



Functions of courtship feeding in black-legged kittiwakes: natural and sexual selection

FABRICE HELFENSTEIN*, RICHARD H. WAGNER†, ETIENNE DANCHIN* & JEAN-MARC ROSSI*

*Laboratoire d'Ecologie, Université Pierre et Marie Curie

†Konrad Lorenz Institute

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Various authors have proposed that courtship feeding evolved under natural selection, sexual selection or both. Using observations of 250 breeding pairs over 3 consecutive years for a total of 77 000 nest-hours, we examined the functional significance of courtship feeding in a seabird, the black-legged kittiwake, *Rissa tridactyla*. We predicted courtship feeding would benefit males and females in different ways: males may invest in future progeny and females may allow copulations in exchange for food or use courtship feeding to assess males' parental quality. Courtship feeding was correlated with clutch size in 1 of 3 years, suggesting that males may increase their reproductive success by provisioning their mates. Courtship feeding, which was individually repeatable between years, was also related to male arrival date. These results suggest that courtship feeding is a reliable index of male quality that females may use for mate appraisal. Because courtship feeding commences after the pair bond is established, it cannot be used as a criterion for mate choice in the pair's first year. However, courtship feeding rate was related to male re-pairing success in the following breeding season. We thus suggest that courtship feeding in kittiwakes could have first evolved under natural selection (the nutrition hypothesis) and subsequently may have become a signal of male quality that females could use to evaluate their mates for future seasons (future mate appraisal hypothesis).

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Male courtship feeding is a widespread behaviour in animals (Lack 1940; Eberhard 1994) whose function has been debated by many authors. Different hypotheses have been proposed to explain the evolution of courtship feeding through natural or sexual selection or both. The female nutrition hypothesis proposes that courtship feeding represents a substantial contribution to the energetic expenditure of egg production (Lifjeld & Slagsvold 1986; Steele 1986a; Gwynne 1988a). In support of this hypothesis, experimentally food-supplemented females lay more or higher quality eggs (Nisbet 1973; Steele 1986a; Salzer & Larkin 1990) and such supplementary food may be offered by courting males (Steele 1986a, b). Courtship feeding thus provides a direct material benefit to females in at least some species and may significantly affect both female and male fitness.

Another explanation for courtship feeding is that females may allow copulations in exchange for food (Nisbet 1973; Thornhill 1976; Gwynne 1986; Simmons

1995; González-Solís et al. 2001). Courtship feeding could give males repeated access to the same female or may enable them to prolong the copulation. This behaviour could then be a behavioural sperm competition strategy by males to increase the probability of fertilizing their partners' eggs (the paternity assurance hypothesis, Birkhead & Møller 1992; Hunter et al. 1993; González-Solís et al. 2001; González-Solís & Becker 2002). Courtship feeding may also serve as a mate-guarding tactic because well-fed females may reduce their foraging trips and spend more time on their nest. The benefits of paternity assurance may be additive with those of nutrition in that the courting male can achieve both advantages via courtship feeding if he succeeds in siring the offspring (Gwynne 1988b; Sherley 1989).

Lack (1940) proposed that females may use courtship feeding to assess and choose a mate, (the mate appraisal hypothesis). For example, in *Drosophila subobscura* (Steele 1986b), courtship feeding influences female mate choice. A male's ability to feed a female may reflect his ability to forage and compete intraspecifically for resources, and thus be correlated with offspring provisioning effort and paternal quality (Wiggins & Morris 1986; Green & Krebs 1995). This is supported by the finding in common terns,

Correspondence: F. Helfenstein, Laboratoire d'Ecologie, Université Pierre et Marie Curie, Bat. A 7ème étage, 7 Quai St Bernard, case 237, F-75252 Paris cedex 05, France (email: fhelfens@snv.jussieu.fr). R. H. Wagner is at the Konrad Lorenz Institute, Austrian Academy of Sciences, Savoyenstrasse 1A, A-1160, Vienna, Austria.

Sterna hirundo, that courtship feeding is correlated with chick feeding rate (Wiggins & Morris 1986). Females may also use the males' ability to feed their mates to adjust their investment in their progeny. The differential allocation hypothesis (Burley 1986) predicts that females paired with high-quality males that feed them at a high rate should invest more in their reproduction, that is, lay more or bigger eggs or feed their offspring at a higher rate.

