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The Influence of Social Context on Animal Behavior:
Implications for Conservation

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy in
Biology

By

Megan Alexandra Owen

ABSTRACT OF THE DISSERTATION

The Influence of Social Context on Animal Behavior:
Implications for Conservation

By

Megan Alexandra Owen

Doctor of Philosophy in Biology

University of California, Los Angeles, 2014

Professor Daniel T. Blumstein, Chair

The pervasive perturbation of natural systems by human activities has rapidly changed the social context of many free-ranging animals, potentially reducing the efficiency of reproductive strategies, as well as the effective population size (N_e). Behavioral flexibility can be beneficial to species confronted with rapid contextual change, and the range of flexibility may ultimately influence whether a species can buy the time needed to respond adaptively to change. From the perspective of conservation management, an understanding of species' behavioral flexibility may improve predictions regarding the effects of rapid environmental change on populations, and facilitate the application of behavioral knowledge to conservation management. Fundamentally,

an animal's decision-making processes are responsible for generating flexible behavioral responses, thus the lability of mechanisms underpinning decision-making influences the flexibility of behavioral responses. Here I evaluate the study of animal decision-making across scientific disciplines. I critically assess the use of animal decision-making in conservation and suggest ways in which decision theory could enhance conservation strategies. My empirical research is focused on the influence of social context on behavioral flexibility in the endangered giant panda (*Ailuropoda melanoleuca*). The panda is a compelling species in which to study behavioral flexibility in the conservation context, because they are solitary, and females are seasonally-monoestrus and ovulate spontaneously. While energetic constraints play a prominent role in reproductive strategies, little is known regarding their mating system or the plasticity of reproductive behavior. Pandas are behaviorally expressive, using multiple modes of signaling during courtship, however, a holistic understanding of multimodal signaling in the species is lacking. Further, although populations are depleted throughout most of their range, the influence of social context on behavior and communication has not been described. Here we show that female signaling effort is generally lower in the exclusive presence of other females, suggesting that females can modify their behavioural efforts during the pre-ovulatory period according to the prevailing social context. We also found that multimodal signaling during social interactions did not consistently evoke an immediate, discrete response from receivers. Together these findings suggest that giant pandas demonstrate a limited degree of flexible behavioral responses dependent upon the prevailing social context.

The dissertation of Megan Alexandra Owen is approved.

Barnett A. Schlinger

Ronald R. Swaisgood

Daniel T. Blumstein, Committee Chair

University of California, Los Angeles

2014

DEDICATION

This work is dedicated to my parents, Diana and Mack Owen, in appreciation for their insistence that education is an unbounded, lifelong endeavor. This work is also dedicated to my children:

Dante, India and Stella. Everything I do is for them.

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Chapters 2 and 3 are in preparation for submission to *Biological Conservation* and *Animal Behaviour* respectively, and are formatted explicitly for these journals.

Chapter 4 is the final submitted form of the manuscript (Dynamics of Male–Female Multimodal Signaling Behavior across the Estrous Cycle in Giant Pandas (*Ailuropoda melanoleuca*), by MA Owen, RR Swaisgood, L McGeehan, X Zhou, and DG Lindburg) published in the journal *Ethology* 119(10): 869-880, (<http://onlinelibrary.wiley.com/doi/10.1111/eth.12128/full>).

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CHAPTER 1: INTRODUCTION

The pervasive perturbation of natural systems by human activities has rapidly changed the environmental and social contexts of many free-ranging animals (Vitousek et al. 1997). While some of Earth's ecosystems may still be classified as "intact" (Caro et al. 2011), the direct alteration of wildlife populations by human activities (e.g., large scale harvest and habitat conversion) and by the byproducts of human activities (including chemical, acoustic, light, and thermal pollution) have had a broad and pervasive reach (Crutzen & Stoermer 2006; Barnosky et al. 2012), ultimately driving the landscape level transformation of terrestrial (Ellis 2011) and marine habitats (Halpern et al. 2008), and the Earth's atmosphere (Zhang et al. 2007), presenting numerous pathways by which animal behaviour and communication may be altered or disrupted (Tuomainen & Candolin 2010). In contrast to environmental change on a geological timescale, these changes have been extremely rapid. And while contemporary evolution is possible (Stockwell et al. 2003; Smith & Bernatchez 2008; Caro et al. 2011), the speed of human driven environmental changes constrains the likelihood of adaptive responses (Sih et al. 2011), and has in fact resulted in large scale extinctions, and dramatic population depletions (Balmford et al. 2003; Barnosky et al. 2012).

Changes in social context are inherently associated with population declines and are commonly associated with range constrictions or habitat alterations such as fragmentation or degradation. Changes in the age structure, sex ratio or range of phenotypic variation within a population or group may reduce the efficiency of reproductive strategies and tactics (Molnár et al. 2014), and reduce the effective population size (" N_e ", Anthony & Blumstein 2000). Further, evolutionarily novel social context may reduce fitness if an organism's evolved behavioral or

decision making flexibility falls outside the range required for reproductive success or survival in the new environment. For example, Whitehead et al. (1997), suggested that the dramatic depletion of large male sperm whales (*Physeter macrocephalus*) in the southeastern Pacific has resulted in a persistent reduction in reproductive rates because females of the species pass up the relatively common smaller males in their search for the now-rare largest males. Thus, the species' evolved decision rule guiding mate choice is no longer adaptive in the aftermath of large-scale human harvest.

Behavioral flexibility and decision-making

In the face of these rapid and pervasive changes, behavioral plasticity (Gross et al. 2010) or flexibility (Kappeler et al. 2013) can be beneficial to species confronted with evolutionary novelty, and the range of plasticity may ultimately influence whether or not a species can “buy time” (Tuomainen et al. 2011) needed to respond adaptively to directional changes in the environment, or increases in environmental variability or uncertainty. Adaptive behavioral plasticity driven by ecological or social gradients has been documented in a range of taxa (Schradin & Lindholm 2011). However, while behavioral plasticity, like phenotypic plasticity, may enhance fitness (Ghalambor et al. 2007; Dingemanse et al. 2010; Tuomainen et al. 2011), plasticity is constrained by a number of factors (Auld et al. 2010; Kappeler et al. 2013), including genetics, development, physiology (Snell-Rood 2013) and generation time (van Schaik 2013). For long-lived, slow-reproducing species, the pace of human-induced environmental change may be too fast to allow for evolutionary adaptation (Chevin et al. 2010; Reed et al. 2010; Sih et al. 2011; Sih 2013).

Behavioral flexibility, in contrast to behavioral plasticity, reflects the capacity of an organism to reversibly fine-tune its behavior in accordance with prevailing environmental and social conditions (Gross et al. 2010; Kappeler et al. 2013). As such, it can be an adaptive response to environmental variability (Tuomainen & Candolin 2010; Milich et al. 2014). However, while ecological and demographic factors have been documented to drive temporal and spatial gradients in behavior (Amcoff et al. 2013), communication (Slabbekoorn & Boer-Visser 2006) and reproductive strategies, (Schradin et al. 2010; Schradin & Lindholm 2011; Botero & Rubenstein 2012), the influence of *transient* characteristics of the *immediate* social context on the flexibility of an individual's social behavior is less well understood (Taborsky & Oliveira 2012). However, there is growing evidence suggesting that behavioral flexibility can enhance fitness in the face of transient environmental variability (Vezina & Salvante 2010; Tinghitella et al. 2013; Mowles 2014). This is especially evident during courtship and breeding encounters (Mowles 2014).

From the perspective of conservation management, an understanding of species' behavioral flexibility may improve our ability to predict the effects of rapid environmental change on populations (Chevin et al. 2010; Sih 2013), and to apply knowledge of behavioral flexibility to animal-based (Whitham & Wielebnowski 2009) conservation triage strategies (Watters et al. 2003; Swaisgood 2007; Watters & Meehan 2007). While species that are less flexible in their behavior may be more susceptible to the impacts of environmental variability, behavioral flexibility may not always enhance fitness if adjustments are made that are energetically costly (e.g., Lombard effect, (Brumm & Zollinger 2011)), or if behavioral compensation compromises success in another dimension. For example, polar bears (*Urusus maritimus*), long adapted to life on the Arctic sea ice, are experiencing unprecedented habitat

transformations as a result of climate change driven reductions in the extent, area and volume of Arctic sea ice (Stroeve et al. 2007). Population projections for this species in the face of habitat losses are dire (Amstrup et al. 2008). While polar bears exhibit a range of opportunistic feeding behaviors (Lunn & Stirling 1985), meeting their evolved metabolic needs on a calorie-poor terrestrial diet is not possible. In some regions, the species' behavioral opportunism may result in a "energetic-trap", if by chasing small prey on land they expend more energy than the consumption of these prey provides (Iverson et al. 2014).

The above example well illustrates how decision-making in response to evolutionary novelty may, or may not, be adaptive and that the prevalence of ecological/evolutionary traps (Schlaepfer et al. 2002) result from the decoupling of animal decision making from the context in which it had evolved (Sih et al. 2011). However, because the sensory, cognitive and strategic stages of decision-making may be differentially impacted by changes in environmental context, identifying which stage or stages of the decision making process are primarily responsible may facilitate the targeted integration of animal decision making into conservation science and strategy. Because decision making is mechanistic, behavioral flexibility may result from flexible sensory integration, cognitive process and decision rules and the ability to integrate current stimuli and information according to evolved decision rules, which may generate behavior that is tuned to current context (Dingemans & Wolf 2013). Understanding the mechanisms that underlie adaptive and maladaptive behavior is especially important in a conservation context because mechanistic understanding allows those mechanisms to be mitigated or manipulated to offset anthropogenic reduction to fitness (Swaisgood 2007).

Social context: mechanisms of influence

Social context may affect an animal's environment or experience, influence decision-making, and shape behavior in a number of ways. Social context may add contextual complexity to courtship interactions, intraspecific competition or dominance relationships, and may result in conditional valuation of individuals or resources (reviewed in Galef & Giraldeau 2001). Public or social information derived from conspecifics may enhance information available for decision-making based on resource quality (Danchin 2004; Valone 2007; Bonnie & Earley 2007) or past performance of individuals. Social context may provide information to, or otherwise influence individuals engaged in social interactions (e.g., "audience effects"), or to those witnessing social interactions (e.g., "eavesdropping") or, more generally, observing the performance of conspecifics or heterospecifics (Goodale et al. 2010).

In fact, the literature reports a wide array of mechanisms demonstrating the pervasive influence of social context on mate or competitor evaluation (Anthony & Blumstein 2000; Xu et al. 2012), the perceived cost associated with specific choices (Galef & Giraldeau 2001; McNamara et al. 2006), reproductive effort (Luttbeg 1996; Johnstone 2001; Ridley et al. 2007), and ultimately how it may influence fitness (Bretman et al. 2011). However, the influence of social context on behavior is dependent upon the permeability of cognitive mechanisms and decision rules to contextual variation (Janetos 1980; Luttbeg 1996; Conradt & Roper 2005; Jennions & Petrie 2007; Fisher & Rosenthal 2007; Reaney 2009; Sumpter & Pratt 2009; Dzieweczynski & Walsh 2010). In the context of reproductive behavior, this permeability must be evaluated from the perspectives of both signalers and receivers.

Reproductive behavior & multimodal signaling

Generally speaking, reproductive behavior can be complex, variable and difficult to characterize (Rundus et al. 2010; Wilgers & Hebets 2011) especially if it is dynamically influenced by extrinsic factors, such as social context (Bretman et al. 2011), or intrinsic factors such as physiology (Hausman & Barb 2010; Ruiz et al. 2010), body condition (Fawcett et al. 2012; Klemme et al. 2012), age or experience (Lunn et al. 1994). Multimodal communication during courtship or intrasexual competition may further challenge our understanding of how the transmission of information between conspecifics is accomplished (Bro-Jørgensen 2010). However, a growing body of research has clarified the range of potential functions it may have in animal communication systems (Candolin 2003; Partan & Marler 2005; Munoz & Blumstein 2012), including the enhancement of information transfer in variable or otherwise “noisy” environments (Parks et al. 2010). In this way, multimodal signaling may be considered a “generalist” strategy that can confer resilience in the face of contextual change.

Multimodal signaling may function in a variety of ways. Multimodal cues may enhance the likelihood of signal reception (Johnstone 1996; Candolin 2003; Parks et al. 2011) and increase responsiveness (Uetz et al. 2009; Bretman et al. 2011), create a signaling threshold needed to elicit a receiver response (Hebets & Uetz 2000), or facilitate the transfer of multiple streams of information (Partan & Marler 1999; 2005; Munoz & Blumstein 2012). Multimodal cues that enhance information transmission would be adaptively advantageous under the temporal and energetic constraints of solitary mating systems (Tengö et al. 1988; Buesching et al. 1998) if they reduce the uncertainty associated with mate search, mate choice, or competing with unfamiliar conspecifics (Schradin & Lindholm 2011). Behavioral systems that have been adaptively shaped by the constraints of environmental variability or uncertainty, provide an

informative context within which to evaluate the sensitivity or resilience of behavior to rapid, human-driven environmental change (Parks et al. 2011).

Interest in the application of animal behavior to conservation has been steadily rising in the last two decades (Blumstein & Fernández-Juricic 2004), and efforts to increase the effectiveness of behavioral approaches to conservation are yet a priority (Caro et al. 2011; Berger-Tal et al. 2011). While it has been noted that application of behavioral knowledge to conservation strategies has been most robustly applied to conservation breeding, translocation and reintroduction (Caro 2007), there is increasing interest in applying behavioral knowledge to both habitat conservation strategies and into individual based (West et al. 2002) and mechanistic predictive models (Molnar et al. 2008). Further, because initial responses to external stimuli are often behavioral (Tuomainen & Candolin 2010; Kappeler et al. 2013), the best means to rapidly assay the impacts of environmental change may be through the study of animal behavior and the underlying mechanisms that generate behavior (Blumstein & Fernández-Juricic 2010).

The dissertation that follows explores the influence of social context on behavioral flexibility, multimodal signaling and animal decision-making in the context of conservation. I begin (Chapter 2) by presenting a synthesis of the literature on animal decision-making, suggesting that by compiling and synthesizing the findings and theory from the varied, and un-integrated, disciplines that have focused on decision making (e.g., behavioral economics, sensory ecology, cognitive psychology, evolutionary biology and behavioral ecology) will enhance our ability to identify the stages in the decision making process that are disproportionately responsible for generating behavior. From each discipline I extract concepts that could be applied to conservation and highlight aspects that have been used to decipher the conservation implications of animal behavior. I follow in Chapter 3 by exploring the influence of social

context on courtship behavior in the solitary, polygynous, spontaneously ovulating, giant panda (*Ailuropoda melanoleuca*) (Schaller et al. 1985). Specifically, I look at the influence of social context on the flexible expression of signaling behaviors during the breeding season. Chapter 4 is focused on the influence of social interaction on social behavior in giant pandas, examining whether the signaling behavior of conspecifics has any influence (inhibitory or enhancement) on social behavior.

Study species

My empirical work is focused on a captive population of giant pandas (*Ailuropoda melanoleuca*) housed at the China Research and Conservation Centre for the Giant Panda (CRCCGP) located in Wolong Nature Reserve, Sichuan China (112.53E, 32.99N). The CRCCGP was founded in 1981 and has been one of the primary captive breeding centers in China with research ongoing since its inception. The population at CRCCGP consists of males, females, sub-adults and cubs, and the size of this population has ranged between 40 and 75 animals in the past decade. The provenance of animals housed at the facility includes both captive and wild born (brought to the facility as ‘rescues’) individuals.

Giant pandas are a compelling species for study of behavioral flexibility. Giant pandas are carnivores that have evolved to exclusively consume a diet of bamboo, resulting in energetic constraints that influence life history (Schaller et al. 1989; Nie et al. 2012) and reproduction (Oftedal & Gittleman 1989). Solitary, seasonally monoestrus and spontaneously ovulating (Monfort et al. 1989; Kersey et al. 2010b), giant pandas have pronounced temporal constraints on locating and choosing an appropriate mate. During the period of follicular development, estrogen levels begin to climb, undergo a rapid elevation and subsequent precipitous drop during

the 2-3 day peri-ovulatory period that coincides with peak female receptivity (Kersey et al. 2010c; Huang et al. 2012). Female signaling behavior during this period is conspicuous, and the onset and maintenance of behavioral estrus is influenced by circulating estrogen levels (Lindburg et al. 2002; McGeehan et al. 2002; Bonney et al. 2008).

Males are seasonally primed for breeding as evinced by seasonally elevated testosterone (Kersey et al. 2010a). However limited data from free ranging giant pandas (Nie et al. 2012) document a different pattern of testosterone elevation than that of captives (Macdonald et al. 2005; Kersey et al. 2010a). In wild pandas, males display steep peak testosterone levels associated with the courtship and mating, falling to non-breeding season baseline during inter-mating intervals (Nie et al. 2012), suggesting that energetic constraints influence the physiology of male reproductive readiness. In captivity, males are capable of breeding with multiple females in relatively quick succession, and over the course of the entire breeding season. In the wild, however energetic constraints (Nie et al. 2012) may limit the number of matings a male may engage in.

Giant pandas are solitary, however a recent study of wild giant pandas (Nie et al. 2011) documented breeding aggregations that included a single estrous female, and 4-6 adult males. Nie et al. (2012) reported that competition between males for access to the estrus females is intense, and dominance appears to be correlated with relative body size and determined via intrasexual competitive interactions. Once established, the dominant male has sole access to the estrus female, but the other males do not disperse until the mating cycle is completed. The population of giant pandas in Foping Nature Reserve, Shaanxi Province, China, is thought to be the densest of any remaining in the wild, and it has been suggested that it reflects historical density (Nie et al. 2012) and so may present a rare snapshot of un-depleted population density

(Wei et al. 2012). These observations shed light on the dynamics of male-male competition, but suggest that further research is warranted especially on the potential role of social information operating in this system. Social information use in this context could plausibly be public information (sensu Nordell & Valone 1998; Oliveira et al. 1998; Danchin 2004), social eavesdropping (Earley 2010) or audience effects (Dzieweczynsk & Walsh 2011).

Giant panda courtship behavior and signaling

Giant panda courtship includes the expression of multimodal signals that include olfactory, vocal and postural elements (Kleinman et al. 1990). Through a series of elegant experiments, the discrete functionality of olfactory (Swaigood et al. 1999; 2000; White et al. 2002; Swaigood et al. 2002; White et al. 2003; 2004; Swaigood et al. 2004) and acoustic (Charlton et al. 2009b; 2009a; 2009c; 2010a; 2010b; 2011; 2012) signals has been described. However, these studies have focused on communicative function of olfactory or acoustic modes in the absence of other modalities, and therefore a holistic understanding of the signaling in the species is lacking (Candolin 2003; Partan & Marler 2005; Bro-Jørgensen 2010; Kasurak et al. 2012). While the results from these studies have informed conservation-breeding efforts and have been incorporated into captive management strategies (Swaigood et al. 2010), copulation is still inconsistently achieved in captivity. The relative over representation of certain founder lineages in the captive population reflects this fact (Zhang 2011), and suggests that further refinement of our understanding of behavioral flexibility, social information use, multimodal communication and social dynamics, will enhance our ability to integrate under-represented pandas into the breeding population (Swaigood et al. 2003; Swaigood & Schulte 2010) as well as to develop predictive mechanistic models of panda mate-search behavior in the wild.

Giant panda conservation status

Human driven changes in giant panda habitat have a long history (Zhu et al. 2010). While the prehistoric range of the giant panda stretched as far south as Myanmar, and included lowland areas (Schaller et al. 1985), during the 18 and 19th centuries, giant panda range was profoundly reduced (Zhu et al. 2010). In the past 100 years, the panda's range has been further reduced, and currently is restricted to six mountain ranges (Qinling, Minshan, Qionglai, Liangshan, Daxiangling, and Xiaoxiangling) in south central China. Remnant populations are highly-fragmented, and while reserve establishment and protections in place since the 1960's may have resulted in a modest increase in the number of wild pandas, population numbers are below carrying capacity, and the long term impacts of selective logging (Zhang et al. 2011), and the intensifying impacts of climate change will continue to threaten the stability of giant panda populations (Songer et al. 2012; Tuanmu et al. 2012). Climate change is expected to have dramatic, and rapid impact on giant panda habitat, exposing them, like many other organisms to evolutionarily novel, and likely unpredictable, conditions. Recent range wide studies have demonstrated that upwards of 60% of giant panda habitat will no longer be climatically suitable within 70 years (Viña et al. 2007; Songer et al. 2012; Tuanmu et al. 2012). Panda range will shift upwards in elevation, further reducing the connectivity of remnant populations, and species of bamboo that populations depend upon will be impacted as well (Tuanmu et al. 2012).

These factors, coupled with the always-present threat of human encroachment into reserves for resource extraction, the spread of disease through contact with invasive species and livestock, remind us that although the trajectory for giant panda populations in the wild and in captivity over the past 20 years has been positive, and that these rebounds are likely the result of

in situ and *ex situ* conservation management, the giant panda is by no means out of the woods (Swaigood et al. 2010). Reintroduction, translocation (Zhu et al. 2010), captive breeding (Zhang & Wei 2006) and projection modeling (Swaigood et al. 2011) will all be important conservation tools applied to giant panda conservation in coming decades.

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**CHAPTER 2: CONTEXTUAL INFLUENCES ON ANIMAL DECISION-
MAKING: SIGNIFICANCE FOR BEHAVIOR-BASED WILDLIFE
CONSERVATION AND MANAGEMENT. *In preparation for submission:*
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ABSTRACT

Survival and successful reproduction require animals to make a broad range of critical decisions amidst a naturally dynamic contextual background. However, human activities have pervasively, and rapidly, extended contextual variation into evolutionarily novel territory, potentially rendering evolved animal decision making mechanisms and strategies maladaptive. We suggest that explicitly focusing on animal decision making (ADM), by compiling and synthesizing findings from studies of sensory ecology, cognitive psychology, behavioral economics and ecological and evolutionary strategies, may enhance our understanding of, and our ability to predict how, human driven changes in the environment (i.e., context) will influence animal populations. Fundamentally, the decisions animals make are mechanistic, and the behaviors that are generated as a result emerge from the combined action of sensory integration, cognitive mechanisms, and strategic rules of thumb, and any of these processes may have a

disproportionate influence on behavior. Although there is an extensive literature exploring ADM, it generally reflects a canalized, discipline-specific approach that is lacking a unified conceptual framework. As a result, there has been limited application of ADM theory and research findings into animal management strategies or predictive models. Here, we review the literature on ADM, with an emphasis on the treatment of context, and discuss the concepts and findings from varied disciplines that may be most applicable to conservation biology. Because changes in population density and age/sex structure are prevalent features of human disturbance, we specifically discuss the influence of social context on decision-making across choice domains. Finally, we discuss, and provide examples that demonstrate, the potential applications of ADM theory to various aspects of applied conservation biology.

