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Female control in yellow-legged gulls: trading paternity assurance for food

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Females in many socially monogamous birds copulate hundreds of times more than necessary for fertilization, although little is known about the benefits of this excess. Females may not directly benefit from high copulation rates, but instead may exploit male interest in copulating to obtain benefits. In species with courtship feeding, females may trade copulations for food (immediate benefits hypothesis). I tested this hypothesis by analysing female behaviour during courtship in yellow-legged gulls, *Larus cachinnans*. Female gulls to some extent controlled sperm transfer, because they moved during copulation bouts, and this behaviour influenced the number of cloacal contacts per mounting that the male achieved. Female control was related to previous feeding by the male, and hence the male courtship feeding rate correlated with the cloacal contact rate. Males that give more food probably enhance their chances of fathering offspring. By analysing within-individual female behaviour, I also found that the number of cloacal contacts was higher when the male fed the female than when he did not, which indicates that female gulls followed a decision rule to resist copulation when food is not given. Overall, these results support the hypothesis that female gulls manipulate their mates to obtain food.

In many animals, intersexual conflict, when mating interests differ between the sexes, has influenced the evolution of male and female sexual behaviour (Trivers 1972; West-Eberhard et al. 1987; Rice 1996). The extent to which males or females influence mating will depend on the level of control that each sex can exert on mating (Borgia 1979; Parker 1979; Clutton-Brock & Parker 1995). In monogamous species, the conflict may continue after the partner has been chosen, and may arise over investment in parental duties such as nest building, incubation, feeding of young, territorial defence and partner cooperation (Winkler 1987; Lessells 1999; Royle et al. 2002). Evolution may favour individuals that can persuade their partner to make a greater investment (Trivers 1972).

Many socially monogamous birds copulate hundreds of times more than is necessary for simple fertilization (Birkhead & Møller 1992). Multiple copulations with the same female are beneficial for males because they devalue the effects of any extrapair copulations (EPCs) in which their mates have engaged (Birkhead & Parker 1997; Birkhead 1998). Multiple copulations with the same male may not be advantageous for females, because one or just a few copulations will provide enough sperm to fertilize an entire clutch (Birkhead et al. 1989; Adkins-Regan 1995), and copulation implies a waste of time and energy, as well as increasing the risk of pathogen transmission (Birkhead & Møller 1992; Hunter et al. 1993; Sheldon 1993). This evidence might suggest that frequent pair copulation is a male strategy that conflicts with female interests (Stockley 1997), yet it is generally accepted that female birds can control the frequency at which copulation takes place (Birkhead & Møller 1992; Hunter et al. 1993; Lens et al. 1997; Delehanty et al. 1998). Female birds may modify their solicitation behaviour, prevent a male from mounting or terminate a copulation attempt before cloacal contact is achieved. Presumably, then, females often gain some additional benefits from repeated copulations with the same male that outweigh any possible costs (Hunter et al. 1993; Heeb 2001).

Several hypotheses have been proposed to explain frequent pair copulation from a female perspective (reviewed in Hunter et al. 1993). These hypotheses can be grouped according to the mechanism through which females are expected to benefit. The beneficial copulation hypotheses state that females obtain direct benefits from high copulation frequency. Possible benefits include beneficial sexually transmitted microbes (Lombardo et al. 1999), fertility assurance, a reduction in the risk of sperm depletion (Birkhead et al. 1987; Sax et al. 1998; Lifjeld

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et al. 2000), information gained about male quality (Tortosa & Redondo 1992; Negro et al. 1996; Catry & Furness 1997; Lens et al. 1997; Villarroel et al. 1998) or benefits obtained from territorial signalling (Negro & Grande 2001). The manipulating males hypotheses suggest that females do not directly benefit from high copulation rates but obtain benefits from male behaviour. Females could trade copulations as paternity assurance for immediate benefits such as food (Tasker & Mills 1981), mate fidelity and future paternal care (Davies et al. 1992; Dixon et al. 1994; Eens & Pinxten 1995; Sheldon & Ellegren 1998) or protection by the partner to reduce harassment from other males (Lijfield 1994; Lovell-Mansbridge & Birkhead 1998).