These hypotheses are not mutually exclusive and courtship feeding may have initially evolved through sexual selection processes (paternity assurance or mate appraisal), and later came to be maintained by natural selection (female nutrition, Nisbet 1973; Simmons 1995). Several processes may operate simultaneously. For example, a male may use courtship feeding to demonstrate his attractiveness or assure his paternity while simultaneously providing nutritional benefits to the female.

The black-legged kittiwake, *Rissa tridactyla*, is a socially monogamous species with biparental care; males and females contribute about equally to nest building, incubation and chick rearing (Coulson & Wooller 1984; Coulson & Porter 1985; Coulson & Johnson 1993; Roberts & Hatch 1993). Neuman et al. (1998) examined courtship feeding in this species but were unable to draw clear conclusions on its adaptive function.

In species in which males suffer a low risk of losing paternity, which is generally the case in seabirds (reviewed in Birkhead et al. 2001), courtship feeding is unlikely to be a paternity assurance strategy. In our population, we observed fewer than 1% of extrapair copulations out of more than 300 copulations, and found only one extrapair young in a genetic analysis of 119 offspring (unpublished data). Thus, paternity confidence is apparently high in kittiwakes. Nevertheless, we examined whether courtship feeding increases the probability of success for a subsequent copulation.

For several seabird species, including kittiwakes, the female nutrition hypothesis is thought to be a likely explanation for the evolution of courtship feeding (Nisbet 1973; Salzer & Larkin 1990; Neuman et al. 1998). This hypothesis predicts a direct effect of courtship feeding on clutch size or egg volume.

Several studies (Coulson & Porter 1985; Coulson & Thomas 1985; Cam & Monnat 2000) have shown that individual kittiwakes vary in their reproductive success, and that differences between individuals in survival and reproduction may be related to differences in individual intrinsic quality. Thus, courtship feeding is likely to vary widely between males, and the benefits of courtship feeding to females may depend on the quality of their mates. Whereas in other species (Wiggins & Morris 1986; Steele 1986b; Green & Krebs 1995) courtship feeding is performed during pair formation, but in kittiwakes it occurs after the pair has already formed. Divorce occurs between seasons, in 19–26% of pairs each year (Coulson & Thomas 1983; Hatch et al. 1993) but divorce soon after pair formation is very rare, occurring only in the circumstance of the partner's death early in the season (J. Y. Monnat, personal communication). When courtship feeding occurs in kittiwakes, pairs are already engaged in

nest building which requires coordination between the members of the pair and is interpreted as evidence of pair stability (Cam et al. 1998). We can thus exclude pair formation as an explanation of courtship feeding. However, in a long-lived species such as the kittiwake, any cues that reliably indicate a male's quality could be used for future pairing. Females may therefore use courtship feeding to decide whether to breed with the same male in the following year. Whereas reproductive success or parental investment may be influenced by extrinsic factors such as predation or the partner's parental effort, courtship feeding is likely to reflect male quality more directly and be a more reliable cue for future pairing. To test the 'future mate appraisal' hypothesis, we examined whether courtship feeding reflects male quality through its relation with arrival date and survival, and through analysis of individual repeatability between years in courtship feeding rate. The hypothesis predicts that pairing success the following year and divorce probability should be influenced by courtship feeding the previous year. Finally, we examined the relation between courtship feeding rate and both male and female parental care. The differential allocation hypothesis (Burley 1986) predicts that, if courtship feeding rate reflects male quality, females, chick-feeding rate should be positively correlated with the rate at which they were fed by their mates. We examined the relation between courtship feeding and male parental ability because we predicted a positive correlation between two behaviours that should require the same foraging skills.

METHODS

Study Site and Data Collection

We studied the kittiwake colonies of Cap Sizun, Brittany, western France, where more than 10 000 individuals have been colour ringed since 1979 (Danchin & Monnat 1992; Danchin et al. 1998; Cam & Monnat 2000). We observed courtship feeding and copulations in 1999, 2000 and 2001 from the early courtship period to the end of the laying period (mid-April to early June) and chick feeding from the start of hatching to the end of fledging (early June to late July). Our observations were made at one cliff with over 250 breeding pairs each year. In the centre of the cliff, we selected subsamples of 68 focal nests in 1999, 84 in 2000 and 122 in 2001. We observed nests in which at least the males were colour ringed. We also confirmed the identity of the resident birds by using wing patterns, which we recorded for all individuals in the sample: the patterns of the black and white dots at the extremity of the wing feathers are highly variable individuals (Cadiou 1993). Wing patterns allowed us to identify unringed mates or any individual whose legs were not visible. Kittiwakes were observed with binoculars from the opposite side of the gully about 30 m away. Behaviour was monitored by continuous sampling (Altmann 1974). Observations were made every day during the focal period and opportunistically throughout the day (from 0830 to 2030 hours).

