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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 reasoning led us to predict that reproductive status would be more important than social context in determining the expression of signalling behaviour.

A strong theoretical framework suggests that social context, mediated by audience effects, also influences signalling behaviour (Matos, Peake, & MacGregor, 2003). We examined how the presence or absence of neighbouring pandas of each sex influenced signalling behaviour. While the giant panda's reliance on spontaneous ovulation may constrain some flexibility, energetic constraints resulting from the panda's foraging strategy may place a premium on social competence, promoting a greater degree of behavioural flexibility than would be otherwise expected. Specifically, we predicted that, because vocal and visual signals moderate face-to-face encounters during courtship (Bonney, Wood, & Kleiman, 1982; Owen et al., 2013; Schaller et al., 1985) and likely entail energetic costs, these modalities would be reduced in the absence of male neighbours, which are the presumed target audience. In contrast, scent-marking behaviour occurs in the absence of conspecifics and operates across longer time frames and larger interanimal distances, and thus is predicted to be less sensitive to audience effects. Because social behaviour between females is limited, we predicted that a female audience would have less influence on signalling behaviour than a male audience.

METHODS

Study Subjects and Facility

We studied female giant pandas at the China Research and Conservation Centre for the Giant Panda at the Wolong National Nature Reserve (hereafter, 'Wolong'; 31°N, 103°E) during the breeding season (February–June) in 1996–2001 and 2003. Giant pandas at Wolong are of mixed provenance, with wild-born individuals broadly representing the giant pandas range. All pandas included in this study were actively included in the Wolong's breeding programme and as such were adult (e.g. female >5 years old, male >6 years old), healthy and considered reproductively fit. We included 15 focal females (8 wild born, 7 captive born) and 21 neighbouring adult individuals in our study (11 females, 10 males). Enclosures consisted of two blocks of 10, linearly arranged 10 × 10 m outdoor pens. Animals had access to an indoor 3 × 5 m den area that was attached to each of the outdoor pens. All animals were housed in separate enclosures. Neighbouring outdoor pens were separated by approximately 7 m of heavy gauge wire mesh and bars, and so offered ample opportunities for visual, chemical and vocal access to neighbours in a protected fashion (Fig. 1. See Swaisgood, Lindburg, Zhou, and Owen (2000) for details of housing and husbandry.

Behavioural Observations and Variables

We conducted 90 min focal observation sessions ($N = 45$) on female giant pandas during the breeding season. Focal sessions occurred between 0645 and 1000 hours and between 1430 and 1600 hours, corresponding to typical peak hours of activity. Focal females were longitudinally sampled over multiple reproductive cycles in different years, and each focal cycle was our sampling unit. This resulted in one to four oestrous cycles per focal female. In total, 210 h of observation were included in the analysis of temporal patterns of behaviour relative to first mating. We only included females in this analysis that either mated naturally or were successfully artificially inseminated (i.e. gave birth), and thus their inclusion was determined post hoc. To explore the influence of social context and reproductive status on behaviour, we calculated mean values for each variable (see below) across each experimental condition (female neighbours, $N = 25$ focal cycles, 33.7 h; male neighbours, $N = 43$ focal cycles, 80.2 h; mixed-sex neighbours, $N = 28$ focal cycles, 36.0 h; control (no neighbours), $N = 26$ focal cycles, 24.5 h; sensu Swaisgood et al., 2000) and used 174.4 h of behavioural observations in our analysis. We used all-occurrence, point-in-time and 1–0 sampling (Martin & Bateson, 1996) to collect behavioural data for both analyses based on an extensive ethogram (Swaisgood & Owen, n.d.). Here we focus our analysis on a subset of behaviours, including: chemosensory behaviours, acoustic signals and visual signalling behaviours (see Table 1 for definitions). We also analysed changes in the percentage of time spent feeding, locomoting and displaying stereotypic behaviours, which were collectively defined as maintenance behaviours. The linear arrangement of pens meant that each focal animal potentially had two neighbours (except when housed in one of the pens at the end of the row; see Fig. 1). We noted, at the beginning of each observation session, the sex and reproductive status of any neighbours.

