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Signalling behaviour is influenced by transient social context in a spontaneously ovulating mammal

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Behavioural flexibility may be a mechanism that confers resilience in the face of rapid environmental changes. However, behavioural flexibility is constrained by a number of factors, including physiology. Giant pandas, *Ailuropoda melanoleuca*, are an endangered ursid found in fragmented habitats at social densities far below their historical carrying capacity. Giant pandas use chemical, visual and acoustic signals to communicate during reproduction. Females are seasonally mono-oestrous, ovulate spontaneously and, thus, fertility and sexual receptivity are temporally constrained. However, because signalling behaviour is energetically costly, the ability to adjust signalling effort according to the presence of an appropriate receiver would be beneficial. Using female giant pandas at the Wolong Breeding Centre in Sichuan, China, we explored the interaction between social context and reproductive status on signalling and maintenance behaviours. To do so, we used linear mixed models and an information-theoretic approach to assess the temporal relationship between signalling behaviours and the timing of first mating. Our results show that signalling behaviour is correlated with time relative to first mating and that multimodal signalling was the best predictor of this timing. Furthermore, we found that social context also influenced signalling behaviours. Specifically, vocal and visual signalling effort were lower in the exclusive presence of other females, reducing the degree of wasted effort. 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 preovulatory period according to the prevailing social context. As an iconic endangered species, the giant panda may benefit from research that informs management. Our study provides information that can be applied to increase the success of conservation breeding efforts and their associated reintroduction programmes.

Individuals in many species have adaptive behavioural flexibility (Kappeler, Barrett, Blumstein, & Clutton-Brock, 2013): they are able to control their behavioural efforts, tactics and energy expenditures (Kappeler et al., 2013; Milich, Bahr, Stumpf, & Chapman, 2014; Tuomainen & Candolin, 2010). While ecological and demographic factors are known to drive temporal and spatial gradients in reproductive strategy and in the relative prevalence of alternative reproductive tactics (Botero & Rubenstein, 2012; Schradin & Lindholm, 2011; Schradin, König, & Pillay, 2010), 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.

A specific type of behavioural flexibility, termed 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 (signalling effort, aggression). For example, if a particularly powerful male does not use all of his potential strength against a particularly weak rival, then it reduces his energetic effort to win access to a female. Individuals may acquire social competence through observation and learning (West, King, & Freeberg, 1996), or through audience effects (Johnstone, 2001). Like most studies of social behaviour, social competence has been best studied in social species, but should be equally advantageous to solitary species, especially when interacting with potentially 'novel' conspecifics.

Behavioural flexibility, and social competence in particular, should have physiological correlates, particularly in the context of

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reproductive behaviour. 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 & 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 spontaneous and induced ovulation (Bakker & Baum, 2000; Nalbandov & Cook, 1976), may determine the degree to which environmental conditions, including social context, may influence the onset of both behavioural oestrus (e.g. social signalling and proceptive behaviour) 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 has induced ovulation (Bakker & Baum, 2000; Basolo & Alcaraz, 2003; Ricklefs & Wikelski, 2002). For example, solitary living is positively correlated with induced ovulation (Clutton-Brock, 2009; Emlen & Oring, 1977; Lariviere & Ferguson, 2003), as is seasonal breeding (Bakker & Baum, 2000). 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 expended 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 (Claus, Over, & Denhard, 2003; Crews & Moore, 1986; Fadem, 1989; Yoerg, 1999), although these species are polyoestrous, cycling year-round, or multiple times throughout the breeding season. By contrast, seasonally monoestrous, spontaneously ovulating species may be even more temporally constrained, leading to the conclusion that socially competent behavioural flexibility should be lacking. However, mistimed or misdirected reproductive effort has disproportionate negative influences on fitness due to the infrequent reproductive opportunities for monoestrous species. If behavioural flexibility enhances successful mating, then selective advantages of social competence may be realized. Further complicating predictions is the role of energetic constraints. In more energy-limited species, selection may favour more conservative deployment of signalling behaviours if their expression is energetically costly, favouring greater social competence to avoid wasting energetic resources.

