

Fabrice Helfenstein · Richard H. Wagner ·
Etienne Danchin

Sexual conflict over sperm ejection in monogamous pairs of kittiwakes *Rissa tridactyla*

Received: 28 October 2002 / Accepted: 30 April 2003 / Published online: 19 June 2003
© Springer-Verlag 2003

Abstract Socially monogamous partners suffer conflicting interests concerning various aspects of reproduction such as parental care, copulation and fertilization. Female black-legged kittiwakes commonly eject their mates' sperm immediately following copulations. Because sperm ejection reduces male sperm competitiveness and paternity assurance, males and females have conflicting interests as regards sperm ejection. Males whose mates ejected their sperm at least once remained longer on their mates' backs after the last insemination which apparently prevented the females from ejecting sperm. These results suggest that compelling females to retain their sperm may be a previously unidentified tactic employed by males to assure their paternity. Females tried to prevent their mates from witnessing sperm ejection by ejecting sperm after their mates departed from the nest. Females were more likely to eject sperm when they terminated the copulations by unbalancing the male. The conflict over sperm ejection was related to the ability of the females to end the copulations which covaried with the body mass of their mates. These findings suggest that conflicts in monogamous pairs also exist over the disposition of sperm.

Keywords Copulation · Kittiwake · Monogamy · Sexual conflict · Sperm ejection

Introduction

Despite the necessity for socially monogamous partners to cooperate, mates often have conflicting interests regarding parental investment, copulation and fertilization (Arnqvist and Rowe 1995; Gowaty 1996; Stockley 1997). For instance, males may benefit by copulating frequently to assure their paternity whereas females may only need to copulate once to achieve fertilization while preferring to minimize the risk of acquiring sexually transmitted diseases or parasites (Birkhead and Møller 1993; Hillgarth 1996; Møller 1998). The sexes have an especially clear conflict of interest when females seek extra-pair copulations (EPCs) (Stockley 1997; Johnsen et al. 1998). It has been proposed that females may select sperm among males to bias paternity toward a more attractive or genetically compatible male (Thornhill 1983; Birkhead and Møller 1993; Olsson et al. 1996; Wilson et al. 1997; Birkhead 1998; Olsson 1999; Pizzari and Birkhead 2000). Female sperm choice may be achieved by sperm ejection immediately following copulation, such as in dunnocks *Prunella modularis* (Davies 1983), feral fowl *Gallus domesticus* (Pizzari and Birkhead 2000) possibly razorbills *Alca torda* (Wagner 1991) and some mammal and insect species (reviewed in Eberhard 1996) in which females mate with multiple males and eject sperm to influence which males fertilize their eggs. Female sperm choice is therefore viewed as a mechanism of sexual selection (Eberhard 1998).

In contrast, sperm choice via sperm ejection by female kittiwakes *Rissa tridactyla* is apparently driven by natural selection to avoid the cost of infertility due to old, degraded sperm. Wagner et al. (submitted) found that sperm ejection occurs following 22% of within-pair copulations in this socially monogamous seabird. In kittiwakes, the criterion for female sperm choice is the age of their mates' sperm that fertilize their eggs (i.e. how long it was stored in their reproductive tract; Wagner et al. submitted) which is associated with hatching failure, a phenomenon that has been suggested in other species (Lodge et al. 1971; Birkhead et al. 1995; Siva-Jothy

Communicated by C.R. Brown

F. Helfenstein · E. Danchin
Laboratoire d'Ecologie,
Université Pierre et Marie Curie,
Bâtiment A 7ème étage, 7 Quai St Bernard, Case 237,
75252 Paris Cedex 05, France

F. Helfenstein (✉) · R. H. Wagner
Konrad Lorenz Institute,
Austrian Academy of Sciences,
Savoyenstrasse 1a, 1160 Vienna, Austria
e-mail: fhelfens@snv.jussieu.fr
Tel.: +43-6767-945789
Fax: +43-1486-212128

2000). Sperm ejection frequency dramatically declines as egg-laying approaches and females that retain their mates' old sperm suffer higher rates of hatching failure (Wagner et al., submitted).