Independent Variables

Social context

Social context reflected the configuration of male and female pandas housed in neighbouring pens (male neighbours, female neighbours, mixed-sex neighbours or no neighbours (control)). The control treatment allowed 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 den area, which was separated from neighbouring pens by concrete walls and so did not afford opportunities for visual or consistently audible vocal contact. Because pandas were typically able to choose whether to be inside their enclosure or in the area outside of their enclosure, we calculated the actual conspecific presence of neighbours, which reflected the amount of time during

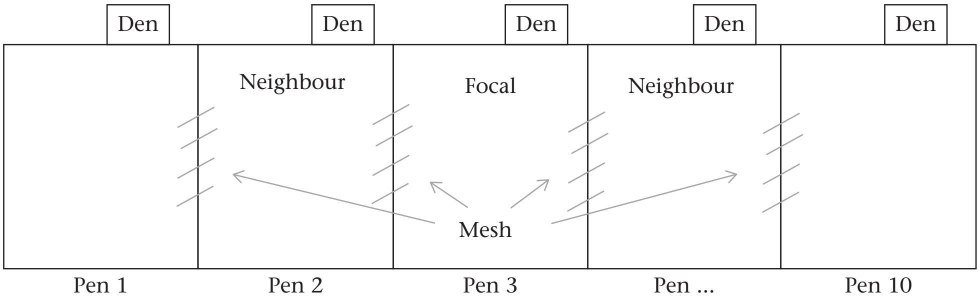

Figure 1. Configuration of panda housing at the Wolong Breeding Center, which consists of two blocks of 10 linearly arranged outdoor pens. Adjacent pens were separated by cinder block construction, with 6 m of wire mesh in the middle span. Pandas had access to an outdoor pen as well as intermittent access to an indoor den area.

Table 1
Ethogram of panda signalling and maintenance behaviours

Behaviour	Definition
Bleat vocalization	Twittering vocalization, similar to a goat's bleat; variable in length and affiliative in intent
Chirp vocalization	High-pitched vocalization, typically short in duration and affiliative in intent
Feed	Consumption, or processing for consumption, of provisioned food, including bamboo and supplementary diet items
Locomote	Directional movement between points; includes walking, climbing or pacing
Moan vocalization	Low-pitched call of variable duration, associated with low-level aggression
Olfactory investigation	Places nose within 5 cm of substrate (or cage divider mesh) and sniffs for more than 1 s; may include flehmen behaviour
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)
Stereotypy	Unvarying, repetitive behaviours without any apparent function or purpose; includes, pirouette, head-toss, paw-sucking or truncated rolling
Visual signal	Composite index of backwards walking, rear present, tail raising or lordosis posture

a focal observation session that neighbours were not in their den area.

Day 0

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

Reproductive status reflects a binning of days relative to peak fertility and included three categories: nonoestrus (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 (Owen et al., 2013; Swaisgood, Lindburg, & Zhang, 2002; Swaisgood et al., 2000).

Statistical Analysis

We used R for all data analyses (R Foundation for Statistical Computing, Vienna, Austria), unless otherwise noted. We transformed all dependent variables to meet assumptions of homoscedasticity. We used an arcsine transformation for all proportional data (bleat, chirp and moan vocalizations, locomote and feed) and a log transformation for all rate data (scent mark, olfactory investigation, visual signalling and stereotypy) (Sokal & Rohlf, 1995). Transformed data were visually inspected (standardized versus fitted residuals) to ensure that they were homoscedastic. We fitted linear mixed-effects models for all variables of interest and we included focal ID and year as random effects in all analyses. We also included actual conspecific presence as a continuous covariate 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 fitted univariate linear mixed-effect models for each behaviour relative to the first day of natural mating, a proxy for ovulation or peak fertility (R package ‘nlme’: Pinheiro, Bates, DebRoy, & Sarkar, 2014). 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 and Schielzeth (2013).

To determine which of the behaviour variables related to signalling best predicted the timing of ovulation, we used an information-theoretic approach and multimodel 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 was developed based on both expert opinion and a comprehensive literature review of reproductive behaviour in the giant panda and other bear species (sensu Burnham, Anderson, & Huyvaert, 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 for the analysis of temporal dynamics. Because highly correlated predictor variables should not be considered in the same model (Burnham et al., 2011), we did not fit models that included additive or interactive effects for bleating and chirping vocalizations. Weight of evidence, a measure of the fit of the best model relative to the next-best model, was calculated for each of the candidate models. 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. We inspected the 95% confidence set models, but we discuss the relative support for models based on the evidence ratio (Richards, Whittingham, & Stephens, 2011) and ΔAICc.