These two groups of alternative hypotheses are not mutually exclusive, and it is likely that females accrue direct benefits as well as benefits derived from their mate. Nevertheless, beneficial copulation (direct benefits) hypotheses suggest that the females are as interested in the copulation as the male is, so, rather than enter into conflict over copulation, both sexes should cooperate. In contrast, manipulating males hypotheses propose that females use the male's interest in copulation to obtain benefits. In a conflicting context, female sexual behaviour may be important in controlling male behaviour and therefore guarantee more help in reproduction (Lumpkin 1983; Gowaty 1996; Rodríguez-Gironés & Enquist 2001). In humans and other primates, for example, females may trade copulations for resources and male help (Alexander & Noonan 1979; Hill 1982; Hill & Kaplan 1988).

The most interesting species with which to test whether females obtain benefits by manipulating males are those in which females are in a position to trade copulations for immediate benefits (immediate material benefits hypothesis). In some bird species, females have occasionally been recorded exchanging EPCs directly for food (Mills 1994; Gray 1997; also in polygynous species: Wolf 1975) or nest material (Hunter & Davis 1998). In species with courtship feeding, females may trade pair copulations for food (Lack 1940; Tasker & Mills 1981), although this has not been tested. This hypothesis arises from evidence of a temporal link between copulations and male feeding in some species (usually copulation follows male feeding; e.g. Cullen & Ashmole 1963; Brown 1967; Calder 1968; Stokes & Williams 1971; Tasker & Mills 1981; Neuman et al. 1998; Arroyo 1999), but not in others (e.g. Royama 1966; East 1981; Kilham 1981; Niebuhr 1981; Greenberg & Gradwohl 1983; Lifjeld & Slagsvold 1986; Birkhead & Lessells 1988; Wiggins & Morris 1988; Simmons 1990; Donázar et al. 1992; Green & Krebs 1995; Lens et al. 1997; Blanchard & Morris 1998; Villarroel et al. 1998; Hatchwell et al. 1999; Mougeot 2000; González-Solis et al. 2001). The best evidence supporting the immediate material benefits hypothesis is found in gull species. In the red-billed gull, *Larus novaehollandiae*, mountings were more likely to be successful when food had been offered previously (Tasker & Mills 1981; Mills 1994), and a similar result was found in black-legged kittiwakes, *Rissa tridactyla* (Neuman et al. 1998). However, in both species, feeding was not essential for successful copulation (Tasker & Mills 1981; Neuman et al. 1998; e.g. in other gull species: Brown 1967; Niebuhr 1981). The links between successful copulation and courtship feeding do not necessarily mean that females trade copulation for food, and alternative hypotheses are possible. For example, Birkhead & Møller (1992, page 150) suggested that the link between food and copulation is a male strategy: 'by providing food for the female and by copulating frequently males will benefit in two ways: directly through increased certainty of paternity and indirectly through increased reproductive success if the food he provides increases the quality or the quantity of offspring produced'. Thus, specific tests must be carried out to identify whether female gulls trade copulations for food.

In this paper I report a field study on female copulation behaviour during the fertile period in the yellow-legged gull, *Larus cachinnans*, that tested whether females exchanged paternity assurance for immediate material benefits. The underlying assumptions of the manipulation hypotheses are that sperm transference is controlled by females and that female control (and hence sperm transfer) is related to courtship feeding. In gulls, several cloacal contacts may occur in a single bout of copulation. I tested (1) whether female behaviour during copulation affected the number of cloacal contacts, and hence (2) whether females resisted copulation when no food was given.