Male kittiwakes are unable to guard their mates (Helfenstein 2002), which is typical of colonial species (Birkhead et al. 1987; Birkhead and Møller 1992; Møller and Birkhead 1993). However, males copulate more than is probably necessary for fertilization (mean \pm SD=14.08 \pm 10.64 copulations per clutch) and copulation frequency peaks 5 days before egg-laying when females are likely to be fertile (Chardine 1987; Neuman et al. 1998; Helfenstein 2002). Male kittiwakes thus appear to attempt to assure their paternity via moderately frequent and well timed copulations as in many non-mate-guarding species (Birkhead et al. 1987). Although females were never observed to pursue EPCs, forced EPCs occasionally occur (Helfenstein 2002). Moreover, copulation interference, which has been reported by Chardine (1986) in another population, has also been observed in our study (Helfenstein 2002). These behaviors indicate the presence of sexually active extra-pair males in the colonies at a time when females are likely to be at their peak of fertility. These males may place pressure on pair males to assure their paternity. A paternity analysis revealing extra-pair paternity to be low to nonexistent (Helfenstein 2002) suggests that males evolved highly effective paternity assurance strategies.

Sperm ejection may thus constitute a reduction of the males' confidence of paternity because it reduces the number of their sperm competing for fertilization if their mates are forcibly inseminated by an extra-pair male. Whereas it is to the advantage of both sexes to avoid hatching failure caused by the retention of old sperm, males exclusively suffer the cost of sperm ejection in terms of reduced confidence of paternity.

Here we report a previously unidentified sexual conflict over the ejection of the males' sperm. The aims of this study are to describe this conflict and to investigate male and female strategies in relation to sperm retention and ejection. Specifically, we examine (1) how males attempt to prevent their mates from ejecting their sperm, (2) the circumstances under which females eject their mate's sperm, and (3) the degree to which body size predicts which sex controls the outcome of copulations and the frequency of sperm ejection. Male quality may alternatively explain the relationship between sperm ejection and male paternity assurance behavior. If low-quality males have low-quality sperm that degrade faster and lead to higher infertility, females may eject their sperm more often (Blount et al. 2001). Low-quality males may also inseminate less sperm during copulation (Dewsbury 1982) or have less motile sperm (Koyama and Kamimura 1999; but see Froman et al. 2002) which provide them with lower sperm competitiveness if their mates are subjected to forced EPCs. Low-quality males are then more likely to try to assure their paternity. We tested whether male quality may explain how frequently a female ejected her mate's sperm and whether males try to

assure their paternity by preventing their mates from ejecting their sperm. We used two variables as measures of male quality: arrival date and courtship feeding. Because early arrival to the colony may indicate good foraging and flight abilities, arrival date is likely to reflect male quality (Møller 1994; Currie et al. 2000; Helfenstein et al. 2003). Courtship feeding rate may also reflect male quality in kittiwakes (Helfenstein et al. 2003) as has been suggested in other species (Wiggins and Morris 1986; Green and Krebs 1995).

Methods

General

The study was conducted during 3 years (1999–2001) in the kittiwake colonies of Cap Sizun (Brittany, western France) where more than 10,000 individuals have been color-banded since 1979 (Danchin and Monnat 1992; Danchin et al. 1998; Cam and Monnat 2000). We observed sexual behavior from the early copulation period to the end of the laying period (mid-April to early-June). Our observations were made at one cliff with over 250 breeding pairs each year. In the center of the cliff, we selected 52 focal pairs in 1999, 64 in 2000 and 115 in 2001 that produced eggs and in which at least one individual was color-banded (in 32% of the pairs both mates were marked). We used unique wing patterns, a method developed by Cadiou (1993), to identify unmarked partners and confirm the identity of the marked birds when their legs were not visible. Kittiwakes were observed with 10 \times binoculars and a 20–60 \times telescope from the opposite side of the gully from a distance of approximately 30 m. Behavior was monitored by continuous sampling (Altmann 1974). Daily observations were made 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. While color-banding the chicks, we captured some adults and weighed them within 5 g using a Pesola spring balance.

Behavioral data

Daily observation ranged from 1 to 10 h totalling 223 h in 1999, 67 in 2000 and 512 in 2001 for a total of 57,736 nest-hours. We recorded observations of copulations and courtship feeding for 112 color-banded females and 91 color-banded males. We recorded the times of the mountings, of the first and last cloacal contacts, and of the dismountings to the nearest second. Following copulation, sperm ejection comprised a conspicuous muscular contraction by the female. Females forcefully expelled from the cloaca white fluid which often carried beyond the nesting cliff, landing in the sea below. In contrast, feces were expelled without force and typically dropped vertically. We focused on the females' cloaca for 90 s after the male dismounted and recorded whether or not sperm was ejected and when. We calculated the duration of the copulation (from mounting to the last cloacal contact), the amount of time the males remained on their mates' backs following the last cloacal contact (i.e. the post-insemination mounting) and the time between the dismounting and the ejection of the sperm. We also recorded the number of cloacal contacts performed and which sex terminated the copulation (Wagner 1996). Copulations were either stopped by the female standing up and unbalancing her mate or by the male dismounting from his mate's back or flying away. Immediately after the copulation, the male either remained on the nest or departed.

