

ON THE FUNCTION OF PRE-LAYING BREEDING SITE ATTENDANCE IN THE NORTHERN FULMAR *FULMARUS GLACIALIS*

OVER DE FUNCTIE VAN DE AANWEZIGHEID OP DE BROEDPLAATS VOORAFGAANDE AAN DE EILEG BIJ DE NOORDSE STORMVOGEL

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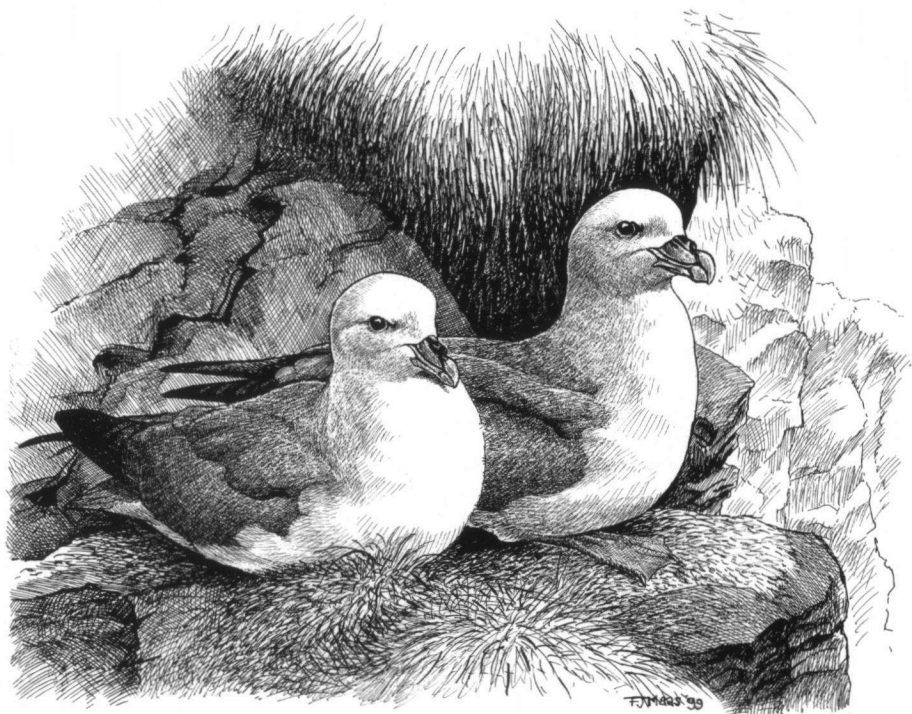
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Northern Fulmars spend considerable periods of time at their breeding sites in the months before egg laying. In this study the function of pre-laying breeding site attendance was investigated. Three potential benefits of prolonged pre-laying colony attendance were considered: (1) site defence; (2) opportunities for engaging in either pair or extra-pair copulations (EPCs); and (3) mate defence. There was no evidence that the function of pre-laying colony attendance was site defence: sites were left unguarded for long periods during the pre-laying period and were not subsequently lost to conspecifics. Neither did it appear that individuals maintained a high frequency of attendance to engage in pair copulations. The available evidence is consistent with the idea that females attended the colony to engage in EPCs; females present at the colony on a high proportion of days during the pre-laying period were more likely to be involved in EPC attempts. Although the possibility that females attended the colony for an as yet unidentified reason and engage in EPCs simply because they were there could not be ruled out. It appeared that males attended the colony in an attempt to prevent their partners from engaging in EPCs. Males maintained a higher level of attendance than females throughout the pre-laying period and seldom left their female partners unaccompanied during the presumed fertile period.

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INTRODUCTION

Seabirds tend to spend the majority of their lives at sea, coming to land only to breed. Individuals must return to their breeding sites to rendezvous and to copulate with their partners after spending the winter apart. In many colonial species individuals are present at the colony for a prolonged period up until the



