Families on the spot: sexual signals influence parent–offspring interactions

Judith Morales[1], Carlos Alonso-Álvarez[2], Cristóbal Pérez[1], Roxana Torres[3], Ester Serafino[1,†] and Alberto Velando[1,*]

[1]*Departamento de Ecoloxía e Bioloxía Animal, Facultade de Ciencias, Universidade de Vigo, 36310 Vigo, Spain*
[2]*Unidad de Ecología, Instituto de Investigación en Recursos Cinegéticos (IREC), Consejo Superior de Investigaciones Científicas (CSIC-UCLM), Ronda de Toledo s/n, Ciudad Real 13005, Spain*
[3]*Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, AP 70-275, México DF 04510, Mexico*

In 1950, Tinbergen described the elicitation of offspring begging by the red spot on the bill of parent gulls, and this became a model system for behavioural studies. Current knowledge on colour traits suggests they can act as sexual signals revealing individual quality. However, sexual signals have never been studied simultaneously in relationship to parent–offspring and sexual conflicts. We manipulated the red-spot size in one member of yellow-legged gull pairs and observed their partners' feeding efforts in relationship to offspring begging. In the enlarged-spot group, partners doubled their effort compared with the other groups. Furthermore, in the reduced-spot group, partners provided food in relationship to offspring begging, contrasting with the fixed effort of the partners of enlarged-spot gulls. Manipulated gulls, independently of treatment, provided food in relationship to chicks begging only when the partner's investment was low, and performed a fixed effort when the partner's contribution was high. Results demonstrate that the red spot in yellow-legged gulls functions as a sexual signal and indicate that parental rules are plastic, depending on the information on offer. Previous evidence and this study indicate that this signal is used by all family members to adjust decision rules. The incorporation of sexual signals in parent–offspring interactions can be crucial in understanding intra-familial conflicts.

Keywords: information exchange; offspring begging; parental care; parent–offspring conflict; sexual conflict; sexual signals

1. INTRODUCTION

Conflicts of interest are widespread in animal societies, where the fitness of one individual depends on the behaviour of others (Hamilton 1964; Trivers 1985). In such evolutionary games, there are multiple interactions between opponents, during which the final outcome of the conflicts may be negotiated (McNamara *et al.* 1999). Wherever individuals interact and disagreements occur, the exchange of information between different parties is fundamental in shaping evolutionarily stable decision rules (Johnstone & Hinde 2006; McNamara *et al.* 2006). Information exchange during conflicts appears to be extremely relevant in social animals (Clutton-Brock & Parker 1995). Thus, for example, information about opponents' quality or reputation determines cooperation or punishment (e.g. Camerer & Fehr 2006; Novak 2006; McNamara *et al.* 2008; Milinski & Rockenbach 2008). Indeed, social skills such as language in humans, or other ways to convey information, are crucial in shaping optimum decision rules (Novak 2006). Therefore, information exchange is probably crucial in the resolution of conflicts in societies (Johnstone & Hinde 2006).

Interactions between parents and young are some of the most common and basic social behaviours exhibited by animals (Godfray 1995). Conflicts of interest may arise between all the members of a family (Hamilton 1964; Trivers 1972). In species with biparental care, there is potential conflict between the male and female parents over how much parental investment each should give (sexual conflict). Because increased parental effort in current reproduction negatively affects future reproduction, organisms commonly restrict their parental effort in order to maximize lifetime reproductive success (Curio 1983; Stearns 1992). Thus, each parent would profit if the other provided more care (Lessells 1999). Also, offspring have different interests from their parents concerning investment (parent–offspring conflict; e.g. Trivers 1974; Parker 1985; Godfray 1995). A key factor in all these conflicts is the degree to which parents negotiate their investments (McNamara *et al.* 1999; Parker *et al.* 2002; Hinde & Kilner 2007). Nevertheless, in spite of the great efforts made to analyse both conflicts separately, their simultaneous action within the framework of intra-familial conflicts has seldom been addressed (Parker *et al.* 2002; Johnstone & Hinde 2006; Hinde & Kilner 2007). In the case of parent–offspring conflict, much effort has been devoted to studying offspring signals (e.g. begging) affecting response rules (e.g. Kilner & Johnstone 1997; Kölliker *et al.* 1998; Royle *et al.* 2002; Roulin & Bersier 2007). Nevertheless, little is known about other sources of information on which parents and offspring base their decision rules. In systems with intense biparental care, sexual signals are expected to be honest indicators of

* Author for correspondence (avelando@uvigo.es).
† Present address: Centro Ricerca Mammiferi Marini (CRIMM), Porto San Paolo (OT), Sardegna 07020, Italy.

parental quality (Kokko 1998; Houston *et al.* 2005). Sexual attractiveness may determine the allocation of resources to reproduction by the partner (i.e. the differential allocation hypothesis; Burley 1988). Therefore, sexual signals may strongly affect the negotiation between mates over offspring care (McNamara *et al.* 1999; Johnstone & Hinde 2006). However, sexual signals have not been considered in the context of a family, where not only the mate, but also the offspring may base their decision rules on the information conveyed by these signals.