We performed all the calculations on copulations that occurred from the peak of sperm ejection, which was 16 days before the laying of the first egg (Wagner et al., submitted) until 2 days after clutch initiation. The sperm storage duration in female birds varies

widely among species (reviewed in Birkhead and Møller 1992) and is unknown in kittiwakes. We conservatively assumed that any sperm transferred between 16 days before and 2 days after laying may fertilize the eggs which numbered from one to three in a clutch.

We recorded pre-laying food delivery by males to their mates. Courtship feeding rate was calculated as the mean daily feeding frequency (feeding bouts h^{-1}) on the period from day -21 (first courtship feeding) to day +2 relative to the laying of the first egg of the pair (Helfenstein et al. 2003).

Data analyses

Proportions were arcsine-transformed to meet statistical assumptions for parametric tests. We checked fit of linear models by analyzing the residuals (normality, homogeneity of variance). When variables departed from a normal distribution, we applied non-parametric statistics. For analyses that focused on female behaviors, we used data from pairs in which the female or both mates were color-banded. Sperm ejection frequency has been found to be highly repeatable within females and between years (ANOVA on the annual proportion of copulations followed by sperm ejection using females observed in at least 2 years, and female identity as a factor; Wagner et al., unpublished data). This allowed us to compute mean sperm ejection proportions for females that had been observed more than once in the 3 years. When investigating male quality in relation to male copulation behaviors we focused on color-banded males and computed means for males that had been observed in two or more years. Because some variables were not available for all the individuals, sample sizes vary between analyses. All analyses were conducted with the (SAS 1999) software and following the statistics in (Sokal and Rohlf 1995).

Results

Sperm ejection behavior

In addition to the difference in appearance between sperm ejection and defecation, there was also a difference in the frequency of each behavior. Females were 290% more likely to extrude a white substance from their cloaca within 90 s after a copulation (19 sperm ejections out of 78 randomly selected copulating pairs: 24.4%) than at other time (5 defecations out of 60 randomly selected resting pairs observed during 90 s: 8.3%; $\chi^2=6.06$, $df=1$, $P=0.014$, $n=138$ females).

Although in some species females may be unable to retain all the sperm transferred during a copulation (Ginsberg and Huck 1989), sperm overflow is expected to occur in species with rapid multiple copulations. Although a mean number (\pm SD) of 14.08 ± 10.64 copulations per clutch (Helfenstein 2002) may be more than necessary to fertilize the eggs, it is a much lower rate than in many non-mate guarding species (Birkhead et al. 1987; Birkhead and Møller 1992). Unsurprisingly, we found no evidence that females ejected sperm because they were unable to store large or multiple ejaculates. Sperm ejection did not depend on the number of cloacal contacts, and presumably inseminations, performed (mean \pm SD of cloacal contacts when sperm ejection occurred: 4.72 ± 2.07 ; mean \pm SD of cloacal contacts when no sperm ejection occurred: 4.93 ± 1.73 ; Wilcoxon-paired signed-rank test: $z=0.62$, $P=0.54$, $n=51$ females). The probability

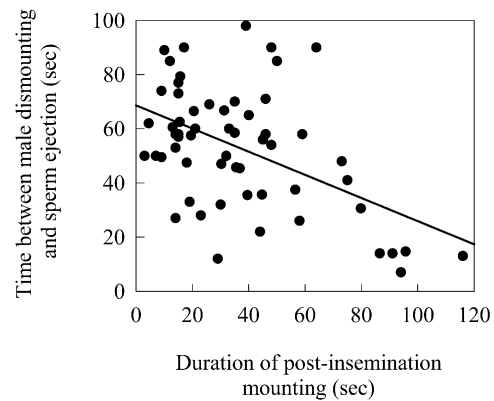


Fig. 1 The time lag between sperm ejection and dismounting in the kittiwake *Rissa tridactyla* in relation to the duration of the post-insemination mounting. The line is the regression line

of sperm ejection after a second copulation in the same day did not depend on the time elapsed since the first one (logistic regression, $\chi^2=0.63$, $df=1$, $P=0.43$, $n=35$ females). The probability of sperm ejection was also not significantly different after the first (mean \pm SD= 0.37 ± 0.44) or the second (mean \pm SD= 0.39 ± 0.42) copulation in the same day (Wilcoxon-paired signed-rank test: $z=0.12$, $P=0.45$, $n=19$ females).