To investigate the influence of reproductive status, social context, and the interaction of these two factors on behaviour, we fitted univariate linear mixed-effect models using JMP v.11 software (SAS Institute Inc., Cary, NC, U.S.A.). As above, we included focal ID and year as random effects, and included actual conspecific presence as a continuous covariate. Denominator degrees of freedom were adjusted using Satterthwaite's correction (Satterthwaite, 1946). We performed post hoc pairwise comparisons using Tukey's HSD to evaluate significant interactions and main effects. Alpha was set at 0.05 for all analyses.

RESULTS

Correlation between Signalling 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 signalling, including bleating, chirping, scent marking and visual signalling (Fig. 2). The temporal dynamics varied across behaviours, with different behaviours being initiated and peaking at different periods of time with respect to presumed ovulation. The relationship between signalling behaviours and the timing of ovulation was best described by the model containing an interaction between the rate of visual signalling, scent marking and the proportion of intervals with the chirp vocalization (Table 2). While the evidence ratio between this and the second-ranked model (visual signalling$*$scent marking) was 3.25 (indicating that the model that included all three signalling modalities was more parsimonious than the bimodal model), the ΔAICc was 1.38, suggesting that the top two models were virtually indistinguishable. Visual signalling appeared in all five models included in the 95% confidence set and was the most influential variable in the model set. However, the importance of multimodal signalling was