To remove uncontrolled variables specific to individual pairs, I used within-female analysis of the influence of courtship feeding and copulation rates, having removed nuisance variables specific to individual pairs. This method may provide valuable insight as to individual decisions. The immediate benefit hypothesis can be restated as a fixed-decision rule within individual females with instructions such as 'resist copulation when food is not given' or 'copulate repeatedly when food is given'. Analysing variation within individual females could represent a powerful method for detecting female decisions regarding their behaviour in relation to the courtship feeding by their partner. I examined whether the number of cloacal contacts was related to previous partner feeding within individual female gulls.

METHODS

Study Colony

The study was carried out in the yellow-legged gull colony on the Islas Cíes, Ría de Vigo, Galicia, Spain, between April and May 1998. The Islas Cíes holds a nesting population of ca. 22 000 pairs of these gulls. In this colony, there is a low interannual variation in the timing of laying, and the first eggs are laid during the first week of May (A. Velando, unpublished data). In a large breeding area, I observed the courtship behaviour of gulls from hides. The observations were made before the first egg was laid in the colony.

Behavioural Observations

I carried out two observational studies: an 'ad libitum' sequential study and a focal study on courtship pairs. In the sequential study, I randomly observed courtship sequences in a large colony (>5000 pairs). The main problem in previous sequential studies analysing courtship feeding and copulation is that many pairs were observed many times, but the sequences were then used as a unit of analysis (i.e. pseudoreplication: Hurlbert 1984). Thus, in my study, I recorded only one sequence per territory. In gulls, the pair retains the same territory during courtship, so this approach would ensure that different pairs were sampled for each sequence (e.g. Fitch & Shugart 1984). I observed 54 and 57 sequences on 30 April and 4 May, respectively. Courtship bouts were defined as uninterrupted courtship segments, during which neither participant engaged with a third individual, and in which the courting birds were within 1 m of each other. A courtship sequence was considered ended when one of the courting individuals moved away or when a courting pair remained inactive for 3 min. The following categories, and their sequence, were recorded: female begging, male head tossing, male courtship feeding, mounting, cloacal contact and female displacement during mounting (Tinbergen 1959; Brown 1967; Tasker & Mills 1981; Alonso-Alvarez & Velando 2001). Mounting was recorded when a male jumped on the female's back, irrespective of whether this ended in cloacal contact. Cloacal contact occurred when the male forced his tail between one of the female's wings and her tail and their cloacas met. Typically, courtship feeding started with females adopting a hunched posture, then tossing their heads and producing a short call (Tinbergen 1959; Brown 1967; Tasker & Mills 1981); in this study, I grouped all these behaviours in the 'female begging' category and recorded them as the number of head tosses (Neuman et al. 1998). Female displacement was recorded when a female moved about or walked while the male was on top (Tasker & Mills 1981).

In the focal study, I observed 21 pairs simultaneously in 1-h blocks from a hide. The nearest territory was 5 m and the furthest 50 m from the hide. I carried out 30 h of observation from 1 to 3 May. Focal female gulls were sampled during the week before their individual laying date (all pairs laid between 3 and 8 May). The following categories and their sequences were recorded: courtship feeding, mounting and cloacal contact. To facilitate the behaviour sampling, I recorded only individual behaviour involving both pair members on the territory; thus, extrapair feedings and copulations were not recorded (in this population, extrapair feedings and unforced EPCs were rare: C. Alonso-Alvarez, unpublished data). On the territories, female gulls were identified on the basis of recognizable bill marks and plumage features such as primary spots and sexed by size differences when both members of the pair were present (Tinbergen 1953; Bolton et al. 1992, 1993; Chardine 2002).

Data Analysis

In the sequential study, the day of observation had no effect on the number of courtship feedings, female displacements, cloacal contacts or mountings recorded ($P > 0.1$), so I pooled the data. The influence of female behaviour during mounting was investigated using a Generalized Linear Model (GLM; Wedderburn 1974; McCullagh & Nelder 1989) with a Poisson distribution and log link. The link function and error distribution in the GLMs were applied taking into account the presumed error distribution of the data and selecting those that minimized the deviance in the model (Crawley 1993; Herrera 2000). The model was fitted with cloacal contacts as a dependent variable and female displacement and female begging as explanatory variables. The number of female begging bouts and cloacal contacts per mounting in relation to courtship feeding were analysed using nonparametric Mann–Whitney tests.

