SHORT COMMUNICATIONS

TIMING OF PAIR AND EXTRA-PAIR COPULATIONS IN THE NORTHERN FULMAR[1]

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Abstract. In most birds, males competing for paternity of a female's offspring attempt copulations most frequently immediately before fertilization. Paternity is determined by the relative numbers and timing of inseminations such that a male inseminating a female frequently at this time has an increased chance of fathering her offspring. In the Northern Fulmar (*Fulmarus glacialis*), fertilization is believed to occur within a few days prior to laying, but extra-pair and pair copulations and paternity defense behaviors start to decline around 20 days before egg laying, and by 9 days prior to egg laying these behaviors are at a minimum. I suggest that inseminations occurring during and after the time of this decline may have a reduced chance of successfully fertilizing eggs due to physiological constraints within the female's reproductive tract.

Key words: copulation, copulation timing, Fulmarus glacialis, Northern Fulmar, sperm competition.

If a female is inseminated by more than one male, the paternity of her offspring will be determined through mechanisms by which the sperm compete for fertilization. Current theory and empirical studies suggest that in birds both the timing of inseminations and the numbers of sperm inseminated are important in determining paternity (Birkhead and Hunter 1990, Birkhead et al. 1995b, Colegrave et al. 1995). This pattern appears to result from a mechanism of passive sperm loss during the period of ovulation combined with variation in numbers and quality of sperm in different ejaculates (Birkhead et al. 1995a, Colegrave et al. 1995). When both timing and frequency of inseminations are important, it is predicted that copulations will peak immediately before fertilization as males attempt to gain both the last insemination and the maximum number of inseminations with a female.

Fertilization has been found to occur 24 hours prior to egg laying in domestic birds that lay at daily intervals (Gilbert et al. 1968, Howarth 1974). Birkhead and Møller (1993) showed that in monogamous species a

peak in copulation frequency occurs three to four days prior to the day the first egg of a clutch is laid, and copulation frequency tends to decline after the onset of egg-laying. In the Northern Fulmar (*Fulmarus glacialis*), behaviorally successful copulations end much earlier, in most cases around 16 days prior to egg laying but in some cases as early as 27 days before laying (Hunter et al. 1992). It is not known exactly when fertilization occurs in the Northern Fulmar, but studies on other procellariiformes suggest that it is likely to follow yolk and albumen formation, so fertilization would occur within the few days prior to laying (Grau 1984, Astheimer and Grau 1985). Consequently, it would appear that copulations end unusually early in fulmars.

Northern Fulmars are long-lived, socially monogamous seabirds (MacDonald 1977a, Dunnet and Ollason 1978). Females engage in extra-pair copulations (EPCs) which give rise to the potential for sperm competition between pair and extra-pair males (Hatch 1987, Hunter et al. 1992). The female lays only one egg in a breeding season, and the pair male invests considerable effort in rearing the offspring, so he should be under strong selective pressure to protect his paternity (Dunnet et al. 1963, Hatch 1987). Hunter et al. (1992) showed that although female fulmars engaged in EPCs, the male partner always fathered the offspring, although the sample size in their study meant a level of extra-pair paternity of less than 4.6% could have gone undetected (95% confidence limits; *n* = 85 females). With the potential for extra-pair males to gain paternity and pair males to lose paternity, why do copulations end so early relative to egg laying in the Northern Fulmar?

The aim of this paper is to explore the timing of extra-pair copulation and paternity defense behaviors in the Northern Fulmar in an attempt to explain why copulations cease to occur so far in advance of egg laying.