A potential example of a signal that may play a role in multiple intra-familial interactions is the red spot on the bill of various gull species. Since the pioneering work of Tinbergen & Perdeck (1950), the red spot in gulls has become a model-signalling system in behavioural studies. Adult gulls of both sexes express this trait. Gull offspring solicit food almost immediately after hatching with begging calls and pecks at the parents' bills, preferentially on the red spot. Tinbergen & Perdeck (1950) showed that this trait stimulates begging in newly hatched chicks, and it has been suggested that the chicks' pecking induces the parent to regurgitate food (Weidmann 1956; Beer 1966). However, the chicks might also inform the parents about their need of food through the intensity of pecking. The red spot could also play a role in the context of sexual selection. The expression of the red spot in gulls is known to vary through the breeding cycle, being enhanced during courtship (Cramp & Simmons 1983). In yellow-legged gulls (*Larus michahellis*), recent studies have revealed that this trait is carotenoid-based and reliably reflects the bearer's antioxidant status (Pérez *et al.* 2008). It is also related to body condition and carotenoid intake in very closely related gull species (Blount *et al.* 2002; Kristiansen *et al.* 2006). The evolution of coloured ornamental traits, especially those based on carotenoids, has been a central topic of sexual selection theory since Darwin (Darwin 1859, 1871; Andersson 1994), but the red spot in gulls may represent a unique case of a coloured signal with a role in intra-familial conflicts over care. Since it has been shown that the signal stimulates chick feeding, the intensity of the signal could also be used by the partner to predict feeding capacity in order to adjust its own investment (e.g. Velando *et al.* 2006). All this indicates that information exchange between all members of a gull family is plausible.

In the present study, we manipulated the red-spot size in one adult yellow-legged gull per nest and monitored its partner's feeding effort, in order to test the hypothesis that the red spot is a signal that affects the partner's reproductive investment (i.e. differential allocation; Burley 1988). Moreover, under the hypothesis that the red spot is a signal that affects decision rules in intra-familial interactions, we also analysed the feeding effort of both parents in relationship to offspring solicitation (the number of pecks directed to the red spot of each parent).

2. MATERIAL AND METHODS

(a) *Field procedures*

The experiment was conducted towards the end of May 2007 in a breeding colony of yellow-legged gulls at Sálvora Island, Galicia, Spain. We searched for nests with three eggs (the modal clutch size in this species) close to hatching, which is visually detectable by a crack or small hole in the shell.
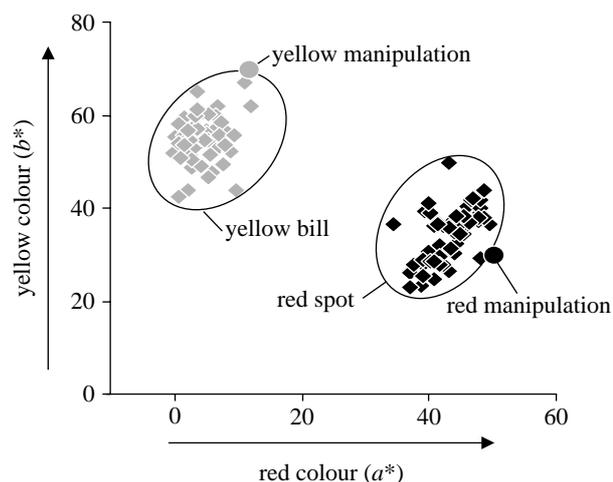

Figure 1. The colour (a^* and b^* in CIELAB colour space) of the red spot and the yellow bill of unmanipulated gulls in our population (from digital photographs of 57 gulls taken in 2004) is compared with the colour of the red and yellow polishes used to manipulate the red-spot size. The colour was measured with image analysis software (ANALYSIS FIVE). For each of three pixels on the central part of the red-spot area, a^* and b^* values in $L^*a^*b^*$ colour space were extracted and averaged. The yellow chroma was obtained in the same way but using three pixels on the yellow part of the bill.

We captured one adult per nest with nest traps (R60 special tilting cage; www.moudry.cz), selecting the first adult captured by the trap. A total of 72 adults were captured (33 males and 39 females) and randomly assigned to one of three treatments. The enlarged-spot group ($n=22$) had the original red spot enlarged with red nail polish (Astor 250), up to the maximum area found in the population (260 mm^2). The reduced-spot group ($n=23$) had the original red spot reduced with yellow nail polish (Yesensy 9) to the minimum area found in the population (78 mm^2). Finally, the control group was divided in two: unmanipulated individuals ($n=14$) and individuals with their original spot area unaltered, but painted over with the red polish and outlined with the yellow one ($n=13$), in order to control for the potential effect of paint colour on the behaviour of gull parents. We confirmed with binoculars that the spot area manipulation had lasted at least until the observation day. We tried to imitate the natural red-spot colour as closely as possible: the yellow and red manipulations were only very slightly over the natural range of red-spot chroma (figure 1), while brightness (L^* in CIELAB colour space) of both polishes was within the natural range of red-spot brightness. The two control groups did not differ in their initial parameters (sex, morphological parameters of manipulated adult, hatching data, observation date and number of chicks), nor in the response variables (provisioning rates performed by both adults and number of pecks; all $p>0.05$). Therefore, they were pooled as a single control group. Similar results were obtained when considering them as two separate groups (available upon request).