In the focal study, I converted behavioural categories into frequencies by dividing the number of behaviours by the number of hours of observation. The association between the courtship feeding rate and the mounting rate and cloacal contact rate were analysed using nonparametric Spearman rank correlation. In the focal study, 13 of 21 females were observed in mountings preceded or not preceded by courtship feeding. I considered individual females as the unit for statistical analysis; thus, the within-pair average of cloacal contacts per mounting was separately computed for mountings preceded and not preceded by courtship feeding. I used the Wilcoxon signed-ranks exact test to compare cloacal contacts in individual females. All tests were two tailed and the alpha level was set at 0.05. Descriptive statistics are expressed as means ± SE.

RESULTS

Female Behaviour During Copulation

Of the 111 courtship sequences recorded, 54 ended in mountings. Female behaviour affected the chances of a successful copulation (Fig. 1). When female displacements were recorded during the copulation, the number of cloacal contacts in the copulation bout was significantly lower than when females did not move (GLM: $F_{1,51} = 55.03$, $P < 0.0001$). When I controlled for female displacement, the association between female begging bouts during the copulation bout and cloacal contacts was also significant (GLM: $F_{1,50} = 7.81$, $P = 0.007$).

Female displacement during copulation was related to previous courtship feeding (Fisher's exact test: $P < 0.0001$; Fig. 2a). Female displacement was recorded only during mountings that had not been immediately preceded by courtship feeding. During mountings preceded by male feeding, female begging was 6.8 times less frequent than during mountings that had not been immediately preceded by male feeding (Mann–Whitney U test: $Z = 5.30$, $N_1 = 22$, $N_2 = 31$, $P < 0.001$; Fig. 2b).

Courtship feeding was not a prerequisite for mounting; thus, 58% of the mountings recorded were not preceded by male feeding. Nevertheless, the probability of cloacal contact was related to previous courtship feeding ($\overline{X} \pm$ SE number of cloacal contacts in mountings preceded by courtship feeding $= 4.27 \pm 0.43$, in mountings with no previous male feeding $= 0.74 \pm 0.19$; Mann–Whitney U test: $Z = 5.30$, $N_1 = 22$, $N_2 = 31$, $P < 0.001$). In total, 43 courtship sequences included courtship feeding, but only 22 ended in mountings. The recorded sequences with

