signals, arms races and the costs of honest signalling. *Florida Entomologist*, *71*, 400–409. https://doi.org/10.2307/3494999

Caves, E. M., Brandley, N. C., & Johnsen, S. (2018). Visual acuity and the evolution of signals. *Trends in Ecology & Evolution*, *33*(5), 358–372. https://doi.org/10.1016/j.tree.2018.03.001

Clutton-Brock, T. H., & Albon, S. D. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour*, *69*(3), 145–170. https://doi.org/10.1163/156853979X00449

Contreras-Garduño, J., Canales-Lazcano, J., & Córdoba-Aguilar, A. (2006). Wing pigmentation, immune ability, fat reserves and territorial status in males of the rubyspot damselfly, *Hetaerina americana*. *Journal of Ethology*, *24*(2), 165–173. https://doi.org/10.1007/s10164-005-0177-z

Dall, S. R., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, *20*(4), 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Dall, S. R. X., & Johnstone, R. A. (2002). Managing uncertainty: Information and insurance under the risk of starvation. *Philosophical Transactions of the Royal Society of London, Series B*, *357*, 1519–1526. https://doi.org/10.1098/rstb.2002.1061

Dawkins, M. S., & Guilford, T. (1991). The corruption of honest signalling. *Animal Behaviour*, *41*, 865–873. https://doi.org/10.1016/S0003-3472(05)80353-7

Dawkins, R., & Krebs, J. R. (1978). Animal signals: Information or manipulation. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 282–309). Oxford, UK: Blackwell Scientific Publications.

Del Giudice, M., & Crespi, B. J. (2018). Basic functional trade-offs in cognition: An integrative framework. *Cognition*, *179*, 56–70. https://doi.org/10.1016/j.cognition.2018.06.008

Dore, A. A., McDowall, L., Rouse, J., Bretman, A., Gage, M. J., & Chapman, T. (2018). The role of complex cues in social and reproductive plasticity. *Behavioral Ecology and Sociobiology*, *72*(8), 124. https://doi.org/10.1007/s00265-018-2539-x

Dugatkin and Godin, 1992Dugatkin, L. A., & Godin, J. G. J. (1992). Prey approaching predators: A cost-benefit perspective. *Annales Zoologici Fennici*, *29*, 233–252.

Dukas, R., & Kamil, A. C. (2000). The cost of limited attention in blue jays. *Behavioral Ecology*, *11*(5), 502–506. https://doi.org/10.1093/beheco/11.5.502

Dunlap, A. S., Papaj, D. R., & Dornhaus, A. (2017). Sampling and tracking a changing environment: Persistence and reward in the foraging decisions of bumblebees. *Interface Focus*, *7*(3), 20160149. https://doi.org/10.1098/rsfs.2016.0149

Elwood, R. W., & Arnott, G. (2012). Understanding how animals fight with Lloyd Morgan's canon. *Animal Behaviour*, *84*(5), 1095–1102. https://doi.org/10.1016/j.anbehav.2012.08.035

Endler, J. A. (2000). Evolutionary implications of the interaction between animal signals and the environment. In Y. Espmark, T. Amundsen, & G. Rosenqvist (Eds.), *Animal signals: Signalling and signal design in animal communication* (pp. 11–46). Trondheim, Norway: Tapir Academic Press.

Engqvist, L., & Taborsky, M. (2017). The evolution of strategic male mating effort in an information transfer framework. *Journal of Evolutionary Biology*, *30*(6), 1143–1152. https://doi.org/10.1111/jeb.13083

Enquist, M., & Leimar, O. (1983). Evolution of fighting behaviour: Decision rules and assessment of relative strength. *Journal of Theoretical Biology*, *102*(3), 387–410. https://doi.org/10.1016/0022-5193(83)90376-4

Espmark, Y., Amundsen, T., Rosenqvist, G. (Eds.) (2000). *Animal signals: Signalling and signal design in animal communication*. Trondheim, Norway: Tapir Academic Press.