We marked captured gulls on the neck with a black spot, in order to easily identify the manipulated adult of each pair during observations. Birds were weighed (± 10 g) and their head, bill and tarsus lengths were measured (± 0.05 mm). The latter parameter allowed confirmation of the sex of captured birds by means of a discriminant function (Bosch 1996), known to be 100 per cent consistent with previously recorded copulatory behaviour

(Alonso-Álvarez & Velando 2003). We photographed the whole bill of each bird (Nikon Coolpix 5200) against a white standard together with a red standard and a millimetric scale. This was done by placing the bill laying in horizontal position inside a black box and keeping a constant distance (15 cm) from the lens to the bill. Illumination was provided by a three-LED lamp (Petzl Tikka) fastened firmly to the inner top of the box and angled 90° to the bottom of the box (i.e. at a distance of 15 cm to the bill for all measurements). The red-spot area was measured by the same person with image analysis software (ANALYSIS FIVE), blindly with respect to treatment. The red-spot area before manipulation, the proportion of sexes, body mass, and bill, tarsus and wing length of experimental birds did not differ between experimental treatments (all $p > 0.3$). The sexes did not differ in red-spot size ($F_{1,70} = 0.015$, $p = 0.90$; mean $\pm$ s.d. in females: 172.78 ± 34.49; males: 173.72 ± 28.76).

We checked nests daily to record the hatching date (hatching day = day zero). Two days after hatching (3.3 ± 0.1 days elapsed from manipulation to observation; there were no differences among treatments: $F_{2,66} = 0.04$, $p = 0.96$), we observed each pair continuously from 10.00 to 15.00 hours. Each observer observed two to six focal pairs simultaneously from a hide that had been put in place the previous day. During the 5 hours of observation time, we recorded chick-provisioning rate (number of regurgitations) performed by both the manipulated bird and its partner, and the number of individual pecks at the bill performed by chicks. Although chicks were individually marked with a small coloured spot on the head (black, blue or green), on many occasions we were not able to identify the specific chick that was pecking. Instead, we recorded the total chick-pecking rates directed to the manipulated gull or to its partner. Three nests could not be observed because adults became reluctant to feed the young after the observer had entered the hide. In three additional nests, the visibility was not good enough to record the number of pecks.

Working permissions and approval of the experimental procedures were given by Parque Nacional de las Islas Atlánticas de Galicia.

(b) *Statistical analyses*
We used SAS software (SAS Institute 2001) for all statistical analyses. We fitted two separate generalized linear models (GENMOD procedure in SAS) with Poisson errors to investigate whether the experiment affected chick pecking rate directed to the manipulated gull or to the partner. Sex of the adult and the number of chicks were included as covariates. In addition, we used another two GENMOD models with Poisson errors to investigate whether the experimental treatment affected the chick-provisioning rate of the manipulated adults or their partners. The number of pecks directed to the adult whose feeding rate was analysed was included as a covariate in the models. This was done to explore the effect of treatment on the relationship between chick-provisioning rate and pecking. Also, the following parameters were included as covariates: chick-provisioning rate of the partner, sex of the adult and the number of chicks. Data dispersion was corrected in all models using the Pearson scale parameter. All main effects and all possible two-way interactions were included in the initial models. Final models were obtained by backward deletion. First, the interaction terms were sequentially removed from the full model when the variance explained did not significantly improve the model
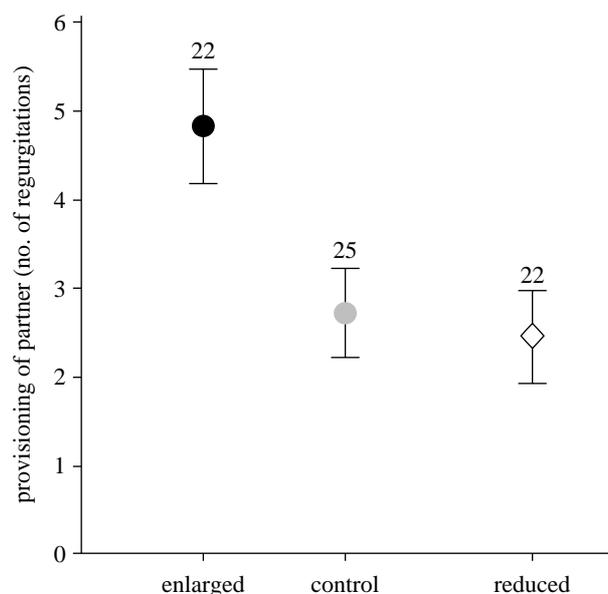
Figure 2. Effect of red-spot size manipulation on the partner's provisioning rate (no. of regurgitations).

($\alpha = 0.05$; Engqvist 2005). After all two-way non-significant interactions were removed from the model, the same deletion procedure was performed with the main effects of the predictor variables. We report the F and p values of the effects of non-significant terms before removing them from the model.

3. RESULTS
(a) *Effect of red-spot manipulation on chick pecking rate*
Treatment did not affect chick pecking rates directed to the manipulated gull ($F_{2,63} = 0.11$, $p = 0.89$; mean $\pm$ s.e. of the enlarged, 0.76 ± 0.27; control, 0.92 ± 0.26; reduced groups, 0.76 ± 0.27). Neither did it affect chick pecking rates directed to the partner ($F_{2,63} = 1.16$, $p = 0.32$; enlarged, 0.95 ± 0.22; control, 0.67 ± 0.21; reduced-spot group, 0.48 ± 0.22). There was no significant effect of the sex of the adult ($F_{1,64} = 2.82$, $p = 0.10$) or the number of chicks ($F_{2,62} = 0.55$, $p = 0.58$).