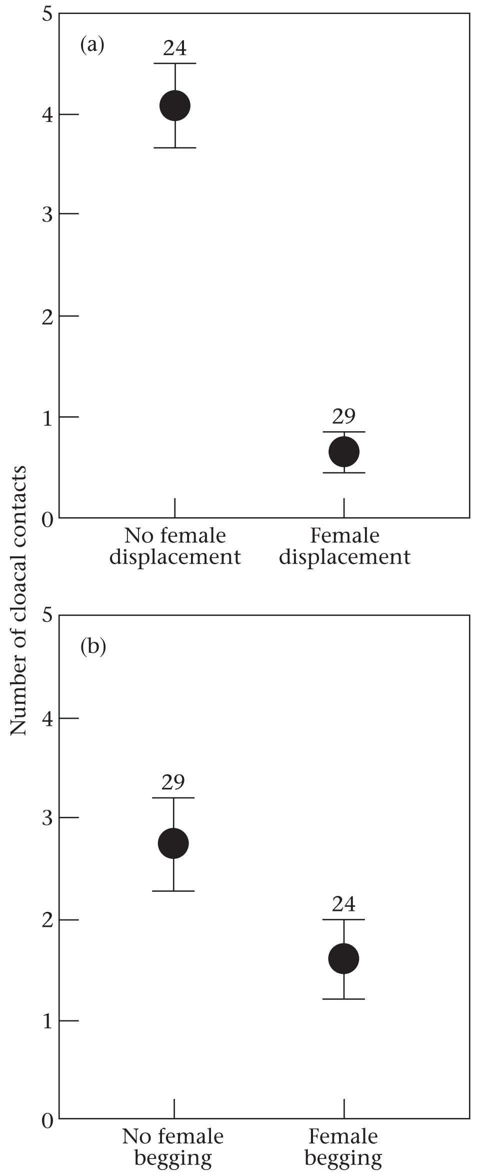

Figure 1. Mean ± SE number of cloacal contacts per mounting in relation to (a) female displacement during mounting and (b) female begging during mounting. The number of sequences is given in each case.

courtship feeding but no mounting were ended when, after feeding, females flew away from the territory (18 of 21 sequences; binomial test: $P = 0.001$).

Courtship Feeding and Copulation Rate

In the focal pairs, the timing of laying did not correlate with courtship feeding, mountings or cloacal contacts ($P > 0.1$). Overall, courtship feeding was positively correlated with pair mountings (Spearman rank correlation: $r_S = 0.71$, $N = 21$, $P < 0.001$; Fig. 3a) and with cloacal contacts ($r_S = 0.80$, $N = 21$, $P < 0.001$; Fig. 3b). In 12 of 13 focal pairs, cloacal contacts per mounting were more frequent after male feeding than in mountings with no courtship feeding (Fig. 4). In each pair, cloacal contacts preceded by male feeding were on average 3.3 times more frequent than cloacal contacts in the absence of previous male feeding (Wilcoxon signed-ranks exact test: $Z = 3.06$, $N = 13$, $P = 0.002$).

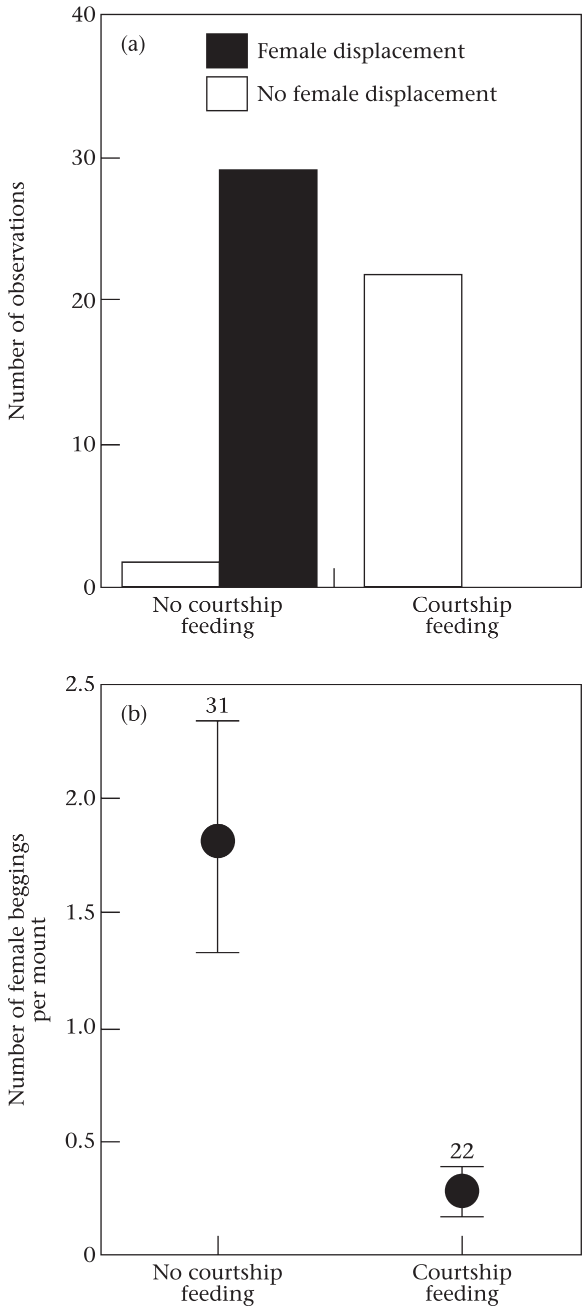

Figure 2. (a) Frequency of female displacement during mounting sequences in relation to previous male feeding. (b) Mean ± SE number of female begging bouts during mounting in relation to previous male feeding.