Fletcher, N. (2007). Animal bioacoustics. In T. D. Rossing (Ed.), *Springer handbook of acoustics* (pp. 785–804). New York, NY: Springer.

Frommen, J. G. (2020). Aggressive communication in aquatic environments. *Functional Ecology*, *34*(2), 364–380. https://doi.org/10.1111/1365-2435.13482

Furlong, E. E., & Opfer, J. E. (2009). Cognitive constraints on how economic rewards affect cooperation. *Psychological Science*, *20*(1), 11–16. https://doi.org/10.1111/j.1467-9280.2008.02244.x

Gfrerer, N., & Taborsky, M. (2017). Working dogs cooperate among one another by generalised reciprocity. *Scientific Reports*, *7*, 43867. https://doi.org/10.1038/srep43867

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, *144*, 517–546. https://doi.org/10.1016/S0022-5193(05)80088-8

Guilford, T., & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour*, *42*, 1–14. https://doi.org/10.1016/S0003-3472(05)80600-1

Guillermo-Ferreira, R., Gorb, S. N., Appel, E., Kovalev, A., & Bispo, P. C. (2015). Variable assessment of wing colouration in aerial contests or the red-winged damselfly *Mnesarete pudica* (Zygoptera, Calopterygidae). *Science of Nature*, *102*, 13.

Hack, M. A. (1997a). Assessment strategies in the contests of male crickets, *Acheta domesticus* (L.). *Animal Behaviour*, *53*(4), 733–747. https://doi.org/10.1006/anbe.1996.0310

Hack, M. A. (1997b). The energetic costs of fighting in the house cricket, *Acheta domesticus* L. *Behavioral Ecology*, *8*(1), 28–36.

Hamer, R., Lemckert, F. L., & Banks, P. B. (2011). Adult frogs are sensitive to the predation risks of olfactory communication. *Biology Letters*, *7*(3), 361–363. https://doi.org/10.1098/rsbl.2010.1127

Höjesjö, J., Axelsson, M., Dahy, R., Gustavsson, L., & Johnsson, J. I. (2015). Sight or smell? Behavioural and heart rate responses in subordinate rainbow trout exposed to cues from dominant fish. *PeerJ*, *3*, e1169.

Hughes, N. K., Kelley, J. L., & Banks, P. B. (2012). Dangerous liaisons: The predation risks of receiving social signals. *Ecology Letters*, *15*(11), 1326–1339. https://doi.org/10.1111/j.1461-0248.2012.01856.x

Johnstone, R. A. (1998). Game theory and communication. In L. A. Dugatkin, & H. K. Reeve (Eds.), *Game theory and animal behavior* (pp. 94–117). Oxford, UK: Oxford University Press.

Knörnschild, M., Fernandez, A. A., & Nagy, M. (2020). Vocal information and the navigation of social decisions in bats: Is social complexity linked to vocal complexity? *Functional Ecology*, *34*(2), 322–331. https://doi.org/10.1111/1365-2435.13407

Knudsen, E. I. (2007). Fundamental components of attention. *Annual Review of Neuroscience*, *30*, 57–78. https://doi.org/10.1146/annurev.neuro.30.051606.094256

Knudsen, E. I. (2018). Neural circuits that mediate selective attention: A comparative perspective. *Trends in Neurosciences*, *41*(11), 789–805. https://doi.org/10.1016/j.tins.2018.06.006

Koops, M. A. (2004). Reliability and the value of information. *Animal Behaviour*, *67*, 103–111. https://doi.org/10.1016/j.anbehav.2003.02.008

Laidre, M. E., & Johnstone, R. A. (2013). Animal signals. *Current Biology*, *23*(18), R829–R833. https://doi.org/10.1016/j.cub.2013.07.070

Laughlin, K., & Mendl, M. (2004). Costs of acquiring and forgetting information affect spatial memory and its susceptibility to interference. *Animal Behaviour*, *68*(1), 97–103.