(b) *Effect of red-spot manipulation on the provisioning rate (number of regurgitations) of the partner*
The chick-provisioning rate of the partner was affected by treatment, being higher in the enlarged-spot group than the control and reduced-spot groups ($F_{2,66} = 4.75$, $p = 0.012$; figure 2). Interestingly, the relationship between the provisioning rate of the partner and the number of pecks directed at its bill was affected by the treatment (table 1). In the enlarged-spot group, the provisioning rate of the partner was not associated with the number of pecks directed to its bill ($\beta = 0.05$; figure 3). By contrast, in the reduced-spot group, the partner's provisioning effort was strongly predicted by the number of pecks directed at its bill ($\beta = 0.70$; figure 3). Finally, in controls, the partner's provisioning effort was marginally associated with the number of pecks directed at its bill, the slope of the association showing an intermediate value between the enlarged- and the reduced-spot groups ($\beta = 0.33$; figure 3). The number of chicks ($F_{2,58} = 1.36$, $p = 0.26$) and the provisioning rate

Table 1. Final generalized linear models (GENMOD procedure in SAS) with Poisson errors showing the significant effects on the provisioning rates of the parents.

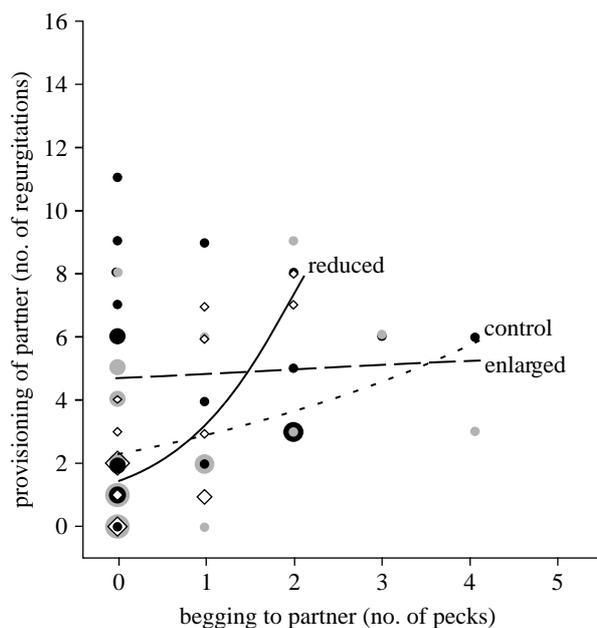|	provisioning of partner			provisioning of manipulated gull		
	F	d.f.	p-value	F	d.f.	p-value
treatment	7.22	2, 60	0.001			
begging to partner	12.02	1, 60	0.001			
treatment × begging to partner	4.28	2, 60	0.018			
begging to manipulated gull				9.93	1, 62	0.002
provisioning of partner				5.13	1, 62	0.027
provisioning of partner × begging to manipulated gull				5.02	1, 62	0.029

Figure 3. Effect of red-spot size manipulation on the relationship between the partner's provisioning rate (no. of regurgitations) and chick begging rate (no. of pecks directed to the partner). Black, grey and white shapes represent, respectively, the enlarged, control and reduced-spot groups. The size of the shapes corresponds to sample size, which ranges from one to five cases.

of the manipulated adult ($F_{1,57}=0.53$, $p=0.47$) were not significant. Also, there was no significant effect of adult sex ($F_{1,56}=0.38$, $p=0.54$) or its interactions with begging to partner ($F_{1,55}=1.16$, $p=0.29$), with treatment ($F_{2,53}=0.66$, $p=0.52$) and with provisioning of the manipulated gull ($F_{1,52}=0.001$, $p=0.95$).

(c) *Effect of red-spot manipulation on the provisioning rate of the manipulated adult*
The provisioning rate of the manipulated adult was not affected by treatment (ANOVA test including treatment alone: $F_{2,66}=0.24$, $p=0.78$). However, when including all the covariates in the model, the provisioning rate of the manipulated adult was affected by the interaction between the number of pecks at its bill and chick-provisioning rate performed by the partner (table 1). Thus, when the provisioning rate of the partner was low, the provisioning effort of the manipulated adult was strongly and positively associated with the number of pecks directed at its bill ($\beta=0.51$; figure 4). This positive effect disappeared when the partners had high provisioning rates ($\beta=-0.04$;
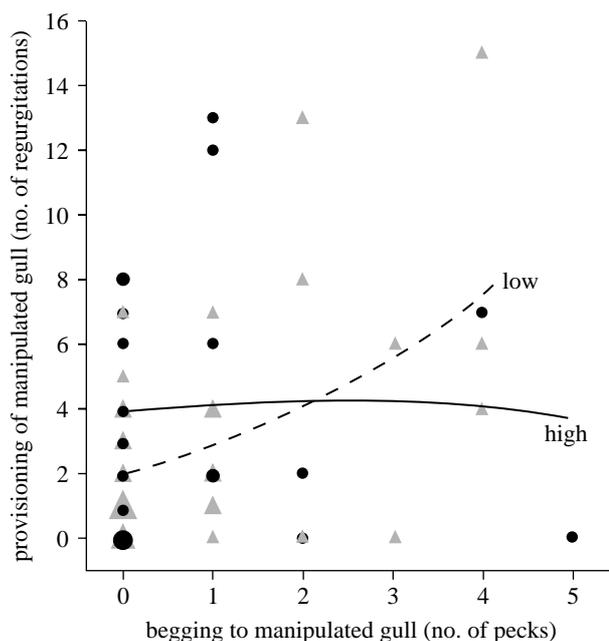

Figure 4. Effect of partner's provisioning rate on the relationship between provisioning effort of the manipulated gull and chick begging rate to the manipulated gull (no. of pecks). For illustrative purposes, we divided partner's provisioning rate into two categories: low (less than five regurgitations, represented by grey triangles) and high (five or more regurgitations, represented by black circles). The size of the circles and triangles corresponds to sample size, which ranges from one to seven cases.