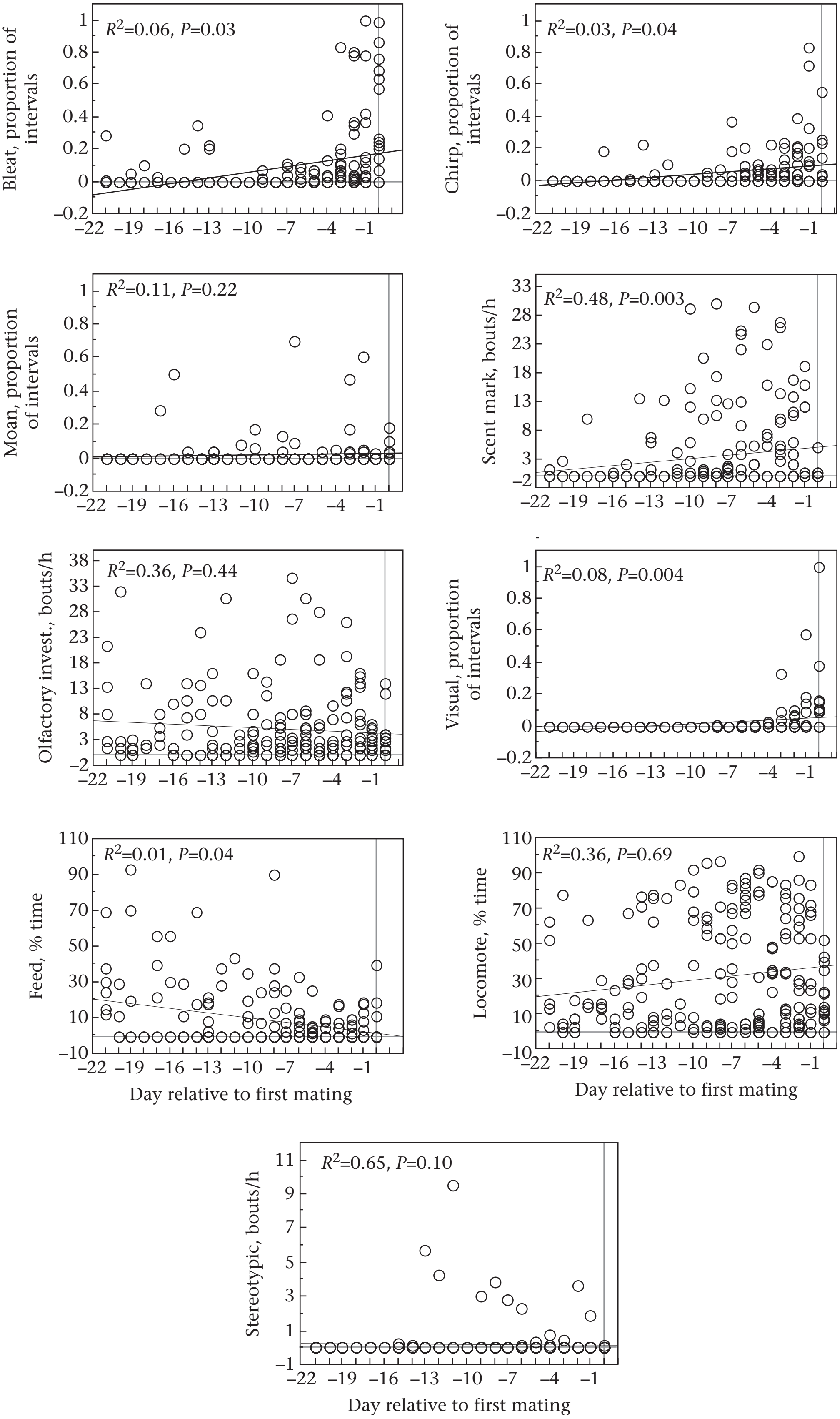

Figure 2. Relationship between day relative to first mating and the expression of signalling and maintenance behaviours. R^2 for each model reflects the conditional R^2, which includes calculation for random factors in goodness of fit.

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

Fixed effects	K	AICc	ΔAICc	ω_i	R^2
VI*SM*CH	**11**	**1353.58**	**0.00**	**0.59**	**0.07**
VI*SM	**7**	**1354.94**	**1.36**	**0.30**	**0.15**
VI*CH	**7**	**1359.18**	**5.61**	**0.04**	**0.03**
VI*SM*BL	**11**	**1360.32**	**6.74**	**0.02**	**0.10**
VI*MO	7	1360.86	7.29	0.02	–
VI	5	1361.23	7.66	<0.01	–
BL*MO	7	1361.34	7.76	<0.01	–
BL*VI	7	1361.85	8.27	<0.01	–
BL*SM	7	1363.23	9.65	0.00	–
BL*OI	7	1365.46	11.88	0.00	–
SM	5	1365.51	11.94	0.00	–
BL	5	1366.05	12.47	0.00	–
MO	5	1367.81	14.23	0.00	–
CH	5	1367.82	14.24	0.00	–
Intercept only	5	1369.73	16.15	0.00	–
OI*MO	7	1369.87	16.29	0.00	–
CH*OI*SM	11	1371.12	17.54	0.00	–
OI	5	1371.41	17.83	0.00	–
CH*OI	7	1371.50	17.92	0.00	–

K: number of parameters; AICc: Akaike Information Criterion adjusted for small sample sizes; ΔAICc: difference in AICc values between models; ω_i: AICc weights, or conditional probability of being the correct model; VI: visual signalling behaviour; SM: scent mark; OI: olfactory investigation; CH: chirp vocalization; BL: bleat vocalization; MO: moan vocalization. The 95% candidate set according to Akaike weight is shown in bold. We provide the conditional R^2 for each model in the confidence set (noted in bold).

conspicuous, and no model with only a single signalling modality was in the 95% confidence set of models.

Influence of Social Context and Reproductive Status on Signalling and Maintenance Behaviours

In general we found that reproductive status had a primary influence on the dynamics of signalling behaviour and was consistently present in all significant models. However, social context also influenced the expression of behaviours related to signalling, and we found significant interactions between social context and reproductive status in three of five signalling behaviours we examined (Fig. 3).

The interaction of reproductive status and social context significantly influenced the expression of the bleat vocalization ($F_{6,77.8} = 4.23$, $P = 0.001$). Main effects of both factors were also significant (reproductive status: $F_{2,76.7} = 33.27$, $P < 0.0001$; social context: $F_{3,76} = 4.78$, $P = 0.004$), and pairwise post hoc evaluation showed that bleating was significantly higher during peak oestrus and significantly lower in the female neighbour treatment. Post hoc evaluation of interactive effects showed that during peak oestrus, when the social context consisted only of females, the proportion of intervals with bleating was significantly lower than when males were present (both in the male neighbour and mixed-sex neighbour treatments) (Fig. 3a). This may be indicative of a suppressive effect on bleating by neighbouring females during peak oestrus. The rates of bleating in the female neighbour treatment were comparable during oestrus and peak oestrus, whereas when males were present, the rate of bleating during peak oestrus was significantly higher than it was during both nonoestrus and oestrus. In the control treatment, female bleats increased in a stepwise fashion between nonoestrus, oestrus and peak oestrus, which was consistent with the temporal pattern we identified in our first experiment (Fig. 2a).