Leimgruber, K. L., Ward, A. F., Widness, J., Norton, M. I., Olson, K. R., Gray, K., & Santos, L. R. (2014). Give what you get: Capuchin monkeys (*Cebus apella*) and 4-year-old children pay forward positive and negative outcomes to conspecifics. *PLoS ONE*, *9*(1), e87035. https://doi.org/10.1371/journal.pone.0087035

Loher, W., & Dambach, M. (1989). Reproductive behavior. In F. Huber, T. E. Moore, & W. Loher (Eds.), *Cricket behavior and neurobiology* (pp. 83–113). Ithaca, NY: Cornell University Press.

Maille, A., & Schradin, C. (2017). Ecophysiology of cognition: How do environmentally induced changes in physiology affect cognitive performance? *Biological Reviews*, *92*(2), 1101–1112. https://doi.org/10.1111/brv.12270

Maynard Smith, J., & Harper, D. (2003). *Animal signals: Oxford series in ecology and evolution* (pp. 1–166). New York, NY: Oxford University Press.

Mesterton-Gibbons, M., & Heap, S. M. (2013). Variation between self- and mutual assessment in animal contests. *The American Naturalist*, *183*(2), 199–213. https://doi.org/10.1086/674443

Milinski, M., & Wedekind, C. (1998). Working memory constrains human cooperation in the Prisoner's Dilemma. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(23), 13755–13758. https://doi.org/10.1073/pnas.95.23.13755

Mokkonen, M., & Lindstedt, C. (2016). The evolutionary ecology of deception. *Biological Reviews*, *91*(4), 1020–1035. https://doi.org/10.1111/brv.12208

Moll, F. W., & Nieder, A. (2015). Cross-modal associative mnemonic signals in crow endbrain neurons. *Current Biology*, *25*(16), 2196–2201. https://doi.org/10.1016/j.cub.2015.07.013

Munoz, N. E., & Blumstein, D. T. (2012). Multisensory perception in uncertain environments. *Behavioral Ecology*, *23*(3), 457–462. https://doi.org/10.1093/beheco/arr220

Nityananda, V. (2016). Attention-like processes in insects. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1842), 20161986. https://doi.org/10.1098/rspb.2016.1986

Niven, J. E., & Laughlin, S. B. (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *Journal of Experimental Biology*, *211*(11), 1792–1804. https://doi.org/10.1242/jeb.017574

Page, R. A., & Bernal, X. E. (2020). The challenge of detecting prey: Private and social information use in predatory bats. *Functional Ecology*, *34*(2), 344–363. https://doi.org/10.1111/1365-2435.13439

Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, *47*(1), 223–243. https://doi.org/10.1016/0022-5193(74)90111-8

Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist*, *166*(2), 231–245. https://doi.org/10.1086/431246

Patricelli, G. L., & Hebets, E. A. (2016). New dimensions in animal communication: The case for complexity. *Current Opinion in Behavioral Sciences*, *12*, 80–89. https://doi.org/10.1016/j.cobeha.2016.09.011

Patricelli, G. L., Krakauer, A. H., & Taff, C. C. (2016). Variable signals in a complex world: Shifting views of within-individual variability in sexual display traits. *Advances in the Study of Behavior*, *48*, 319–386.

Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M., & Bonhoeffer, S. (2005). Evolution of cooperation by generalized reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1568), 1115–1120.

Polnaszek, T. J., & Stephens, D. W. (2014). Why not lie? Costs enforce honesty in an experimental signalling game. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1774), 20132457.

Ręk, P. (2014). Do aggressive signals evolve towards higher reliability or lower costs of assessment? *Journal of Evolutionary Biology*, *27*(12), 2605–2613. https://doi.org/10.1111/jeb.12512

Römer, H. (2020). Insect acoustic communication: The role of transmission channel and the sensory system and brain of receivers. *Functional Ecology*, *34*(2), 310–321. https://doi.org/10.1111/1365-2435.13321

Rutte, C., & Taborsky, M. (2007). Generalized reciprocity in rats. *PLoS Biology*, *5*(7), e196. https://doi.org/10.1371/journal.pbio.0050196