Regular visits to the colony from January to April allowed us to estimate a male's arrival date which was the first day on which an individual was spotted. The date at which nest construction was completed (Cam et al. 1998) and the size of the clutch were determined by daily inspection of the nests.

No licences or permissions were required to conduct this study.

Behavioural Observations

Total time spent daily in observation ranged from 1 to 10 h for a total of 99 h in 1999, 100 h in 2000 and 507 h in 2001 for a total of 76 986 nest-hours. Courtship feeding consists of the regurgitation of food; the male of ten extends his throat widely to deliver a large bolus. It may last up to 30 min when a male attempts to regurgitate a large undigested fish against the scales. Males sometimes failed to regurgitate the bolus and left without feeding the female. We recorded food solicitation by females and food delivery by males. We also recorded mountings without cloacal contacts (i.e. unsuccessful copulations) and complete copulations with cloacal contacts (i.e. successful copulations). When copulations were successful, the number of cloacal contacts was noted. We recorded whether successful and unsuccessful copulations were preceded by food delivery.

Courtship feeding rate and copulation rate were calculated as the mean daily feeding frequency (feeding bouts/h) and daily copulation rate (number of copulations/h) from day -20 to day +1 (day 0 is the laying of the pair's first egg). In 2000, we estimated the amount of food that the male delivered at each feeding bout. We scored each bolus size on a three-point scale (1, 2 and 3) corresponding approximately to a small piece of food, half a fish and a whole fish. The quantity of food delivered during each feeding bout is the sum of the scored bolus sizes. For 2000, we were then able to estimate of the total number of feeds and total amount of food given to the females by males.

To compare the proportion of successful copulations (i.e. number of copulations in which cloacal contact was achieved/number of times the male mounted his mate) with and without prior feeding within pairs, we used a Wilcoxon test for paired samples (Sokal & Rohlf 1995). The more inseminations a male performs the higher his probability of achieving fertilization (Birkhead & Møller 1992). In kittiwakes, copulations may comprise several cloacal contacts, and presumably inseminations. We then compared the number of cloacal contacts of copulations that were and were not preceded by courtship feeding. As previously, we used a Wilcoxon pairwise test. Between pairs, we tested the relation between the percentage of successful copulations and the mean courtship feeding frequency.

Chick Feeding

The total time spent daily in observation ranged from 1.15 to 6 h (summing to 147 h in 1999, 177 h in 2000 and

135 h in 2001 for a total of 21 630 nest-hours). Chick feeding was recorded for the pairs that had successfully reached the chick-rearing period and in which at least the males were colour ringed (47 pairs in 1999, 58 pairs in 2000 and 33 pairs in 2001).

We recorded food deliveries by males and females during the 10 days after hatching. The chick feeding rate was estimated as the number of feeding bouts/h.

Male Quality

In birds, early arrival is generally correlated with breeding success and individual quality (Møller 1994). Early arrival may maximize the chance of producing a second clutch when the first has been depredated. Furthermore, early arrival indicates good migration ability (foraging and flight abilities; Møller 1994). We tested whether mean arrival date per individual was related to mean reproductive success (scored on a four-point scale corresponding to failure in reproduction, one, two or three chicks fledged, and coded as 0, 1, 2 or 3). Early-arriving males were predicted to feed their females more.

Kittiwakes show positive phenotypic correlations between fitness components that are generally considered to emerge from heterogeneity in quality between individuals (Cam & Monnat 2000). Consequently, the differences in survival probability lead to older individuals being of higher quality (Cam & Monnat 2000). If courtship feeding reflects individual quality, we predicted a positive correlation between males' age at death, that is, the males' survival ability, and courtship feeding rate. In our population, the individual resighting rate is not statistically different between years and not significantly different from one, regardless of breeding status (Danchin & Monnat 1992; Cam et al. 1998). Because no kittiwakes formerly breeding in our population have been observed in other study populations (J.-Y. Monnat, unpublished data), we assumed that any missing bird was dead. The age at death was estimated as the bird's age in the last year it was seen.