figure 4). Including treatment in the final model did not change the results (provisioning of partner × begging to manipulated adult: $F_{1,60}=6.17$, $p=0.016$; treatment: $F_{2,60}=1.30$, $p=0.28$). Neither the number of chicks ($F_{2,58}=2.34$, $p=0.10$) nor sex of the manipulated adult ($F_{1,57}=0.05$, $p=0.82$) were significant. Also, there were no significant effects of the interaction between sex and other covariates (sex of the adult × treatment: $F_{2,55}=0.92$, $p=0.41$; sex of the adult × begging to the manipulated gull: $F_{1,54}=0.73$, $p=0.40$; sex of the adult × provisioning of partner: $F_{1,53}=0.46$, $p=0.50$).

4. DISCUSSION
The results demonstrate that decision rules in familial conflicts depend on the reliable information conveyed by sexual signals (the red spot), and suggest that they may also be influenced by the provisioning rate of the partner and offspring begging behaviour. Partners

doubled their provisioning effort in the enlarged-spot group, supporting the role of sexual signals in breeding decisions (i.e. differential allocation hypothesis; Burley 1988). Moreover, in the reduced-spot group, partners fine-tuned their feeding effort according to offspring begging behaviour, contrasting with the fixed effort showed by partners of enlarged-spot gulls. Manipulated gulls, independently of treatment, provided food in relationship to chick pecking when the partner's investment was low, but performed a fixed effort when the partner's contribution was high. Overall, these findings suggest that parents may use multiple information sources to adjust their investment and that rules over parental care are plastic, varying from flexible to fixed depending on the information on offer (McNamara *et al.* 1999; Hinde 2006; Johnstone & Hinde 2006).

Heinroth & Heinroth (1928) pointed out that gull chicks show a strong tendency to peck at red objects, and Tinbergen's (Tinbergen & Perdeck 1950; Tinbergen 1953) and later studies (e.g. Dawkins & Impekoven 1969; Alessandro *et al.* 1989; Griswold *et al.* 1995) have shown that the red spot on the bill of various gull species is a stimulus that elicits chick pecking. This previous evidence together with the present study show that the red spot is involved in interactions both between the breeding pair and between parent and offspring, thus becoming the first case of a 'familial' signal. This signal may play a role in parent–offspring communication only in the first few days after hatching, when chick pecking behaviour is prompted by the red spot (Tinbergen & Perdeck 1950). Interestingly, parents seem to have control; for example, parents sometimes only simulate regurgitation after repeated pecking by the chick (Hendersson 1975). Similarly, we found that regurgitation was not always proportional to chick pecking, as parental effort was adjusted to pecking rate in certain situations, but not in others (e.g. when the partner's effort was high).

We found that partners enhanced their effort when their mate had an enlarged red spot. Parental investment should be affected by the mate's quality or parental abilities (Chase 1980; Houston & Davies 1985; Cunningham & Russell 2000), particularly in long-lived species (Jones & Montgomerie 1992; Velando & Alonso-Álvarez 2003; Krebs & Putland 2004). In species with biparental care, sexual signals are expected to be the modest, but honest, indicators of parental abilities or resources available, thus revealing direct benefits to the mate (Kokko 1998). In gulls, the red spot reliably indicates some aspects of individual quality, such as antioxidant status, carotenoid intake and condition (Blount *et al.* 2002; Kristiansen *et al.* 2006; Pérez *et al.* 2008), as well as egg quality (Blount *et al.* 2002; Kristiansen *et al.* 2006). Thus, gull parents may gain direct benefits when their mate shows a large red spot. However, indirect benefits are also possible (Kokko 1998; Houston *et al.* 2005; Velando *et al.* 2005), so that the signal could reflect the bearer's genetic quality, which offspring may inherit. This may apply to both sexes when care is equally provided by males and females (Kokko 1998), and may explain why we did not find sex differences in provisioning rules. It has been proposed that dissimilar opportunities for extra-pair copulations might cause provisioning rules to differ between males and females (Kölliker *et al.* 1998). However, the mechanisms of paternity assurance (Velando 2004) and the consequent

low extra-pair paternity in gulls (Gilbert *et al.* 1998) may in part explain why, in our study, both sexes followed similar rules over investment. Accordingly, previous studies in monogamous species have shown that males and females can benefit equally if they increase parental effort according to the mate's advertisement or its level of investment (reviewed in Kraaijeveld *et al.* 2007).