DISCUSSION

Female yellow-legged gulls sometimes moved during copulation bouts, and this behaviour influenced the number of cloacal contacts per mounting that males

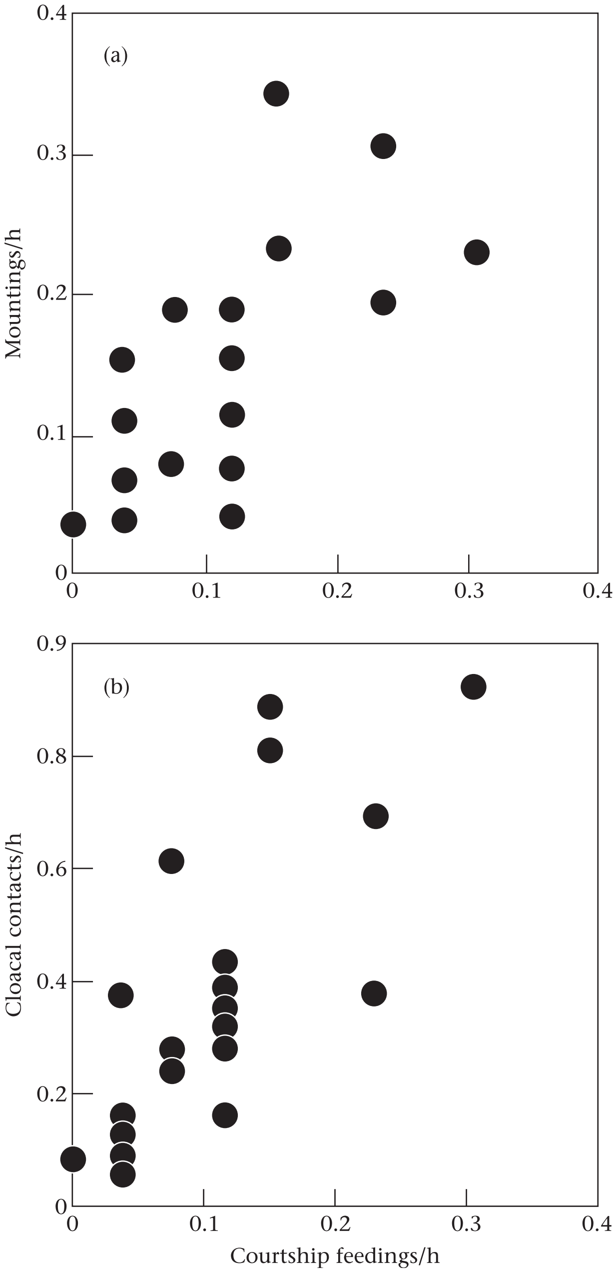

Figure 3. Relation between male courtship feeding rates in 21 focal pairs and (a) pair mounting rates and (b) pair cloacal contact rates.