Repeatability of courtship feeding rate of the same male in different years was derived from a one-way ANOVA with male identity as a factor (Lessells & Boag 1987; Falconer & Mackay 1996). This analysis included any male that was observed at least twice over the 3 years.

Pairing Success the Next Year and Divorce Probability

We measured pairing success as the time a male took to obtain a mate which was calculated as the pairing date minus the arrival date. We defined the pairing date as the first day on which we observed courtship feeding. Because observations began later in 2000, this estimation was available only for 2001. We defined divorce as a change of mate when the previous mate was still alive.

Data Analyses

We used polytomous regression for discrete dependent variables with three levels (clutch size: one, two or three

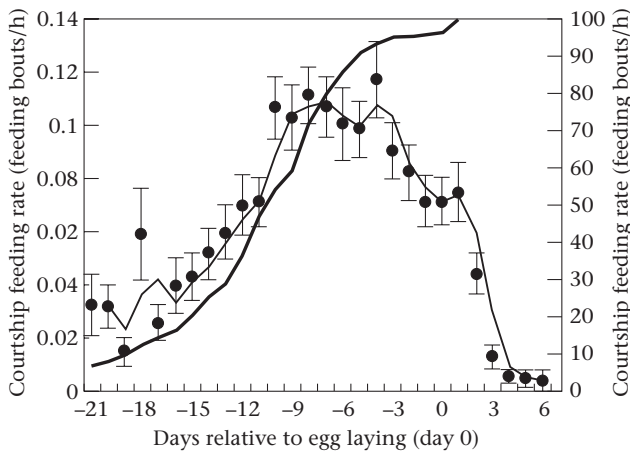


Figure 1. Timing of nest building (thick curve, percentage of completed nests) and courtship feeding (thin curve, mean frequency \pm SE).

eggs; Genmod procedure in SAS (SAS Institute 1999), multinomial distribution with a multilogit link function. We checked the fit of the model with likelihood-ratio and goodness-of-fit tests. We used general linear model regression when both dependent and explanatory variables were continuous (GLM procedure in SAS, SAS Institute 1999). The fit of linear models was checked by residual analyses.

Variables were square-root-transformed, log transformed or arcsine transformed (for ratio) when necessary to fit modelling assumptions. When variables departed from a normal distribution, we applied nonparametric statistics. We use two-tailed statistical tests.

When individuals were observed in more than 1 year we computed individual means over the 3 years or treated each year separately.

RESULTS

We observed 1390 courtship feedings over a total of 76 986 nest-hours in 3 years. The first courtship feeding was observed 21 days before clutch initiation and the last 6 days after the first egg of the pair was laid, with a peak between day -10 and day -4 before laying (Fig. 1). The daily courtship feeding rate varied between pairs from 0 to 0.52 feeding bouts/h ($\bar{X} \pm \text{SE} = 0.075 \pm 0.06$ bouts/h, $N = 274$ pairs). In 2000, we calculated that a female obtained from her mate an average of 15.4 whole fish (based on the mean quantity of food delivered/h, with a 14-h daylight period over 20 days: $\bar{X} = 0.055$ fish/h $\times 14$ h $\times 20$ days). Nest building commenced before courtship feeding. Consequently, about 5% were built before the first courtship feeding and about 75% were completed by the peak (Fig. 1). We thus assume that pairs were already formed by the time courtship feeding commenced.