Apart from the red-spot size, yellow-legged parents seemed to be influenced by other information sources (partner's effort and the number of pecks performed by offspring) to adjust their parental care, although these traits were not manipulated and the interpretations should thus be taken with caution. One possibility is that the perceived probability of failure in the current reproduction affected parental decision rules (McNamara *et al.* 1999; Royle *et al.* 2002). For instance, young at increased probability of starving are expected to benefit to a greater degree from additional resources than those chicks at a lower probability (Godfray & Johnstone 2000). Hence, parents should fine-tune their effort in relationship to begging, being more responsive when parental investment confers disproportionately high fitness returns to the offspring (Godfray & Johnstone 2000). Consistent with this, parent gulls responded accurately to chick pecking only when the partner's ornament expression or contribution were low, i.e. when there was a high probability of failure. By contrast, when the partner's ornament expression or investment were high (diminishing marginal fitness returns), parents provisioned offspring at a constant rate, thus avoiding the potential costs of evaluating offspring need. Similar risk-based rules are expected in central economic models of optimal investment of capital, such as that of Markowitz (i.e. investors select from the set of optimal risk–return options; Markowitz 1952; Gigerenzer 2008). Nevertheless, as we have not manipulated chick begging, we cannot be sure whether it is a causal factor for variation in provisioning rate. Alternatively, the number of pecks performed by gull chicks could be reliable only when breeding conditions are poor (Godfray & Johnstone 2000). However, exactly the opposite is expected in theory (Royle *et al.* 2002). Furthermore, according to previous studies, the expression of the red spot may enhance the number of pecks, entailing costs (if pecking is costly) to the offspring that prevent them from cheating. Although the present study failed to find an effect of the size of the red spot on chick pecking rate, the experiments performed by Tinbergen did find such an effect (Tinbergen & Perdeck 1950; Tinbergen 1953). Nevertheless, super-stimuli (exaggerated versions of a signal) may provoke unnatural responses, so Tinbergen's results should be treated with caution.

An interesting question arises as to how parents evaluate the partner's effort to adjust their own investment. One possibility is that they directly observe the partner's behaviour, as described in previous studies (Hinde 2006 and references therein). Gull parents engage in complex rituals that offer excellent opportunities for a direct and dynamic assessment of their mates' quality or parental effort. For instance, there is a brief ritual between mates during nest relief, sometimes including pre-copulatory behaviour (Hendersson 1975), and parents commonly feed the chicks in the presence of the partner (J. M. Morales, C. Alonso-Álvarez, C. Pérez, E. Serafino & A. Velando 2007, personal observation). Moreover, parents can also indirectly assess their partners' contributions by

evaluating brood need, quality or behaviour (Wright & Dingemanse 1999; Johnstone & Hinde 2006).

Our study highlights the crucial role of information exchange in the interactions between family members and different sources of information that are used in different contexts. Information about the likely success of a breeding attempt is known to affect parental decisions in insects (Alexander 1974; Agrawal *et al.* 2001), fish (Steinegger & Taborsky 2007; Pike *et al.* 2008), birds (Kilner *et al.* 1999; Kilner 2002; Velando *et al.* 2006; Griggio & Pilastro 2007) and mammals (Hudson & Trillmich 2008). Information exchange between family members may also explain the occurrence of flexible or fixed provisioning rules across species (Velando & Alonso-Álvarez 2003; Hinde & Kilner 2007). Furthermore, information is relevant in all negotiation games, whether between family members or unrelated individuals, in social interactions (McNamara *et al.* 1999, 2008; Novak 2006).

In conclusion, our results, together with previous evidence, strongly suggest that the red spot on the bill of various gull species is used by all family members to adjust decision rules. Offspring are known to exhibit begging displays or colourful gapes to convey honest information to their parents (e.g. Kilner & Johnstone 1997; Kölliker *et al.* 1998; Royle *et al.* 2002). Similarly, sexual signals may also play a role in the interactions between parents and offspring, although they have been narrowly considered in the context of sexual selection.

REFERENCES

Agrawal, A. F., Brodie III, E. D. & Brown, J. 2001 Parent–offspring coadaptation and the dual genetic control of maternal care. *Science* **292**, 1710–1712. (doi:10.1126/science.1059910)

Alessandro, D., Dollinger, J., Gordon, J. D., Mariscal, S. K. & Gould, J. L. 1989 The ontogeny of the pecking response of herring gull chicks. *Anim. Behav.* **37**, 372–382. (doi:10.1016/0003-3472(89)90085-7)

Alexander, R. D. 1974 The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5**, 325–383. (doi:10.1146/annurev.es.05.110174.001545)

Alonso-Álvarez, C. & Velando, A. 2003 Female body condition and brood sex ratio in yellow-legged gulls *Larus cachinnans*. *Ibis* **145**, 220–226. (doi:10.1046/j.1474-919X.2003.00149.x)

Andersson, M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.

Beer, C. G. 1966 Incubation and nest-building behaviour of black-headed gulls. V: the post-hatching period. *Behaviour* **26**, 189–214. (doi:10.1163/156853965X00183)

Blount, J. D., Surai, P. F., Nager, R. G., Houston, D. C., Møller, A. P., Trewby, M. L. & Kennedy, M. W. 2002

Carotenoids and egg quality in the lesser black-backed gull *Larus fuscus*: a supplemental feeding study of maternal effects. *Proc. R. Soc. Lond. B* **269**, 29–36. (doi:10.1098/rspb.2001.1840)

Bosch, M. 1996 Sexual size dimorphism and determination of sex in yellow legged gulls. *J. Field. Ornithol.* **67**, 534–541.

Burley, N. 1988 The differential-allocation hypothesis: an experimental test. *Am. Nat.* **132**, 612–618. (doi:10.1086/284877)

Camerer, C. F. & Fehr, E. 2006 When does 'economic man' dominate social behavior? *Science* **311**, 47–52. (doi:10.1126/science.1110600)

Chase, I. D. 1980 Cooperative and non-cooperative behaviour in animals. *Am. Nat.* **115**, 827–857. (doi:10.1086/283603)

Clutton-Brock, T. H. & Parker, G. A. 1995 Punishment in animal societies. *Nature* **373**, 209–216. (doi:10.1038/373209a0)

Cramp, S. & Simmons, K. E. L. 1983 *Handbook of the birds of Europe, the Middle East and North Africa. The birds of western Palearctic vol. 3*: *waders to gulls*. Oxford, UK: Oxford University Press.