The production of chirp vocalizations was significantly influenced by the interaction of social context and reproductive status ($F_{6,77.8} = 4.93$, $P = 0.0003$), and the effect of status alone was also significant ($F_{2,76.7} = 3.31$, $P = 0.04$; Fig. 3b). Post hoc comparison showed that chirping rate was significantly higher during peak oestrus than during nonoestrus. However, social context alone was not significant ($F_{3,76} = 2.12$, $P = 0.12$). Post hoc evaluation of interactive effects showed that both the male neighbour and control treatments were comparable during peak oestrus, with significantly elevated rates of chirping relative to the female neighbour or mixed-sex neighbour treatments. These results suggest that the presence of conspecific females had an inhibitory influence on chirping during peak oestrus (Fig. 3b). We found no significant effects for our analysis of the moan vocalization ($F_{6,77.8} = 1.10$, $P = 0.37$; reproductive status: $F_{2,76.7} = 2.33$, $P = 0.10$; social context: $F_{3,76} = 1.16$, $P = 0.34$). However, examination of treatment means revealed that moan was most frequently uttered during oestrus in the mixed-sex and control treatments (Fig. 3c).

Chemosensory behaviours were not consistently influenced by social context. In the case of olfactory investigation (Fig. 3d), we found no significant effects, and neither reproductive status nor social context, was statistically significant (reproductive status*social context: $F_{6,77.8} = 1.19$, $P = 0.32$; reproductive status: $F_{2,76.7} = 1.50$, $P = 0.23$; social context: $F_{3,76} = 2.70$, $P = 0.06$). In contrast to affiliative vocal signals (bleat and chirp), reproductive status alone significantly influenced the rate of scent marking ($F_{2,76.7} = 10.51$, $P < 0.0001$), and neither social context ($F_{3,76} = 0.23$, $P = 0.12$) nor the interaction of social context and reproductive status was significant ($F_{6,77.8} = 0.91$, $P = 0.49$). These results indicate that scent marking was little influenced by social context. Post hoc evaluation of scent marking showed that a significantly higher rate of scent marking occurred during oestrus (Fig. 3e).

Visual signalling (Fig. 3f) was significantly influenced by the interaction of social context and reproductive status ($F_{6,77.8} = 3.61$, $P = 0.01$), as was reproductive status alone ($F_{2,76.7} = 9.34$, $P = 0.0002$). Social context alone did not have a significant effect on visual signalling ($F_{3,76} = 1.51$, $P = 0.22$). Visual signals were observed at very low levels during nonoestrus and oestrus, and the presence of a male clearly increased the rate of expression during peak oestrus. Post hoc evaluation demonstrated that visual signalling in the male neighbour treatment was significantly higher than in all other treatment groups, and very low levels of visual signalling were observed when social context consisted exclusively of females (Fig. 3f).

Feeding behaviour was not influenced by social context or reproductive status (reproductive status*social context: $F_{6,77.8} = 0.64$, $P = 0.70$; reproductive status: $F_{2,76.7} = 0.71$, $P = 0.49$; social context: $F_{3,76} = 1.50$, $P = 0.23$; Fig. 3g). Reproductive status had a significant effect on locomotion ($F_{2,76.7} = 4.80$, $P = 0.01$), with levels during oestrus being significantly higher than those during peak oestrus. However, neither social context nor the interaction effect was significant (reproductive status*social context: $F_{6,77.8} = 0.18$, $P = 0.98$; social context: $F_{3,76} = 2.13$, $P = 0.12$; Fig. 3h). We found that stereotypic behaviour was influenced by the interaction of reproductive status and social context ($F_{6,77.8} = 3.89$, $P = 0.002$), and reproductive context alone ($F_{2,76.7} = 7.24$, $P = 0.001$). Post hoc evaluation showed significantly lower rates of stereotypic behaviour during peak oestrus in the female neighbour treatment than during peak oestrus and nonoestrus in the other treatments. Social context alone did not have a significant effect on stereotypic behaviour ($F_{3,76} = 2.13$, $P = 0.12$; Fig. 3i).