METHODS

The study was carried out on a cliff nesting colony of fulmars on Fair Isle (59°32'N, 01°37'W), Shetland. The colony consisted of 91 breeding pairs, occupying an area of about 15 × 15 m. All individuals in the study site could be observed simultaneously and were recognizable by unique color band combinations and/or distinctive culmen markings (Hunter et al. 1992). The birds were observed continuously by two recorders al-

ternating 4-hr observation periods, from dawn until dusk each day for the duration of the pre-laying season, from 27 March until the day the last egg was laid on 29 May 1988. As fulmars copulate only on the nest site (Hatch 1987) and only during daylight hours (pers. observ.), this record accounts for all copulation attempts for all birds at the study site in the 1988 breeding season. The date of egg laying, accurate to within 24 hr, was obtained for 79 of these pairs. This allowed patterns of activity relative to egg laying to be determined. The day the egg was laid is referred to as day 0, one day before the day the egg was laid is referred to as day −1 and so on.

During the pre-laying period, a complete record was made of all copulation attempts and related behaviors. The following information specific to pair copulation activity was recorded for each copulation attempt: (1) the identity of the male and female involved, and the site and time at which the activity occurred, (2) whether the copulation attempt was behaviorally successful, and (3) for failed copulations, the sex of the individual terminating copulation. A copulation was recorded as being behaviorally successful if cloacal contact was observed. Studies of both wild and captive species have shown that not all apparent cloacal contacts result in apposition of the cloacae, followed by ejaculation and successful insemination, and further that even with apparently successful insemination, sperm is not always transferred (Birkhead et al. 1988, Hunter et al. 1996). In the present study, the best measure of copulation success that could be attained was apparent cloacal contact. The female was recorded as responsible for causing the failure of a copulation if she moved or flew away or threw the male from his mounted position, whereas the male was considered responsible if he fell, dismounted, or failed to position himself in such a way that cloacal contact could be achieved.

Frequencies of copulations per individual per day were highly variable and not normally distributed, so patterns of copulation behavior are presented as numbers of individuals engaging in copulations each day.

RESULTS AND DISCUSSION

I predicted that extra-pair copulation (EPC) and paternity assurance behaviors should persist up until the time of fertilization. If fertilization occurs in the few days prior to laying, then both extra-pair and pair copulations should peak immediately before this time.

Most EPCs occurred during the period day −39 to day −9 (Fig. 1a). There were no EPC attempts after day −6 and the last behaviorally successful EPC for any female occurred on day −9, despite the presence of females at the colony after this time (unpubl. data). Contrary to the prediction that males should inseminate females immediately prior to fertilization, no peak in EPCs occurred within the 4 to 5 days prior to laying.

The number of pairs engaging in copulations showed a similar pattern to that of pairs engaging in EPCs (Fig. 1b). A high number of pairs engaged in both copulation attempts and behaviorally successful copulations over the period day −34 to day −21 (30–44 pairs involved in copulation attempts; 27–38 pairs involved in behaviorally successful copulations). After this time, the numbers of pairs engaging in copulations
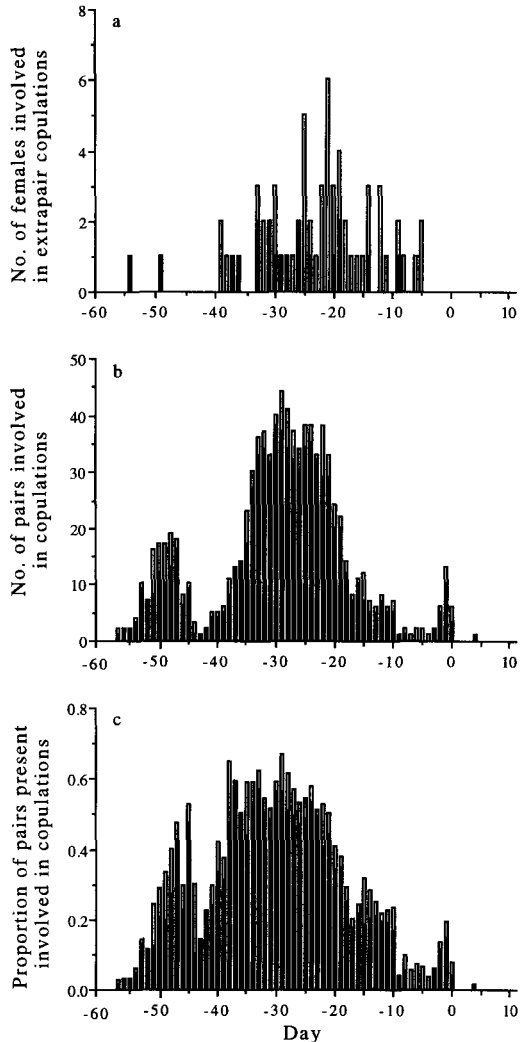