Keywords: decision-making, environmental variation, context

1. Introduction

Animals make many decisions each day. They may decide whether or not to forage in a certain area based on the expected rewards of doing so traded off against any risks of doing so. They decide when to look around for predators, when to run, when to hide, and when to sleep. On a good day, they may make decisions about whom to mate with and how much to energy to allocate to a given reproductive event. But these decisions are not made in a vacuum.

Environmental context is an integral part of animal decision making (hereafter “ADM”) because the adaptive value of decisions varies based on context. And, as humans change the environment, and change the demographic structure of animal populations, humans change the context under which decisions are made.

While correlations between anthropogenic change and changes in behavior, population

parameters and environmental characteristics have been broadly documented (Crutzen and Stoermer, 2006; IPCC, 2007; Parmesan and Yohe, 2003; Parmesan, 2006), an understanding of how key properties of the ADM process influence resultant changes has been lacking, however interest is rising (Robertson et al., 2013; Sih et al., 2010, 2011, 2013). Countless examples of clearly maladaptive behavioral responses to a human-modified environment have been documented. From sea turtles (*Caretta caretta*; *Chelonia mydas*) being misdirected by city lights (Tuxbury and Salmon 2005), seabirds and condors (*Gymnogyps californianus*) eating plastic trash (Houston et al. 2007), kangaroo rats (*Dipodomys stephensi*) digging burrows along roadside berms (Shier et al. 2012), the literature is replete with examples of behaviors generated by evolved ADM that no longer work. But what mechanisms are responsible for these bad decisions? Is it that in the current environment, a cue no longer consistently represents the resource it once had? Is information integration more challenging amidst a more cluttered background? Do the decision-rules long used to guide mate search strategies and mate choice set them up for “failure” in a modified social landscape? Is it a combination of sensory mis-match, cognitive overload and a now-ill-fitting decision rule? Because ADM is inherently mechanistic (Blumstein and Bouskila, 1996), explicit study of decision-making can provide a ready framework from within which to identify critical sensory, cognitive or strategic processes that are potentially disproportionately responsible for generating behavior, and ultimately influencing demographic parameters.

Sih (2010) provided a mechanistic framework, founded in signal detection theory (Tanner and Swets, 1954; Wiley, 2006), to examine how mismatches between evolved cue-response systems may influence ADM and thus determine the susceptibility of some species to the negative effects of rapid environmental change (as exemplified by the jewel beetle

(*Julodimorpha bakewelli*) erroneously mating with brown glass bottles (Robertson et al. 2013)). This cue-response framework can facilitate the development of explicit, quantitative predictions regarding both short and long-term impacts on animals inhabiting degraded or disturbed habitats when behavior is predominantly generated by a species stereotypic response to external stimuli. This framework also provides a model from which to approach the extraction of findings from other disciplines focused on ADM to conservation research and management.

Beyond the mechanisms of sensory inputs and cognitive processing, decision rules that link assessment to the ultimate fitness payoff shape the role of information gathering and the guidelines an animal uses for option sampling (Luttbeg, 1996). Thus decision rules may also have a fundamental influence on how contextual variation influences ADM and may have a disproportionate influence on behavioral responses to environmental change. For example, species that utilize decision rules based on character-trait threshold or absolute valuation (Jennions and Petrie, 1997) to evaluate options may be influenced by changes in context in a different way than those that utilize comparative evaluation (Reaney, 2009), consensus (Conradt and Roper, 2008; Sumpter and Pratt, 2009), sequential sampling (i.e., comparative Bayes tactic, (Luttbeg, 1996)), or a “best-of-n” strategy (Janetos, 1980) (Table 1). Species using absolute or threshold valuation may pay increased search costs when confronted with changes in resource availability. If the trait-value criteria are rendered rare by human-induced change, these costs could have profound effects on fitness; in theory animals could keep searching forever if the (optimal) criteria no longer exists in the current environment. For example, Whitehead et al. (1997) suggested that the dramatic depletion of large male sperm whales (*Physeter macrocephalus*) in the southeastern Pacific has resulted in a persistent reduction in pregnancy rates because females of the species pass up the relatively common smaller males in their search

for the now-rare largest males. Thus, a threshold-based decision rule has intensified the population losses initiated by the rapid and large-scale human harvest of the species.

By contrast, the decisions made by species using comparative or sequential strategies may make “the best of a bad situation,” settling for the best of the available options. This may have relatively positive effects on fitness if it saves significant search costs, but also could result in potentially maladaptive or fitness compromising decisions. For example, if, during dispersal and habitat selection an animal settles for the best available habitat of the N habitats sampled, they could end up settling in (or *settling for* perhaps) habitat associated with extremely low fitness (sensu “evolutionary and ecological traps”, Battin 2004; Robertson et al. 2013). These examples illustrate how changing environmental context can alter the fitness associated with different ADM mechanisms, with implications for population-level performance and, hence, of conservation concern.

The relative importance of animal behavior to conservation biology is still, and somewhat surprisingly, debated (Berger-Tal et al., 2011; Blumstein and Fernandez-Juracic 2010; Caro and Sherman, 2011); however, the potential for behavior-based studies to both reveal and address anthropogenic impacts has been broadly demonstrated (Blumstein et al. 2002; Blumstein 2006; Fernandez-Juracic et al. 2005; Shier and Swaisgood 2006; Swaisgood & Schulte 2010), if not fully realized (Berger-Tal et al. 2011, Caro 2007). We contend, however, that the relatively unexplored (from a conservation perspective) and mechanistic approach to the study of ADM will enhance our ability to predict how both behavior and population demography will change in the face of rapid anthropogenic environmental change.

1.1 The ADM Process

Blumstein and Bouskila, (1996) outlined a generalizable mechanistic framework and standardized terminology for the ADM process. Taken together, the ADM process includes sensory, cognitive and behavioral processes. ADM begins with the acquisition of information via sensory inputs (i.e., stimulus filtering and perception). Evaluation of information gained through perception occurs via higher-level cognitive processes that result in an “informational state” (i.e., “representation”, Real, 1991; Shettleworth, 2010). Decisions are made based on the informational state, and result in behavioral actions that change (or maintain) the state of the organism. Ultimately, the outcomes of actions taken are re-evaluated, thereby consolidating experience into information that can influence future decisions (i.e., learning, Fawcett et al., 2012; Lebiere and Anderson, 2011; or Bayesian updating—revising probabilities based on prior knowledge or experience--, Biernaskie et al., 2009; Luttbeg and Langen, 2005; Trimmer et al., 2011; Valone, 2006) (Figure 1). Each step of the process may also be influenced by both the intrinsic state of the receiver (e.g., body condition, reproductive condition, past experience; here referred to as “personal information”) (Blumstein and Bouskila, 1996; Pompilio et al., 2006; Pompilio and Kacelnik, 2010), and the environment or context (e.g., habitat, social grouping, spatial or temporal arrangement of the choice set or public information) (Bateson, 2002; Danchin et al., 2004; Freiden and Kacelnik, 2011).

Disparate scientific disciplines have approached the study of ADM in very different ways, and the resulting discipline-specific technical lexicon reflects the lack of a common theoretical framework or empirical synthesis (Sanfey, 2007). Psychological studies of ADM have used both cognitive approaches (Lebiere and Anderson, 2011) and behavioral economic theory (Bateson, 2002; Bateson and Healy, 2005) to construct paradigms that guide both experimental design and the interpretation of results. Cognitive approaches investigate the

higher-level mental processes that underlie information acquisition and the role cognitive traits play in generating behavior (Dukas, 2004). The behavioral economic approach to the study of ADM is founded in stripping away context to expose underlying optimization processes (or the “utility function”) (Real, 1991). However, in nature, decisions are not made in a vacuum (Rosati and Stevens, 2009), so it is easy to appreciate that contextual variation is a constant and pervasive feature of ADM, and is in fact an important source of valuable information (Danchin et al., 2004; Franks et al., 2003; Janetos, 1980; Lebiere and Anderson, 2011).

Behavioral ecological approaches typically frame ADM in optimization strategies that reflect adaptive decision-making (McNamara and Houston, 2009). In contrast to the behavioral economic approach, behavioral ecologists have incorporated a functional perspective, integrating contextual complexity and interpreting results in the context of adaptive trade-offs (Dill 1987; Waksberg et al., 2009). Behavioral ecological studies focusing on decision-making rules (hereafter “decision rules”) examine the framework that governs information acquisition and option evaluation. For example, Janetos (1980) and Janetos and Cole (1981) tested models of decision rules animals may use when searching for mates or food and noted that animals either search for and evaluate all possible options, or that they may sample a subset of options and choose the best among them (e.g., “best-of-n” strategy). Heuristic models of ADM (Hutchinson and Gigerenzer, 2005) are based on the idea that there are costs and time constraints on decision-making in nature. Thus, whether decision rules are fundamentally economic or ecologically optimized, information-gathering shortcuts (or “rules of thumb”) are the rule, rather than the exception.

There is an extensive literature of empirical and theoretical research explicitly focused on ADM in the disciplines of sensory ecology, cognitive psychology, behavioral economics,

behavioral ecology and evolutionary biology. However, there has been little intellectual exchange between these disciplines, and, as a result, a unified conceptual framework is lacking, which has limited the application of research findings to conservation and wildlife management. In this review, we provide an overview of ADM theory, and describe some of the fundamental concepts guiding the study of ADM in sensory ecology, experimental psychology, behavioral economics, evolutionary biology and behavioral ecology. We provide definitions for terms commonly used among disciplines, and we explore the influence of context on the ADM process across choice domains and discuss the potential implications and applications of contextually modulated ADM on conservation management.

2. A brief survey of ADM theory: From signal detection theory to heuristics

2.1 Signal detection theory and sensory ecology

Signal detection theory (SDT) provides a quantitative framework for assessing cue-response systems, by measuring the information-bearing content of a cue or signal against any aspect of the background that may obscure signal reception (often referred to as “noise”). Adapted from statistical decision theory (see section 2.4), SDT can be explicitly used to predict how an organism’s response will change in association with cue (signal) strength or other measurable characteristics. For example, Ord and Stamps (2008) used this framework to demonstrate how the use of an alert display by *Anolis* lizards enhanced the efficacy of information carrying visual displays, increasing the chances of successful signal reception at greater distances. As a result, explicit predictions could be made regarding the signal strength required to successfully communicate with conspecifics under varying environmental conditions.

Within the SDT framework, context is included as a fundamental driver of cue-response relationships, and thus it can be readily utilized to examine the influence of human driven environmental changes on ADM. In the context of animal conservation, SDT has been increasingly used empirically (Erbe and Farmer, 1998), or invoked in theoretical discussions (Sih et al., 2010) and in the interpretation of otherwise descriptive findings (Nie et al., 2012). For example, Sih et al. (2010) provided numerous examples of cue-response mismatches resulting from anthropogenic changes to the environment (e.g., sea turtles hatchlings mis-directed by light pollution), and theoretically demonstrated how SDT could be used to explicitly predict the strength and direction of these changes.

Signaling in communication systems is an important arena in which anthropogenic alteration in context may disrupt signal transmission, with important consequences for mating, competition, and social integration and stability. Wollerman and Wiley (2002) tested the influence of background noise on signal reception in tree frogs (*Hyla ebraccata*), demonstrating that female responses to calls from males were prone to error in the face of even moderate background noise. Erbe and Farmer (1998) took an applied approach, using this framework to examine how masking noise from different types of ocean vessels influenced conspecific signal detection in beluga whales (*Delphinapterus leucus*). The authors were then able to apply their results directly to shipping management and make explicit policy recommendations based on the predictable impact of different classes of ocean vessels on beluga communication. In chemical communication, airborne or waterborne pollutants may disrupt signaling. For example, female swordtail fish (*Xiphophorus birchmanni*) show diminished preference for conspecific males and are more likely to hybridize in the presence of pollutants associated with agricultural runoff and sewage (Fisher et al., 2006). Similarly, anthropogenic alteration of substrates important for

chemical signaling may impede efficient communication to the detriment of mating or other important social functions. Owen et al. (In review) suggest that reductions in the extent and volume of arctic sea ice not only reduces access to prey for threatened polar bears, but may also fragment the signaling substrate that allows this widely dispersed and solitary species to locate one another for mating. Nie et al. (2012), after finding that giant pandas (*Ailuropoda melanoleuca*) select scent mark sites based on optimal topographic, microhabitat and substrate surface characteristics, suggested that “signaling habitat” should also be preserved alongside foraging and other resource habitat, reasoning that anthropogenic alteration of panda habitat may reduce signal transmission detection probability, increase energetic output, and impede mating. These predictions could be explicitly tested empirically using SDT.

From these examples it is clear that for threatened and endangered species, or species facing rapid habitat degradation or losses, disruption of cue response systems may have dire implications for species persistence. SDT can be readily applied to conservation or management problems, generating predictions that can be tested empirically (Rabin et al., 2003; Sih et al., 2010; Sih, 2013) as well as providing a framework that can promote the use of SDT in future research.

2.2 Cognitive constraints and experimental psychology

Optimality models aside, animals do not possess perfect information about their world and many approaches have sought to understand the constraints limiting information acquisition and ADM. Cognitive constraints, the frequent subject of study among experimental psychologists, can be defined as “limits on memory and neuronal processing of information” (Real, 1991) and, from the ADM perspective, result in imperfect integration of all possible information-bearing stimuli

(Lebiere and Anderson, 2011). These limits may be determined by physical properties that limit perception (e.g., acoustic frequency or light wavelengths) or by processing limitations that constrain the quantity of information that can be handled (e.g., Weber's law).

Psychophysical and behavioral studies have demonstrated that cognitive constraints are an essential factor in the adaptive evolution of ADM and thus profoundly influence the information utilized for decision-making (Dukas, 2004). For example, female mate choice in Tungara frogs (*Engystomops pustulosus*) is dominated by a preference for males with more complex calls (Bernal et al., 2009). However, Akre et al. (2011) demonstrated that the perception of calling complexity is constrained by Weber's Law, and accordingly found that it is the ratio of male calling complexity between competing males, and not complexity *per se*, that defines attractiveness. Thus, if the number or quality of males is reduced due to human activities females may choose males subjected to less rigorous competition. Chan et al. (2011) found that Caribbean hermit crabs (*Coenobita clypeatus*) exposed to an aerial predator were distracted by boat noise, as measured by a delay in their behavioral response to the predator stimulus. When the crabs were exposed to an additional stimulus (flashing lights), the predator avoidance behavior was further delayed. These results demonstrate potential cognitive constraints on information processing, and demonstrate how anthropogenic stimuli may influence ADM by reducing cognitive efficiency. Similarly, Teixeira et al. (2007) reviewed the many ways that biological stress may impede conservation translocations, emphasizing how stress impairs cognitive processes and decision-making. Other anthropogenic stressors may also alter contextual influences on cognitive constraints with detrimental effects on ADM.

Cognitive processes may be adaptively specialized (Cosmides et al., 2010; MacPhail and Bolhuis, 2001; Perdue et al., 2011) or may function as general processes that carry-over into

different choice domains, across taxa or sexes (Lebiere and Anderson, 2011). Numerous studies have demonstrated that ADM specialization in caching behavior is correlated with differing environmental and social conditions (Pravosudov and Clayton, 2002; Van der Wall, 2000). Specifically, animals that live in highly seasonal environments where caching is prevalent exhibit both a greater degree of problem solving ability, and concomitantly larger hippocampus volume (Shettleworth, 2001). General-purpose rules, as their name implies, provide a broad-spectrum cognitive framework for ADM that is applicable across choice domains and operates across taxa and sex classes. While general-purpose rules are often characterized as “powerful and flexible”, adaptive specialization may equally be characterized as powerful in that it provides “custom” problem solving tools to cope with particular challenges. Such specialization, however, is only beneficial in the context of the environmental challenges to which the cognitive process is adapted. As in other forms of adaptive specialization, species with specialized cognitive abilities may be disproportionately affected by anthropogenic change, and more susceptible to ecological or perceptual traps (Patten and Kelly, 2010) because cognitive specialization is no longer adaptive.

2.3 Rational decision making and behavioral economics

Economic theory has had a profound influence on the study of ADM (Bateson, 2002; Bateson et al., 2002; McNamara and Houston, 1996; Monteiro et al., 2013; Simon, 1959) and was developed out of expected utility theory in the mid-20th century (i.e., the von Neumann-Morgenstern utility theorem). Expected utility theory, as applied to ADM, simply states that a decision maker will choose an option based on the product of an option’s usefulness (i.e., “utility-value”) and its associated risk. A central prediction emerging from behavioral economic

theory is that ADM will be “rational”; in other words, the choices that animals make will be “consistent across contexts” (Schuck-Paim et al., 2004, p. 2305) (Table 2). Conversely, decisions that are intransitive or inconsistent across contexts are termed “irrational”.

Notably, however, irrational ADM has been widely documented in diverse taxa (Bateson, 2002; Bateson et al., 2002; Edwards and Pratt, 2009; Freiden and Kacelnik, 2011; Hurly and Oseen, 1999; Latty and Beekman, 2011; Schuck-Paim and Kacelnik, 2002; Shafir, 1994). Within the behavioral economics literature, irrational ADM is often described as “anomalous” (Waite and Fields, 2000), expressed only under specific circumstances (Houston, 1997; Schuck-Paim and Kacelnik, 2002), or interpreted as reflecting cognitive biases (e.g., Weber’s law, Waite and Fields, 2000). However, a growing body of literature suggests an adaptive or ecological perspective lies at the heart of this seeming irrationality (Haselton and Buss, 2000; Haselton and Buss, 2009; Houston et al., 2007a; Houston et al., 2007b; Johnson et al., 2013) and that cognitive or ecological constraints on ADM are the rule rather than the exception in nature (Janetos, 1980), and greatly influence how information is gathered and used. Further, we suggest that information regarding the resilience of ADM in a rapidly changing environment may be reflected in contextual influences on otherwise rational decisions.

We found no examples in the literature where behavioral economic studies of ADM were directly applied to animal conservation or management. However, results may be broadly applicable if the interpretation of results is reframed within the milieu of rapid environmental change. For example, Schuk-Paim et al. (2004) found that adding an irrelevant decoy to a set of food options influenced foraging choices in starlings (*Sturnus vulgaris*). However, this influence was dependent upon the state of the chooser. Thus irrational decision-making in this context reflected the contextual influences on decision-making in the real world that may be driven by

changes in body condition, degraded public information or socially acquired information. Thus while the stripped down laboratory setting of most behavioral economic studies of ADM, coupled with the exclusion of context, has left behavioral economics ill-adapted to conservation, findings such as these may provide valuable concepts for conservation behavior and reflect the inherent sensitivity or resilience of some species to the negative effects of rapid changes to the environment.

2.4 Information theory and evolutionary biology

Information is a principal theme in biology (Maynard-Smith, 2000) and can be broadly characterized as facilitating a reduction in uncertainty (Dall et al., 2005; Danchin et al., 2004; McNamara and Dall, 2010; Schmidt et al., 2009). As Maynard-Smith (2000) suggested, the information value of genes, compounds, and signals spans disciplines and processes. McNamara and Dall (2010) take Maynard-Smith's concept further and suggest that: "information *processing*" is central to biology and to biological phenomena (p. 231), and provide a mathematical proof demonstrating how more information never reduces an organism's fitness. However some studies show that there is not a linear relationship between information quantity and optimal behavior, suggesting a leveling off of payoffs as information quantity increases (Hutchinson and Gigerenzer, 2005; Scheibehenne et al., 2010; Ward et al., 2008), which may reflect the added costs of the time it takes to process more information. Information saturation may be a fundamental property of natural systems, and may be founded in fundamental psychophysical properties (e.g., Weber's law, Stamps et al., 2005) or cognitive constraints that may result in compromised behavioral performance.

As with signal detection theory (section 2.1), statistical decision theory provides a framework from which to analyze the way animals use information (Dall et al., 2005; McNamara and Houston, 1980; Schmidt et al., 2009), including personal information (i.e., information obtained directly through interaction with the environment) and public information (information obtained through observation of the performance of others; Danchin et al., 2004; Fletcher, Jr. and Miller, 2008). SDT capitalizes on information to create decision rules that model the steps of ADM processes and assign probabilities to behavioral actions or outcomes. Empirical studies can be utilized to test the fit of various decision rules (Mabry and Stamps, 2008), and assess their outcomes across contextual, information carrying, gradients. For conservation biologists, incorporating contextual gradients that vary in terms of characteristics that have been altered by human activities, can be assessed for their differential influence on survival or reproductive success.

2.5 Heuristics, strategy and behavioral ecology

Unlike behavioral economists, behavioral ecologists have historically been interested in the evolution of adaptive ADM (Dill, 1987). Rosati and Stevens (2009) argue that natural selection does not result in animals that “adhere to economic theory” and acknowledge that the growing body of evidence suggests an adaptive role for contextual variation, and not an error producing one. Another perspective on adaptive ADM suggests that while strategic ADM may result in erroneous choices, the costs of bad decisions are often negligible (Waite and Field, 2000). In situations where the fitness pay off is higher, animals should be more inclined to take risks in ADM, thus producing more “errors” (McNamara and Houston, 1986; Houston, 1997; Johnson et al., 2013) and so, on average, there is a net gain. Further the pervasive asymmetry between the

costs associated with false positive and false negative errors may drive the adaptive value of ADM errors (Johnson et al., 2013) and, particularly germane this asymmetry is predominantly driven by contextual variation. Adaptive ADM incorporates the dynamic nature of the environment including the variability of context, personal information, individuality and time, presuming that the trade-offs between costs and benefits inherent to optimal ADM are expressed *in context* (Lima, 1989).