Northern Fulmars at nest site *Noordse Stormvogels op het nest* (F.J. Maas)

time of laying (e.g. Common Guillemot *Uria aalge*, Birkhead 1978; Least Auklet *Aethia pusilla*, Jones 1992; Northern Fulmar *Fulmarus glacialis*, Dunnet *et al.* 1963). Attendance at the colony is likely to carry costs such as loss of time otherwise available for feeding. However, there are also three potential benefits of prolonged pre-laying colony attendance: (1) site defence; individuals may attend the colony in order to defend their breeding site from others. A number of studies of colonial seabirds have shown that breeding sites vary in quality and that breeding success is affected by site quality (Potts *et al.* 1980; Hudson 1982; Birkhead *et al.* 1985; Hatchwell 1991). As a result there is likely to be competition for good sites, and pairs that have secured good sites may have to defend them. One or both members of the pair could carry out site defence. (2) Opportunities for engaging in either pair copulations or extra-pair copulations (EPCs); individuals may attend the colony in order to seek opportunities to engage in pair copulations with their breeding partner or extra-pair copulations with others (Gladstone 1979; Wittenburger & Hunt 1985; Birkhead & Møller 1992). Both genetic and non-genetic benefits can be gained from engaging in extra-pair copulations. Genetic benefits take the form of additional offspring for males and good or diverse genes for females. Non-genetic benefits include fertilisation assurance, courtship feeding and paternal care (Birkhead & Møller 1992). For long-lived seabirds, the most important non-genetic benefit of engaging in EPCs may be the potential for gaining future reproductive partners (Hatch 1987); (3) mate defence; males may attend the colony in order to defend their mates from the extra-pair copulation attempts of others (Hatch 1987; Hatchwell 1988). Mate defence would carry genetic benefits for males and females similar to those outlined above.

The Northern Fulmar is a long-lived, socially monogamous seabird that breeds colonially and is site- and mate-faithful (Dunnet & Ollason 1978a; MacDonald 1977a; Ollason & Dunnet 1978). Breeding is highly synchronous within any local population (Dunnet & Ollason 1978b; Dunnet *et al.* 1963). The female lays one egg in each breeding season and does not relay if that egg is lost (Hatch 1987). Extra-pair copulation attempts are frequent and 16% of females are involved in behaviourally successful EPCs, although paternity is always secured by the pair male (Hunter *et al.* 1992). In some groups of seabirds and particularly in the Procellariiformes, a pre-laying exodus from the colony occurs immediately prior to egg-laying (Warham 1990). Yolk deposition in the Northern Fulmar takes 23 days, similar to other Procellariiformes, and the function of the pre-laying exodus may be to allow females to feed at sea during this costly egg production period, while males

may feed during the exodus in preparation for their first long incubation shift (Dunnet *et al.* 1963; Astheimer & Grau 1990).

The aim of this study is to report the pattern of pre-laying attendance of Northern Fulmars in a colony on Fair Isle, Shetland (UK) and to assess whether patterns of attendance are related to site or mate defence or extra-pair activity.

METHODS

The study was carried out on a cliff dwelling colony of Northern Fulmars on Fair Isle (59°32'N, 01°37'W), Shetland. The study population consisted of 91 breeding pairs, occupying an area of about 15 m x 15 m of cliff-face. Dates of egg laying were obtained for 77 of these pairs allowing patterns of attendance relative to egg-laying to be determined. Day 0 was defined as the day the egg was laid, day -1 was one day before the egg was laid, day -2 was two days before the egg was laid and so on. All individuals in the study site could be observed simultaneously and were recognisable by unique colour ring combinations and/or distinctive culmen markings (Hatch 1987; Hunter *et al.* 1992). Individuals were sexed by their positions during copulation. The presence or absence of individuals at each site and the identity and hence sex, of single individuals were recorded at 12.00 h GMT 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.

During the pre-laying period a record was made of all copulation attempts and related behaviours. The birds were observed continuously by two recorders alternating 4 hr observation periods, from dawn until dusk each day. The following information was recorded for each copulation attempt: 1) the identity of the male and female involved (i.e. whether it was a pair or extra-pair copulation); and 2) the outcome, that is whether the copulation attempt was behaviourally successful. A copulation was recorded as behaviourally successful if cloacal contact was observed (Hunter 1998).

RESULTS

A partial pre-laying exodus occurred during the period 2-13 May (the first egg was laid on 14 May). On 2 and 3 May there were very high winds which may have resulted in exceptionally low numbers of birds at the colony. On the remaining days of the exodus between 19% and 37% of breeding birds were present at the colony on any one day.

If the function of pre-laying attendance in the Northern Fulmar is site defence, it would be predicted that a high proportion of sites would be occupied by at least one member of the pair throughout the pre-laying period up to the day of egg-laying. This was not the case (Fig. 1). During the period 1-10 April, more than 75% of sites were unoccupied on any one day and during the periods 2-4 and 7-11 May, more than 50% of sites were unoccupied. Furthermore, if individuals attend the colony to defend their sites, it would be predicted that breeding sites left unguarded would be lost to incoming individuals. Although nest sites were sometimes temporarily taken over during the absence of a pair, no such take-over was seen to persist after the return of the original site holder(s). So it seems unlikely that nest site defence is the primary reason for colony attendance.