Cunningham, E. J. A. & Russell, A. F. 2000 Differential allocation and 'good genes': comment from Cunningham & Russell. *Trends Ecol. Evol.* **16**, 21. (doi:10.1016/S0169-5347(00)02049-8)

Curio, E. 1983 Why do young birds reproduce less well? *Ibis* **125**, 400–404. (doi:10.1111/j.1474-919X.1983.tb03130.x)

Darwin, C. 1859 *On the origin of species by means of natural selection*. London, UK: Murray.

Darwin, C. 1871 *The descent of man, and selection in relation to sex*. London, UK: Murray.

Dawkins, R. & Impekoven, M. 1969 The 'peck/no-peck decision-maker' in the black-headed gull chick. *Anim. Behav.* **17**, 243–251. (doi:10.1016/0003-3472(69)90009-8)

Engqvist, L. 2005 The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Anim. Behav.* **70**, 967–971. (doi:10.1016/j.anbehav.2005.01.016)

Gigerenzer, G. 2008 *Gut feelings: the intelligence of the unconscious*. New York, NY: Viking.

Gilbert, L., Burke, T. & Krupa, A. 1998 No evidence for extra-pair paternity in the western gull. *Mol. Ecol.* **7**, 1549–1552. (doi:10.1046/j.1365-294x.1998.00488.x)

Godfray, H. C. J. 1995 Evolutionary theory of parent–offspring conflict. *Nature* **376**, 133–138. (doi:10.1038/376133a0)

Godfray, H. C. J. & Johnstone, R. A. 2000 Begging and bleating: the evolution of parent–offspring signalling. *Phil. Trans. R. Soc. Lond. B* **355**, 1581–1591. (doi:10.1098/rstb.2000.0719)

Griggio, M. & Pilastro, A. 2007 Sexual conflict over parental care in a species with female and male brood desertion. *Anim. Behav.* **74**, 779–785. (doi:10.1016/j.anbehav.2007.01.007)

Griswold, D. A., Harrer, M. F., Sladkin, C., Alessandro, D. A. & Gould, J. L. 1995 Intraspecific recognition by laughing gull chicks. *Anim. Behav.* **50**, 1341–1348. (doi:10.1016/0003-3472(95)80049-2)

Hamilton, W. D. 1964 The genetical evolution of social behaviour. *J. Theor. Biol.* **7**, 1–52. (doi:10.1016/0022-5193(64)90038-4)

Heinroth, O. & Heinroth, M. 1928 *Die Vögel Mitteleuropas*. Berlin, Germany: Hugo Behrmöller.

Hendersson, B. A. 1975 Role of the chick's begging behavior in the regulation of parental feeding behavior of *Larus glaucescens*. *Condor* **77**, 488–492. (doi:10.2307/1366101)

Hinde, C. A. 2006 Negotiation over offspring care?—a positive response to partner-provisioning rate in great tits. *Behav. Ecol.* **17**, 6–12. (doi:10.1093/beheco/ari092)

Hinde, C. A. & Kilner, R. M. 2007 Negotiations within the family over the supply of parental care. *Proc. R. Soc. B* **274**, 53–60. (doi:10.1098/rspb.2006.3692)

Houston, A. I. & Davies, N. B. 1985 The evolution of cooperation and life history in the dunnock *Prunella modularis*. In *Behavioural ecology: the ecological consequences of adaptive behavior* (eds R. Sibly & R. Smith), pp. 471–487. Oxford, UK: Blackwell.

Houston, A. I., Székely, T. & McNamara, J. M. 2005 Conflict between parents over care. *Trends Ecol. Evol.* **20**, 33–38. (doi:10.1016/j.tree.2004.10.008)

Hudson, R. & Trillmich, F. 2008 Sibling competition and cooperation in mammals: challenges, developments and prospects. *Behav. Ecol. Sociobiol.* **62**, 299–307. (doi:10.1007/s00265-007-0417-z)

Johnstone, R. A. & Hinde, C. A. 2006 Negotiation over offspring care—how should parents respond to each other's efforts? *Behav. Ecol.* **17**, 818–827. (doi:10.1093/beheco/arl009)

Jones, I. L. & Montgomerie, R. 1992 Least auklet ornaments: do they function as quality indicators? *Behav. Ecol. Sociobiol.* **30**, 43–52. (doi:10.1007/BF00168593)

Kilner, R. M. 2002 Sex differences in canary (*Serinus canaria*) provisioning rules. *Behav. Ecol. Sociobiol.* **52**, 400–407. (doi:10.1007/s00265-002-0533-8)

Kilner, R. & Johnstone, R. A. 1997 Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.* **12**, 11–15. (doi:10.1016/S0169-5347(96)10061-6)

Kilner, R. M., Noble, D. G. & Davies, N. B. 1999 Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature* **397**, 667–672. (doi:10.1038/17746)

Kokko, H. 1998 Should advertising parental care be honest? *Proc. R. Soc. Lond. B* **265**, 1871–1878. (doi:10.1098/rspb.1998.0515)

Kölliker, R., Richner, M., Werner, I. & Heeb, P. 1998 Begging signals and biparental care: nestling choice between parental feeding locations. *Anim. Behav.* **55**, 215–222. (doi:10.1006/anbe.1997.0571)

Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Komdeur, J. 2007 The evolution of mutual ornamentation. *Anim. Behav.* **74**, 657–677. (doi:10.1016/j.anbehav.2006.12.027)

Krebs, E. A. & Putland, D. A. 2004 Chic chicks: the evolution of chick ornamentation in rails. *Behav. Ecol.* **6**, 946–951. (doi:10.1093/beheco/arh078)

Kristiansen, K. O., Bustnes, J. O., Folstad, I. & Helberg, M. 2006 Carotenoid coloration in great black-backed gull *Larus marinus* reflects individual quality. *J. Avian. Biol.* **37**, 6–12. (doi:10.1111/j.0908-8857.2006.03667.x)

Lessells, C. M. 1999 Sexual conflict. In *Levels of selection in evolution* (ed. L. Keller), pp. 75–99. Monographs in Behaviour and Ecology. Princeton, NJ: Princeton University Press.