McNamara et al. (2012) have suggested that irrational ADM is more appropriately interpreted as “strategic”, reflecting the imperfect nature of information gathering in natural settings. These ideas are consistent with the constraints on ADM outlined by Janetos (1980) and Janetos and Cole (1981) (e.g., time, memory, mobility) and recast the information “skimming” associated with heuristic characterizations as tactical “cherry picking”. McNamara et al. (2012) further argue that making decisions quickly is an adaptive strategy that reflects a *cumulative* rationality, shaped by experience and the real world constraints of incomplete information and little time to act. Freidin and Kacelnik (2011) demonstrated this context-dependent irrational ADM in European starlings (*Sturnus vulgaris*), showing that starlings’ performance on a decision-making task was reduced when contextual information was incorporated in simultaneous choice tests. However, in sequential choice tests, the starlings’ performance improved. Freidin and Kacelnik (2011) concluded that the sequential presentation was more akin to the natural setting (Lebiere and Anderson, 2011) and suggested that incorporating ecologically relevant context into the study of ADM is required for a holistic understanding of the process.

Heuristics (or simple algorithmic process models, Hutchinson and Gigerenzer, 2005) are cognitive processes that provide a shortcut to ADM via “skimming” partial information from all that is available (Gigerenzer and Goldstein, 1996; Edwards and Pratt, 2009; Gigerenzer and

Gaissmaier, 2011). By limiting the amount of time, and energy, involved in information gathering, it has been suggested that the “fast and frugal” (Gigerenzer and Goldstein, 1996) character of heuristic approaches enhances ADM efficiency but limits accuracy (Gigerenzer et al., 1996; Gigerenzer and Gaissmaier, 2011). However, because it is impossible for an animal to sample all possible options (Janetos, 1980), mechanisms that promote the use of “rules of thumb” or comparative valuation may be adaptively advantageous (Bateson and Healy, 2005; Bouskila and Blumstein, 1992; Latty and Beekman, 2011; McNamara et al., 2013; Reaney, 2009). In this regard, a heuristic approach to information gathering may be adaptive, or be representative of general ADM processes that function across choice domains. Regardless, the accuracy of decisions made using a heuristic approach may be compromised if the information available in the environment is no longer a good predictor of what, on average, will enhance fitness. This is well illustrated by the potential costs of erroneous decisions made while inspecting predators, a risky strategy employed by prey species to gain fitness-enhancing information about potential predators (Brown et al. 1999; Fishman, 1999). Inter-population variation indicates that prey co-evolved with dangerous predators display greater caution when inspecting predators (Magurran 1986). Species that have evolved in a context that promoted risk taking may be more vulnerable in human altered landscapes, such as those with more dangerous introduced predators or habitat modifications that reduce escape options and increase vulnerability. In these human-modified landscapes the consequences once-adaptive information acquisition strategies may entail greater than historical risk, with errors having profound impacts on fitness.

2.6 Synthesis and summary of ADM approaches and the role of context

Common themes emerge from each of the disciplines we have reviewed, and taken together, the ADM process as a whole can be best described, and key mechanisms responsible for generating observed behavior identified, by compiling and synthesizing results from each. Does environmentally driven variation in behavior result from sensory constraints? Do cognitive constraints limit an animals' ability to retrieve salient information when confronted with irrelevant environmental stimuli? Are strategic decision rules obsolete when the demography of a population has changed dramatically? If constraints on information gathering are the rule, rather than the exception, will contextual changes render the information landscape inadequate to make critical decisions that will, on average, enhance fitness? McNamara and Dall (2010) suggest that functional approaches to studies of ADM, as exemplified above, would be enhanced by the "judicious application of economics theory" (p. 231), and by taking an explicit information approach (Stephens, 2007). The same can be said for incorporating the other, rather compartmentalized, disciplines we have discussed here. Signal detection theory provides a ready and quantifiable framework within which to make predictions regarding how changes in external stimuli may influence behavior via the capacity of a species' sensory apparatus. Cognitive psychology provides a body of literature that tests the constraints on information processing, after signals are received. Information theory provides an adaptive framework within which to assess the overall performance of a dynamic chain of elements. Heuristic and strategic approaches to the study of ADM reflect the real world limits on information acquisition and overarching strategies that may enhance fitness over the course of an animal's lifetime. Taken together, these concepts are consistent with adaptive theories of ADM and provide a balanced framework from which to consider the contextual modulation of ADM processes in animals. The extent to which these varying processes are utilized will influence how organisms respond to

rapid environmental change, and will determine whether these responses are adaptive or maladaptive. The different approaches to studying these processes related to ADM will yield different sources of information and, collectively, provide a new toolbox that can be applied to understanding, predicting, and mitigating against animals' fitness-reducing responses in a changing world.

3. Social modulation of ADM

3.1 What is “social context”?

“Social context” describes a number of characteristics that emerge from the specific composition of individuals in a population and is an aspect of an organism's biotic environment that can be influenced, or even transformed, by human activities (Blumstein and Fernández-Juricic, 2010; Newby et al., 2013). Population density, age structure, sex ratio and the range of phenotypic variation in a population are all among characteristics that contribute to an organism's social context. In particular, social context is an integral component of reproductive strategies and may influence reproductive behavior at all stages of the reproductive process (Kokko and Rankin, 2006; Procter et al., 2013). Social context may influence mate search strategies, courtship communication, intrasexual competition and reproductive behavior (Procter et al., 2013; Wade et al., 2013), as well as critical decisions in other realms that ultimately influence fitness (e.g., foraging, migration, settlement; Mabry and Stamps, 2008; Ratikainen et al., 2010). Table 3 provides illustrative examples of empirical studies examining the influence of social context on animal behavior, demonstrating a broad array and long history of research on diverse taxa. However, note that very few empirical studies explicitly investigated the influence of social context on ADM *per se*. The following examples illustrate some of the ways in which ADM can

be socially modulated. They also provide a number of scenarios in which rapid shifts in contextual variation may present evolutionarily novel conditions from which animals must make decisions (Palumbi, 2001; Sih et al., 2011; Sih 2013) or drive ecological traps when social information is no longer an accurate proxy for habitat quality (Robertson and Hutto, 2006; Sih et al., 2013).

3.2 Social modulation of information acquisition

Information acquisition may be socially modulated in a number of ways. Information enhancement results from conspecifics gaining cues regarding the quality of a resource or habitat (e.g., public information, Danchin et al., 2004; Fletcher, Jr. & Miller 2008; Valone, 2007).

Audience effects and eavesdropping may influence foraging, vigilance (Ridley et al., 2007) or contest behaviors (Fitzsimmons and Bertram, 2013). Conspecific attraction is a mechanism that guides some species to make settlement decisions based on social cues or the presence of conspecifics (Ahlering et al., 2010; Fletcher Jr., 2006; Fletcher Jr. and Sieving, 2010).

Information acquisition regarding predator dangerousness may also be socially modulated, and mobbing behaviour has been documented in a wide array of taxa, from guppies (*Poecilia reticulata*; Magurran and Seghers, 1994) to meerkats (*Suricata suricatta*; Graw and Manser, 2007) as a way of reducing the risks associated with information gathering.

In cases of quorum or consensus ADM, the information bearing role of conspecifics can be amplified, as seen by the increased speed and accuracy of decisions made by highly social, swarming or shoaling animal groups (reviewed in Chittka et al., 2009; Contradt and Roper, 2005; Sumpter and Pratt, 2009). In these cases, threshold effects and positive feedback often (but not exclusively) facilitate the recruitment of individuals to consensus action (Evison et al., 2012;

Petit et al., 2009; Petit and Bon, 2010; Sumpter and Pratt, 2009).

Social context can also influence information acquisition by influencing the available options or perceived value of each element in a choice set (Xu et al., 2011), or influencing the perceived cost associated with specific choices (Galef and Giraldeau, 2001; but see Giraldeau et al., 2002). For example, intraspecific competition or dominance relationships may result in conditional valuation of a resource choice set (reviewed in Galef and Giraldeau, 2001). However, apart from aggregations of highly social species, the effect of social modulation on information use and decision rules is less clear (but see Seppänen et al., 2007).

3.3 Social modulation of search decisions

For highly social species that move in groups, social modulation of search decisions is prevalent. For schooling and flocking species, group size can be positively correlated with search decision accuracy (Couzin, 2008). For species in less structured social groups, the search for food, habitat and mates, can be influenced by signals from conspecifics or by social information available in the environment. For example, in the social bobolink (*Dolichonyx oryzivorus*), nest-searching decisions were influenced by the calls of conspecifics heard in the previous year's nest searching (Nocera et al., 2006), suggesting that social information had a lasting impact on nest site selection.

For typologically solitary species, search strategies (Janetos, 1980; Janetos and Cole, 1981), population density and population structure should determine the degree to which social context influences courtship and other socially mediated behaviors (Schradin et al., 2011) even though the acquisition of social cues indirectly (i.e., adaptively extended social information use, Seppänen et al., 2007) is widespread amongst solitary species, and across choice domains. For

example, Clark (2007) demonstrated that timber snakes (*Crotalus horridus*) used conspecific scent to find foraging sites, thus influencing both movement and resource acquisition decisions. Of note, the reliability and accessibility of indirect cues is also vulnerable to anthropogenic disturbance (Fisher et al., 2006; Ward et al., 2008).

3.4 Social modulation of courtship and mate-choice decisions

Regardless of social typology, group composition, age structure and option quality may drive comparative valuation during mate choice (Jennions and Petrie, 1997) (Table 3). Royle et al. (2008) focused on the influence of social context on mate choice in green swordtails (*Xiphophorus helleri*) and also found that potential mates were conditionally valued depending how they were presented relative to other conspecific options. Bateson and Healey (2005) noted that if comparative valuation is a property of mate choice in natural systems, the signaler may also be influenced by the context and adjust signaling effort if it knows its relative value compared to other options in the choice set (e.g., Doutrelant et al., 2001). If mate value is evaluated relative to the other possible mates, a signaler need only be a better choice relative to the other options in the choice set. This strategy may put males at a selective advantage if they can adjust their competitive or display effort from situation to situation, reducing costs associated with signaling.

3.5 Social modulation of predation risk

Predation risk can be modulated by the presence of conspecifics or heterospecifics, and thus social context can have a profound influence on the utility of a resource (Fletcher, Jr. and Miller 2008). Anti-predator behavior requires animals to make decisions by assessing the degree of

danger based on available information and deciding whether to flee, freeze, warn conspecifics, or attack or inspect the predator. Because any of these behaviors will take time away from maintenance behaviors such as feeding, resting, or reproductive behavior (such as courtship and parental care), they can be costly. Decision rules that govern these processes should be efficient and flexible in order to integrate contextual information into the ADM process. There is also little room for error, as predator avoidance ADM errors are associated with sudden and dramatic loss of fitness.

Social organization and group size effects on anti-predator behavior have been widely documented (Elgar 1986). Blumstein (2006) analyzed the relationship between sociality and anti-predator behavior in birds and found that cooperative breeders were generally more wary than non-cooperative breeders. Similarly, Blumstein and Daniel (2003) found that the size of social aggregations influenced vigilance behavior in red kangaroos (such “group size effects” are widely reported in many species—Caro 1994). These authors posited that species living in open habitats perceive less predation risk and experience greater protection from predation when socially aggregated, and so could spend more time feeding. The mechanisms that underpin this relationship may reflect the information-providing role of conspecifics in this domain (e.g., signaling and public information; Valone 1989), dilution effects (Dehn 1990) or the enhanced capacity to mob or threaten predators when in a large group (Dugatkin and Godin, 1992a). Social context may also influence anti-predator behavior if prey individuals can assess the likelihood of being preyed upon relative to other individuals in the group. For example, a large, healthy adult may be a less likely target than young, old or injured individuals. Integrating this information may influence how an animal decides to allocate potentially costly anti-predator behavior.

4. Conservation applications and implications

The scale, pace and pervasiveness of anthropogenic influences on natural systems is unprecedented (Crutzen and Stoermer, 2006; IPCC, 2007; Parmesan and Yohe, 2003; Parmesan, 2006). Habitat loss, habitat fragmentation (Fletcher Jr., 2006; Sih et al., 2011), and selective harvesting may drive changes in population density and age/sex structure that ultimately influence the social context in which animals make critical decisions (e.g., Allee effects-- Courchamp et al., 1999; Molnár et al., 2008) or render evolved search strategies inefficient or maladaptive (Sih et al., 2011). For example, Lamberson et al. (1992) found that search-efficiency declined significantly in northern spotted owls (*Stix occidentalis caurina*) when the population size fell below a certain threshold. Habitat degradation via noise (reviewed in Patricelli and Blickley, 2006), light (reviewed in Longcore and Rich, 2004), and chemical pollutants (Fisher et al., 2006) may also reduce the efficacy of signals, or availability of public information, and so influence the quality, accuracy and availability of information used for social ADM (Bateson, 2007). Systematic and persistent changes in body condition, driven by changes in resource availability, may also influence decisions guiding risk-taking and parental investment (Coleman et al., 1985) because animals in poorer condition may prioritize survival over reproductive or foraging needs. Together, these effects demonstrate the dynamic nature of social context and the potential for shifts in social context to drive species depletion.

While incorporating ADM theory into conservation is not a new idea (Swaisgood, 2007), it is rarely overtly integrated into conservation strategy (but see Table 4 for some examples to the contrary). Nonetheless, it is evident that understanding how an animal makes decisions, including the sensory, cognitive, and strategic processes that govern each stage of the process, would enhance both applied conservation management and our understanding of how

disturbance will influence critical behavioral domains and, ultimately, fitness. Sih et al. (2010, 2012) have provided a detailed framework for applying these concepts, and have specifically demonstrated how an evolutionary mismatch between cue-response systems can drive maladaptive behavioral responses. The mismatch between cues and behavioral responses demonstrates how the sensory and cognitive stages of ADM can generate inappropriate behavior and influence fitness. The degree to which an organism can learn (Fawcett et al., 2013) or update (Valone, 2006) may also influence the fitness impacts or persistence of species in the face of this mismatch if this promotes the ability to contextualize novel stimuli (e.g., human predators). For example, noise stimuli associated with urban landscapes can have a negative impact on avian fitness, due to the impedance or energetic impacts on communication needed for reproduction and survival (Warren et al., 2006). However, peregrine falcons (*Falco pegrinus*) can exploit urban landscapes to their advantage, and commonly use elevated buildings for perching and nesting, successfully staging a comeback from the brink of extinction through the use of city buildings and bridges (Bell et al., 1996). For this species, the acoustic stimuli associated with high-density urban areas has been contextualized, and does not impede successful reproduction or foraging.

4.1 Ecological traps

The ecological trap concept, in which animals display an active preference for lower-quality habitat conferring lower fitness (Battin, 2004; Robertson and Hutto, 2006; Robertson et al., 2013; Schlaepfer et al., 2002), provides a number of examples that demonstrate both the influence of context on ADM and the relevance of ADM to conservation. Without an understanding of ecological trap theory and ADM underpinning, conservation practitioners may

inadvertently set ecological traps for species they are trying to manage. In one possibility, creation of artificial burrows has been adopted as a “quick-fix” for loss of fossorial mammal-engineered habitat for burrowing owls, *Athene cunicularia hypugaea*. This conservation-dependent species readily uses these artificial burrows (Belthoff and Smith, 2003), but little research has addressed the optimal placement of burrows to provide other resources that the owls require. If burrowing owls’ settlement decisions are guided primarily by burrow availability—historically indicating that the habitat also supports fossorial mammals and possibly predictive of other habitat factors important to burrowing owls, such as prey availability—then owls may be deceived into settling in an ecological trap. In this context, a better understanding of ADM may make managers more attuned to the possibility that their actions may have unforeseen consequences.

Further, ecological traps provide examples of contextual influences on ADM at both the level of cognitive mechanisms (i.e., “perceptual traps”; Patten and Kelly, 2010) and evolutionary strategy (Robertson and Hutto, 2006). If contextual cues no longer provide reliable information about habitat or resource quality, previous ADM strategies that would “on average” be fitness enhancing, may now be maladaptive. And if habitat cues are no longer efficiently transmitted or received, then decision-makers will miss out on high quality resources. The use of social information (e.g., “conspecific attraction”) provides a ready example demonstrating how the formation of ecological traps may be socially modulated.

4.2 Conspecific cueing

There are notable examples of ADM theory being applied, either implicitly or explicitly, to behavior-based wildlife management, particularly in the contexts of habitat re-colonization,

captive breeding and in applying an individual based approach to projection models (Table 4). For example, the use of socially acquired public information by colonial nesting and territorial species has prompted the strategic use of decoys to attract animals to ecologically appropriate, yet underutilized, habitat (Arnould et al., 2013; Stamps, 1988). While numerous applications of varied types and configurations of decoys (e.g., visual, acoustic or olfactory conspecific cues) have been successfully utilized to trigger settlement decisions, there are cases where they have not been successful, even when focal species are colonial (Ahlering et al., 2010; Fletcher Jr., 2006; Fletcher Jr. and Sieving, 2010).

These mixed results suggest that a more detailed understanding of the interaction between decision strategies, cognitive constraints, and environmental context, could enhance the success of using conspecific attraction as a management tool (Fletcher, Jr. and Miller, 2008; Patten and Kelly, 2010; Robertson and Hutto, 2006). For example, Forsman et al. (2008) demonstrated that older male great tits (*Parus major*) were more likely to use social information for nest site selection than younger males. This effect, when integrated into an applied management strategy, can be used to enhance the success of re-colonization strategies. The use of social information may also differ between age or sex classes. For example, Forsman et al. (2008) found that older male great tits (*Parus major*) were more likely to use public information when choosing a nest site than younger males. A better understanding of contextual influences on ADM in relation to conspecific cueing may also help avoid misguided approaches when using this potentially powerful conservation tools. If animal settlement decisions are based upon an integrated index of several ecological factors important to fitness, the risk of luring animals to ill suited habitat is less than if animals are using conspecific cues as the only or primary cue to habitat quality. Clearly, from a conservation viewpoint, hunters' use of decoys to attract waterfowl is an

ecological trap.

4.3 Captive breeding

Captive breeding is an area of applied conservation that has integrated decision theory, either implicitly or explicitly, to increase the success rate of pairings, and often this has involved contextual manipulation (Swaisgood et al., 2010). Because breeding pairs in captivity are often identified based on genetic considerations, an understanding of behavioral decision rules, and how they are socially modulated can be a powerful tool used for promoting both breeding success and the genetic health of small populations. For example, Martin and Shepherdson (2012) showed that various measures of reproductive success in the pygmy rabbit (*Brachylagus idahoensis*) were socially modulated, with females demonstrating increased fitness when allowed to mate with familiar or preferred males. Integrating these social influences on reproductive success with necessary genetic management, can greatly improve the long-term success of captive breeding programs.

In another example, Fisher et al. (2003) hypothesized a simple decision rule guiding mate choice in the asocial pygmy loris (*Nyctecebis pygmaeus*). While not explicitly identified as such, the decision rule the authors tested was a “best-of-n” strategy. Fisher and colleagues utilized scent as a proxy for the presence of conspecifics and manipulated the perceived social environment of estrus females; familiarizing each with a genetically preferred male (via scent) so that she “chose” him when she was ready to mate. This type of adaptive management strategy can be effectively applied to species that use comparative valuation to choose between potential mates. For example, mate “choice sets” can be manipulated to ensure that a genetically appropriate mate is preferred. Further, stimuli that indicate receptivity (*sensu* Xu et al., 2011)

can be manipulated to prime sexual motivation in otherwise unmotivated animals (Roberts and Gosling, 2004). In either of these applied contexts, an understanding of the decision rule underpinning choice will enable the efficient design of conservation management strategies.

4.4 Reintroduction and translocation

The success rate of both reintroduction and translocation is generally low (Wolf et al. 1998; Fischer and Lindenmayer 2000), However, a number of studies have demonstrated how the integration of decision theory may enhance the likelihood of success. Specifically, socially modulated ADM has been incorporated into reintroduction and translocation efforts for solitary species, such as the Stephen's kangaroo rat (SKR: *Dipodomys stephensi*) and black rhinoceros (*Diceros bicornis*). In the case of the SKR, Shier and Swaisgood (2011) found that after translocation, settlement decisions were socially modulated and that fitness increased when SKR were translocated with neighbors. Neighbor-translocated SKR established territories closer to the release site and had higher survival rates and greater reproductive success than those SKR that were not translocated with neighbors. Similarly, black rhinoceros translocated with unfamiliar conspecifics into smaller reserves met with less success than those released into larger reserves with lower social density, due to the effects of excessive social conflict not found in stable groups of rhinos (Linklater and Swaisgood, 2008). Socially modulated ADM offers a plausible explanation of these results, as rhinos appear to make decisions about escalated fighting based on the degree of familiarity and social density.

4.5 Projection models

Integrating behavioral decision rules into projection models of population abundance and persistence has been underutilized. However, the growing use of behavior-based individual (agent) based modeling (IBM) provides a coherent and valuable framework (*sensu* Goss-Custard et al., 2006; Semeniuk et al., 2012) for incorporating multiple aspects of ADM, from sensory constraints to overarching decision rules, into projection models. For example, Croft et al. (2012) developed an IBM to explore the influence of social group size on collision risk to address management concerns regarding the rate of fatal interactions between wildlife and wind turbines. Using the IBM approach, these authors identified interactions between group size and social interactions, on both navigational efficiency and group cohesion and suggested that this information would be essential for developing effective and protective management strategies for birds in the face of this growing sector of the energy industry.

Incorporating behavior rules into projection models is not limited to the IBM approach. For example, Molnár et al. (2010) developed an encounter rate model for polar bears (*Ursus maritimus*) to predict how female mate searching efficiency would be influenced by climate change driven habitat fragmentation. In their mechanistic model, they found that reductions in mating success were non-linearly sensitive to varying degrees of reduced search efficiency. While this work did not integrate a decision rule *per se*, the sensitivity of varying degrees of mate search efficiency suggest that the accuracy of projections could be enhanced by an understanding of the decision rules and cognitive constraints governing mate search in the species. For example, if male bears utilize an absolute or threshold decision rule to locate females that are in adequate body condition (via chemical cues, *sensu* Hurst et al., 1996), then the influence of reduced body condition or population depletion on mate search could be more pronounced than if they used a comparative or “best-of-n” strategy. For this species, identifying

the mechanisms of mate search is essential because many populations have experienced changes in the operational sex ratio due to selective harvest (Derocher et al., 1997; Molnár et al., 2008), and reductions in body condition due to sea ice loss. An understanding of the decision rules polar bears use to choose between potential mates would enhance the accuracy of predictive models (Derocher et al., 2010).