Male reactions to sperm ejection

Males appeared to prevent their mates from ejecting their sperm by remaining on the females' backs after the last cloacal contact. Males remained on their mates' backs a mean (\pm SD) of 29.96 ± 28.78 s (median: 22.0 s, range: 1–279 s, $n=621$ copulations) and sperm ejection never occurred while a male stood on his mate's back. Males often appeared to struggle to maintain balance while their mates were shifting position. Among those cases in which sperm ejection occurred, the longer males remained on their mate's back, the sooner the females ejected sperm after males dismounted ($F_{1,56}=18.38$, $P < 0.0001$, $n=58$ females; Fig. 1).

Males whose mates ejected their sperm at least once remained on their mates' backs longer after the last cloacal contact (mean \pm SD= 34.22 ± 21.96 s, $n=60$ females) than males whose mates were never observed ejecting their sperm (mean \pm SD= 23.12 ± 12.53 s, $n=41$ females; t -test, $t=2.80$, $df=99$, $P=0.006$, Fig. 2a). Among the pairs in which the female had ejected their mate's sperm at least once, males spent significantly more time on their mates' backs after the first sperm ejection (mean \pm SD= 38.36 ± 24.08 s) than before (mean \pm SD= 22.66 ± 14.55 s; Wilcoxon-paired signed-rank test, $T_s=35$, $P < 0.01$, $n=20$ females; Fig. 2b). The duration of the copulation (from the mounting to the last cloacal contact) did not depend on whether or not females had ejected their mates' sperm (mean \pm SD copulation duration with sperm ejection: 52.03 ± 21.96 s, $n=58$ females; and without sperm ejection:

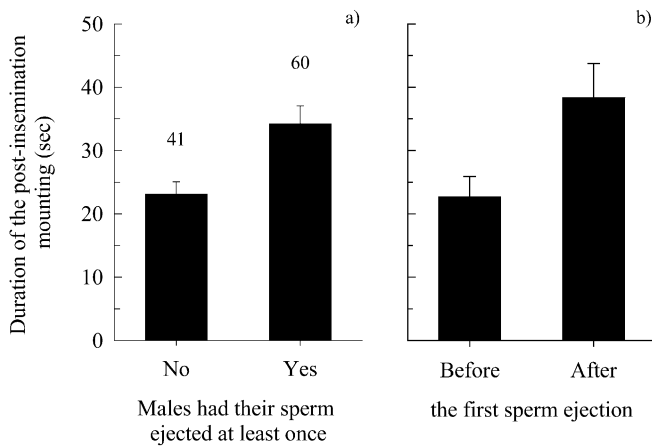


Fig. 2 a Mean duration of the post-insemination mounting (mean \pm SE) depending on whether or not females had ejected their mates' sperm at least once. Numbers above the bars refer to sample sizes. b Within-pair comparison of the mean duration of the post-insemination mounting (\pm SE, $n=20$ females) during copulations taking place before and after the first copulation followed by sperm ejection

52.76 \pm 16.73 s, $n=38$ females; t -test, $t=0.59$, $df=94$, $P=0.56$).

There was a positive relationship between the mean duration of the post-insemination mounting and the mean proportion of copulations followed by sperm ejection ($F_{1,99}=6.87$, $P=0.01$, $n=101$ females). This analysis may however reflect more the way males react to the ejection of their sperm by their mates than the influence of duration of the post-insemination mounting on the probability of sperm ejection.

There was no relationship between sperm ejection and two measures of male quality (see Introduction): (1) arrival date ($r_s=-0.08$, $P=0.58$, $n=46$ males) and (2) courtship feeding rate ($r_s=0.05$, $P=0.70$, $n=76$ males). Arrival date and courtship feeding rate also did not correlate with the duration of the post-insemination mounting ($r_s=0.11$, $P=0.44$, $n=50$ males and $r_s=0.03$, $P=0.82$, $n=80$ males, respectively). There was also no relationship between courtship feeding rate and the frequency with which males departed from the nest after a copulation ($r_s=0.02$, $P=0.87$, $n=80$ males). However, males that arrived seasonally late to the colony were more likely to leave the nest immediately after a copulation ($r_s=0.35$, $P=0.012$, $n=50$ males).