The Nutrition Hypothesis

Out of 274 breeding pairs over 3 years, only 21 males (7.7%) were never observed providing any food to their

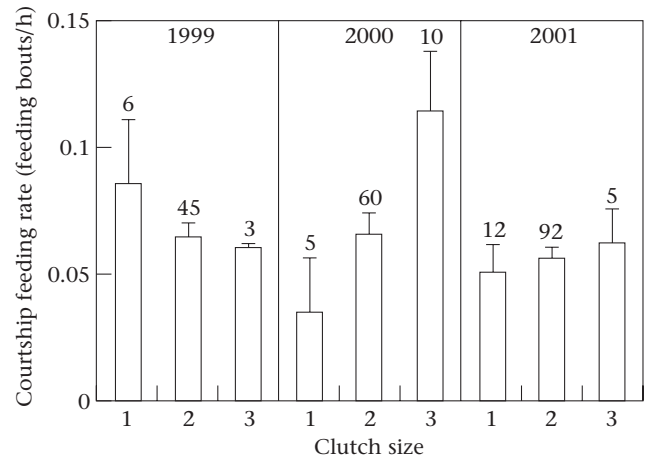


Figure 2. The relation between courtship feeding rate and clutch size. Values given are mean frequencies \pm SE. Numbers above bars refer to sample size.

mates. There was a positive correlation between courtship feeding rate and clutch size in 2000 but not in the other 2 years (polytomic regression modelling cumulative probabilities for an ordinal variable with more than two levels: 1999: $\chi^2_1 = 0.62$, $N = 54$ pairs, $P = 0.43$; 2000: $\chi^2_1 = 6.88$, $N = 75$ pairs, $P = 0.009$; 2001: $\chi^2_1 = 0.25$, $N = 115$ pairs, $P = 0.62$; Fig. 2). This was reflected by a greater proportion of three-egg clutches in 2000 (13.3%) than in 1999 and 2001 (4.4 and 5.6%, respectively). Clutch size was also correlated with laying date in 2000 and 2001, but not in 1999 (1999: $\chi^2_1 = 2.47$, $N = 54$ pairs, $P = 0.12$; 2000: $\chi^2_1 = 11.65$, $N = 75$ pairs, $P = 0.0006$; 2001: $\chi^2_1 = 7.51$, $N = 115$ pairs, $P = 0.006$). Laying date and courtship feeding were significantly correlated only in 2000 (1999: $F_{1,52} = 2.17$, $P = 0.146$; 2000: $F_{1,73} = 6.90$, $P = 0.012$; 2001: $F_{1,113} = 0.03$, $P = 0.86$). The year 2000 was also characterized by early laying (1999: $\bar{X} \pm \text{SD} = 133.5 \pm 6.39$ Julian days; 2000: 125 ± 6.31 Julian days; 2001: 134.4 ± 8.12 Julian days; $F_{2,241} = 40.57$, $P < 0.0001$) and a higher variance in courtship feeding rate (1999: $\sigma^2 = 1 \times 10^{-3}$; 2000: 6×10^{-3} ; 2001: 2×10^{-3}).

In 2000, clutch size was related to the total amount of food delivered in terms of the total number of feeds ($\chi^2_1 = 6.10$, $N = 75$ pairs, $P = 0.014$) and the estimated quantity of food delivered ($\chi^2_1 = 4.87$, $N = 75$ pairs, $P = 0.027$).

Courtship Feeding and Copulations

Courtship feeding did not increase the probability that a copulation would be successful (proportion of successful copulations without prior feeding: $\bar{X} \pm \text{SD} = 0.72 \pm 0.23$; with prior feeding: 0.74 ± 0.34 ; Wilcoxon paired test: $Z = 0.54$, $N = 37$ pairs, $P = 0.71$). Courtship feeding was also unrelated to the number of cloacal contacts made during the copulation (mean number of cloacal contacts without prior feeding: $\bar{X} \pm \text{SD} = 4.31 \pm 1.70$; with prior feeding: 4.19 ± 2.05 ; Wilcoxon paired test: $Z = 0.65$, $N = 49$ pairs, $P = 0.74$). There was also no significant correlation between the mean frequency of courtship feeding per pair and the percentage of successful copulations ($F_{1,63} = 0.92$,

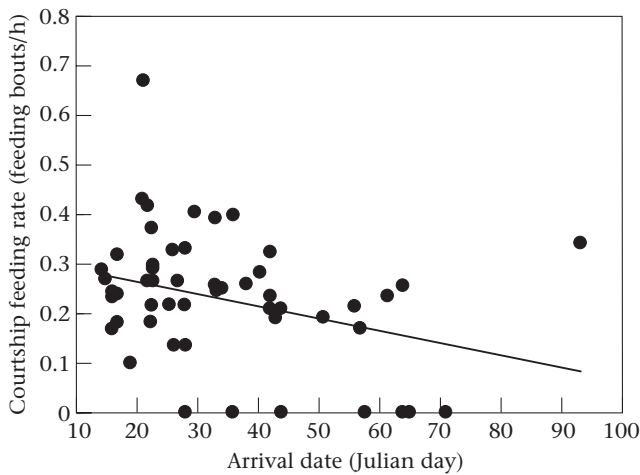


Figure 3. The relation between arrival date and courtship feeding rate. Values are means over the 3 years of the study. Courtship feeding rates are square-root transformed to meet statistical assumptions.