Here we explore the interplay of temporal constraints driven by physiology, energetic constraints and social context on the reproductive behaviour of the seasonally monoestrous, spontaneously ovulating, giant panda, *Ailuropoda melanoleuca*. Giant pandas are a long-lived, large-brained, wide-ranging, solitary and endangered (IUCN, 2013) carnivore, turned bamboo specialist, that has a limited and highly fragmented range in the mountains of south-central China (Wei et al., 2012). The panda's foraging strategy, while providing reliable access to a stable food supply, is a highly energy limited and energetic considerations appear to constrain many life history characteristics, including communication and mating strategies (Nie, Swaisgood, Zhang, Hu, et al., 2012; Nie, Swaisgood, Zhang, Liu, & Wei, 2012; Nie, Zhang, Swaisgood, & Wei, 2011; Schaller, Hu, Pan, & Zhu, 1985). The polygynous mating system of the giant panda is characterized by strong male–male competition for access to oestrous females (Nie, Swaisgood, Zhang, Liu, et al., 2012; Schaller et al., 1985). Behavioural oestrus is brief, lasting less than 2 weeks, ending with a notably short window of fertility of 1–3 days annually (Lindburg, Czekala, & Swaisgood, 2001). Because reproductive behaviour in pandas appears to be coupled to rapid changes in circulating oestrogen levels associated with follicular development and ovulation, it is unclear whether and how transient extrinsic factors influence female signalling behaviours (Owen, Swaisgood, McGeehan, Zhou, & Lindburg, 2013).

Giant pandas exhibit a range of chemical, acoustic and visual signals during breeding (Kleiman & Peters, 1990; Swaisgood, Zhang, Zhou, & Zhang, 2006; Swaisgood, Zhou, Zhang, Lindburg, & Zhang, 2003). Pandas rely on a sophisticated chemical communication system to coordinate social behaviour prior to face-to-face encounters, using signals to advertise identity, age class, sex and reproductive status (Swaisgood, Lindburg, White, Zhang, & Zhou, 2004). Once pandas are in direct contact, vocal behaviour conveys a rich range of information to conspecifics. For example, changes in chirp acoustic structure in females provide temporally specific information to panda males regarding the timing of ovulation and sexual receptivity (Charlton, Keating, Li, Huang, & Swaisgood, 2010) and male bleat vocalizations advertise testosterone levels to potential mates (Charlton et al., 2011; Charlton, Swaisgood, Zhang, & Snyder, 2012). Although visual signals are not well studied (but see Owen et al., 2013), several proceptive displays are known to increase during the periovulatory period (Lindburg et al., 2001).

Despite this scientific attention to the social signals used by giant pandas, a holistic understanding of panda social behaviour is lacking (but see Nie, Swaisgood, Zhang, Hu, et al., 2012; Owen et al., 2013), which can be a detriment to conservation strategies that rely on good scientific information (Swaisgood, Wei, Wildt, Kouba, & Zhang, 2010; Wei et al., 2015). Critical to moving some conservation management actions forward is a better understanding of social and reproductive behaviour. Although panda conservation breeding programmes have advanced rapidly, breeding difficulties remain and the production of more animals for release is needed to maximize the success of reintroduction programmes. Thus, the goals of our study are two-fold. First, to document, in detail, patterns of reproductive signalling behaviour as an informative tool to guide conservation breeding management decision making. Second, to examine, for the first time in this species, the degree of behavioural flexibility to better understand how pandas might respond to anthropogenically mediated changes in social context.

To address these knowledge gaps, we investigated the temporal dynamics of female giant panda behaviour during the breeding season at a large conservation breeding facility within the panda's range in China with a specific aim of determining the degree of behavioural flexibility present in the female panda's expression of oestrus across varying social contexts. As a spontaneously ovulating species, the panda is expected to follow a fairly reliable sequential pattern of signals to ensure that the timing of ovulation is adequately conveyed to prospective mates; mistimed matings will entail severe fitness costs. We examined the temporal dynamics of behaviours relative to the timing of fertility, and then compared the fit of linear mixed models consisting of unique signalling behaviours (scent marking, vocalizations and visual signals), as well as multiple interacting signalling behaviours, to determine whether independently, or combined, these provided temporally explicit clues to impending ovulation. Predictions emanating from these analyses are nonspecific but should support the general hypothesis that different signalling assemblages will increase and peak at different times with regard to the timing of ovulation. Specifically, long-lasting chemical signals involved in opposite-sex recruitment and advertisement of impending fertility should be used to a greater degree earlier in the reproductive cycle, whereas acoustic and visual signals should be used primarily during direct encounters of courtship. Specific temporal patterning can highlight function and motivation, subject to post hoc interpretation. This line of