4.6 Mechanistic modeling of behavior based on ADM and acoustic impact: Noise disturbance and denning polar bears

The most efficient way to measure behavioral responses to environmental change or evolutionary novelty is through controlled exposure experiments (Cox et al., 2006), and the value of adaptive management strategies has been well documented. However, for many conservation dependent species, controlled exposure to disturbance stimuli is not feasible due to ethical concerns or regulatory constraints (e.g., Marine Mammal Protection Act 1972). In these cases, modeling approaches must be employed in order to generate predictions regarding the impacts of disturbance on individuals and populations. As exemplified above, contextual variation and behavioral decision rules can be incorporated into models (sensu Goss-Custard et al. 2006), and the biological validity may be further enhanced if models also incorporate sensory capacity (sensu Erbe 2002), cognitive constraints, and life history dynamics, in order to enhance the biological validity and predictive value of models (Ellis et al. 2013).

Industrial scale resource extraction provides a number of examples wherein wildlife managers are faced with potentially profound transformation of habitat, and often little biologically based understanding of how to most effectively mitigate disturbance, beyond spatial buffer zones or protected areas (Blumstein et al. 2003). For example, oil and gas activities

overlap temporally and spatially with polar bear maternal denning habitat on the North Slope of Alaska (Lentfer & Hensel 1980). While these activities have been ongoing in the region for decades, concerns persist, and in fact have intensified, regarding their impact on denning polar bears (Aars et al. 2006). In this case, as in others, logistical, ethical and regulatory constraints preclude the execution of controlled noise exposure experiments with denning females. Thus, both the circumstances leading to premature den abandonment (Amstrup 1993), and the cumulative impact on reproductive success from disturbance (Owen & Bowles, 2011), are poorly understood. However, it is likely that the magnitude and nature of the disturbance response are influenced by the combined interaction of sensory capacity, cognitive processes, life history (e.g., parity and the influence of residual reproductive effort), body condition, and social context. Social context may influence critical decision making for parturient female bears because abandoning the den post-partum may have more serious consequences (i.e., litter loss), than abandoning the den pre-partum. Further, changes in demography associated with climate change driven sea ice losses in the Arctic may increase the probability of potentially predatory male polar bears remaining on land over winter.

Owen et al. (unpublished) have proposed an individual behavior-based approach to estimating the degree of noise disturbance experienced by parturient females in dens, and the potential ramifications for individuals and populations. These authors have developed a conceptual model (figure 2), based on the mechanistic model of decision-making adapted from Blumstein and Bouskila (1996; figure 1). The authors propose that more refined estimates of disturbance can be developed, and modeled according to changes in the social and environmental context, by including the species' sensory capacity, cognitive constraints, behavioral ecology (acoustic communication and maternal care), energetics and life-history, to estimate female

behavior in the face of a range of acoustic and seismic stimuli. While substantial data are still needed to parameterize aspects of the model, recent research has provided some needed information. Owen and Bowles (2011) utilized a psychoacoustic approach to measure polar bear hearing sensitivity, and have incorporated noise transmission data collected from the field (MacGillivray et al. 2009; O'Neill et al. 2012; Owen et al. 2013), as a first step towards estimating zones of impact (sensu Erbe 2002; Richardson et al. 1995). However, modeling individual and population level effects will require integrating decision rules (developed from behavioral ecology in the denning and maternal care context), along with energetics and life history variation.

5. Conclusions

The study of ADM has emerged in disparate fields, including signal detection theory, cognitive psychology, behavioral economics and behavioral ecology. While the distance between these fields is great, and the context in which each has addressed the same overall process differs in terms of its approach, overriding themes emerge from all, and these themes offer valuable insight into the process of ADM. Context is clearly important, however limitations on sensory input and processing (i.e., information overload, Bernays and Wicslo, 1994) may also influence ADM. Identifying how fundamental principles interact with contextual themes may have tremendous value in conservation and enhance the success rate of behavior-based management strategies, by providing targeted, and quantitative predictions for both behavioral and larger scale changes in the face of environmental change.

The potential for behavior based studies to both reveal, and address, anthropogenic impacts is clear, as demonstrated by both a rich literature documenting both correlations between

human generated changes in the environment and changes in behavior (Warren et al. 2006), and the application of animal behavior theory to conservation management (Ahlering et al. 2010). Likewise, incorporating ADM theory into conservation biology could refine our understanding of how anthropogenic stimuli and activities will influence species over time, and may also provide mitigation tools that can be applied to conservation management (Sih et al., 2011). Mitigation tools can be developed based on an understanding of what aspect (sensory, cognitive, ecological) of the decision-making process drives behavioral responses and ultimately, larger scale patterns.

Table 1. Glossary of terms commonly used by behavioral ecologists to describe the decision-rules that guide the choices animals make across choice domains (i.e., for mate search, movement, predator avoidance, resource acquisition). We provide working examples of decision rule for a generic animal in the context of mate search, illustrating how different rules influence the process of decision making. We also suggest the potential fitness implications associated with decision-rules that are no longer optimal in an altered environment.

Term	Definition	Example	Fitness implications in rapidly altered social context
Absolute valuation	Decision is based on a trait meeting a specific criteria value	Male must weigh 350 kg	-Increased search costs if large males have become rare -Reduced fitness due to lost reproductive opportunities
Comparative valuation	Simultaneous, relative valuation of a trait based on two or more options	Female simultaneously compares the attributes of two or more males	-“Fixed” search cost -Potential for reduced fitness if sub-par male traits confer reduced trait value to offspring
Best-of-n	Sampling of a fixed number of options. Chooser bases decision on best “quality” option sampled.	Female evaluates 4 males, chooses to mate with the largest of them	-“Fixed” search costs -Potential for reduced fitness if male traits are subpar
Threshold	Sampling of options continues until a threshold value of a particular trait is identified.	Male must weigh <i>at least</i> 350 kg	-Increased search costs if large males have become rare -Reduced fitness due to lost reproductive opportunities
Sequential sampling	Sequential assessment of options.	Female compares the attributes of two or more males in turn	-Search costs dependent upon whether female uses a best-of-n, absolute or threshold strategy for

			mate choice -Potential for reduced fitness if sub-par male traits confer reduced trait value to offspring or if search costs increase due to deplete population density or male quality
Consensus	Social animals choose between a number of options and follow the option with the most “votes”	Swarming or flocking species	-Population density influences the speed and accuracy of decision making
Heuristic rules of thumb	Fast and frugal approach to information gathering	Decisions made on incomplete information	-Search costs reduced -Incomplete assessment of mate quality may result in erroneous decisions

Table 2. Fundamental concepts associated with the behavioral economic theory of ADM. Note within the realm of classical behavioral economic theory, it is assumed that individuals have complete and accurate information when making decisions, and that there are no cognitive limitations to processing all available information.

Term	Definition
Rationality	Prevailing axiom of economic ADM. Rational decisions are transitive, complete and consistent regardless of contextual variation.
Transitivity	Consistent valuation of options regardless of context.
Completeness	Preferences based on a single dimension will hold regardless of the magnitude of the trait in that dimension.
Independence of irrelevant alternatives	Inclusion of an additional “irrelevant” option to a choice set does not change the preference order expressed between relevant options.

Table 3. Empirical studies of socially-modulated ADM. While this table illustrates the taxonomic breadth and prevalence of socially modulated decision-making, it does not constitute an exhaustive search on the topic.

Domain	Species	Reported Mechanism	Reference
Resource Acquisition	European starling (<i>Sturnus vulgaris</i>)	Copying	Templeton and Giraldeau (1996)
	Ant (<i>Leptothorax albipennis</i>)	Consensus	Franks et al. (2003)*
	Acorn ant (<i>Temnothorax curvispinosus</i>)	Consensus	Edwards and Pratt (2009)*+
	German cockroach (<i>Blattella germanica</i>)	Consensus	Ame et al. (2006)*
	Cliff swallow (<i>Petrochelidon pyrrhonota</i>)	Public information	Brown et al. (1991)
	Nine-spine stickleback (<i>Pungitius pungitius</i>)	Public information	Webster and Laland (2012)
	Red winged blackbird (<i>Agelaius phoeniceus</i>)	Copying	Avery (1994)
	Domestic sheep (<i>Ovis aries</i>)	Consensus?	Dumont and Boissy (2000)
	Budgerigar (<i>Melopsitacus undulates</i>)	Facilitation	Soma and Hasegawa (2004)
	Timber rattlesnake (<i>Crotalus horridus</i>)	Copying	Clark (2007)
Movement/ Settlement	Budgerigar (<i>Melopsitta caundulatu</i>)	?	Valone and Giraldeau, (1993)+
	White-headed capuchin (<i>Cebus capucinus</i>)	Consensus	Petit et al. (2009)*
	Ant (<i>Temnothorax sp.</i>)	Consensus	Sumpter and Pratt (2009)*

	Harvestman (<i>Prionostemma sp.</i>)	Public information	Donaldson and Grether (2007)
	Pharroh ant (<i>Monomorium pharoonis</i>)	Consensus	Evison et al. (2012)*
	Bush grasshopper (<i>Ligurotettix coquilletti</i>)	Copying	Muller (1998)
	Collared flycatcher (<i>Ficedula albicollis</i>)	Public information	Doligez et al. (2004)
	Blue tit (<i>Cyanistes caeruleus</i>)	Public information	Parejo et al. (2007)
	Black-throated blue warbler (<i>Dendroica caerulescens</i>)	Public information	Betts et al. (2008)
	Great tit (<i>Parus major</i>)	Public information	Nicolaus et al. (2012)
Predator Avoidance	Fathead minnow (<i>Pimephales promela</i>)	Public Information	Pollack et al. (2006)
	Chimpanzee (<i>Pan troglodytes</i>)	Dilution	Kutsukake (2006)
	Common frog (<i>Rana temporaria</i>)	?	Nicieze (1999)+
	Tammar wallaby (<i>Macropus eugenii</i>)	Dilution	Blumstein et al. (1999)
	Red kangaroo (<i>Macropus rufus</i>)	Dilution	Blumstein and Daniel (2003)
	Ringed salamander (<i>Ambystoma annulatum</i>)	Public information	Crane et al. (2012)
Social Interactions	Guppy (<i>Poecilia reticulata</i>)	Copying	Dugatin and Godin (1992b), Briggs et al. (1996)
	Tungara frog (<i>Physalaemus pustulosus</i>)	?	Kirkpatrick et al. (2006)+

Siamese fighting fish (<i>Betta splendens</i>)	Audience	Doutrelant et al. (2001)
	Eavesdropping	Doutrelant and McGregor (2000), Oliveira et al. (1998) Peake et al. (2002)
Great tit (<i>Parus major</i>)		
Swordtail (<i>Xiphophorus helleri</i>)	Comparative	Royle et al. (2008)*
Wolf spider (<i>Schizocosa ocreata</i>)	Comparative	Uetz and Norton (2007)
Pygmy swordtail (<i>Xiphophorus multilineatus</i>)	Comparative	Morris et al. (2010)
	Frequency dependent preferences	Tudor and Morris (2011)
Florida crickets (<i>Orthoptera, gryllidae</i>)	Comparative	Sadowski et al. (2001)
Pygmy loris (<i>Nycticebus pygmaeus</i>)	Comparative	Fisher et al. (2003)
Guppy (<i>Poecilia reticulata</i>)	Social feedback	Price and Rodd (2006)
African clawed frog (<i>Xenopus laevis</i>)	Public information	Xu et al. (2011)
Zebra finch (<i>Taeniopygia guttata</i>)	Social feedback	Royle and Pike (2010)
White headed capuchin (<i>Cebus capucinus</i>)	Consensus	Petit et al. (2009)

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- * decision-making was explicitly tested, + social modulation not found.

Table 4. Representative studies where animal decision rules were explicitly identified and applied to conservation/management issues. Applications include the inclusion of behavior in individual based modeling (IBM) or predictive models of population dynamics (PM), the use of psychophysics to assess the impact of anthropogenic stimuli (PA), the use conspecific attraction to influence settlement (CA), or the inclusion of ADM theory into captive breeding programs (CB).

Application	Conservation/ management concern/goals	Aspect(s) of animal decision making incorporated	Reference
IBM	Habitat use by caribou (<i>Rangifer tarandus</i>) in areas industrialized by oil & gas	Risk aversion	Semeniuk et al. (2010)
IBM	Impact of recreationist activity on blue butterfly (<i>Lycaeides melissa</i>)	Reproductive success and habitat choice	Bennett et al. (2013)
IBM	Habitat selection by white fronted geese (<i>Anser albifrons</i>)	Foraging decisions	Amano et al. (2006)
IBM	Habitat loss and shorebird mortality	Density dependent mortality	Goss-Custard et al. (2002)
PM	Population growth rates	Social modulation of social interactions	Sutherland and Norris (2002)
PA	Noise masking of intraspecific communication in beluga whales (<i>Delphinapterus leucas</i>)	Conspecific signal detection	Erbe and Farmer (1998)
PA	Noise masking of intraspecific communication in avian communities	Conspecific signal detection	Halfwerk et al. (2011)
CA	Degraded habitat, translocation	Use of public information	Ward and Schlossberg (2003)

CA	Temporal variation in settlement decisions by loggerhead shrikes (<i>Lanius ludovicianus</i>)	Use of public information	Etterson (2003)
CB	Mate choice in captivity in harvest mice (<i>Micromys minutus</i>)	Olfactory manipulation of mate choice	Roberts and Gosling (2004)

Figure 1. Stages of the decision-making process (modified and expanded from Blumstein and Bouskila, 1996). Context may influence each stage of the decision-making process. Personal information may have influence over all stages once a stimulus has been integrated. Sensory capacity, selection on the sensory apparatus and experience are part of the prior, and the posterior is formed after the evaluation process.

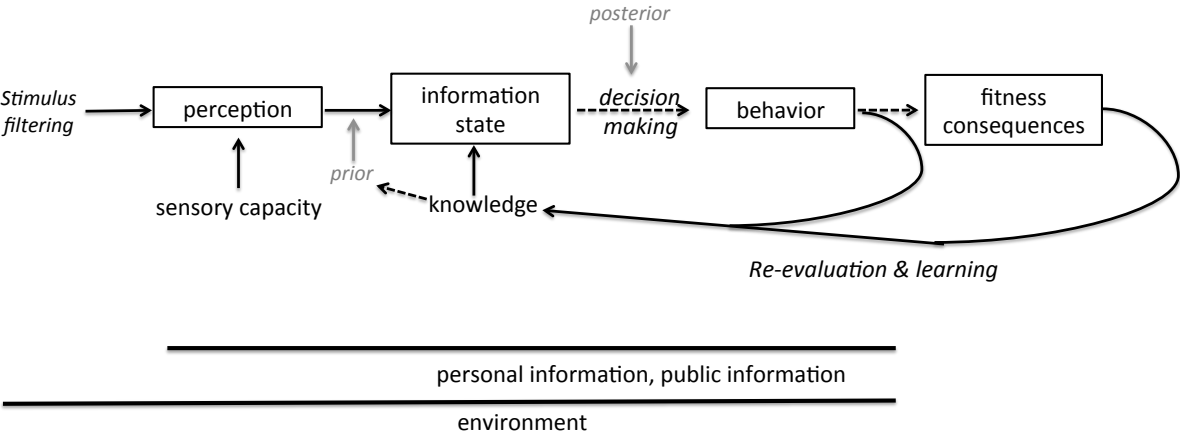
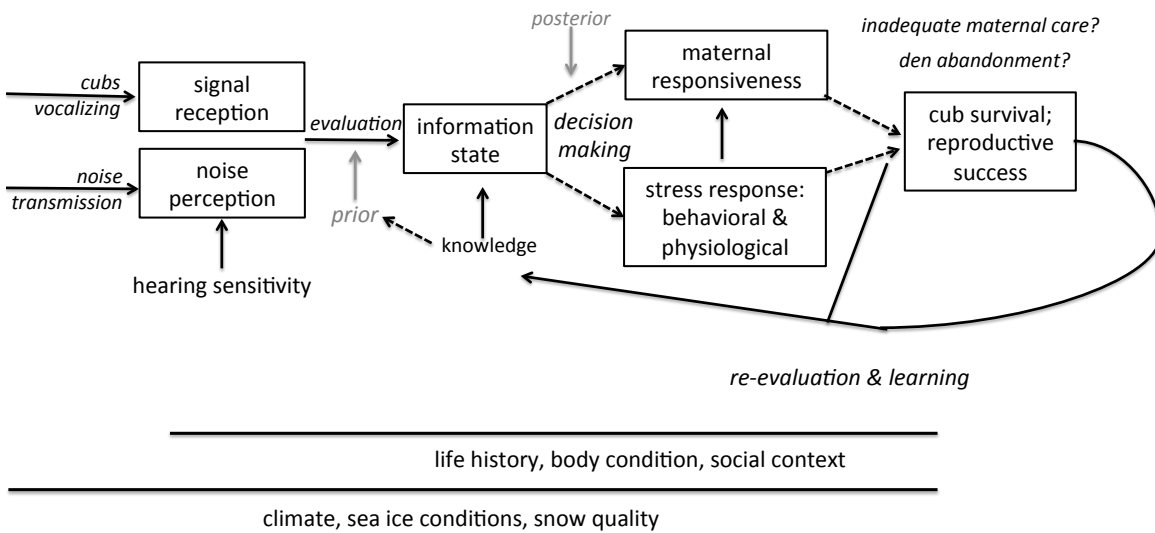


Figure 2. Conceptual model, based on the ADM model (figure 1), of the influence of industrial noise exposure on reproductive success in the polar bear. This model is founded in species' sensory ecology, utilizing psychophysics, cognitive psychology, behavioral ecology, energetics and physiology to estimate the response and predict impacts on fitness. This model approximates the influence of all these factors on the chances of success in a single or multiple reproductive events.



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CHAPTER 3: TRANSIENT SOCIAL CONTEXT INFLUENCES COURTSHIP SIGNALING BEHAVIOUR IN A SOLITARY, SEASONALLY-MONOESTRUS, SPONTANEOUSLY OVULATING MAMMAL: THE GIANT PANDA (*AILUROPODA MELANOLEUCA*). *In preparation for submission: Animal Behaviour.*

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Abstract

Behavioural flexibility may confer resilience in the face of rapid changes in the environment resulting from human activities. However, behavioural flexibility is constrained by a number of

factors, including physiology. The giant panda (*Ailuropda melanoleuca*) is a solitary, wide-ranging and endangered ursid occupying fragmented habitat at social densities below historical carrying capacity. Giant panda females are seasonally mono-oestrus, and ovulate spontaneously, which limits a female's capacity to adjust the timing of fertility in accordance with the presence of an appropriate mate, and the onset and maintenance of signaling behaviour may be deterministic. Because signaling behaviour is energetically costly, the ability to adjust signaling effort according to the presence of an appropriate receiver would be beneficial in an anthropogenically altered social context, especially given the substantial energetic constraints on reproduction imposed by the species' energy-poor diet. To examine the influence of social context and time relative to ovulation on giant panda behaviour, we studied female giant pandas during the breeding season at the Wolong Breeding Centre in Sichuan, China. We used linear mixed-models and an information theoretic approach to assess the temporal relationship between signaling behaviors and the timing of first mating of the season. We also explored the interaction between social context and reproductive status on the expression of signaling and maintenance behaviours. We found that while most signaling behaviours provided temporally explicit clues to presumed reproductive fertility, social context also influenced the expression of signaling behaviour. Specifically, female signaling effort was generally lower in the exclusive presence of other females. Thus, in spite of the temporal constraints that spontaneous ovulation might impose on sexually proceptive and receptive behaviour, females can modify their behavioural efforts during the pre-ovulatory period according to the prevailing social context.

Keywords: Behavioural flexibility, social context, courtship, energetic constraints, spontaneous ovulation

Introduction

Courtship can be costly, and increases in energetic output associated with signaling and social behaviour (Vezina & Salvante 2010; Mowles 2014) are typically coupled with decreases in feeding and self-maintenance behaviours (Abrahams 1999). Further, the risks of injury and energetic costs associated with intra-sexual competition can be great (Promislow 1992; Clutton-Brock 2007), as can be the survival compromising effects of sexually selected ornaments (Basolo & Alcaraz 2003). Given these costs, sexual selection can appear to contradict adaptive strategies (Emlen & Oring 1977; Clutton-Brock 2009). However, mechanisms regulating courtship and mating behaviour may be influenced by ecological, physiological and social factors (Crews & Moore 1986) and thus animals can modulate courtship behaviour according to changes in the environment, and so exploit opportunities to reduce associated costs and enhance fitness (Schradin & Lindholm 2011). Decreasing the costs of courtship and mating behaviour may be an especially valuable strategy for species that exhibit strong energetic constraints on reproduction.

Behavioural flexibility reflects the ability for an animal to reversibly fine-tune its behavioural effort and tactics (and therefore energy output) in accordance with current environmental conditions (Kappeler et al. 2013), and thus can be an adaptive response to environmental variability, whether natural or human-driven (Tuomainen & Candolin 2010; Milich et al. 2014). However, while ecological and demographic factors have been documented to drive temporal and spatial gradients in reproductive strategy, and the relative prevalence of alternative reproductive tactics (Schradin et al. 2010; Schradin & Lindholm 2011; Botero & Rubenstein 2012), the influence of the potentially *transient* characteristics of the *immediate* social context on the flexibility of an individual's social behaviour is less well understood. Yet,

the potential for behavioural flexibility to enhance fitness in the face of transient environmental variability is clear, especially during courtship and breeding encounters (Vezina & Salvante 2010; Tinghitella et al. 2013; Mowles 2014).