$P=0.34$; power of the test: $\phi=0.84$). Overall, 79% of the successful copulations ($N=1247$) occurred without prior courtship feeding.

The Future Mate Appraisal Hypothesis

Courtship feeding repeatability and male quality

Courtship feeding frequency by individual males was repeatable between years ($r=0.40$, $F_{39,60}=2.29$, $P=0.002$). Age at death and mean courtship feeding rate were not significantly correlated ($r_s = -0.19$, $N=22$, $P=0.40$). Arrival date was correlated with individual reproductive performance for males but not for females (mean individual arrival date versus mean reproductive performance: males: $F_{1,53}=8.91$, $P=0.004$; females: $F_{1,73}=1.11$, $P=0.30$). As predicted if courtship feeding ability reflects overall male body condition, mean arrival date was negatively correlated with mean courtship feeding rate ($F_{1,52}=6.40$, $P=0.015$; Fig. 3). Courtship feeding rate was not correlated with male chick-feeding frequency ($F_{1,46}=1.51$, $P=0.23$; power of the test: $\phi=0.78$) or with female chick-feeding frequency ($F_{1,46}=0.27$, $P=0.61$; power of the test: $\phi=0.93$).

Courtship feeding, pairing success and divorce

Consistent with the prediction that males that provision at high rates are more attractive to females, males that fed their mates more in 2000 paired faster in 2001 ($F_{1,20}=8.28$, $P=0.009$ (Fig. 4). For this analysis we used individuals that re-paired with the same female and individuals that changed mate, but the sample size was too small to introduce pair status as a covariate. There was no-significant difference in the predicted direction for males that divorced at least once during the study to feed their mates less ($\bar{X} \pm SD=0.045 \pm 0.032$ feeding bouts/h, $N=10$) than males that never divorced (0.088 ± 0.092 feeding bouts/h, $N=27$; Mann-Whitney U test: $Z=1.56$, $P=0.12$).

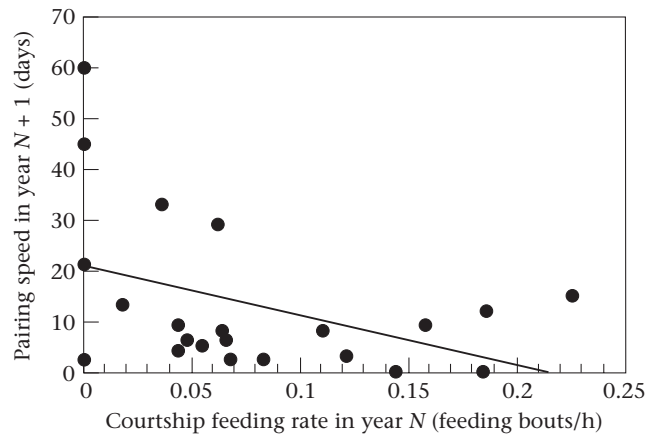


Figure 4. Male pairing success in year $N+1$, as estimated by the time needed for a male to acquire a mate from the day it arrived (pairing date–arrival date) in relation to the male's courtship feeding rate in year N .

DISCUSSION

We found partial support for the nutrition hypothesis in that courtship feeding increased with clutch size in one year. We also found support for the future mate appraisal hypothesis because males that provided high rates of courtship feeding paired faster in the following year. These results suggest that both natural and sexual selection may operate simultaneously in kittiwakes, as suggested for some other species (Nisbet 1973; Steele 1986a, b; Simmons 1995). We also found that males did not obtain copulations in exchange for food which is unsurprising in a species in which males suffer a low risk of losing paternity. Courtship feeding also did not covary with subsequent male chick provisioning. Although such a relation might be expected if males use similar foraging skills to feed either their mates or their chicks, the balance between the parental contributions of monogamous mates is complex and a number of hypotheses make opposing predictions (Wright 1998).