FIGURE 1.   Patterns relative to egg laying of (a) numbers of female Northern Fulmars involved in attempted and behaviorally successful extra-pair copulations per day (n = 79 females), (b) numbers of pairs involved in attempted and behaviorally successful pair copulations per day (n = 79 pairs), and (c) numbers of pairs involved in attempted and behaviorally successful pair copulations per pairs present per day (7 ≤ n ≤ 79 pairs). Day 0 is the day the egg was laid. Solid bars indicate successful copulations, open bars indicate copulation attempts.

dropped steadily until during the period day −9 to day −3 a maximum of two pairs were involved in copulations on any one day. Unlike the pattern for extra-pair copulation behavior, a number of pairs engaged in copulations early in the pre-laying period. A small number of pairs engaged in copulations immediately prior to egg laying (13 pairs involved in copulation

attempts; 10 pairs involved in behaviorally successful copulations).

Pair copulation behavior started to decline approximately 20 days prior to egg laying, and from 9 days before egg laying onwards both extra-pair and pair copulation behavior were at a minimum. Similar patterns of behavior have been observed in albatrosses: females ashore during the pre-laying exodus did not engage in copulations, despite the presence of males (Astheimer et al. 1985). Hatch (1987) found a similar pattern for fulmars in Alaska. He explained the drop in copulations as a function of one or both members of a pair being absent from the colony on a pre-laying exodus (Fisher 1952, Warham 1990). This pre-laying exodus of between 9 and 20 days has been measured by a number of workers including Dunnet et al. (1963), MacDonald (1977b), and Hatch (1990). During the present study, there was no indication of a complete exodus. Attendance was reduced during the period day −15 to day −3, but at least 30% of females and 40% of males were present each day during this time (unpubl. data). It may be that food was available in the region of the colony and individuals were able to forage relatively close to the breeding site and so avoid a complete exodus (Warham 1990). If the decline in the number of pairs involved in copulations each day was due to this partial absence of individuals, then I predicted that the number of pairs involved in copulation activity as a proportion of the number of pairs present would remain high.

The pattern of the number of pairs involved in copulations per pair present per day relative to the female cycle was similar to that of the absolute number of pairs involved in copulations per day (Fig. 1c). This suggests that the decline in copulation behavior from day −20 did not result from a partial exodus.

I tested whether the decline in copulations resulted from females being unwilling to copulate during the period immediately before laying by examining the pattern of female-determined copulation failure. Although the highest proportion of females causing some failure of copulation attempts (60.0%, 3/5) occurred within the period day −9 to day −5, there was no significant variation over the pre-laying period ($\chi^2_{10} = 12.0$, $P = 0.3$; Fig. 2). Thus, the decline in copulations immediately prior to laying does not appear to result from females being unwilling to copulate. Interestingly, the lowest proportion of females involved in causing failures (20.8%, 5/24) occurred within the period day −4 to day 0. For part of this time the female would have had a shelled egg in her oviduct, and may have avoided struggling away from her partner's copulation attempts in order to avoid damaging the egg and consequently herself.

Even if females were controlling the decline in behaviorally successful copulations, the number of males attempting copulations would remain high. The proportion of pairs present engaging in copulation attempts declined over the period day −20 to day −10 and was low from day −9 to day −3 (Fig. 1c).