Social competence refers to the capacity for fitness enhancing behavioural flexibility during social interactions (Abrahams 1999; Oliveira 2009; Taborsky & Oliveira 2012). Social competence decouples classically defined performance traits (such as body size, speed, strength) from behavioural performance (signaling effort, aggression) because, for example, a particularly powerful individual will not have to utilize all of its potential strength against a particularly weak rival, thereby reducing the energetic effort required to achieve the goal of winning access to a female. Social competence may be achieved through observation and learning, experience (West et al. 1996), or through audience effects, which influence behavioural efforts or trigger the physiological responses that drive behaviour. Like most studies of social behaviour, social competence has been best studied in social species. However, social competence should be equally advantageous to solitary species, especially when navigating potentially “novel” conspecifics. Like the more general concept of behavioural flexibility, social competence is underpinned by physiological flexibility, particularly in the context of reproductive behaviour.

The interplay between behavioural flexibility and physiology is not well understood (Bakker & Baum 2000). It is, however, clear that adaptive responses to environmental change can be constrained by physiology (Ricklefs & Wikelski 2002). In the context of courtship and breeding, endocrine control of the onset and maintenance of reproductive behaviours (both proceptive and receptive) have been well documented in a vast array of taxa (reviewed in Bakker and Baum 2000), as have environmental and social influences on these processes (Greene & Drea 2014). Ovulatory mode, alternatively defined as bimodal (i.e. either spontaneous *or*

induced) or as occurring over a continuum between the two (Nablandov 1976; Bakker & Baum 2000), may determine the degree to which environmental conditions, including social context, may influence the onset of both behavioural oestrus and sexual receptivity. Indeed, we can make predictions regarding life history traits and responsiveness to environmental stimuli based on ovulatory mode, especially if a species demonstrates induced ovulation (Bakker & Baum 2000; Ricklefs & Wikelski 2002; Basolo & Alcaraz 2003). For example, solitary living is positively correlated with induced ovulation (Emlen & Oring 1977; Lariviere & Ferguson 2003; Clutton-Brock 2009), as is seasonal breeding (Bakker & Baum 2000), and the advantages of induced ovulation for both of these traits are intuitive: induced ovulation ensures that reproductive resources (i.e., energy and gametes) are not utilized until a reproductive opportunity presents itself.

In contrast to induced ovulation, spontaneous ovulation should temporally constrain the flexibility of reproductive behaviour because the timing of ovulation is not influenced by coital or pheromonal stimuli (Bakker & Baum 2000). However, there are notable examples of social context influencing the onset or length of behavioural oestrus in spontaneously ovulating species, if not ovulation itself. For example, Yoerg (1999) found that the oestrous cycle of the solitary, spontaneous ovulating Heermann's kangaroo rats (*Dipodomys heermanni*) was lengthened when females were socially isolated. Other examples of pheromonally induced behavioural flexibility during oestrus have been documented in the grey short-tailed opossum (*Monodelphis domestica*) (Fadem 1989), whiptail lizard (*Cnemidophorus inornatus*) (Crews et al. 1986) and domestic goats (*Capra aegargrus*) (Claus et al. 2003). However these species, like the Heermann's kangaroo rat, are polyoestrus; cycling year-round, or multiple times throughout the breeding season. In contrast, seasonally monoestrus, spontaneously ovulating species may be the most temporally

constrained class of sexually reproducing organism. And, because the degree to which a mistimed or mis-directed reproductive effort influences fitness is greater in seasonally mono-oestrus species, selection for social context to drive some degree of behavioural flexibility during courtship should be especially advantageous.

Here we explore the interplay of temporal constraints driven by physiology, energetic constraints and social context on the courtship behaviour of the giant panda (*Ailuropoda melanoleuca*). The giant panda is a long-lived, large brained, wide ranging, solitary and endangered (IUCN 2013) carnivore that has a limited, and highly fragmented, range in the mountains of south central China (Wei et al. 2012). The giant panda mating system is polygynous and male-male competition for access to oestrus females has been documented (Schaller et al. 1985; Nie et al. 2012). Giant panda females are seasonally monoestrus and ovulate spontaneously (Durrant et al. 2003). Captive studies of giant panda courtship and breeding behaviour have documented a period of proceptive behaviour (“oestrus”) lasting 10-14 days, followed by a short period of sexual receptivity (“peak-oestrus”, 1-3 days). Behavioural oestrus is correlated with a steady pre-ovulatory rise in oestrogen levels, followed by a precipitous fall in oestrogens typically occurring on the first day of natural breeding (McGeehan et al. 2002; Czekala et al. 2003; Kersey et al. 2010). These factors, coupled with the energetic constraints that likely influence all aspects of giant panda reproduction and survival (Schaller et al. 1985), would suggest that some degree of behavioural flexibility during courtship would be advantageous. However, because reproductive behaviour in the species appears to be coupled with the rapid changes in circulating oestrogen levels associated with follicular development and ovulation, it is unclear whether transient extrinsic factors would influence the expressive range of signaling behaviours exhibited by females during this period (Owen et al. 2013).

In fact, giant pandas are behaviourally expressive during courtship and breeding, exhibiting a range of chemical, acoustic and visual signals (Kleiman & Peters 1990; Swaisgood et al. 2003; 2006). Giant pandas rely on scent communication to coordinate social behaviour (reviewed in Swaisgood et al. 2004) and prior to face-to-face encounters (Swaisgood et al. 1999; 2000; 2002). Because scent marks are temporally persistent, chemical communication is a key modality used by solitary species (Ralls 1971). Previous research has documented a range of information contained in giant panda scent marks, including signaller identity, age-class, sex and reproductive status. Further, identifying information is conveyed in both the deposition strategy (e.g., scent mark height, White et al. 2003) and chemical constituents (Hagey & MacDonald 2003) of scents. While male giant pandas use scent to both advertise individual status and to respond to conspecific signals, female giant panda use scent primarily to advertise reproductive status, via temporally sensitive cues to prospective male suitors. And, while chemical communication has been documented in other species of bear (American black bear: Burst & Pelton 1983 ; brown bear: Tschanz et al. 1970; Clapham et al. 2012; 2013; polar bears: Owen *In review*), the giant panda is the only species that has a large anogenital scent gland, and that exhibits unique and energetically demanding marking behaviours (e.g., the “handstand” scent mark exhibited by males).

Scent marking facilitates the coordination of social behaviour prior to face-to-face encounters, vocal behaviour is the predominant signaling modality during proximate social encounters. Giant pandas are, arguably, the most vocally expressive bear species. Giant pandas have a repertoire that includes a range of both affiliative and aggressive vocalisations (Kleiman & Peters 1980). Bleats and chirps are affiliative vocalisations that are predominantly expressed during the breeding season by both females and males (Kleiman & Peters 1990). Recent research

has identified a rich range of information conveyed to conspecifics by both bleats (Charlton et al. 2009b; 2009a; 2009c; 2011) and chirps (Charlton et al. 2010). Changes in the acoustic structure of the chirp provide temporally specific information to male conspecifics regarding the timing of ovulation and sexual receptivity (Charlton et al. 2010). Visual signals have not received the same degree of study (but see Owen et al. 2013), however oestrus-related increases in the rates of backwards walking, rear-present, tail-raising and lordosis posture are typically associated proceptive behaviour during the peri-ovulatory period.

Although social signaling during the breeding season is conspicuous, giant panda social behaviour is poorly understood, especially in regards to the influence of social context on reproductive behaviour. Social grouping during the breeding season has occasionally been documented in the wild (Nie et al. 2011, 2012), but it is not known whether social grouping is correlated with population density, which was likely higher in the panda's evolutionary past. Recent studies conducted in the Foping Nature Reserve, Shaanxi Province, China (Nie et al. 2012b) documented breeding aggregations centered around a single oestrous female being courted 4-6 adult males. Nie et al. (2011) described intense competition between males for access to an oestrous female. In these accounts, the winning male would gain sole access to the oestrus female. However the loser males became spectator males over time, and the aggregation did not disperse until the mating cycle was completed. In a study of captive giant pandas, Owen et al. (2013) found that intersexual social interactions were influenced by behaviour of opposite conspecifics primarily during peak-oestrus. While these observations shed light on giant panda social behaviour, it remains unknown how population density or other factors driven by human activities and habitat loss have influenced social behaviour in the species.

We investigated the temporal dynamics of female giant panda behaviour relative to the first day of natural mating, a proxy for ovulation or peak fertility (Huang et al. 2012). We compared the fit of linear-mixed models consisting of unique signaling behaviours (scent marking, vocalisations and visual signals), as well as multiple interacting signaling behaviours, to determine whether singly, or in concert, these provided temporally explicit clues to impending ovulation or peak fertility. We also assessed the relative influence of social context, (as characterized by the presence or absence of same sex, opposite sex or mixed sex conspecifics in neighbouring pens) and reproductive status on signaling behaviour. We hypothesized that female signaling behaviour would be predominantly influenced by reproductive status. However, because of the energetic constraints on giant panda behaviour, we predicted that social context may influence signaling effort. Specifically, we predicted that, because vocal and visual signals moderate face-to-face encounters during courtship (Bonney et al. 1986; Schaller et al. 1984; Owen et al. 2013), these modalities would be dampened in the absence of male neighbours. In contrast, because, scent-marking behaviour serves to advertise female reproductive status prior to face-to-face encounters (Swaisgood et al. 2004), we predicted that the rate of chemical signaling would be elevated in the absence of males in an effort to attract a male suitor.

Methods

Study subjects and facility

We studied female giant pandas at the China Conservation and Research Centre for the Giant Panda at the Wolong National Nature Reserve (hereafter, “Wolong”; 31°N, 103°E). Giant pandas at Wolong are of mixed provenance, with wild born individuals broadly representing the giant pandas range. Table S1 provides background information on focal females (n=15), neighbouring

females (n=21) and neighbouring males (n=14) included in this study. All pandas included in this study were actively included in the Wolong's breeding program and as such were adult, healthy, and considered reproductively fit. Enclosures consisted of linearly arranged 9 x 8 m outdoor enclosures. Animals had access to a 3 x 6 m den area that was attached to each of the outdoor pens. The outdoor enclosures are separated by approximately 7m of heavy gauge wire mesh and bars, and so offer ample opportunities for visual, chemical and vocal access to neighbours in a protected fashion (Figure 1). At Wolong, adult male and female giant pandas are singly housed. See Swaisgood et al. (2000) for details of housing and husbandry.

Behavioural observations and variables

We conducted 90-min focal observation sessions on female giant pandas during the breeding season over an eight-year period. Focal sessions occurred from 0645-1000h and from 1430-1600h, corresponding to typically peak hours of activity. In total 276 h of behavioural observations were included in the analysis of social context and reproductive status, and 210 h of observation were included in the analysis of temporal patterns relative to first mating. We only included females in this analysis that either naturally mated or were successfully artificially inseminated (i.e., gave birth). We used all occurrence, point in time, and 1-0 sampling (Martin & Bateson 1996) to collect behavioural data based on an extensive ethogram (Swaisgood et al., unpublished). Here we focus our analysis on a subset of behaviours, including: chemosensory behaviours, acoustic signals, and visual signaling behaviours (See Table 1 for definitions). We also analyzed changes in the percent time feeding, locomoting, and stereotypic behaviours. The linear arrangement of pens meant that each focal animal had potentially two neighbours (except

when housed on one of the pens at the end of the row) (Figure 1). We noted, at the beginning of each observation session, the sex and reproductive status of any neighbours.

Independent variables:

Social Context reflected the configuration of male and female pandas housed in neighbouring pens. We include four treatment levels for Social Context: Male, Female, Mixed Sex and Control (no neighbours). The control treatment allows us to distinguish between effects resulting from the lack of a male, versus the unique presence of females. Pandas in our study also typically had access to an adjoining sleeping area, which was separated from neighbouring pens by concrete walls and so did not afford opportunities for visual or consistently audible vocal contact. Because animals were typically able to choose whether to be in the inside or outside area of their enclosure, we calculated the Actual Conspecific Presence (ACP) of neighbours, which reflected the amount of time during a focal observation session that neighbours were not in their sleeping area. ACP was binned into three-levels (1: <33%; 2: 34-66%; 3: 67-100%) and included as a random effect in all analyses. Including this variable allowed us to evaluate the importance of concurrent visual access to neighbours in mediating any audience effects of neighbours on signaling and other behaviour.

“*Day 0*” reflects the first day of natural mating, or the first day of artificial insemination if no mating occurred, and is a proxy for inferred peak fertility or presumed ovulation. Huang et al. (2012) found that the first mating recorded during the period of sexual receptivity accounted for 84% of paternity in giant pandas housed at Wolong, and so is strongly indicative of fertility and presumed ovulation.

Reproductive Status reflects a binning of days relative to peak fertility, and includes three categories: Non-oestrus (days -21 to -8), Oestrus (days -7 to -2), Peak-oestrus (days -1 to +1). This generalized categorization of reproductive status has been used previously (Swaisgood et al. 2000; 2002; Owen et al. 2013).

Statistical analysis

We used R for all data analyses (R Core Team 2013). We transformed all dependent variables to meet assumptions of homoscedasticity. We used an arcsine transform for all proportion data (bleat, chirp and moan vocalisations, locomote and feed) and a log transform for rate data (scent mark, olfactory investigation, visual signaling and stereotypy) (Sokal & Rohlf 2006).

Transformed data were visually inspected (standardized vs. fitted residuals) to ensure that they were homoscedastic. We fitted linear mixed effects models (package: 'nlme' (Pinheiro et al. 2014)) for all variables of interest. We included Focal ID as a random factor in both analyses and also included ACP as random effects in our analysis of the influence of social context and reproductive condition.

To examine the correlation between behaviour and time relative to presumed ovulation, we fit univariate linear mixed effect models for each signaling behaviour, relative to the first day of natural mating, a proxy for ovulation or peak-fertility. For each of these models we calculated the conditional R^2 , an estimate of the total variance explained by both the fixed and random factors and thus the fit of the model, using the method described by Nakagawa & Schielzeth (2013).

To determine which signaling variables best predicted the timing of ovulation, we used an information-theoretic approach and multi-model selection, using the Akaike information

criterion corrected for small sample sizes “AICc” (Burnham & Anderson 2002) to compare the fit of candidate models. The complete model set for all analyses were developed based on both expert opinion and a comprehensive literature review of reproductive behaviour in the giant panda and other bear species (*sensu* Burnham et al. 2011). As a result we considered additive and interaction models of some, but not all possible, combinations of predictor variables. This resulted in 19 models (including an intercept-only model) for the analysis of temporal dynamics. Because highly correlated predictor variables should not be considered in the same model (Burnham et al. 2011; Freckleton 2011), we did not build models that included additive or interactive effects for bleating and chirping vocalisation. Weight of evidence was calculated for each of the candidate models, and while we used a 95% confidence set, we discuss the relative support for models based on the evidence ratio (Richards et al. 2011). For the best model in each confidence set, we calculated the conditional R^2 , an estimate of the total variance explained by both the fixed and random factors and thus the fit of the model, using the method described by Nakagawa & Schielzeth (2013). Following these same guidelines, we fit five models (including an intercept-only model), for each behaviour of interest, for our analysis of the influence of social context and reproductive status on behaviour. We used R package “AICcmodavg” (Mazerolle 2013) to construct AIC tables and calculate the weight of evidence for models and the relative importance (Burnham & Anderson 2002) for each analysis.

RESULTS

Experiment 1: Correlation between signaling and maintenance behaviours and day relative to ovulation

We found strong positive correlations between the day relative to presumed ovulation, and the expression of behaviours related to conspecific signaling, including bleating, chirping, scent marking and visual signaling (Figure 2). The temporal dynamics vary across behaviours, with different behaviours being initiated and peaking at different periods of time with respect to presumed ovulation. However, we found no relationship between moaning, olfactory investigation and stereotypy and the time relative to first mating. We also found that both locomotion and feeding were weakly associated (non-significant relationship) with time relative to first mating. Locomotion showed a positive trend relative to day of first mating and feeding showed a negative trend relative to the day relative to first mating. Figure 2 provides a marginal R^2 values as a measure of the goodness of fit each model.

The relationship between signaling behaviours and the timing of ovulation was best described by the model containing an interaction between the rate of visual signaling, scent marking and the proportion of intervals with the chirp vocalisation (VI*SM*CH, Table 2). The evidence ration between this and the second ranked model (VI*SM) was 3.25, indicating the model that included all three signaling modalities was over 3 times stronger than the bimodal model. Visual signaling appeared in the top four models included in the 95% confidence set, and was the most influential variable in the model set. However, the importance of multimodal signaling was striking, and no model with only a single signaling modality was in the 95% confidence set of best models.

Experiment 2: Relative influence of social context and reproductive status on signaling and maintenance behaviours

In general we found that reproductive status had a primary influence the dynamics of signaling behaviour and was found in each of the topped ranked models. However, however social context also influenced the expression of signaling behaviour, and the interactive or additive effect of social context along with reproductive status were found in 4 of 5 signaling behaviours we examined. Model comparisons for signaling behaviours can be found in Table 3.

The model containing an interaction between reproductive status and social context (ST*SO) best explained the dynamic expression of the bleat vocalisation. This model had a conditional probability of 0.97, and the evidence ratio between it and the next best model in the candidate set was 428.24, indicating there was very little evidence in support of the second ranked model. Inspection of mean values shows that the proportion of intervals with bleating was dramatically lower when the social context consisted only of females (figure 3a), suggesting a suppressive effect on bleating by neighbouring females. In the control treatment, female bleats increased in a stepwise fashion between non-oestrus, oestrus and peak oestrus conditions, which was consistent with the temporal patterns we identified in our first experiment. However, when males were present (both in the Male and Mixed treatments) the rate of bleating during peak-oestrus was substantially higher than both non-oestrus and oestrus treatments, suggesting that the presence of males prompted females to increase their bleating effort during peak oestrus.

The model containing both social context and reproductive status (SO + ST) best explained the dynamic expression of the chirp vocalisation, and the interaction between social context and reproductive status (SO*ST) was the second ranked model. However, the evidence ratio between these two models was 10.11, indicating that there was little support for this second model. Examination of treatment means shows that both Male and Control treatments were comparable, with the most elevated rates of chirping during peak-oestrus. By contrast, in the

Female and Mixed treatments, very low levels of chirping were observed during peak-oestrus, suggesting that the presence of conspecific females had an inhibitory influence on chirping during peak-oestrus (fig. 3b).

The interaction between reproductive status and social context (ST*SO) best explained the dynamics of moan vocalisations, and the evidence ratio between this model and the second ranked model (ST) was 17.56, indicating that there was little evidence in support of this second ranked model. Examination of treatment means shows that moan was most prominently emitted during oestrus in the Mixed and Control treatments (Fig. 3c).

The intercept only model was the top ranked model for olfactory investigation, with social context (SO) a close second. The evidence ratio between these two models was 2.17, suggesting there was little evidence in support of it. Indeed, the third ranked model that contained only reproductive status (ST), had an evidence ratio of 2.20, suggesting that all three of these models were equally strong. Examination of treatment means showed fairly consistent levels of olfactory investigation throughout the study period, however it was substantially lower during peak-oestrus in the Female treatment.

In contrast to vocal signals (bleat and chirp), scent mark, was best explained by the model that only contained reproductive status (ST). This model explained 89% of the variation in the data, and the evidence ratio between it and the second ranked model (ST+SO) was 8.46. These results indicate that scent marking was not influenced by social context. Examination of treatment means (figure 3e) shows a consistent pattern in all treatments, with the highest rate of scent marking occurring during oestrus.

Visual signaling was best explained by the model containing an interaction between reproductive status and social context (ST*SO). This model had a conditional probability of 0.95

compared to other model configurations, and the evidence ratio between it and the second ranked model was 20.14. Visual signals were nearly absent during non-oestrus and oestrus, and the presence of a male clearly increased the rate of expression. Virtually no visual signals were emitted when social context consisted exclusively of females (Figure 3f).

Model comparison for maintenance and stereotypic behaviours can be found in Table 4. Social context influenced feeding behaviour, and the best model included SO only. The evidence ratio was 3.93 relative to the second ranked model (ST+SO). Females tended to feed more during the oestrus and peak-oestrus in the Female treatment (Figure 3g). Locomotion was influenced by both social context and reproductive status, and the ST+SO was the best model in the confidence set. Reproductive status (ST) alone was the second ranked model, and we found evidence for it that was nearly as strong as the top-ranked model with an evidence ratio of 1.2. We found no clear pattern for the expression of stereotypic behaviour, and no model in our set of candidate models best explained the data, and the 95% candidate set included the interaction between reproductive status and social context (ST*SO), intercept only, and reproductive status only (ST).

DISCUSSION

Behavioural flexibility, or social competence, may be reflected by changes in signaling effort, as a function of changes in social context. While the giant panda's reproductive physiology may constrain flexibility, the omnipresent energetic constraints due to the species' reliance on low energy bamboo may promote behavioural flexibility, consistent with other life-history characteristics governed by energetic efficiency, including movement patterns and chemical signaling (Schaller et al. 1985; Nie et al. 2011; 2012b; 2012a; Zhang et al. 2014). Considering

the species' physiological and energetic constraints, we hypothesized that giant panda signaling behaviour would be correlated with the timing of peak-fertility, however we also hypothesized that energetic constraints on reproductive behaviour would drive the evolution of behavioural flexibility in response to variable social context. Therefore, we predicted that female giant pandas would modulate their signaling effort in the absence of male conspecifics. Based on the differential efficacy of signaling modalities, we predicted that vocal and visual signaling behaviour would be reduced in the absence of an appropriate receiver, and that chemical signals, designed to convey information regarding reproductive status in the absence of conspecifics (Swaisgood et al. 2004), would not be affected. To a large extent, these predictions were upheld.

While our results demonstrated that chemical, vocal and visual signaling behaviours changed predictably in females with the approach of ovulation, we also found that the model that best predicted the timing of natural mating included the interaction of scent marking, chirping and visual signaling, suggesting that, together, these signals provide an information-rich, non-redundant message to conspecifics. While research has shown that the changes in the acoustic structure of the chirp vocalisation during the peri-ovulatory period provide explicit information regarding pending fertility (Charlton et al. 2010), we found that the rate of chirping was relatively less informative than the interaction between the rate of chirping, scent marking and visual signaling. Thus, the rate of signaling relative to other signals likely conveys the most temporally explicit information to male conspecifics. Consistent with this finding, previous research has demonstrated the importance of multi-modal signaling in pandas over shorter time frames (Owen et al. 2013).