Markowitz, H. 1952 Portfolio selection. *Journal of Finance* **7**, 77–91. (doi:10.2307/2975974)

McNamara, J. M., Gasson, C. E. & Houston, A. I. 1999 Incorporating rules for responding into evolutionary games. *Nature* **401**, 368–371. (doi:10.1038/43869)

McNamara, J. M., Binmore, K. & Houston, A. I. 2006 Cooperation should not be assumed. *Trends Ecol. Evol.* **21**, 476–478. (doi:10.1016/j.tree.2006.07.005)

McNamara, J. M., Barta, Z., Fromhage, L. & Houston, A. 2008 The coevolution of choosiness and cooperation. *Nature* **451**, 189–192. (doi:10.1038/nature06455)

Milinski, M. & Rockenbach, B. 2008 Punisher pays. *Nature* **452**, 297–298. (doi:10.1038/452297a)

Novak, M. A. 2006 Five rules for the evolution of cooperation. *Science* **314**, 1560. (doi:10.1126/science.1133755)

Parker, G. A. 1985 Models of parent–offspring conflict. V. Effects of the behaviour of the two parents. *Anim. Behav.* **33**, 519–533. (doi:10.1016/S0003-3472(85)80075-0)

Parker, G. A., Royle, N. J. & Hartley, I. R. 2002 Intrafamilial conflicts and parental investment: a synthesis. *Phil. Trans. R. Soc. Lond. B* **357**, 295–307. (doi:10.1098/rstb.2001.0950)

Pérez, C., Lores, M. & Velando, A. 2008 The availability of nonpigmentary antioxidant affects red coloration in gulls. *Behav. Ecol.* **19**, 967–973. (doi:10.1093/beheco/arn053)

Pike, T. W., Samanta, M., Lindström, J. & Royle, N. J. 2008 Behavioural phenotype affects social interactions in an animal network. *Proc. R. Soc. B* **275**, 2515–2520. (doi:10.1098/rspb.2008.0744)

Roulin, A. & Bersier, L.-F. 2007 Nestling barn owls beg more intensely in the presence of their mother than in the presence of their father. *Anim. Behav.* **74**, 1099–1106. (doi:10.1016/j.anbehav.2007.01.027)

Royle, N. J., Hartley, I. R. & Parker, G. A. 2002 Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol. Evol.* **17**, 434–440. (doi:10.1016/S0169-5347(02)02565-X)

SAS Institute 2001 *The SAS system for Windows, version 9.0.* Cary, NC: SAS Institute Inc.

Stearns, S. C. 1992 *The evolution of life histories.* New York, NY: Oxford University Press.

Steinegger, M. & Taborsky, B. 2007 Asymmetric sexual conflict over parental care in a biparental cichlid. *Behav. Ecol. Sociobiol.* **61**, 933–941. (doi:10.1007/s00265-006-0322-x)

Tinbergen, N. 1953 *The herring gull's world.* London, UK: Collins.

Tinbergen, N. & Perdeck, A. C. 1950 On the stimulus situation releasing the begging response in the newly hatched herring gull chick (*Larus argentatus argentatus* Pont.). *Behaviour* **3**, 1–39. (doi:10.1163/156853951X00197)

Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man 1871–1971* (ed. B. Campbell), pp. 136–179. Chicago, IL: Aldine Press.

Trivers, R. L. 1974 Parent–offspring conflict. *Am. Zool.* **14**, 249–264. (doi:10.1093/icb/14.1.249)

Trivers, R. L. 1985 *Social evolution.* Menlo Park, CA: Benjamin/Cummings.

Velando, A. 2004 Female control in the yellow-legged gull: trading paternity assurance for food. *Anim. Behav.* **67**, 899–907. (doi:10.1016/j.anbehav.2003.08.019)

Velando, A. & Alonso-Álvarez, C. 2003 Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *J. Anim. Ecol.* **72**, 846–856. (doi:10.1046/j.1365-2656.2003.00756.x)

Velando, A., Torres, R. & Espinosa, I. 2005 Male coloration and chick condition in blue-footed booby: a cross-fostering experiment. *Behav. Ecol. Sociobiol.* **58**, 175–180. (doi:10.1007/s00265-005-0911-0)

Velando, A., Beamonte-Barrientos, R. & Torres, R. 2006 Pigment-based skin color in the blue-footed booby: an honest signal of current condition used by females to adjust reproductive investment. *Oecologia* **149**, 535–542. (doi:10.1007/s00442-006-0457-5)

Weidmann, R. 1956 The social behaviour of the black-headed gull with special reference to incubation and food-begging behaviour. PhD thesis, Oxford University.

Wright, J. & Dingemanse, N. J. 1999 Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. *Anim. Behav.* **58**, 345–350. (doi:10.1006/anbe.1999.1152)