It is possible that the decline in behaviorally successful copulations over the period day −20 to day −9 results from fertilization occurring at some point during this time. If so, eggs fertilized during this period
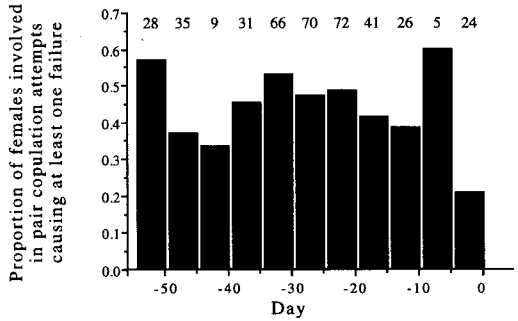

FIGURE 2.   Females that caused at least one copulation failure as a proportion of those involved in pair copulation attempts, relative to egg laying. Day 0 is the day the egg was laid. Number of females involved in pair copulation attempts in each 5-day period are given above the columns.

would show some signs of development by the day of laying. Northern Fulmar eggs show no signs of early development (pers. observ.), so it seems unlikely that fertilization occurs during or immediately after the period day −20 to day −9.

It appears that for the Northern Fulmar, males do not gain behaviorally successful EPCs with females after day −9 of the participating female's cycle, although they continue to attempt EPCs up until day −6 of the same cycle. Also, the incidence of pair copulations starts to decline around day −20, and from day −9 onwards pair copulations are at a minimum, indicating that pair males reduce their efforts to protect their paternity from day −20 onwards. Finally, females are left alone by their male partners more often from day −11 (unpubl. data), indicating that males no longer sustain pre-copulatory mate defense after this time. The available evidence suggests that the outcome of sperm competition for the Northern Fulmar is established on or before day −9, releasing males from the pressures of obtaining EPCs and protecting paternity.

Why should the outcome of sperm competition be determined so far in advance of egg laying? One possible causal explanation concerns the timing of egg formation. Egg formation and development have been well documented in domestic birds which produce large clutches and lay at 24-hr intervals. The completion of yolk formation is followed immediately by ovulation, fertilization, secretion of albumen, laying down of shell material, and finally oviposition. The interval from ovulation to oviposition in most birds studied is 24 hr (Romanoff and Romanoff 1949). Yolk deposition takes 7–11 days in Chickens, 5–7 days in Japanese Quail (*Coturnix coturnix*), and 12–15 days in Turkeys (*Meleagris gallopavo*) (Bacon and Cherms 1968, Bacon and Koontz 1971, Gilbert 1972). In fulmars and other procellariiformes, yolk deposition takes much longer: 23 days in the Northern Fulmar, 20 days in the Black-browed Albatross (*Diomedea melanophris*), 21 in the Grey-headed Albatross (*D. chrysostoma*), 23 in the Grey-faced Petrel (*Pterodroma macroptera gouldii*), and 30 in the Royal Albatross (*D.*

epomorpha) (Grau 1984, Astheimer et al. 1985, Astheimer and Grau 1990).

In a number of seabird species, a period referred to as the lag phase exists between the completion of yolk formation and egg laying. During the lag period, albumen and shell membrane materials are synthesized in readiness for rapid completion of the egg following ovulation (Grau 1984, Astheimer 1986). The lag period appears to result from a delay in ovulation rather than a delay in oviposition of the fertilized egg (Grau 1984, Astheimer and Grau 1985, Astheimer 1986). The Black-browed and Royal Albatrosses have a lag period of 9 days and the Grey-headed Albatross 12 days (Grau 1984, Astheimer et al. 1985). These lag periods occur during the pre-laying exodus. Although it is not known, it seems likely that fulmars have a lag period of similar duration and timing relative to laying.