The nutrition hypothesis predicts a direct relation between courtship feeding and clutch size which we found in 1 of 3 years. The lack of this relation in the other 2 years might have been caused by the small variance in clutch size in kittiwakes. Hence, a relation between courtship feeding and clutch size may be revealed only in years with high food abundance when some males can provide much more food to their mates, resulting in more three-egg clutches. Although courtship feeding did not covary with clutch size in 2 years, it is logical that it provides nutritional benefits in all years. Courtship feeding occurs during egg development, when females' nutritional needs are high (Robbins 1981; Perrins 1996; Nager et al. 1997; Ramsay & Houston 1997; Reynolds 2001). During this period females spend most of their time on the nest (unpublished data) and 92.3% of males were seen delivering food to their mates, suggesting that females depend on their partners to feed them. Direct contributions by males to clutch size or clutch quality have been empirically and experimentally shown in several species such as katydid, *Requena verticalis* (Simmons 1995), common

terns (Nisbet 1973) and glaucous-winged gulls, *Larus glaucescens* (Salzer & Larkin 1990), and suggested in kittiwakes (Neuman et al. 1998). Male kittiwakes are therefore likely to be naturally selected to increase their fitness by provisioning their mates. Alternatively, this relation may be the result of assortative mating by individual quality reflected through the clutch size of females and feeding ability of males. Experiments are needed to separate the effects of courtship feeding on clutch size versus male and female quality and to test whether providing supplementary food increases not only clutch size, but also egg volume which we were unable to measure.

The differential allocation hypothesis predicts that courtship feeding rate may be related to clutch size or egg volume because females paired to high-quality males, which feed them often, may invest more in their progeny (Burley 1986). Although our data did not allow us to disentangle the direct effect of courtship feeding from female differential allocation on clutch size, the lack of a relation between female parental effort and courtship feeding frequency is inconsistent with this hypothesis.

Our finding that a male's courtship feeding rate in one year influences his re-pairing success the following year supports the future mate appraisal hypothesis. This hypothesis predicts that males provision their mates in proportion to their intrinsic quality. Two of our results support this prediction: the courtship feeding rates of individual males were repeatable between years and males that had provisioned at high rates were also those that had arrived early at the breeding areas. Arrival date is thought to indicate individual quality because the ability to arrive early implies that individuals have acquired enough fat reserves to migrate or that they migrated faster (Møller 1994). There may also be strong selection for early arrival because it allows individuals to claim better breeding sites and to pair earlier and with higher quality mates (Møller 1994, 2001). As in other studies (reviewed in Møller 1994; Lozano et al. 1996), early arrival of male kittiwakes was associated with higher reproductive success. Hence, early arriving males that provide a large number of courtship feeds may be high-quality males. Given that only males with high foraging ability and competitiveness for resources are likely to provide large amounts of food to satisfy both their mates' and their own energetic needs, courtship feeding is likely to be an honest signal of male quality (Zahavi 1975).

We found that courtship feeding occurred after nest building started, and therefore presumably after pair formation. Females therefore could not use a male's ability to feed them to choose a mate for the current breeding season. Instead, we found that a male's courtship feeding rate in one year influenced his re-pairing success in the following year. We also found a trend that males that never divorced fed their females twice as much as males that divorced at least once, a nonsignificant difference based on a small sample size. Although we were unable to separate re-pairing from new pair bonds, two studies of kittiwakes have revealed that a large majority of pairs remain together in the following year, with 74% and 81% re-pairing (Coulson & Thomas 1983; Hatch et al. 1993). Thus most males that fed at high rates and paired rapidly

in the following year were likely to have re-paired with the same mate. These results suggest that courtship feeding may indicate male's attractiveness and can be used by his own mate or by other females. In addition to courtship feeding rate, males probably possess multiple traits that females use in mate choice. An experiment is required to distinguish between the effects of male quality and courtship feeding ability on male pairing success in the following year.

In conclusion, we propose that, like other behaviours such as chick feeding or foraging success (Lotem et al. 1999), courtship feeding in kittiwakes, and possibly in other species, may have first evolved under natural selection and later came to be used by females as a sexually selected signal of male quality to decide whether to re-pair with their mates in the following season.

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