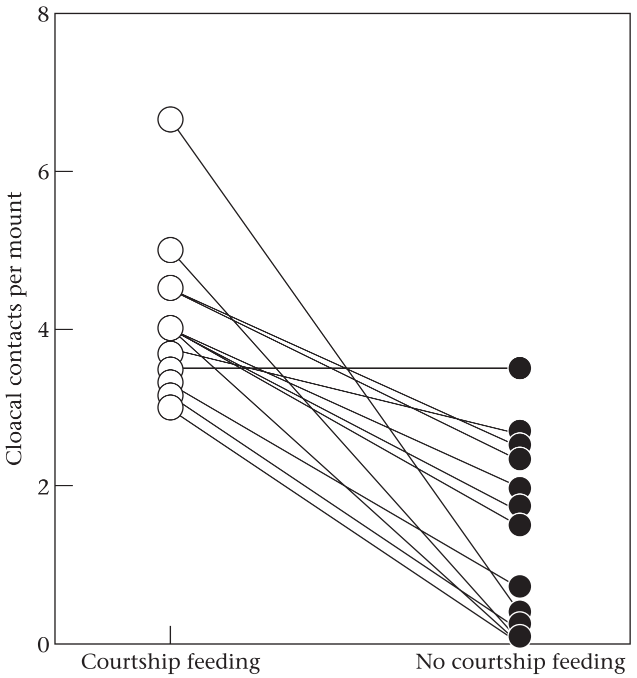

Figure 4. Average cloacal contacts per mounting in 13 focal pairs in relation to courtship feeding. A pair of points connected by a line represents individual females.

achieved. This result strongly suggests that females control the sperm transference in this species. Female control is a prerequisite for the manipulation hypotheses, but is rarely if ever tested for. In studies of red-billed gulls, the majority of mountings were ended by a movement of the female (Tasker & Mills 1981; Mills 1994), although there were no data relating successful copulation to female behaviour. Forceful termination of copulation by females that results in failure to transfer sperm has been recorded in many taxa (Eberhard 1996, page 126). In some bird species, females may control copulation rates through modifications of their solicitation behaviour or rejection of males (e.g. Birkhead & Møller 1992; Hatchwell & Davies 1992; Lens et al. 1997; Delehanty et al. 1998; Lovell-Mansbridge & Birkhead 1998). In species with repeated cloacal contacts, females may also control sperm transfer by evasive behaviour during copulation bouts, as female yellow-legged gulls did during this study.

The immediate benefits hypothesis argues that males are interested in copulation because it is the best way to ensure their paternity. There are two assumptions underlying this argument. The first is that sperm competition occurs. In gulls, EPCs are common (MacRoberts 1973; Fitch & Shugart 1984; Mills 1994; Bukacinska et al. 1998), resulting in extrapair fertilization in some species (Bukacinska et al. 1998; but see Gilbert et al. 1998). In a detailed study, Mills (1994) showed that approximately 80% of females were involved in EPCs. In the population of yellow-legged gulls that I studied, successful EPCs, mostly forced copulations, represent more than 10% of all copulations (Alonso-Alvarez 2001). In this species, successful EPCs include those arising from active female solicitation as well as those forced by males (Alonso-Alvarez 1998). In gulls, males invest heavily in their offspring, so paternity assurance is important and is a prerequisite for male parental investment (Fitch & Shugart 1984).

The second assumption is that males depend on frequent copulations to increase their chances of fathering offspring. Two main paternity guard strategies are generally found in birds: mate guarding and frequent copulations (Birkhead & Møller 1992). If males use mate guarding rather than frequent copulation to protect their paternity, they will not need to copulate as often. The frequent copulation strategy is expected particularly in birds that, because of ecological constraints, cannot guard their mate efficiently; this occurs in colonial breeders whose feeding grounds are not near the nest (Fitch & Shugart 1984; Birkhead & Møller 1992). In the population that I studied, female yellow-legged gulls were unattended for 25% of the fertile period (Alonso-Alvarez 1998). Thus, male gulls are not able to guard their mates fully and probably use the frequent copulation strategy to ensure paternity. Another question is whether all cloacal contacts in a bout result in sperm transfer (Hunter et al. 2000; Wedell et al. 2002). During the fertile period in the yellow-legged gull, I found that females forced their mates to dismount by movements and by food solicitation during mountings not preceded by feeding. Male courtship feeding rates correlated with cloacal contact rates; thus, males that gave more food probably enhanced their chances of fathering offspring.