Grau (1984) has suggested that the protracted lag period may have been a feature of reproduction in primitive birds. With the evolution of increased clutch sizes and reduced laying intervals, many birds may have been forced to reduce the lag period. The procellariiformes, which lay only one egg per clutch, may not have been under such pressure, and hence the protracted lag period is still a feature of their reproductive biology. In addition, both yolk formation and albumen synthesis are costly in terms of both protein and energy, such that females in a system in which food is ephemeral and widely dispersed, e.g., as in a marine environment, might gain by carrying out each process separately (Whittow and Rahn 1984, Astheimer 1986).

The timing of the reduction in EPC and paternity assurance behaviors outlined above coincides with the completion of yolk deposition and initiation of albumen and shell membrane synthesis. There are two possible explanations for the observed pattern of copulation behavior: (1) ovulation and fertilization occur immediately after the completion of yolk deposition on or around day −9, or (2) fertilization occurs within a few days of egg laying but the biochemical environment within the female reproductive tract changes towards the end of yolk deposition or the onset of the lag phase making it impossible for sperm to survive outside the protected surroundings of the sperm storage tubules. Regardless of the timing of fertilization, the fertile period would effectively end at or around the beginning of the lag period. If the fertile period ends at this time, there would be no benefit for males in pursuing extra-pair copulations or attempting to protect their pair paternity. Such a mechanism would explain the behaviors observed in this study. A detailed investigation of the female reproductive tract during egg formation would be needed to examine this hypothesis further.

In summary, in the Northern Fulmar extra-pair and pair copulations and paternity defense behaviors start to decline around 20 days before egg laying, and by 9 days prior to egg laying these behaviors are at a minimum. Inseminations occurring after this time may be unsuccessful due to physiological constraints within the female's reproductive tract.

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SONG SPARROW MALES USE FEMALE-TYPICAL VOCALIZATIONS IN FALL[1]

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Abstract.   In many species of north temperate-zone passerines, females do not sing, but rather use female-specific calls for acoustic communication. In a resident population in Washington state, banded adult male Song Sparrows (*Melospiza melodia*) outside the breeding season used a vocalization (chitter call) previously believed to be used only by females. This phenomenon has not been observed previously because most field studies of temperate passerines are confined to the breeding season. In this population, juvenile males attempt to establish territories in fall when they do not yet sing fully crystallized songs. Use of female-typical vocalizations by adult males outside the breeding season may allow adults of both sexes to communicate about territories to juvenile males who cannot yet sing the full adult songs males typically use to communicate territorial boundaries.

Key words: calls, communication, female-typical calls, Melospiza melodia, *nonbreeding season, Song Sparrow, territoriality.*

In oscine songbirds, both males and females communicate with vocalizations. Whereas male songs are

used to compete with other males and to attract and increase the receptivity and fecundity of female mates (Searcy and Andersson 1986, Kroodsma and Byers 1991), females of most north temperate species do not sing. Female vocalizations are used socially in competition with other females (Beletsky 1983), to indicate species, sex or individual identity (Beecher et al. 1985), to alert others to the presence of a predator (Marler 1955), in pair bond formation or maintenance (Beletsky 1983), to coordinate reproductive effort within the pair (Lehrman 1964, Cheng 1992), during copulation solicitation (Baker and Baker 1988), and to communicate with young (Beecher et al. 1985, Medvin and Beecher 1986). Song Sparrow (*Melospiza melodia*) females sing only rarely (Nice 1943, Arcese et al. 1988) and have a variety of calls, some of which typically are used only by females (chitter, chet, sweep buzz; Fig. 1c, d, e, respectively; also Nice 1943) and some of which are used by both sexes (low chip contact call, high chip alarm call, threat vocalization growl; Fig. 1a, b, f. respectively; also Nice 1943). The most distinctive of these calls is the chitter. Females direct the chitter call both to their mates as a form of inciting, and to conspecific intruders during the early stages of aggressive encounters. They also use the chitter call during copulation solicitations and upon leaving the nest during incubation (Nice 1943). To date, only females have been reported to use this call. The purpose of this paper is to report observations of males in a resident population using the female-typical chitter call during the nonbreeding season. The chitter call is