Alternatively, individuals may attend the colony in an attempt to gain genetic benefits by engaging in either extra-pair or pair copulations. If so, it would be predicted that individuals with high levels of pre-laying attendance would be involved in more copulation attempts than those with low attendance.

Comparing males involved in EPC attempts with those not involved, there was no difference in the proportion of time spent at the colony between individuals engaging in EPCs and those not (Mann-Whitney *U*-test: $z = 1.46$, $n = 32,45$, $P = 0.1$). By contrast, females involved in EPC attempts were present at the colony on a higher proportion of days than those not involved in any EPC attempt (Mann-Whitney *U*-test: $z = 2.20$, $n = 44,33$, $P = 0.03$). This pattern may arise simply as a result of males directing EPCs towards females that spend more time at the colony. This potentially confounding factor would be overcome if only females that solicited copulations were considered. However, it was not possible in this study to identify the sex initiating a copulation attempt, except in the small number of cases in which a female went to the site of a male to engage in an EPC. Instead unforced EPC attempts are considered. Unforced EPCs may be initiated by either sex and are behaviourally indistinguishable from pair copulation attempts, indicating a level of co-operation by both male and female. Females involved in unforced EPC attempts were present at the colony on a higher proportion of days during the pre-laying period than those not involved in any unforced EPC attempt (Mann-Whitney *U*-test: $z = 2.53$, $n = 56,21$, $P = 0.01$). By contrast, neither males nor females gained more pair copulation attempts by being present at the colony on a high proportion of days (male: $z = 1.09$, $n = 77$, n.s.; female $z = 0.62$, $n = 77$, n.s.).

It appears, then, that females are involved in more unforced EPCs by maintaining high attendance at the colony. However, there is no evidence for

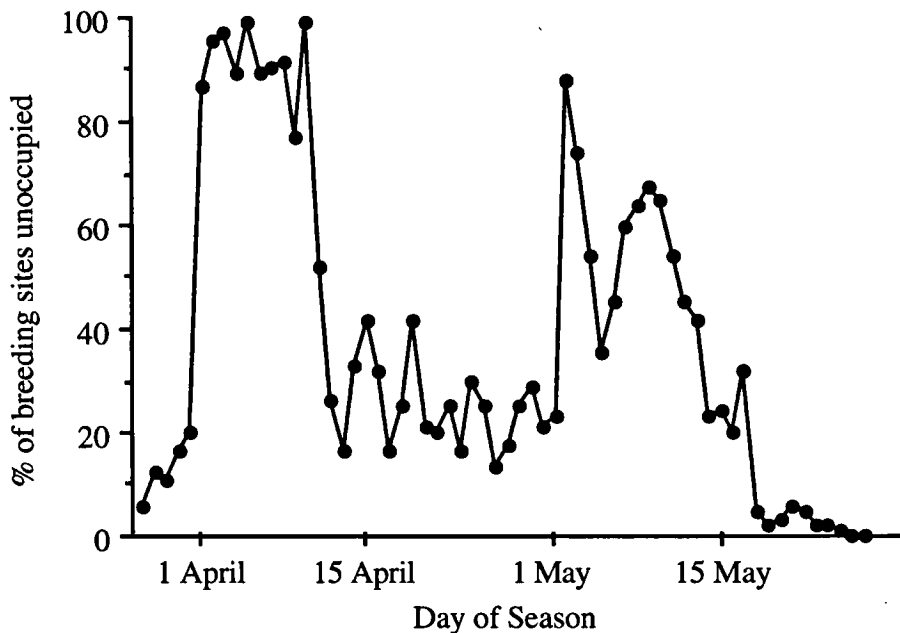


Figure 1. Pattern of site occupancy relative to calendar date. Mean date of egg laying was 18 May (± 3 days SD, $n = 91$ pairs).

Figuur 1. De aanwezigheid van Noordse Stormvogels op de broedplaats gedurende het jaar. De eileg vond gemiddeld rond 18 mei plaats (SD ± 3 dagen, $n = 91$ paren).

females gaining more pair copulations, nor for males gaining either extra-pair or pair copulations by maintaining high attendance at the colony.