Sakaluk, S. K., & Belwood, J. J. (1984). Gecko phonotaxis to cricket calling song: A case of satellite predation. *Animal Behaviour*, *32*(3), 659–662. https://doi.org/10.1016/S0003-3472(84)80141-4

Sartori, P., Granger, L., Lee, C. F., & Horowitz, J. M. (2014). Thermodynamic costs of information processing in sensory adaptation. *PLoS Computational Biology*, *10*(12), e1003974. https://doi.org/10.1371/journal.pcbi.1003974

Searcy, W. A., & Nowicki, S. (2005). *The evolution of animal communication: Reliability and deception in signaling systems*. Princeton, NJ: Princeton University Press.

Smith, M. E., & Belk, M. C. (2001). Risk assessment in western mosquitofish (*Gambusia affinis*): Do multiple cues have additive effects? *Behavioral Ecology and Sociobiology*, *51*(1), 101–107. https://doi.org/10.1007/s002650100415

Stanca, L. (2009). Measuring indirect reciprocity: Whose back do we scratch? *Journal of Economic Psychology*, *30*(2), 190–202. https://doi.org/10.1016/j.joep.2008.07.010

Stephens, D. W. (1989). Variance and the value of information. *The American Naturalist*, *134*(1), 128–140. https://doi.org/10.1086/284969

Stevens, J. R., Volstorf, J., Schooler, L. J., & Rieskamp, J. (2011). Forgetting constrains the emergence of cooperative decision strategies. *Frontiers in Psychology*, *1*, 235. https://doi.org/10.3389/fpsyg.2010.00235

Sueur, C., & Mery, F. (2017). Social interaction in animals: Linking experimental approach and social network analysis. *Frontiers in Psychology*, *8*, 35.

Székely, T., Moore, A. J., & Komdeur, J. (Eds.) (2010). *Social behaviour: Genes, ecology and evolution*. Cambridge, UK: Cambridge University Press.

Tibbetts, E. A. (2008). Resource value and the context dependence of receiver behaviour. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1648), 2201–2206.

van Doorn, G. S., & Taborsky, M. (2012). The evolution of generalized reciprocity on social interaction networks. *Evolution: International Journal of Organic Evolution*, *66*(3), 651–664. https://doi.org/10.1111/j.1558-5646.2011.01479.x

Varela, S. A. M., Teles, M. C., & Oliveira, R. F. (2020). The correlated evolution of social competence and social cognition. *Functional Ecology*, *34*(2), 332–343. https://doi.org/10.1111/1365-2435.13416

Vehrencamp, S. L. (2000). Handicap, index, and conventional signal elements of bird song. In Y. Espmark, T. Amundsen, & G. Rosenqvist (Eds.), *Animal signals: Signalling and signal design in animal communication* (pp. 277–300). Trondheim: Tapir Academic Press.

Waite, T. A. (2002). Interruptions improve choice performance in gray jays: Prolonged information processing versus minimization of costly errors. *Animal Cognition*, *5*(4), 209–214. https://doi.org/10.1007/s10071-002-0146-7

Weitekamp, C. A., & Hofmann, H. A. (2014). Evolutionary themes in the neurobiology of social cognition. *Current Opinion in Neurobiology*, *28*, 22–27. https://doi.org/10.1016/j.conb.2014.06.005

Wilczynski, W., & Ryan, M. J. (2010). The behavioral neuroscience of anuran social signal processing. *Current Opinion in Neurobiology*, *20*(6), 754–763. https://doi.org/10.1016/j.conb.2010.08.021

Wiley, R. H. (1994). Errors, exaggeration and deception in animal communication. In L. A. Real (Ed.), *Behavioural mechanisms in evolutionary ecology* (pp. 157–189). Chicago, IL: University of Chicago Press.

Zahavi, A. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, *53*(1), 205–214. https://doi.org/10.1016/0022-5193(75)90111-3

Zahavi, A. (1977). The cost of honesty: Further remarks on the handicap principle. *Journal of Theoretical Biology*, *67*(3), 603–605. https://doi.org/10.1016/0022-5193(77)90061-3