Sexual conflict over copulation duration

Copulations were either terminated by the males dismounting from their mates' backs or by the females unbalancing their mates, forcing them to dismount. Males remained on the female's back for a shorter period of time after the last insemination when the female ended the copulation (mean \pm SD duration of the post-insemination mounting: 22.33 \pm 20.26 s) than when the male ended the copulation (31.43 \pm 20.74 s; Wilcoxon-paired signed-rank

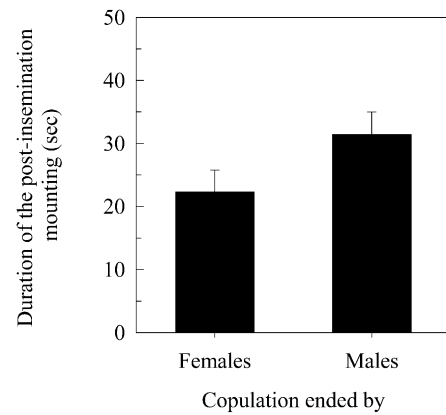


Fig. 3 Within-pair comparison of the mean duration of post-insemination mountings (\pm SE, $n=34$ females) depending on the sex that terminated the copulation

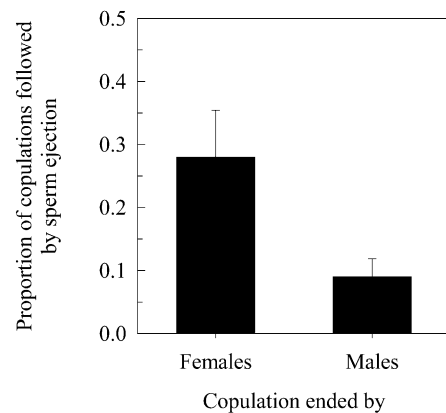


Fig. 4 Within-pair comparison of the mean proportion (\pm SE, $n=35$ females) of the copulations followed by sperm ejection depending on the sex that terminated the copulation

test, $z=2.86$, $P=0.004$, $n=34$ females; Fig. 3). When females stopped the copulation they were three times more likely to eject sperm (mean \pm SD sperm ejection frequency: 0.28 \pm 0.44) than when males ended the copulation (0.09 \pm 0.17; Wilcoxon-paired signed-rank test, $z=2.65$, $P=0.008$, $n=35$ females; Fig. 4), suggesting that females may have ended copulations in order to eject sperm expeditiously.

Females ejected sperm more than twice as often when their mates departed after the copulation (mean \pm SD sperm ejection frequency: 0.35 \pm 0.41) than when they remained on the nest (0.16 \pm 0.29; Wilcoxon-paired signed-rank test, $z=3.67$, $P<0.0003$, $n=55$ females), suggesting that females avoid ejecting sperm in their mates' presence.

Sexual conflict and body mass

The proportion of copulations followed by sperm ejection was not correlated with female body mass ($r_s=-0.16$,

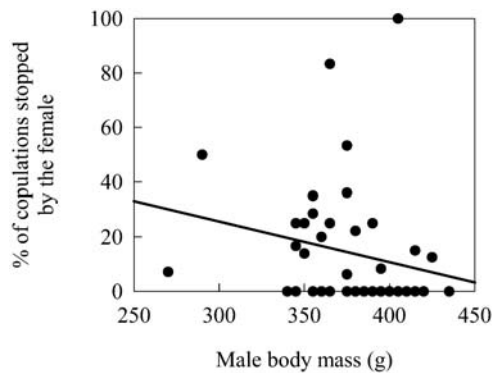


Fig. 5 Proportion of the copulations stopped by the females in relation to their mates' body mass. The line is the regression line

$P=0.19$, $n=70$ females), male body mass ($r_s=0.02$, $P=0.91$, $n=43$ males) or the difference in body mass between mates ($r_s=0.18$, $P=0.38$, $n=26$). The amount of time that males remained on their females' backs after the last insemination was also not correlated with female body mass ($r_s=-0.08$, $P=0.53$, $n=71$ females), male body mass ($r_s=-0.21$, $P=0.16$, $n=45$ males) or the difference in body mass between mates ($r_s=-0.01$, $P=0.97$, $n=28$). The frequency with which females stopped the copulation did not depend on their own body mass ($r_s=-0.18$, $P=0.14$, $n=71$ females) but was significantly correlated with their mates' body mass ($r_s=-0.40$, $P=0.007$, $n=45$ males) (Fig. 5) and with the difference in body mass between mates ($r_s=-0.44$, $P=0.02$, $n=28$), suggesting that male control over copulation depended on their size.