The temporal dynamics of varying signaling behaviour in female pandas also provides potential mates with predictive information at different stages of oestrus; early signals, such as

scent marking, likely function to alert and recruit potential mates, while later signals, such as affiliative vocalisations and visual displays, may serve to coordinate mating and induce reproductive behaviour and physiology in support of breeding. This interpretation is consistent with the finding that wild male pandas show elevations in energetically-expensive testosterone only when oestrous females are encountered (Nie et al. 2011); the current study exposes the potential behavioural mechanisms that may mediate this physiological effect. Importantly, energy limitations are greatest during the mating season in pandas, due to the seasonal decrease in the quality of bamboo forage (Schaller et al. 1985; Zhang et al. In review), placing a premium on efficiency. These ecological constraints may set the stage for the evolution of enhanced social competence in this solitary species, as the ability to adjust behavioural investments in social signaling would be especially advantageous. Trends in non-signaling behaviour also showed evidence of being shaped to promote reproduction, as indicated by the increased tendency to locomote and decreased tendency to feed as ovulation approached. These alterations in behavioural priorities likely reflect the necessity of sacrificing energy-acquisition behaviours in favor of investing time and energy in locating or recruiting mates. In fact, the increase in locomotory behaviour may be part of a signaling strategy to increase the range of signal dispersion, and therefore encounter rate by potential mates (Swaigood et al. 2002). That these shifting motivational priorities are apparently canalized by past selective forces is evidenced by the continuation of these behavioural shifts even in a captive environment that is more homogeneous than natural environments.

In this context of energetic constraints operating during the mating season it is perhaps unsurprising that, while the relationship between reproductive status and signaling behaviour is strong, we still found evidence for the social modulation of some signaling behaviours. Signals

that are used during face-to-face encounters (e.g., affiliative vocalisations and visual signals) were influenced by the interaction of social context and reproductive status. Specifically, these behaviours were generally inhibited in the female-only treatment and most fully expressed with a male audience. These results suggest the role of energetic constraints in shaping behavioural flexibility or social competence in the species. Signaling behaviour can be energetically demanding and comes with opportunity costs (Smith & Harper 2003; Searcy & Nowicki 2005), and in these females reproductive signals reflect wasted effort if directed at female conspecifics. Furthermore, these results suggest that panda females do not compete with other females for access to males, because the signaling effort in the female-only treatment was generally lower than that documented in the control treatments, including for the more aggressive vocalisation, moan. Consistent with this hypothesis, mating aggregations documented in nature contain a single female and multiple males, and no female-female competition has been reported (Schaller et al. 1985; Nie et al. 2011, 2012a).

Because our results demonstrate differential influences on behaviour in the female and control treatments, we can also distinguish to some degree between changes in behaviour driven by the *absence* of a male versus changes driven by the *exclusive presence* of females. That male and mixed sex treatments typically had similar patterns suggests that it is not simply the presence of a female that is correlated with reduced signaling; it is the exclusive presence of a female. Because signaling was typically less inhibited in control treatments, it may be inferred that social uncertainty (as evidenced by the lack of conspecifics) facilitated signaling, whereas the presence of inappropriate receivers provided information that allowed signalers to make adjustments in signaling effort, potentially conserving energy in the process. Similarly, the presence of male panda rivals, as inferred from chemical signals, facilitates male social behaviour with potential

mates (Bian et al. 2013), providing another example of flexibility and social competence, with males apparently investing more in female courtship when potential competition makes it necessary. It is plausible that over the course of an animal's reproductive lifetime, these adjustments may enhance fitness (Han et al. 2014), especially in an energy-limited species such as the giant panda. Audience effects that promote the fine-tuning of signaling behaviour to target specific conspecifics are one important means by which signaling behaviour can be made more efficient.

Species that are able to muster flexible behavioural responses may be more resilient to the rapid changes in the environment that have been broadly documented as a result of human activities (Tuomainen & Candolin 2010). Panda populations are far below their potential carrying capacity and pandas live in a highly fragmented landscape (Wei et al. 2012). Climate change is expected to have dramatic, and rapid impact on remaining giant panda habitat, further reducing the connectivity of remnant populations (Songer et al. 2012; Vina et al. 2012). Giant pandas, therefore, much like other declining species, exist at lower social densities and may experience shifts in demographic structure. That they also show behavioural flexibility in response to changing social context may mean that, as a species, they will be better equipped to cope with anthropogenically-mediated changes in social context. However, caution is warranted because there will likely be limits to this flexibility. Our results also provide guidance to managers of conservation breeding programs, allowing them to predict the timing of ovulation using behavioural cues and suggest a strategy which incorporates social context as a management tool to enhance the display of sexual behaviours and reproductive output (see also Swaisgood et al. 2006).

Understanding how animals respond to variations in social context has broad conservation applications, and can be used to predict population dynamics in the face of changes in population density or changes in age/sex structure (Whitehead et al. 1997), for manipulating social context in the captive environment for conservation breeding (Yoerg 1999; Fisher et al. 2004; Swaisgood & Schulte 2010), and for increasing the potential for success in both reintroductions and translocations (Shier & Swaisgood 2010). Therefore, an understanding of how sensitive animals are to changes in social context is important. Because underestimating the complexity of reproductive behaviour can have dire consequences for species requiring conservation or harvest management (Anthony & Blumstein 2000; Rowe & Hutchings 2003), we suggest that further research be done examining the influence of social context on behavioural flexibility, especially in the under-studied solitary species.

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Figure 1. Configuration of panda housing at the Wolong Breeding Center. Pens are arranged linearly. Bears have access to an outdoor pen as well as intermittent access to an indoor den area.

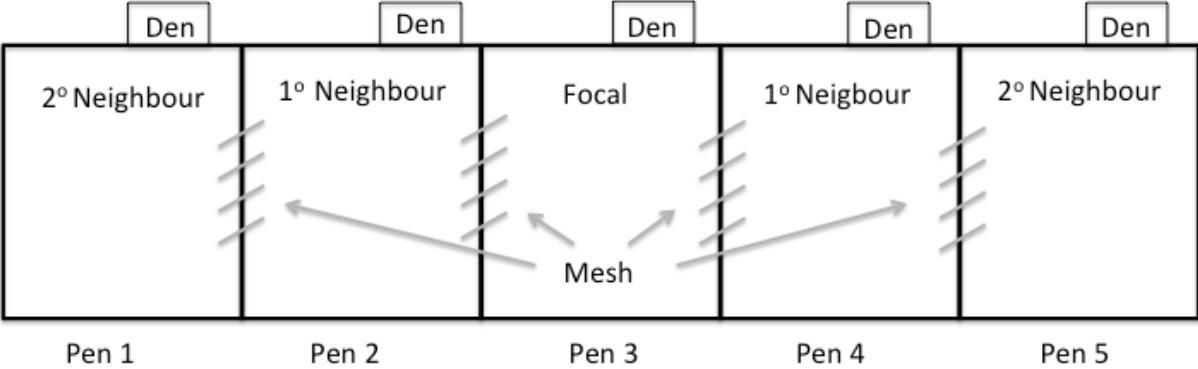


Table 1. Giant panda ethogram (signaling and maintenance behaviours only).

Behaviour	Definition
Bleat vocalisation	Twittering vocalisation, similar to a goat's bleat. Variable in length and affiliative in intent.
Chirp vocalisation	High pitched vocalisation, typically short in duration, affiliative intent.
Moan vocalisation	Low-pitched call of variable duration, associated with low-level aggression.
Scent mark	Anogenital rubbing against an object or substrate (e.g., ground, tree, rock) in any marking posture (e.g., squat, reverse, leg-cock, or handstand).
Olfactory investigation	Places nose to substrate and sniffs for more than 1 second. May include flehmen behaviour.
Visual signal	Composite index of backwards walking, rear present, tail-raising or lordosis posture.
Locomote	Directional movement between points. Includes walking, climbing or pacing.
Feed	Consumption, or processing for consumption, of provisioned food, including bamboo and supplementary diet items.
Stereotypy	Unvarying, repetitive behaviours without any apparent function or purpose. Includes, pirouette, head-toss, paw-sucking or truncated rolling.

Table 2. Performance of linear mixed effects models predicting the timing of ovulation or peak-fertility.

Fixed effects	K	AICc	Δ AICc	ω_i
<i>VI*SM*CH</i>	10	1307.99	0.00	0.70
<i>VI*SM</i>	6	1310.35	2.70	0.22
<i>VI*CH</i>	6	1314.84	6.85	0.02
<i>VI*SM*BL</i>	10	1315.26	7.27	0.02
<i>BL*SM</i>	6	1315.83	7.84	0.01
<i>VI*BL</i>	6	1317.46	9.47	0.01
<i>SM</i>	4	1317.75	9.76	0.01
<i>VI</i>	4	1317.96	9.97	0.01
<i>BL*OI</i>	6	1319.69	11.70	0.01
<i>VI*MO</i>	6	1320.18	12.19	0.00
<i>BL</i>	4	1321.06	13.07	0.00
<i>CH</i>	4	1321.81	13.82	0.00
<i>BL*MO</i>	6	1322.91	14.92	0.00
<i>CH*OI*SM</i>	10	1323.19	15.20	0.00
Intercept only	3	1324.09	16.10	0.00
<i>MO</i>	4	1324.64	16.65	0.00
<i>CH*OI</i>	6	1324.99	17.00	0.00
<i>OI*MO</i>	6	1325.53	17.54	0.00
<i>OI</i>	4	1325.61	17.62	0.00

The Akaike score adjusted for small sample sizes (AICc), differences between models (Δ AICc) and weights, or conditional probability of being the correct model, (ω_i) are given. The 95% candidate set is in bold. *VI*=Visual signaling behaviour; *SM*=Scent mark; *OI*=Olfactory investigation; *CH*=Chirp vocalisation; *BL*=Bleat vocalisation; *MO*= Moan vocalisation.

Table 3. Comparison of 95% candidate models for the influence of social context and female reproductive status on signaling behaviours. The complete model set included an intercept only model for each behaviour analyzed. Evidence ratio reflects the weight of evidence between the first and second ranked models.

Behaviour	<i>Models</i>	K	AICc	Δ AICc	ω_i	Evidence Ratio
Bleat vocal	<i>ST*SO</i>	15	-162.20	0.00	1.00	4283.2
	<i>ST</i>	6	-145.90	16.72	0.00	
Chirp vocal	<i>ST+SO</i>	9	-505.25	0.00	0.86	10.11
	<i>ST*SO</i>	15	-506.68	4.63	0.08	
	<i>ST</i>	6	-499.67	5.58	0.05	
Moan vocal	<i>ST*SO</i>	15	-659.06	0.00	1.00	679.51
	<i>ST</i>	6	-641.41	17.65	0.00	
Scent mark	<i>ST</i>	6	274.40	0.00	0.89	8.46
	<i>ST+SO</i>	10	278.60	4.21	0.11	
	<i>ST*SO</i>	16	288.1	13.72	0.00	
Olfactory investigation	<i>Intercept only</i>	4	338.39	0.00	0.65	3.05
	<i>SO</i>	7	340.62	2.23	0.21	
	<i>ST</i>	6	341.99	3.61	0.11	
Visual display	<i>ST*SO</i>	15	-422.25	0.00	0.94	20.14
	<i>ST</i>	6	-416.25	6.01	0.05	

Random factors included in all models include Subject ID and Actual Conspecific Presence (ACP). The Akaike score adjusted for small sample sizes (AICc), differences between models (Δ AICc) and weights, or conditional probability of being the correct model, (ω_i) are given. The 95% candidate set is in bold. ST=Reproductive status; SO=Social context.

Table 4. Comparison of 95% candidate models for the influence of social context and female reproductive status on maintenance behaviours. For each behaviour analyzed, the complete model set included an intercept only model. Evidence ratio reflects the weight of evidence between the first and second ranked models.

Behaviour	<i>Models</i>	K	AICc	Δ AICc	ω_i	Evidence Ratio
Feed	<i>SO</i>	7	-157.31	0.00	0.78	3.93
	<i>ST+SO</i>	9	-154.38	2.74	0.20	
Locomote	<i>ST+SO</i>	9	102.36	0.00	0.54	1.20
	<i>ST</i>	6	102.73	2.37	0.45	
	<i>SO</i>	6	112.84	10.47	0.01	
Stereotypic	<i>ST*SO</i>	7	-749.71	0.00	0.53	1.88
	<i>Intercept only</i>	4	-748.45	1.26	0.28	
	<i>ST</i>	6	-742.42	2.29	0.17	

Random effects included in each model include subject ID, and ACP (actual conspecific presence). The Akaike score adjusted for small sample sizes (AICc), differences between models (Δ AICc) and weights, or conditional probability of being the correct model, (ω_i) are given. The 95% candidate set is in bold. SO= Social context, ST= Reproductive status.

Supplemental Table 1. Giant pandas included in this study, as either focals or neighbours. All captive born individuals were born at the Wolong Breeding Centre. Provenance of wild individuals includes the county from which they were recovered.

ID #	Sex	Provenance	ID #	Sex	Provenance
SB498	F	Wild- Chongzhou	SB382	F	Wild- Wolong
SB371	F	Captive	SB475	F	Captive
SB418	F	Wild- Taibai	SB404	F	Captive
SB385	F	Captive	SB476	F	Captive
SB358	F	Wild- Baoxing	SB394	M	Captive
SB432	F	Captive	SB413	M	Captive
SB439	F	Captive	SB415	M	Wild- Baoxing
SB544	F	Wild- Mianning	SB305	M	Wild- Baoxing
SB499	F	Wild- Dijianyan	SB455	M	Captive
SB230	F	Wild- Quinchuan	SB298	M	Wild- Baishuiji
SB437	F	Captive	SB308	M	Wild- Baoxing
SB374	F	Wild- Leibuo	SB492	M	Captive
SB447	F	Wild- Pingwu	SB377	M	Wild- Foping
SB397	F	Wild- Baoxing	SB479	M	Captive
SB414	F	Wild- Baoxing	SB381	M	Wild- Wenshuan
SB446	F	Wild- Pingwu	SB399	M	Captive
SB444	F	Wild- Baoxing	SB329	M	Wild- Baoxing
SB434	F	Captive	SB357	M	Wild- Nanping

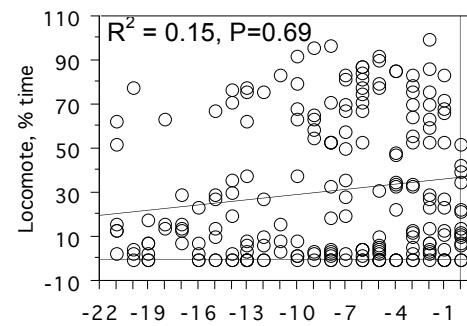
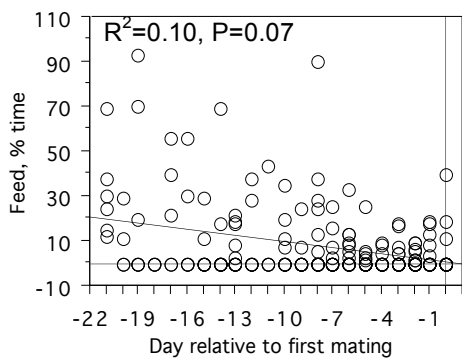
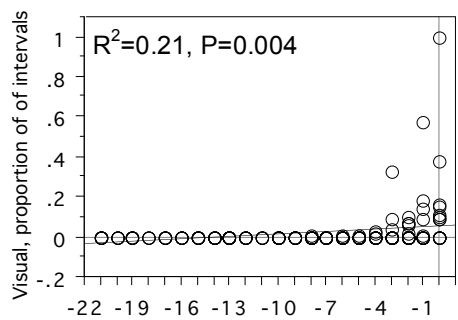
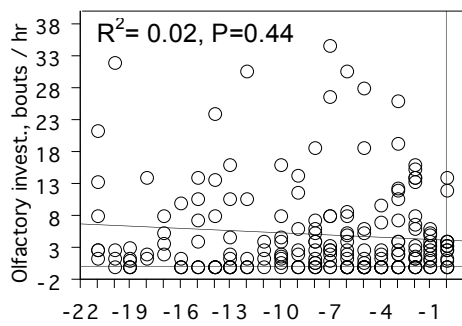
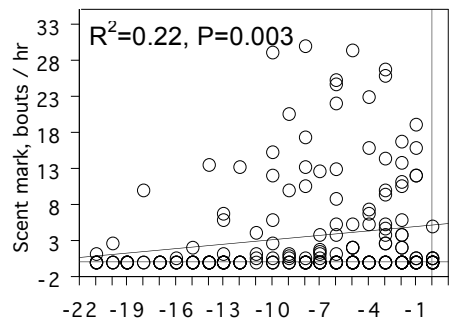
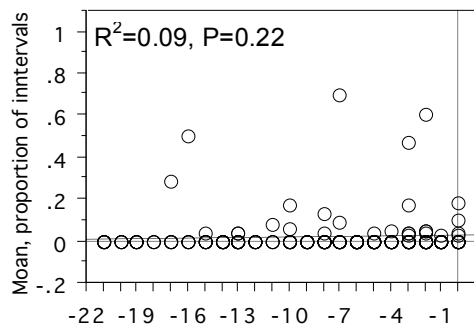
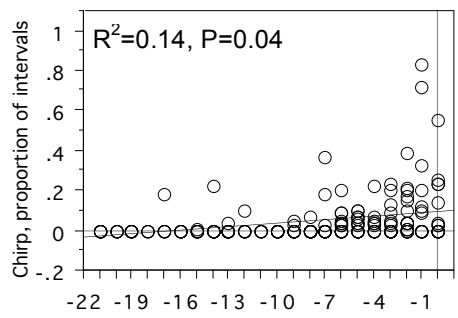
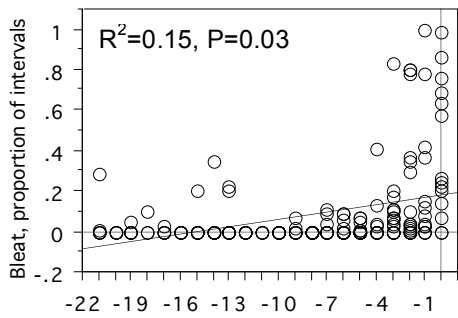
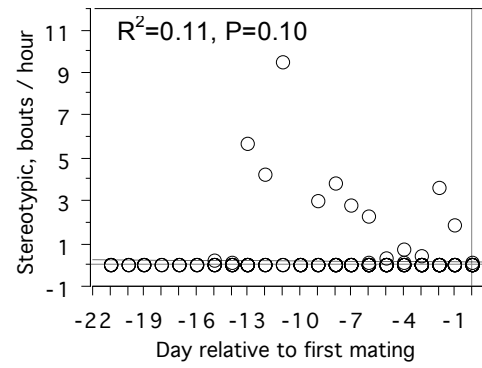


Figure 2. Relationship between day relative to first mating and the expression of signaling and maintenance behaviours. R^2 for each reflects the conditional R^2 , which includes calculation for random factors in goodness of fit.



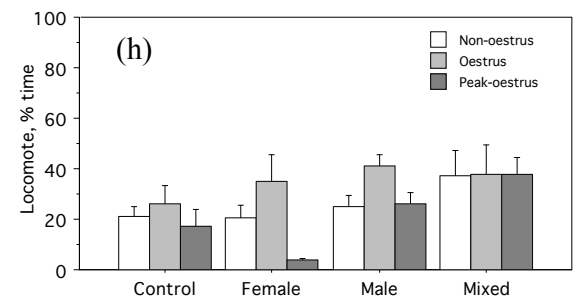
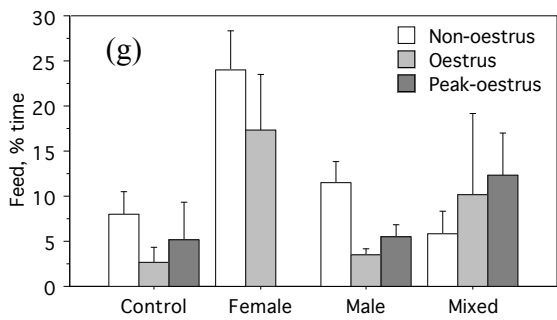
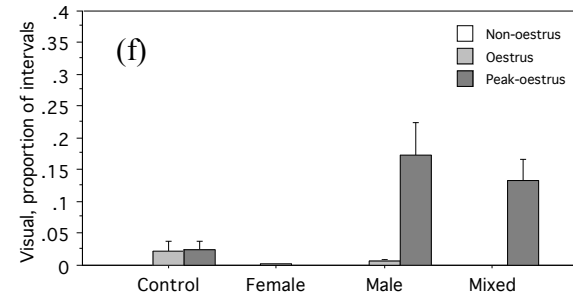
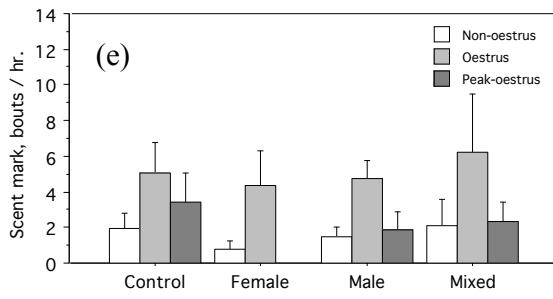
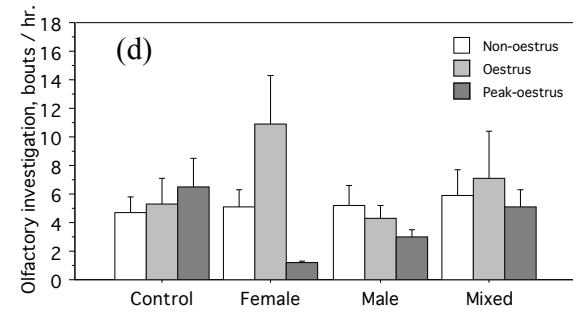
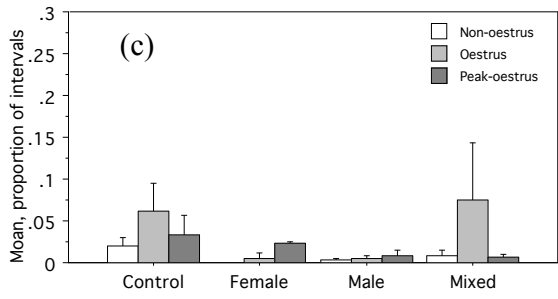
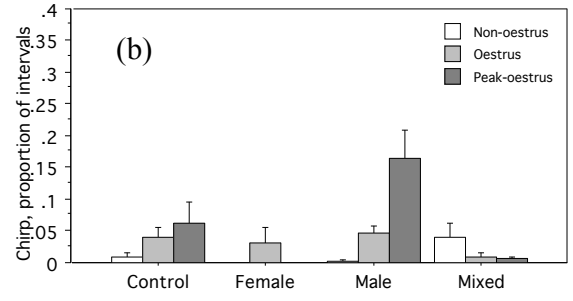
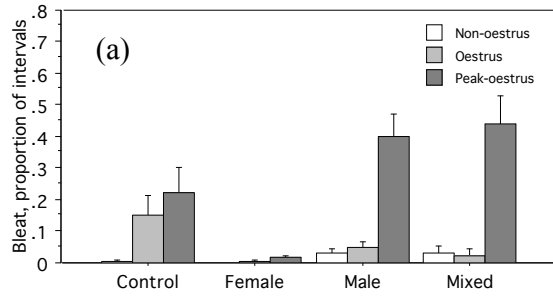
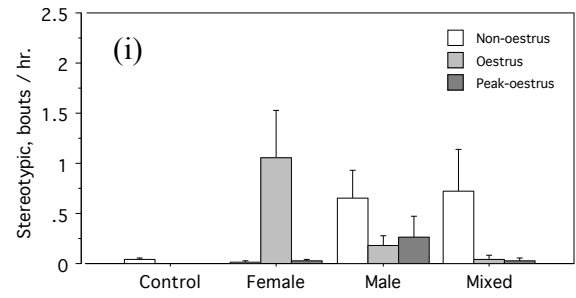


Figure 3. The influence of social context and reproductive status on female giant panda behaviour including mean \pm SEM of (a) bleat vocalisation, (b) chirp vocalisation, (c) moan vocalisation, (d) olfactory investigation, (e) scent mark, (f) visual signal, (g) feed, (h) locomote, and (i) stereotypy.