Finally, if males attempt to protect the paternity of the offspring they will help to raise by defending their mates from EPCs, then it is predicted that male attendance will be higher than female attendance during the female's fertile period. This will arise because each male will attempt to be at his nest site to defend his female when she returns from feeding. The exact timing of the fertile period is not known for Northern Fulmars. In most species studied, fertilisation occurs 24 hours prior to egg laying and the fertile period ends at

this time, on day -1 (Birkhead & Møller 1992). Hunter (1998) has suggested that in female Northern Fulmars, although fertilisation is likely to take place within a few days of egg laying, the fertile period ends between nine and 20 days prior to egg-laying due to physiological changes in the females reproductive tract. So, inseminations after this time are incapable of fertilising eggs. Hence, if male Northern Fulmars attempt to protect their partners from EPCs it is predicted that male attendance will be higher than female attendance in the period immediately before day -9.

The patterns of male and female attendance varied relative to egg laying during the 52 days prior to laying (Fig. 2a). Attendance was high on days -52 to -50 and reached a peak during the period from day -32 to day -21. After the initial high attendance and during the period day -15 to day -5, attendance was relatively low for both males and females, with less than 60% of individuals of either sex being present. The overall pattern of attendance from day -55 to day +11 was similar for each sex (Spearman rank correlation, $r_s = 0.73$, $n = 67$, $P < 0.001$). Assuming the fertile period to have ended on day -9, then a higher proportion of males than females were in attendance prior to the end of the fertile period (Wilcoxon signed rank test: $z = 5.66$, $n = 46$ days, $P < 0.001$). Even if the fertile period continues to day -1 a higher proportion of males than females were in attendance during the pre-laying period (Wilcoxon signed rank test: $z = 6.20$, $n = 55$ days, $P < 0.001$). By contrast, during the post-laying period there was no difference in the proportion of males and females in attendance (Wilcoxon signed rank test: $z = 1.51$, $n = 12$, $P = 0.1$).

If males attempt to defend their mates, it is predicted that females will rarely be left alone by their partners during the females' fertile periods. The patterns of attendance of unaccompanied males and females varied with respect to egg laying (Fig. 2b). The proportion of females observed to be alone at their sites was very low (4.2%, 2/48) during the period day -34 to day -12. After this time it rose to 14.3% (2/14) on day -9 and remained at this level until day 0 when it increased to 26.7% (20/75) and persisted during the first ten days of incubation. The proportion of males observed to be alone during the period day -20 to day -2 was always greater than 17.7% (6/34) and rose as high as 51.9% (14/27) on day -6. Immediately after laying, the proportion of males observed alone increased to 72.3% (34/47). The post-laying pattern of sex observed alone at the site reflects the tendency for females to take a short (<24 hr) initial incubation shift and males to follow with a long shift (Dunnet *et al.* 1963; Hatch 1990; Mougin 1967). If the fertile period ends on day -9 a smaller proportion of females than males were left alone on any day prior to the end of the fertile period (Wilcoxon signed rank test: $z = 5.62$, $n = 45$, $P < 0.001$).