Discussion

In kittiwakes there appears to be a conflict between mates over the retention of the male's sperm. Whereas females often eject their mate's sperm, the males, by remaining on their mate's back at the end of the copulation, appear to try to prevent sperm ejection. Wagner et al. (unpublished data) found that female kittiwakes generally eject sperm that would have become old and possibly damaged by the time of fertilization, and retain fresh sperm as laying approaches. Frequent sperm ejection results in higher hatching success and may be mainly, if not solely, driven by natural selection in kittiwakes (Wagner et al., unpublished data). However, because EPCs, though infrequent, may be forced in kittiwakes, male kittiwakes may risk losing paternity. Sperm ejection, because it reduces the number of their sperm in their mates' reproductive tract, may lower males' confidence of paternity. Hence, the balance of the costs and benefits of sperm ejection may differ between mates. Female birds, and presumably female kittiwakes, invest a large amount of energy in their eggs (Bolton et al. 1992; Nager et al. 1997; Ramsay and Houston 1997; Neuman et al. 1998) and suffer a net cost when an egg fails to hatch. In contrast, males may benefit more from a reduced hatching rate if they sire all the

chicks than from a brood that entirely hatches but may contain extra-pair offspring. Males may thus have developed behavioral strategies to prevent their mates from ejecting their sperm in order to maximize their probability of paternity.

We never observed sperm ejection while the males stood on their mates' backs following the last cloacal contact, suggesting that males tried to prevent the females from ejecting their sperm by remaining on their backs. Females may have been unable to perform the conspicuous muscular contraction while bearing the male's full weight. It is also possible that females never ejected sperm while mounted in order to avoid allowing their mates to perceive the ejection of their sperm. Our results also suggest that males adjust their copulation behavior to their mates' behavior, remaining on the females' backs longer when they have previously ejected their sperm (Fig. 3). By compelling their mates to retain their sperm, males may increase the probability that their sperm will reach the females' sperm storage tubules and eventually achieve fertilization (Brillard and Bakst 1990; Bakst et al. 1994).

Females may be constrained by a time threshold beyond which sperm ejection is no longer efficient and sperm become stored in their reproductive tracts. Females may reduce this constraint by adjusting the timing of sperm ejection according to the amount of time their mates had remained on their backs. Females ejected their mates' sperm rapidly when males remained a long time on their backs, whereas they tended to delay sperm ejection when their mates dismounted soon after the last cloacal contact (Fig. 2). Females may delay sperm ejection, waiting for their mate to depart from the nest, in order to avoid them witnessing sperm ejection. Notably, sperm ejection occurred three times more often when females stopped the copulations than when males did. By ejecting sperm more frequently when their mates leave the nest just after the copulation, females may prevent their mates from witnessing sperm ejection and subsequently trying to prevent it. In addition, females often shortened copulations by unbalancing their mates.

Because low-quality males may have low-quality sperm that degrade faster (Blount et al. 2001), their mates may be more likely to eject their sperm. In turn, low-quality males, in which sperm may also be less competitive, may try to prevent their mates from ejecting their sperm to assure their paternity. However, there was no correlation between our measures of male quality (arrival date and courtship feeding rate) and sperm ejection frequency or the duration of the post-insemination mounting. Thus, males seem to adjust their behavior solely in response to their mates' behavior, i.e. whether or not they ejected their sperm, and not according to their own quality.

Females terminated an average of 14.9% (± 24.9) of the copulations, ranging from 0 to 100%, suggesting that some females were more likely than others to control the duration of copulations. Simply because it may be more difficult for females to stand up and make a heavy male

dismount, male body mass may determine how likely females are to be able to stop the copulation. Indeed, females paired with heavy males were less likely to stop the copulations. However, the ability of males to remain on their mates' backs may either be due to their ability to prevent their mates from standing up or to the females not attempting to unbalance them. This may explain the lack of direct relationships between male body mass, post-insemination mounting duration and sperm ejection frequency. Our results nevertheless suggest that male kittiwakes are able to perceive the risk of losing paternity through their mates' behavior because they increased the duration of the post-insemination mount after their mates had ejected their sperm.