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CHAPTER 4: DYNAMICS OF MALE-FEMALE MULTIMODAL SIGNALING BEHAVIOR ACROSS THE ESTROUS CYCLE IN GIANT PANDAS (*AILUROPODA MELANOLEUCA*), *Ethology* (2013) 119:869-880.

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Abstract

Giant panda courtship behavior includes multimodal signaling assemblages consisting of olfactory, vocal and postural elements. While signaling is generally conspicuous, successful copulation is inconsistently achieved in captivity, even when female behavioral and physiological data indicate that ovulation is imminent. We set out to characterize these complex patterns of social behavior by observing interactions between 26 unique pairs of giant pandas housed in adjoining pens throughout the females' reproductive cycle. We categorized social behaviors from a transactional perspective, and examined social exchanges via analyses of the relative frequency of social behaviors, and via the sequential relationship between male and female social behavior. From non-estrus to peak-estrus, we found that the relative frequency of female affiliative and sexual behavior increased, and that the relative frequency of ambivalent and aggressive behavior decreased. Male behavior was fairly constant, except for sexual behavior, which increased during peak-estrus, when it was facilitated by female sexual behavior. Sequential analysis of social interactions showed that preceding behavior had a significant influence over the other panda's response behavior primarily during peak-estrus, suggesting that pandas are most responsive to conspecific signaling during the peri-ovulatory period. However, behavioral momentum was a dominant feature of the intra-individual transitions. Females maintained sexual, ambivalent and neutral behavior during interactions significantly more than would be expected by chance, with male behavior bearing little influence once the behavior was initiated. A similar pattern was also observed in males, who maintained affiliative, interested and neutral behaviors. Overall, our data suggest that the multimodal signals used by giant pandas during courtship do not consistently evoke a discrete, immediate response from receivers.

Instead, signals appear to advertise reproductive condition and influence potential mates over longer timeframes, suggesting the potential tonic role of communication.

Keywords: multimodal signaling, courtship communication, giant panda, sequential analysis

Introduction

Communication during courtship can be complex and difficult to characterize, especially if intersexual exchanges are temporally dynamic and include multimodal signaling (Wilgers & Hebets 2011). Signal theory suggests that communication is a dynamic process wherein the ultimate outcome of an exchange is not predetermined, but dependent upon the information exchanged by individuals. Of course, underlying physiological state, past reproductive performance and body condition may also influence both the information exchanged, and the outcome of intersexual exchanges (Rowe 1999; Fawcett & Johnstone 2003; Scheuber et al. 2004;). These factors may also drive the use of multiple cues in communication (Gerhardt 1991, Galeotti et al. 1997) allowing signals to be transmitted over multiple sensory channels simultaneously. Multimodal signaling, or multiple cues, may provide redundant information, enhancing the chances of signal reception and responsiveness, act synergistically, thereby creating a signaling threshold needed to elicit a receiver response, or they may facilitate the transfer of multiple streams of information with multimodal cues functioning independently even though they are received simultaneously (Partan & Marler, 1999, 2005). Additionally, the use of multimodal signaling may reduce the costs of mate choice (Candolin 2003).

The giant panda (*Ailuropoda melanoleuca*) is an excellent model for the study of communication during courtship. An endangered species, with conservation breeding as an important component of the overall conservation strategy (Wildt et al. 2006; Swaisgood et al. 2010, 2011), the panda historically was notoriously difficult to breed in captivity. For successful captive breeding management, interpreting when a breeding encounter is moving towards copulation, or towards potentially injurious failure, may depend on the correct interpretation of social exchanges between the male and female over the course of the reproductive cycle. Given the short window of opportunity for breeding, it is imperative that managers accurately assess

multimodal behavioral assemblages, displayed by both females and males, *prior* to pairing for mating in order to ensure the safety of the animals and to promote successful copulation (Swaisgood et al. 2004). Moreover, managers must understand how these dynamics change over the course of the female reproductive cycle to allow judicious decisions regarding mating management.

Female giant pandas have a single, annual estrus, with mating receptivity lasting only 1-3 days (Schaller et al. 1985). Females undergo a 10-14 day period of follicular development prior to ovulation, which appears to be spontaneous (Durrant et al. 2003). During follicular development, estrogen levels begin to climb, undergo a rapid elevation and subsequent precipitous drop during the 2-3 day peri-ovulatory period (Kersey et al. 2010). Female behavior appears to be strongly coupled to circulating estrogen levels, and the behavioral repertoire of estrous females appears to be equivocal whether or not a male is present (Bonney et al. 1982; Lindburg et al. 2001; McGeehan et al. 2002). Due to the brevity of the window of female receptivity and the concomitant period of rapid hormonal changes and spontaneous ovulation, signals that both accurately reflect the female's reproductive condition and facilitate assessment by male conspecifics, must be conveyed to males for successful reproduction.

During the spring breeding season the coordination of courtship is primarily dependent on the exchange of olfactory signals prior to face-to-face encounters, and acoustic signals once males and females are in proximity. Signaling assemblages during face-to-face encounters are further complicated by the prominence of visual displays and other behaviors employed during social interactions, such as approaches, backwards walking, rear present, and lordosis (Kleiman 1984; Swaisgood et al. 2004). Taken together, these dynamic assemblages demonstrate a clear role for multimodal communication during courtship in this species.

Past research has focused on isolating chemical (Swaisgood et al. 2004) and vocal signals (Charlton et al. 2009a, 2009b, 2010a, 2010b, 2011, 2012) to determine their motivational and functional significance. However, while this reductionist approach has been remarkably successful, we still do not understand how these signal assemblages function together during the courtship process. Here, to gain a more holistic understanding of social interactions, we use a transactional approach to characterize panda social behavior (Lyons et al. 1992). When social exchanges are characterized in a transactional manner, it becomes easier to analyze how the behavior of one individual influences the behavior of another during naturally occurring social exchanges. If information exchange between male and female pandas has influence over the other's behavior or facilitates cooperation, then we would expect to see sequential dependency between male and female behaviors, and distinct patterns of the facilitatory and inhibiting effects of certain behaviors. However, if signaling behavior is not tightly coupled to discrete responses in the receiver, then intra-individual behavioral momentum, more than social exchange, may characterize the sequence of behaviors during breeding encounters. Behavioral momentum is generally defined as a resistance to change, even when confronted with variable stimuli (Nevin & Grace 2000).

Here we characterize for the first time the temporal dynamics of giant panda social exchanges during the breeding season. In an attempt to better understand the significance of the displays used during panda courtship, we examine how the female's reproductive condition influences the nature of these social interactions and how individuals respond to naturally occurring composite social displays.

Methods

Animals and housing

Study subjects included 10 adult females and 5 adult males at least 5.5 years of age. The animals were housed at the Wolong Breeding Center in Sichuan, China. For details of housing and diet, refer to Swaisgood et al. (1999). The pandas were housed in enclosures consisting of a 9 x 8 m outdoor portion and 3 x 6 m indoor den. Pandas had access to one or two neighbors housed in adjoining pens through cage bars running nearly the entire length of the wall separating them (7 m). Attached to the cage bars is a wire mesh precluding all but minimal direct physical contact. Neighboring pandas, therefore, had ample olfactory, visual and auditory, but limited tactile and gustatory access to one-another.

Behavioral Observations

We observed interactions between males and females housed in adjoining pens throughout the females' reproductive cycle during a breeding season (February-May). Behaviors were characterized using a transactional approach (Lyons et al. 1992) wherein the observer integrates multiple sources of information into a few meaningful, functional categories. This differs from the traditional ethological approach of recording discrete motor patterns and attempting to reconstruct the functional context during the analytical phase.

All social interactions were scored according to the categories of behavior defined in Table 1. Categorization of the functional significance of vocalizations follows Kleiman and Peters (1990). Behavioral categories are mutually exclusive and exhaustive. A social transaction commenced when one panda approached to within two body lengths (hereafter, "proximity") of another and remained in proximity for ≥ 5 s. The approacher's initial behavior was categorized, as was the approachee's response. Each change in behavior by one of the participants

necessitated a response in the other, even if that response was to maintain the same behavior in spite of the other party's change in behavior. This scoring protocol yields a chain of behaviors alternating between actions by one participant and the other. A transaction was terminated when one panda departed to greater than two body lengths or both animals remained neutral (see Table 1) while in proximity. We conducted 224 focal observations on individual animals during peak activity periods (06:45-10:00 h and 14:30-16:00 h), recording all interactions with neighboring animals. Observation sessions were 60-90 min for females, and 45 min for males. These observations yielded data for 26 unique male-female pairs. Data were recorded in real-time, using pencil and paper.

Data Analysis

Non-sequential data

For each male-female pair housed in adjoining pens, we calculated total frequency of each behavior type and divided that number by the total amount of time the pair was observed during each phase of the female's reproductive cycle, yielding an average behavioral rate per hour for each pair, for each reproductive period. We then calculated the relative frequency of each behavior (specific behavior ÷ total # of behaviors). Because some pairs were not housed in adjacent pens throughout the duration of the study, we were unable to obtain data for every pair during every phase of the reproductive cycle. For purposes of analysis, we divided the female reproductive cycle into three distinct phases: (1) 'Peak-estrus' was defined as the three-day period including the day before, the day of, and the day after successful mating. In cases where no mating occurred (N=4), we used the peak in vulvar swelling (Durrant et al. 2003). (2) Because the duration of behavioral estrus is variable (Swaigood, unpublished data), we chose to define

'estrus' by the presence of the following, not explicitly social, behavioral and physical indices: elevated scent-marking, water play, backwards walking, rolling, masturbation, and vulvar swelling and reddening. (3) The 'non-estrus' period included the days prior to 'estrus' and more than three days post 'peak-estrus.' We included these post-estrus data after first determining that there were no substantive differences between the pre- and post-estrus periods. We categorized male interactive data according to the reproductive condition of the female with which he interacted.

Of the behaviors defined in Table 1, 'shows interest' occurred too infrequently in females to merit analysis, and both ambivalence and aggression were very rarely expressed by males, and so were also excluded from analysis. We inspected residual plots of behavioral data for deviations from normality and subjected all data to Hartley's Fmax test for heterogeneity of variance (Sokal & Rohlf 2006) and transformed data to meet the assumptions of normality. We present mean \pm SE for the untransformed relative frequency data. We fitted a linear mixed-effect model in R (R Core Development Team 2011) using the 'lme4' package (Bates et al. 2013) for each of the behavioral variables of interest. To assess changes in behavior between stages of the estrus cycle, we performed Tukey HSD for each behavior to test for differences between treatment means: (1) non-estrus versus estrus, (2) non-estrus versus peak-estrus and (2) estrus versus peak-estrus.

Sequential data analysis

The same behavior categories included in the non-sequential analyses from males and females were also analyzed for sequential dependence. 'Sexual' was also excluded from analysis during non-estrus and estrus. These criteria for excluding data ensured that all behaviors

analyzed met the requirement that sequential analyses be based on behaviors that comprise at least 20% of the total frequency (Bakeman & Gottman 1997). To avoid the problem of data pooling (Machlis et al. 1985), for each male-female pair we calculated the average frequency for each possible transition from one interactive behavior to another ('behavioral dyads'). To test for sequential dependence, we constructed six transition matrices for preceding and following behavioral elements, one for each sex in each of the three reproductive periods, and subjected each table to log-linear analysis (Likelihood Ratio Chi Square test) using ILOG (Bakeman & Robinson, 1994). We calculated first-order conditional probabilities (lag 1) to assess the immediate response of each sex to the actions of the other, and probabilities (lag 2) to determine whether a subject's last previous action affected subsequent behavior (i.e., 'behavioral momentum'). Because our data collection protocol required that each action by one animal be followed by a response by another animal, all lag 1 analyses represent male-to-female or female-to-male transitions, whereas lag 2 analyses arise from intra-individual transitional probabilities. We also calculated higher-order conditional probabilities, but report only lag 1 and lag 2 results here because the others failed to attain statistical significance, in part because fewer long sequences were available for analysis. Alpha was set at <0.05 . Following the logic of Fisher's LSD posthoc test in ANOVA, we used adjusted residuals to determine the significance of transitions between specific behavioral dyads ($Z \geq |1.96|$) only where the omnibus test indicated significant table- and row-wise sequential constraints (i.e., evidence for non-random occurrence of behavioral transitions). We used standardized residuals for one table (F \rightarrow M at lag 1, peak-estrus) to determine the significance of behavioral dyads. Standardized residuals are a more conservative test than adjusted residuals (Bakeman & Quera 1995). We used the heterogeneity

G-statistic (Sokal and Rohlf, 2006) to test for reproductive period effects on sequential dependence.

Prior to analyses, we took several steps to ensure that the data met the assumptions of the analysis. One fundamental problem that we encountered was that of structural zeroes, which occur where consecutive codes cannot repeat (Bakeman & Gottman 1997). According to our scoring protocol, an individual's action could not be followed by another action by the same individual. In consequence, half of the potential behavioral transitions are structural zeroes. In addition, male sexual behavior required that the female first exhibited sexual behavior, rendering structural zeroes for several other transitions. Most traditional sequential analyses cannot handle this many structural zeroes, but the log-linear method we employed uses an iterative process to yield a valid analysis. Another assumption unique to sequential analysis is stationarity, which requires that the probabilistic structure not change over time (Bakeman & Gottman 1997). To test for stationarity for each table, we used the G-test for repeated observations in ILOG (Bakeman & Robinson 1994) to determine whether transitional probabilities differed between the first and second half of observation sessions (see Bakeman & Gottman 1997). We ensured that our table sample size met the requirements that the total sample size be at least four times the number of cells not structurally zero. Row-wise sample size was deemed adequate if it met the standard Chi Square test assumption that no expected frequency be less than five (Siegel & Castellan 1988).

Results

All results are presented using the following compound (Sex-Behavior) coding scheme: Sex: 'F' (female), 'M' (male); Behavior: 'SX' (sexual), 'AF' (affiliative), 'SI' (shows interest), 'NU' (neutral), 'AM' (ambivalent), 'AG' (aggressive) (Table 1).

Rate of social behavior

The overall rate of all behavioral elements observed by both sexes during interactions changed significantly across the reproductive cycle ($F_{2, 17}=10.4, P=0.001$). The rate of interactive behaviors was slightly elevated, albeit non-significantly, during estrus (9.8 ± 2.2) compared with non-estrus ($6.4 \pm 1.8; P=0.52$), and showed a dramatic increase during peak-estrus (40.3 ± 6.5) relative to estrus ($P=0.002$). Below we present analyses for the relative frequency of social behaviors. Relative frequency yields information on the probability of a particular behavioral response, given that an interaction has occurred; thus it is not influenced by the substantive changes in overall interaction rates across the reproductive cycle.

Patterns of female social behavior during interactions with males

Females were responsible for approaching males proportionately more often than the converse during estrus than either non-estrus ($P=0.01$) or peak-estrus ($P=0.04$; main effect: $F_{2, 17}=3.7, P=0.04$) (Fig. 1). Female approach rates varied with reproductive period, albeit not quite significantly ($F_{2, 17}=2.9, P=0.08$), a trend resulting from incremental increases from non-estrus to estrus and estrus to peak-estrus (non-significant planned comparisons).

Table 2 provides a summary of results for models run on each social behavior for both female and male data. Figure 2 displays the relative frequencies (mean \pm SEM) of female

interactive behavior across the three reproductive periods. The proportion of F-AG behavior in interactions with males changed across the reproductive cycle (albeit non-significantly; Fig. 2a) with an overall trend towards reduced aggressiveness from non-estrus to peak-estrus. Pairwise comparisons revealed that the females were significantly less likely to respond aggressively to males in peak-estrus than during non-estrus. The relative frequency of F-AM behavior decreased in a stepwise fashion from non-estrus to peak-estrus and the main effect was significant (Fig. 2b). Females also displayed a significantly lower relative frequency of ambivalent behavior from non-estrus to estrus, and between non-estrus and peak-estrus. The relative frequency of F-NU behavior also declined significantly over the course of the estrus cycle, and neutral behavior constituted a proportionally lower amount of female behavior during peak-estrus and estrus as compared to non-estrus (Fig. 2c)

Females significantly altered the relative frequencies of AF behavior across the three reproductive conditions (Fig. 2d), an effect largely attributable to the marked increase in the relative frequency of AF from estrus to peak-estrus. Pairwise comparisons of relative frequency showed a significant increase in the proportion of AF responses from non-estrus to peak-estrus (Fig. 2d). The relative frequency of F-SX responses toward males was significantly affected by reproductive period with females displaying more SX behavior during peak-estrus than estrus and non-estrus (Fig. 2e).

Patterns of male social behavior during interaction with females

Males approached females at the same rate regardless of female reproductive condition ($F_{2, 17}=1.9, P=0.18$), although there was a trend to approach females more in peak-estrus than estrus ($P=0.07$), and males were responsible for a higher proportion of approaches during non-

estrus (Fig. 1). The relative frequencies of male responses to females in differing reproductive conditions are shown in Figure 3. Model and pairwise comparison statistics are provided in Table 2. The relative frequency of NU, SI and AF responses by males to females were not influenced by female reproductive condition, although the relative frequency of both SI and AF showed an increasing trend from non-estrus to estrus. However, the relative frequency of M-SX covaried significantly with female reproductive condition, with a marked increase across the reproductive cycle. Pairwise comparisons showed significantly elevated relative frequencies of SX behavior from males during peak estrus compared to both estrus and non-estrus.

Sequential analysis of behavior transitions

Table 3 displays the conditional probabilities of inter- and intra-individual behavioral transitions for males and females, respectively. These descriptive statistics show clearly that some behaviors are often associated with corresponding behaviors in the opposite sex. For example, males displayed NU behavior following female AG 78% of the time during peak-estrus, but only 27% of the time when a female displays AM behavior. By contrast, males displayed AF behavior 56% of the time following female AM behavior. These conditional probabilities demonstrate well how female and male behavior is synchronized over the longer time frame of the interaction or day, but do not demonstrate that the subject displays a discretely different response following individual displays of the other panda. Transition matrix analysis, reported below, was used to determine how these individual displays alter the ongoing pattern of behavior during an interaction.

Stationarity

All transition tables analyzed met the assumption of stationarity (lag 1: female-to-male transitions during non-estrus: $G_6^2 = 2.7$, NS; estrus: $G_6^2 = 2.7$, NS; and peak-estrus: $G_8^2 = 9.0$, NS; lag 1 for male-to-female transitions during non-estrus: $G_6^2 = 2.6$, NS; estrus: $G_6^2 = 7.6$, NS; and peak-estrus: $G_{12}^2 = 8.2$, NS; intra-individual lag 2 transitions for females during non-estrus: $G_6^2 = 5.1$, NS; estrus: $G_7^2 = 2.0$, NS; and peak-estrus: $G_{15}^2 = 4.2$, NS; intra-individual (lag 2) transitions for males during non-estrus: $G_4^2 = 3.9$, NS; estrus: $G_4^2 = 1.1$, NS; and peak-estrus: $G_9^2 = 7.2$, NS).

Inter-sexual behavioral transitions (lag 1)

Sequential data at lag 1 were significantly heterogeneous between reproductive stages for both the $F \rightarrow M$ transitions ($G_8 = 46.2$, $P < 0.001$) and for the $M \rightarrow F$ transitions ($G_{18} = 77.6$, $P < 0.001$).

Female to male (F → M) behavioral transitions

We found significant evidence of sequential constraints operating during peak estrous ($G_8^2 = 46.0$, $P < 0.001$) periods, but not during non-estrous ($G_6^2 = 8.2$, NS) or estrus ($G_6^2 = 3.5$, NS) (Table 3a).