Overall, my results strongly support the hypothesis that females manipulate their mates to obtain material benefits, i.e. that female gulls trade male interests (paternity assurance) for immediate benefits (food) in a sexual conflict context. Nevertheless, alternative hypotheses could be proposed. In some species, females may select their mates by their courtship feeding because it is a good indicator of male parental quality (e.g. Nisbet 1973; Wiggins & Morris 1986). In gulls, the good-parent choice hypothesis is inconsistent with the fact that courtship feeding and copulation rates are much more frequent in the week before laying, a month after pair formation (e.g. Brown 1967; Niebuhr 1981; Tasker & Mills 1981; Chardine 1987; Neuman et al. 1998). However, under a female choice model, females could use the food contribution of their mates to assess their quality and to influence ova fertilization: poor-quality males (bad food providers) will be less likely to father offspring. In this context, male feeding should be considered as a trait under sexual selection by female choice. Discriminating between sexual conflict and sexual selection models can be difficult and confusing (for a detailed discussion, see Eberhard 2001; Cordero & Eberhard 2003), in this case, discriminating between females manipulating male behaviour and females exerting mate choice. In a study on herring gulls, *L. argentatus*, male courtship feeding during the prelaying period correlated with both the time spent incubating and brooding and with the frequency of chick feeding by males (Niebuhr 1981); however, in this example, it is difficult to discriminate whether courtship feeding was an indicator of male quality, whether males invested more in offspring when there was a greater probability of parentage, or both.

In my study, the evidence suggests that female yellow-legged gulls manipulate their mates. First, they obtained naturally selected advantages, i.e. direct benefits from their behaviour, as predicted by the manipulation hypothesis. This hypothesis assumes that these direct benefits will outweigh any indirect benefits predicted by sexual selection models (Eberhard 2001; Cordero & Eberhard 2003). In gulls, food given by the male in courtship feeding is important for female fitness. In the lesser black-backed gull, *L. fuscus*, a closely related species, supplementary feeding experiments showed that additional food during the prelaying period has a strong influence on the number, quality and sex of the eggs laid, and also on offspring survival (Bolton et al. 1992, 1993; Nager et al. 1999, 2000). A second source of evidence arises from this study; within-female analysis reveals that the number of cloacal contacts with the same male (i.e. with the same quality) was higher when food had been given previously than in bouts with no previous food given. This result suggests that female behaviour during copulation bouts is influenced directly by food given rather than by male quality.

In some cases, males gave food and were not able to mount because females left the territory, suggesting female deceit. A further indication that conflict occurs is that many female food-begging bouts did not result in male feeding. In fact, typically courtship feeding starts with females food begging and males initially attempting to avoid food regurgitation; in some cases males do not regurgitate (Tinbergen 1953; Brown 1967; Tasker & Mills 1981). Often males bring food only half way out of their bill before swallowing it again and may respond aggressively to females afterwards. Female gulls, when soliciting food, imitate chick solicitation, and males feed the female in exactly the same way as they feed chicks (Tinbergen 1959). Female behaviour may be exploiting response biases in the male's neural machinery (Ryan 1998). The theory of manipulation assumes a continuous arms race between interacting individuals (Dawkins & Krebs 1978; Krebs & Dawkins 1984). This evolutionary scenario is a good model for understanding male and female behaviour in monogamous birds (Wachtmeister 2001). Indeed, courtship feeding in gulls bears the hallmarks of an unending coevolutionary spiral between the two sexes (Parker 1979; Sakaluk 2000). Such unending conflict may explain why in some species, such as gulls, females trade copulation for food, but not in others. In a coevolutionary process, there is no reason to assume that male and female evolution in different taxa will converge on the same counteradaptations.

In conclusion, this study supports the predictions of the immediate benefits hypothesis: (1) female gulls controlled copulation access, (2) female control was related to male courtship feeding, and (3) within-female analysis revealed that they followed a decision rule by resisting copulation when food is not given. Overall, these results support the hypothesis that female gulls manipulate their mates to obtain food.

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