DISCUSSION

Our studies demonstrate, for the first time, the degree of socially modulated behavioural flexibility, and the interplay between such flexibility and the constraints of reproductive status, present in the reproductive signalling behaviour of a spontaneously ovulating seasonally monoestrous mammal. In this test with giant pandas, we

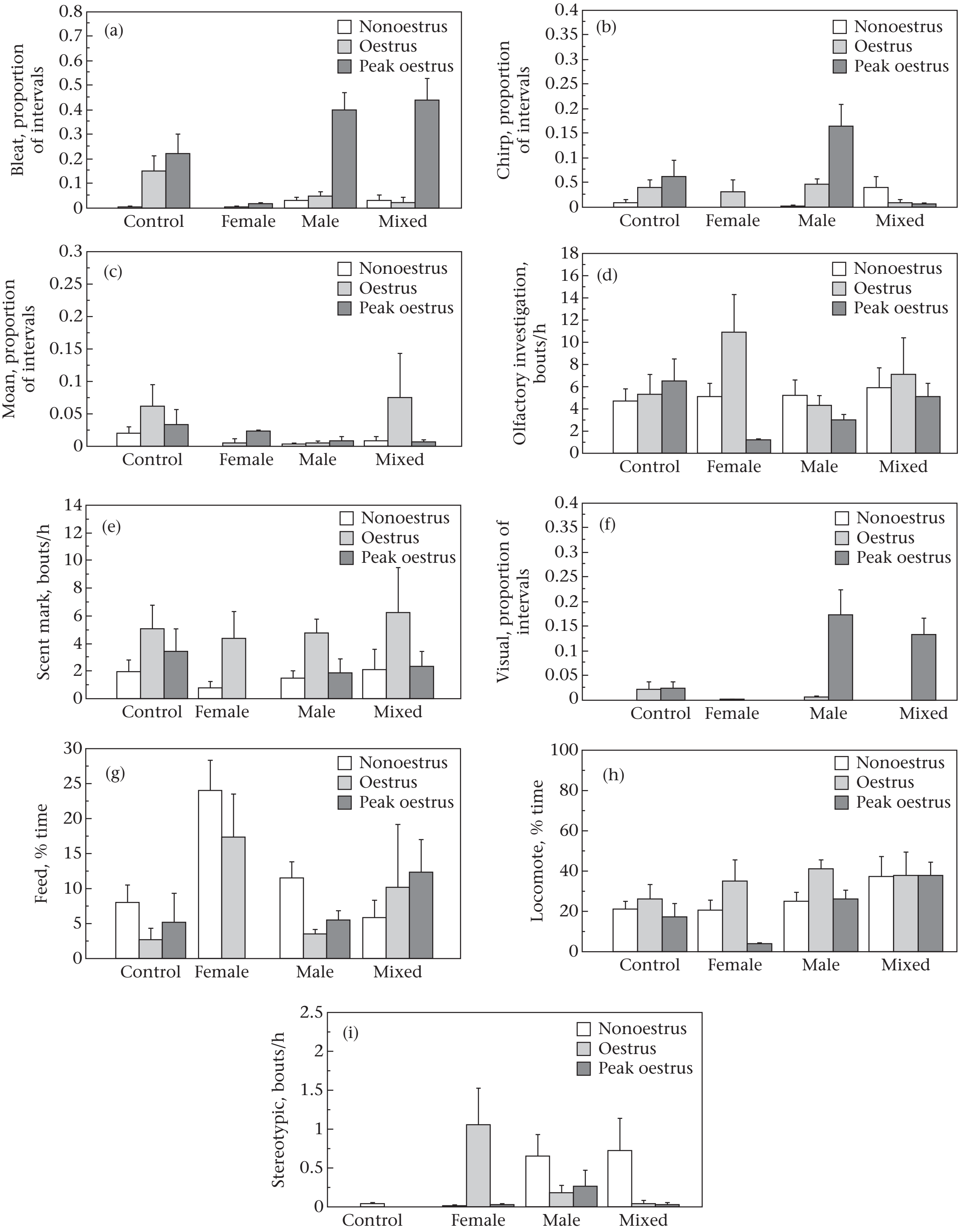

Figure 3. Influence of social context and reproductive status on female giant panda behaviour: (a) bleat vocalization, (b) chirp vocalization, (c) moan vocalization, (d) olfactory investigation, (e) scent mark, (f) visual signal, (g) feed, (h) locomote and (i) stereotypy. Values are means ± SE.