The peak-estrus table for the $F \rightarrow M$ transitions had adequate sample size ($N = 290.2$) and all rows contained cells with expected average frequencies > 5 . These data were sequentially constrained at lag 1 ($G_8^2 = 46.0$, $P < .001$). Inspection of cell-wise 'Z' scores found the following transition to be significant: F-AG behavior strongly inhibited M-NU behavior ($Z = -4.13$, $P < 0.001$). Interestingly, F-SX facilitated MNU ($Z = 3.13$, $P < 0.002$), and inhibited M-SI ($Z = -3.06$, $P < 0.01$) and M-AF ($Z = -2.03$, $P < 0.05$). These effects were likely the consequence of high probability of F-SX being followed by M-SX (0.65) by any male otherwise exhibiting affiliative

or ambivalent behavior. Note that the transitional probability of F-SX→F-SX was 0.65.

However, this score was not significant ($Z=0.01$, NS) due to the computational constraints of the structural zeros.

Male to female (M→F) behavioral transitions

Reproductive period had a significant effect on M→F behavioral transitions at lag 1 ($G_{18} = 77.6$, $P<0.001$). However, the effect was not homogenous across all reproductive conditions.

We found significant evidence of sequential constraints operating during the non-estrous ($G_6^2=14.4$, $P=0.025$) and peak estrous ($G_{12}^2=73.5$, $P<0.001$) periods, but not during estrus ($G_6^2=5.4$, NS) (Table 3b). During the non-estrous period M-NU had an inhibitory effect on F-AG ($Z=-2.86$, $P<0.01$) and had a facilitatory effect on F-AF ($Z=-1.96$, $P<0.05$) behavior. M-SI inhibited F-AF ($Z=-2.38$, $P<0.01$) behavior. Although non-significant, F-AG behavior was most common in response to M-SI (29%) or M-AF (24%).

Although the estrous period was not sequentially constrained, examination of Table 3 reveals a general increase in F-AM responses and a corresponding reduction in F-NU responses. In contrast with the non-estrous period, estrous females responded with F-AF behavior equally regardless of the preceding behavior (although M-AF behavior appears to have a slight, but non-significant, facilitatory effect on F-AF behavior).

The peak estrous period yielded the most pronounced effects on M→F behavioral transitions (Table 3b). F-SX among peak estrous females was facilitated by M-SX ($Z=4.74$, $P<0.0001$). M-SX behavior also inhibited the expression of both F-NU ($Z=-1.06$, $P<0.05$) and F-AF ($Z=-3.93$, $P<0.0001$) behavior, probably an incidental consequence of the high proportion of F-SX responses (71%) to M-SX behavior. M-AF behavior significantly inhibited F-AG ($Z=-$

3.12, $P < 0.001$) and F-NU ($Z = -1.96$, $P < 0.05$), and facilitated F-AM ($Z = 3.11$, $P < 0.001$). Peak-estrous females were also most likely to display F-NU ($Z = 2.29$, $P < 0.01$) behavior when the preceding behavior by the male was Neutral (29%).

Intra-individual behavior transitions (lag 2)

Sequential data at lag 2 were significantly heterogeneous between reproductive stages for both the F→F transitions ($G_8 = 46.2$, $P < 0.001$) and for the M→M transitions ($G_{18} = 77.6$, $P < 0.001$). However, due in part to the shorter interactive behavior 'chains' between males and females during non-estrus and estrus, only the peak-estrus table met the sample size requirements for lag 2 analyses. Analysis of the peak-estrus table revealed significant sequential constraints on intra-individual behavioral transitions for females ($G_{16}^2 = 50.4$, $P < 0.001$) (Table 3c)

Behavioral transitions F→F

The peak-estrus table for the F→F transitions did have adequate sample size ($N = 233.5$) and all rows contained cells with expected average frequencies > 5 . Peak-estrus data were sequentially constrained at Lag 2 for the F→F transition ($G_{16}^2 = 50.4$, $P < 0.001$) (Table 3c). Subsequent analysis of behavioral dyads yielded eight significant behavioral transitions. Several behaviors, F-AM ($Z = 3.10$, $P = 0.002$), F-NU ($Z = 4.05$, $P < 0.0001$) and F-SX ($Z = 2.68$, $P < 0.01$) appeared to carry behavioral momentum in that their expression facilitated significantly more of the same behavior regardless of the intervening male response. F-AG also facilitated the subsequent expression of F-AM ($Z = 2.78$, $P < 0.01$), while F-NU inhibited F-SX ($Z = -3.43$, $P < 0.001$), and F-SX inhibited both F-AM ($Z = -2.03$, $P < 0.05$) and F-NU ($Z = -1.97$, $P = 0.05$).

Behavioral transitions M→M

The peak-estrus table for the M→M transitions did have adequate sample size (N=220.1) and all rows contained cells with expected average frequencies >5. Peak-estrus data were sequentially constrained at lag 2 for the M→M transitions ($G^2 = 106.4$, $P \ll .001$) (Table 3d). Behavioral momentum was evident for 3 out of 4 male transactional categories (M-SI: $Z = 5.58$, $P < .0001$; M-AF: $Z = 3.56$, $P < .001$; M-NU $Z = 8.18$, $P \ll .00001$). M-SI inhibited both M-AF ($Z = -2.78$, $P < .01$) and M-NU ($Z = -2.66$, $P < .01$). M-AF facilitated M-SX ($Z = 3.95$, $P < .0001$). M-AF had a strong inhibitory effect on both M-SI ($Z = -3.47$, $P < .001$) and M-NU ($Z = -4.50$, $P < .00001$). M-NU inhibited transitions to both M-AF ($Z = -2.74$, $P < .01$) and M-SX ($Z = -4.70$, $P < .00001$).

During non-estrus and estrus, for both the F→F transitions and the M→M transitions, small sample size did not allow us to investigate sequential dependency, however, visual inspection of Table 3, c-d strongly suggests that primarily self-facilitatory effects characterize many interactive behaviors during non-estrus and estrus, as evidenced by most transitional probabilities being greater than 50%. In one notable exception, F-AM tended to transition to F-AF 48% of the time during estrus.

Discussion

Our results underscore the dramatic changes in male-female interactions over the course of the female estrous cycle and provide insight into how behavior is synchronized during courtship. As the fertile period approaches there was an upsurge in the rate of behavioral interactions between males and females, and the rates of most types of social behaviors increased. Although the overall rate of some non-affiliative behaviors also increased, analyses of

the relative frequencies of social transactions shows a clear shift by females away from aggressive, neutral and ambivalent behaviors, which are gradually replaced by more affiliative and sexual behaviors. By contrast, males responded similarly to females across the reproductive period, consistently showing high levels of interest and affiliative behavior regardless of her status. Only the relative frequency of sexual behavior increased during peak-estrus, when it was enabled by female proceptive sexual behavior. Two behaviors proved to be limited largely to only one sex. Only males “showed interest” in females, making non-vocal efforts to interact with females, whereas only females showed “ambivalent” behavior where vocalizations indicated both aggressive and affiliative motivation simultaneously.

Taken together, these results indicate that males remain relatively constant in their efforts to interact with and court females, whereas females respond to males aggressively during early phases of the courtship process and gradually become more receptive and proceptive toward males as peak-estrus approaches. These findings are consistent with what is known about these reproductive processes in the wild (Schaller et al. 1985). Several days before mating, several males aggregate around an estrous female, which interacts intermittently with males while largely avoiding them (often by climbing a tree) until mating occurs (Nie et al. 2012). Our analysis of the transactional behaviors in captive pandas provides a proximate communication mechanism by which the male pursues and courts females while the female deters males until she is capable of conceiving. Presumably, the female’s behavior also promotes mating with relatively high quality males capable of sustaining both male-male competition and courtship with females (Nie et al. 2012).

We know from previous work that components of the signal assemblages studied here, as well as others such as olfactory signals that were not studied here, are strongly associated with

reproductive behavior and hormones. Our sequential analyses demonstrate further the coupling of behaviors leading up to sexual behavior (although since our animals were separated, this could not include copulation). Strong conditional probabilities illustrate tight linkage between behaviors even when transitions are not significant. For example, we can state that during peak-estrus males are highly likely to respond to female aggressive behavior with neutral behavior (no vocalization, no directed movement) and to engage in affiliative behavior (typically bleating vocalizations) when the female shows ambivalence (typically a mix of bleating, chirping, barking and moaning). The frequent display of ambivalent behavior by females strongly suggests that this varying complex signal composite serves as a functional unit, most likely indicating to the male that sexual behavior is imminent but that the female is not yet fully receptive.

As noted earlier, when these conditional probabilities are analyzed in the context of an ongoing interaction with a great deal of intra-individual behavioral momentum, these response probabilities, though common, are not often statistically significant. The Markov Chain analysis revealed a striking number of significant “maintenance chains” underscoring how these interactions are dominated by behavioral momentum. This might suggest strong coupling of panda social displays to circulating estrogen and testosterone levels, which govern the use of social displays with little sensitivity to feedback from the displays and actions of the other animal. Alternatively, these displays may operate over longer time frames than can be assessed in Markov Chain analysis. While signals are conspicuous and often emphatically broadcast during social interactions, they often fail to evoke a response in the immediate time frame. For example, while the rate and relative frequency of female affiliative increased significantly over the estrus cycle, it typically did not elicit any specific behavior from males *within* a social interaction. Although outside the scope of the current analysis, it seems highly improbable that

these social displays have no effect on the opposite sex over longer timeframes. The nature of these behaviors, which are repeated frequently over the course of many days, is consistent with the precepts of “tonic communication” (*sensu* Schleidt 1973). It seems plausible that these repeated social displays function cumulatively to alter motivational priorities and hormonal states of receivers such that they become more sexually motivated and less aggressive, in much the same manner that long-lasting chemical signals have been shown to act for this species (e.g., Swaisgood et al. 2004). Thus, the various visual and auditory signals that comprise the transactional behaviors researched in the present study do not appear to evoke discrete immediate responses from receivers, but most likely advertise reproductive condition and influence potential mates over longer timeframes.

Conclusions

Our data here differ from previous efforts to dissect individual signals used during courtship communication and determine signal meaning in isolation. Instead we have studied the complex composite of signals and other behaviors that giant pandas employ during courtship, much in the same way a manager attempting to breed pandas might see these interactions. We see additional value in our approach in that it can provide useful tools and guidelines for breeding managers. Our transactional behavior scoring system simplifies complex behavior and helps discern larger patterns. Managers can adopt and adapt this approach to track the behavior of pandas in their charge and compare the rates, relative frequencies, and sequential conditional probabilities reported here to their own observations. This foundation will assist in their endeavor to understand the reproductive readiness of pandas and to examine the effects of management activities on social displays supporting breeding.

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Table 1.

Operational definitions of interactive behaviors.

Behavior category	Code	Definition
Aggressive	AG	Animal emits the vocalizations huff, snort, chomp, honk, moan, bark, growl or roar (connoting defensive or offensive threat), and/or paw swat and charge.
Neutral	NU	Animal shows no overt response other than simply observing the other party.
Shows Interest	SI	Animal responds to the other party by sniffing the other participant, pushing or pulling at the fence between, or swaying or pacing back and forth within proximity of the other animal. Emission of any vocalization results in categorization according to the appropriate vocally defined behavior.
Ambivalent	AM	Animal alternates between vocalizations associated with Aggressive and Affiliative responses, or emits vocalizations intermediary between these two categories (e.g., 'chirpy bark').
Affiliative	AF	Animal emits bleats or chirps.
Sexual	SX	Female presents anogenital region to male. Male sniffs or licks anogenital region and/or nudges or paws at anogenital region through wire mesh. Note that the female must first display 'Sexual' before it is possible for the male to respond with 'Sexual.'

Table 2. Results for linear mixed effects models of social behavior, according to female reproductive condition. Tukey HSD was used for pair-wise comparisons between each of the stages of the reproductive cycle: non-estrus (NE), estrus (E) and peak-estrus (PE). For pairwise comparisons we report Z-score, P-value.

		F _{2,15}	P	Pairwise comparisons					
				NE-E		E-PE		NE-PE	
<i>Female:</i>	Neutral	8.78	0.003	2.66,	0.02	-1.36,	0.36	-4.12,	<0.001
	Affiliative	10.56	<0.002	-2.51,	0.03	1.98,	0.12	4.58,	<0.001
	Ambivalent	6.00	<0.02	-3.47,	<0.002	-1.89,	0.14	1.58,	0.25
	Aggressive	3.59	<0.05	1.55,	0.15	-0.66,	0.79	-2.55,	0.03
	Sexual	16.79	<0.001	-2.27,	0.06	3.36,	0.002	5.76,	<0.001
<i>Male:</i>	Neutral	0.18	0.93	-0.52,	0.86	0.00,	1.00	0.52,	0.86
	Show interest	0.50	0.62	0.45,	0.89	-0.54,	0.85	-1.01,	0.56
	Affiliative	2.09	0.16	-1.79,	0.17	-0.06,	0.99	1.75,	0.19
	Sexual	14.51	<0.003	-1.46,	0.30	3.64,	<0.001	5.25,	<0.001

Table 3. Conditional probabilities of dyads at lag 1 (a. female to male; b. male to female) and lag 2 (c. female to female; d. male to male).

	Non-estrus				Estrus				Peak-estrus#				
	NU	SI	AF	N/A	NU	SI	AF	N/A	NU	SI	AF	N/A	SX
AG	0.36	0.47	0.17	N/A	0.52	0.27	0.20	N/A	0.78	0.20	0.02	N/A	*
AM	0.17	0.14	0.69	N/A	0.43	0.22	0.35	N/A	0.27	0.17	0.56	N/A	*
NU	0.43	0.39	0.18	N/A	0.55	0.29	0.17	N/A	0.66	0.22	0.12	N/A	*
AF	0.47	0.15	0.38	N/A	0.33	0.27	0.40	N/A	0.34	0.23	0.43	N/A	*
SX	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.27 ⁺	0.01 ⁻	0.06 ⁻	N/A	0.65

	Non-estrus#				Estrus				Peak-estrus#				
	AG	AM	NU	N/A	AG	AM	NU	N/A	AG	AM	NU	N/A	SX
NU	0.04	0.03	0.48	N/A	0.45 ⁺	0.22	0.17	N/A	0.32	0.25	0.25	N/A	0.29
SI	0.27	0.05	0.53	N/A	0.12 ⁻	0.25	0.16	N/A	0.25	0.25	0.04	N/A	0.19
AF	0.24	0.08	0.31	N/A	0.33	0.14	0.28	N/A	0.09	0.39	0.00	N/A	0.05
SX	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.02	N/A	0.05 ⁺

	Non-estrus				Estrus				Peak-estrus#				
	AG	AM	NU	N/A	AG	AM	NU	N/A	AG	AM	NU	N/A	SX
AG	0.50	0.21	0.21	N/A	0.00	0.69	0.02	N/A	0.04	0.11	0.38	N/A	0.23
AM	0.00	0.55	0.00	N/A	0.00	0.03	0.34	N/A	0.09	0.48	0.02	N/A	0.23
NU	0.04	0.00	0.86	N/A	0.09	0.00	0.07	N/A	0.77	0.16	0.02	N/A	0.52 ⁺
AF	0.07	0.02	0.06	N/A	0.81	0.00	0.02	N/A	0.12	0.64	0.00	N/A	0.07
SX	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.01	N/A	0.05 ⁻

	Non-estrus				Estrus				Peak-estrus#				
	NU	SI	AF	N/A	NU	SI	AF	N/A	NU	SI	AF	N/A	SX
NU	0.73 ⁺	0.23	0.05	N/A	0.65	0.12	0.19	N/A	0.74 ⁺	0.09	0.10	N/A	0.07
SI	0.26	0.54	0.17	N/A	0.15	0.65	0.10	N/A	0.18 ⁻	0.33 ⁺	0.09	N/A	0.41
AF	0.15 ⁻	0.31	0.49 ⁺	N/A	0.23	0.17	0.47	N/A	0.14 ⁻	0.04 ⁻	0.35 ⁺	N/A	0.47 ⁺
SX	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.21	0.14	0.37	N/A	0.27

#= Significant tablewise G2; ‘+’ = Significant, positive ‘Z’ score for the behavioral dyad; ‘-’ = Significant negative ‘Z’ score for the behavioral dyad; ‘#’ = Structural zero

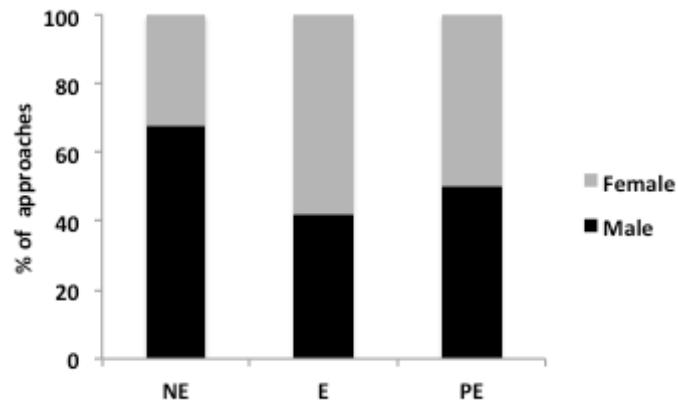


Figure 1. Percentage of interactions initiated by females and males, according to reproductive condition. Reproductive condition is represented by NE: non-estrus, E: estrus and PE: peak-estrus.

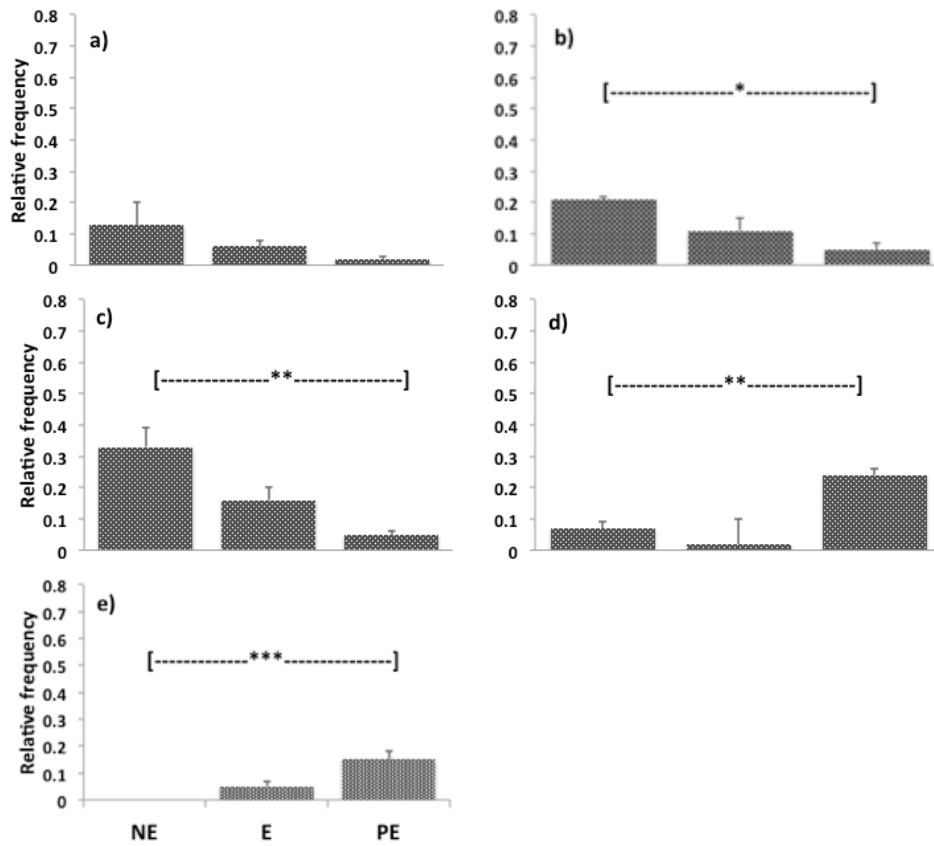


Figure 2. Relative frequency of female social behaviors during interactions with males across the female reproductive cycle (\pm SEM). Social behaviors include: (a) aggressive; (b) ambivalent; (c) neutral; (d) affiliative and (e) sexual. Abbreviations for female reproductive condition: NE: Non-estrus; E: Estrus; PE: Peak-estrus. * $P < .05$, ** $P < 0.01$, *** $P < .001$

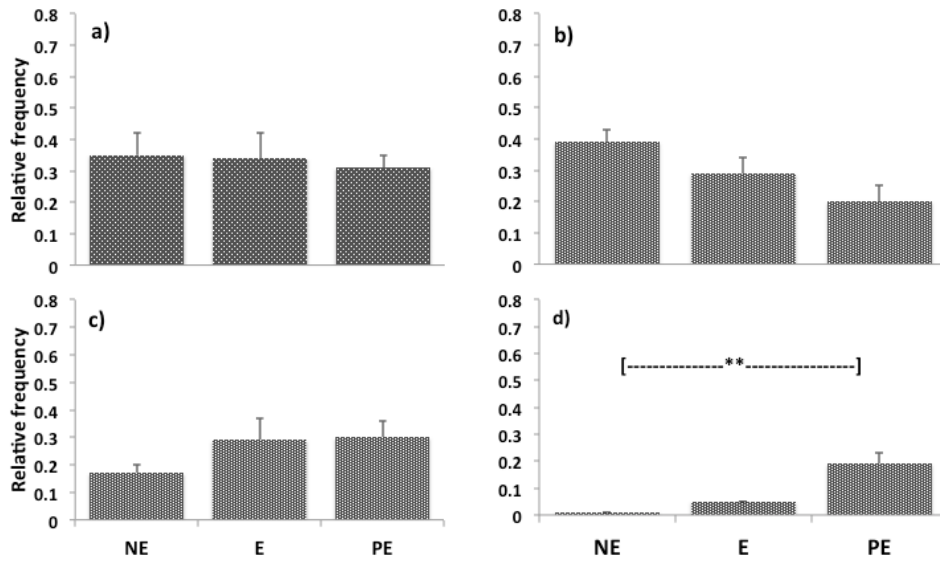


Figure 3. Relative frequency of male social behaviors during interactions with females, across the female reproductive cycle (\pm SEM). Social behaviors include: (a) neutral; (b) shows interest; (c) affiliative and (d) sexual. Abbreviations for female reproductive condition: NE: Non-estrus; E: Estrus; PE: Peak-estrus. ** $P < 0.01$.

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