If males remain on their mates' backs to prevent them from ejecting their sperm, we might predict a negative relationship between the duration of the post-insemination mounting and sperm ejection frequency, yet we found a positive relationship. This prediction however, does not account for our finding that males remain on their mates' backs longer after apparently witnessing sperm ejection once (Fig. 2a, b). This male response is the likely explanation of this positive relationship and suggests that, combined with other paternity assurance tactics (Helfenstein et al., unpublished data), it may help explain the low extra-pair paternity frequency in kittiwakes.

Further research on paternity assurance strategies may fruitfully examine seemingly simple behaviors such as males remaining on their mates' backs after copulation because it may be a strategy to prevent the females from ejecting their sperm. Males pressuring their mates to retain their sperm appears to be a previously unrecognized paternity assurance strategy. Kittiwake behavior adds a new dimension to the study of sexual conflict in monogamous species by illustrating that conflicts may arise over the disposition of sperm.

Acknowledgements We thank T.R. Birkhead, D. Blomqvist, B. Kempenaers and two anonymous referees for their helpful comments on the manuscript. We are grateful to A. Degeorges, J. Guillaumin, F. Martayan, J-Y. Monnat and V. Nepoux for their help in field work and data collection. We thank Bretagne Vivante-SEPNEB for providing access to the Réserve Naturelle du Cap-Sizun. This work is part of the CNRS Research Group for Behavioural Ecology (GDR 2155) and complies with the current laws of the country in which it was performed.

References

- Altmann J (1974) Observational study of behaviour: sampling methods. *Behaviour* 49:227–267
- Arnqvist G, Rowe L (1995) Sexual conflict and arms races between the sexes: A morphological adaptation for control of mating in a female insect. *Proc R Soc Lond B* 261:123–127
- Bakst MR, Wishart GJ, Brillard J-P (1994) Oviducal sperm selection, transport, and storage in poultry. *Poult Sci Rev* 5:117–143
- Birkhead TR (1998) Cryptic female choice: criteria for establishing female sperm choice. *Evolution* 52:1212–1218
- Birkhead TR, Møller AP (1992) Sperm competition in birds. Evolutionary causes and consequences. Academic Press, London
- Birkhead TR, Møller AP (1993) Why do females make it so difficult for males to fertilize their eggs? *J Theor Biol* 161:51–60
- Birkhead TR, Atkin L, Møller AP (1987) Copulation behavior of birds. *Behaviour* 101:101–138
- Birkhead TR, Veiga JP, Fletcher F (1995) Sperm competition and unhatched eggs in the House Sparrow. *J Avian Biol* 26:343–345
- Blount JD, Møller AP, Houston DC (2001) Antioxidants, showy males and sperm quality. *Ecol Lett* 4:393–396
- Bolton M, Houston D, Monaghan P (1992) Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. *J Anim Ecol* 61:512–532
- Brillard J-P, Bakst MR (1990) Quantification of spermatozoa in the sperm-storage tubules of turkey hens and the relation to sperm numbers in the perivitelline layer of eggs. *Biol Reprod* 43:271–275
- Cadiou B (1993) L'accession à la reproduction: un processus social d'ontogénèse. Cas de la mouette tridactyle (*Rissa tridactyla*). Thesis, Université de Rennes, Rennes, France
- Cam E, Monnat J-Y (2000) Stratification based on reproductive state reveals contrasting patterns of age-related variation in demographic parameters in the kittiwake. *Oikos* 90:560–574
- Chardine JW (1986) Interference of copulation in a colony of marked Black-legged Kittiwake. *Can J Zool* 64:1416–1421
- Chardine JW (1987) The influence of pair-status on the breeding behaviour of the Kittiwake *Rissa tridactyla* before egg-laying. *Ibis* 129:515–526
- Currie D, Thompson DBA, Burke T (2000) Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. *Ibis* 142:389–398
- Danchin E, Monnat J-Y (1992) Population dynamics modelling of two neighbouring kittiwake *Rissa tridactyla* colonies. *Ardea* 80:171–180
- Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implication for the study of coloniality. *Ecology* 79:2415–2428
- Davies NB (1983) Polyandry, cloaca-pecking and sperm competition in dunlocks. *Nature* 302:334–336
- Dewsbury DA (1982) Ejaculate cost and male choice. *Am Nat* 119:601–610
- Eberhard WG (1996) Female control: sexual selection by cryptic female choice. Princeton University Press, Princeton, N.J.
- Eberhard WG (1998) Female roles in sperm competition. In: Birkhead TR, Møller AP (eds) Sperm competition and sexual selection. Academic Press, San Diego, pp 91–145
- Froman DP, Pizzari T, Feltmann AJ, Castillo-Juarez H, Birkhead TR (2002) Sperm mobility: mechanisms of fertilizing efficiency, genetic variation and phenotypic relationship with male status in the domestic fowl, *Gallus gallus domesticus*. *Proc R Soc Lond B* 269:607–612
- Ginsberg JR, Huck UW (1989) Sperm competition in mammals. *Trends Ecol Evol* 4:74–79
- Gowaty PA (1996) Battles of the sexes and origins of monogamy. In: Black JM (ed) Partnerships in birds. Oxford University Press, Oxford, pp 21–52
- Green DJ, Krebs EA (1995) Courtship feeding in Ospreys *Pandion haliaetus*: a criterion for mate assessment? *Ibis* 137:35–43
- Helfenstein F (2002) Stratégies de reproduction et conflits sexuels: le cas d'une espèce coloniale, la mouette tridactyle *Rissa tridactyla*. PhD thesis, Université Pierre et Marie Curie, Paris, France
- Helfenstein F, Wagner RH, Danchin E, Rossi J-M (2003) Functions of courtship feeding in black-legged kittiwakes: natural and sexual selection. *Anim Behav* 65:1027–1033
- Hillgarth N (1996) Ectoparasite transfer during mating in ring-necked pheasants *Phasianus colchicus*. *J Avian Biol* 27:260–262
- Johnsen A, Lifjeld JT, Rohde PA, Primmer CR, Ellegren H (1998) Sexual conflict over fertilizations: female bluethroats escape male paternity guard. *Behav Ecol Sociobiol* 43:401–408
- Koyama S, Kamimura S (1999) Lowered sperm motility in subordinate social status of mice. *Physiol Behav* 65:665–669