have also explored this phenomenon in a species with many life history characteristics governed by energetic efficiency, including movement patterns and chemical signalling (Nie, Swaisgood, Zhang, Hu, et al., 2012; Nie, Swaisgood, Zhang, Liu, et al., 2012; Nie et al., 2011; Schaller et al., 1985; Zhang et al., 2014). As we hypothesized for a spontaneously ovulating mammal needing to convey precise information on reproductive status, signalling behaviour was tightly correlated with and highly predictive of the timing of ovulation. Yet we also found some behavioural flexibility in the expression of reproductive signalling, and this showed that pandas allocate signalling effort efficiently in a manner sensitive to the social audience. During peak oestrus, when the overarching pattern is one of relatively elevated vocal and visual signalling, the exclusive presence of females was correlated with a significantly lower signalling effort than in other social contexts. This indication of social competence is consistent with our hypothesis that energetic constraints would infuse some degree of behavioural flexibility on this signalling system to increase efficiency, even in the face of temporal constraints imposed by their reliance on spontaneous ovulation. We did not observe social influences on the emission of chemical signals, an expected finding since chemical signals are designed to convey information regarding reproductive status in the absence of conspecifics (Swaisgood et al., 2004).

While our results demonstrated that chemical, vocal and visual signalling 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 signalling. Previous research has shown that the changes in the acoustic structure of the chirp vocalization during the periovulatory 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 and the rates of scent marking and visual signalling, and that this multimodal assemblage of signals probably conveys the most temporally explicit information to male conspecifics. Consistent with this finding, previous research has demonstrated the importance of multimodal signalling in pandas over shorter time frames (Owen et al., 2013).

Results from our analysis of social context demonstrate differential influences on behaviour in the female neighbour and control treatments. Furthermore, we can distinguish some changes in behaviour driven by the absence of a male versus changes driven by the exclusive presence of females. Because male neighbour and mixed-sex neighbour treatments had similar patterns (in the case of the bleating vocalization and visual signalling), our results suggest that it is not simply the presence of a female that is correlated with relatively reduced signalling; it is the exclusive presence of a female. Because signalling was typically less inhibited in control treatments, it may be inferred that social uncertainty (as evidenced by the lack of conspecifics) facilitated signalling, whereas the presence of inappropriate receivers provided information that allowed signallers to make adjustments in signalling effort, potentially conserving energy by reducing the rate of signal production. 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 only when potential competition makes it necessary. It is plausible that over the course of an animal's reproductive lifetime, these adjustments may enhance fitness (Hofmann et al., 2014), especially in an energy-limited species such as giant pandas. Audience effects that promote the fine-tuning of signalling behaviour to target specific conspecifics are one important means by which signalling behaviour can be made more efficient.

Species that exhibit behavioural flexibility may be more resilient to the rapid changes in the environment occurring as a result of human activities (Claus et al., 2003; Tuomainen & Candolin, 2010). Panda populations are small and highly fragmented (Wei et al., 2012), and climate change is expected to have a dramatic and rapid impact on remaining giant panda habitat, further reducing the connectivity of remnant populations (Songer, Delion, Biggs, & Huang, 2012; Viña et al., 2010). 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.

Understanding how animals respond to variations in social context has broad conservation applications, including both in situ and ex situ contexts. Such knowledge can be used for manipulating social context in the captive environment for conservation breeding (Fisher, Swaisgood, & Fitch-Snyder, 2003; Swaisgood & Schulte, 2010; Yoerg, 1999) and for increasing the potential for success in both reintroductions and translocations (Shier & Swaisgood, 2011). Our results also provide guidance to managers of conservation breeding programmes, allowing them to predict the timing of ovulation using behavioural cues, and suggest a strategy that incorporates social context as a management tool to enhance the display of sexual behaviours and reproductive output (see also Swaisgood et al., 2006). We point to the specific temporal dynamics of various behaviours with regard to peak fertility as detailed in Fig. 2. Conservation managers go to great effort to predict when a female will be fertile so that mating introductions can be properly timed; poorly timed introductions fail and sometimes result in injurious aggression (Swaisgood et al., 2006). Managers should understand that, according to our results, one or two variables alone will not reliably predict the timing of fertility, but that a suite of these variables working in concert will. Managers may also benefit from the knowledge that the presence of male neighbours evokes female vocalizations that indicate enhanced sexual motivation (bleats, chirps) and thus can be used as a tool to promote natural mating. Understanding the signalling dynamics in the reproductive context will contribute to the goals of conservation breeding, their associated reintroduction programmes and a better understanding of how anthropogenic change may alter breeding success in wild populations.

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