- Lodge JR, Fehheimer NS, Jaap RG (1971) The relationship of in vivo sperm storage interval to fertility and embryonic survival in the chicken. *Biol Reprod* 5:252–257
- Møller AP (1994) Sexual selection and the barn swallow. Oxford University Press, Oxford
- Møller AP (1998) Sperm competition and sexual selection. In: Birkhead TR, Møller AP (eds) *Sperm competition and sexual selection*. Academic Press, San Diego, pp 55–90
- Møller AP, Birkhead TR (1993) Cuckoldry and sociality: a comparative study of birds. *Am Nat* 142:118–140
- Nager R, Rügger C, Van Noordwijk AJ (1997) Nutrient or energy limitation on egg formation: a feeding experiment in great tits. *J Anim Ecol* 66:495–507
- Neuman J, Chardine JW, Porter JM (1998) Courtship feeding and reproductive success in Black-legged Kittiwakes. *Colon Waterbirds* 21:73–80
- Olsson M (1999) Sperm choice and sperm competition: suggestions for field and laboratory studies. *Oikos* 84:172–175
- Olsson M, Shine R, Madsen T, Gullberg A, Tegelström H (1996) Sperm selection by females. *Nature* 383:585
- Pizzari T, Birkhead TR (2000) Female feral fowl eject sperm of subdominant males. *Nature* 405:787–789
- Ramsay SL, Houston DC (1997) Nutritional constraints on egg production in the blue tit: a supplementary feeding study. *J Anim Ecol* 66:649–657
- SAS (1999) SAS user's guide, v. 8.02. SAS Institute, Cary, N.C., USA
- Siva-Jothy MT (2000) The young sperm gambit. *Ecol Lett* 3:172–174
- Sokal RR, Rohlf JF (1995) *Biometry*, 3rd edn. Freeman, New York
- Stockley P (1997) Sexual conflict resulting from adaptations to sperm competition. *Trends Ecol Evol* 12:154–159
- Thornhill R (1983) Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *Am Nat* 122:765–788
- Wagner RH (1991) Evidence that female razorbills control extra-pair copulations. *Behaviour* 118:157–169
- Wagner RH (1996) Why do female birds reject copulations from their mates? *Ethology* 102:465–480
- Wiggins DA, Morris RD (1986) Criteria for female choice of mates: courtship feeding and parental care in the common tern. *Am Nat* 128:126–129
- Wilson N, Tubman SC, Eady PE, Robertson GW (1997) Female genotype affects male success in sperm competition. *Proc R Soc Lond B* 264:1491–1495