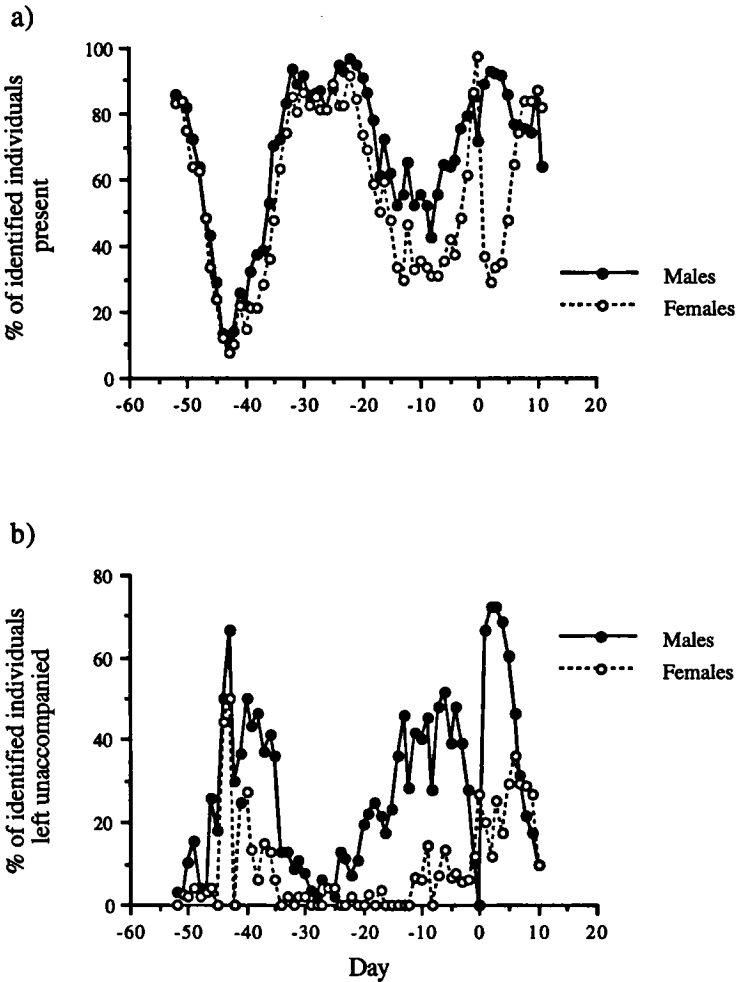


Figure 2. Pattern of attendance of breeding individuals relative to egg-laying for: (a) males and females ($n = 77$ pairs); and (b) unaccompanied males and females ($n = 77$ pairs). Day 0 is the day the egg is laid.

Figuur 2. Aanwezigheid van broedvogels in vergelijking tot de datum van eileg: (a) mannetjes en vrouwtjes ($n = 77$ paren) en (b) niet-begeleide mannetjes en vrouwtjes ($n = 77$ paren). Dag 0 is de datum waarop het ei werd gelegd.

Similarly, if the fertile period continues up until day -1 a smaller proportion of females than males were left alone on any day during the pre-laying period (Wilcoxon signed rank test: $z = 6.18$, $n = 54$, $P < 0.001$). However, during the post-laying period there was no difference between the sexes in the numbers of individuals left alone (Wilcoxon signed rank test: $z = 1.78$, $n = 10$, n.s.) The proportion of females left alone was lower before than after (and including) day -9, the presumed end of the fertile period (Mann-Whitney U -test: $z = 3.18$, $n = 45,20$, $P < 0.001$). Similarly, a lower proportion of females was left alone prior to egg-laying than after egg-laying (Mann-Whitney U -test: $z = 4.48$, $n = 54,11$, $P < 0.001$). There was no difference in the proportion of females left alone during the presumed infertile period prior to laying (day -9 to day -1) and the post-laying period (Mann-Whitney U -test: $z = 0.49$, $n = 9,11$, n.s.).

The higher incidence of male than female attendance, and the finding that females are rarely left alone during the period day -34 to day -12, both support the idea that males are attempting to protect their partners from EPCs. If so, it would be predicted that females involved in EPC attempts will have been left alone by their partner for longer periods than those not involved in EPC attempts. However, females involved in attempted EPCs were not more likely to be left unaccompanied by their mates during the pre-laying period than those that were not involved in any EPC attempt (Mann Whitney U -test $z = 0.48$, $n = 44,33$, n.s.). That is, there was no relationship between the amount of time a female was left unaccompanied by her mate and the likelihood of her being involved in extra-pair copulation activity.

DISCUSSION

Many studies have reported a pre-laying exodus in Northern Fulmars and other Procellariiformes during which individuals are absent from the colony (Fisher 1952; Warham 1990). Dunnet *et al.* (1963) reported a pre-laying exodus during which only 3-10% of their Orkney population was present, MacDonald (1977b) found only 8-23% of his Aberdeenshire population present during the exodus, and Hatch (1987) found less than 10% of individuals present during the exodus in the Semidi Islands, Alaska. In the Fair Isle population studied here, only a partial exodus appears to have occurred over the period 2-13 May. Except for the first two days of this period when high winds occurred and all but a few birds were absent, between 19% and 37% of breeding birds were present. It is possible that food was available relatively close to the colony so foraging individuals could return frequently to the breeding site (Warham

1990). It appears that the pre-laying exodus might have had little or no constraining effect on the behaviour of individuals in this study.

There was no evidence to support the idea that for Northern Fulmars the function of pre-laying colony attendance was site defence. Nest sites were left unguarded for long periods during the pre-laying period and were not subsequently lost to conspecifics. Both MacDonald (1980) and Hatch (1987) in their studies of Northern Fulmar site attendance came to similar conclusions. Females present at the colony on a high proportion of days during the pre-laying period were more likely to be involved in EPC attempts. However, without further study it is not possible to say whether females maintain a presence at the colony specifically to engage in EPCs or whether they attend the colony for some other, as yet unidentified, reason and experience a high rate of EPCs as a consequence. There was no relationship between the amount of time a female was left unaccompanied by her mate and the likelihood of her being involved in extra-pair copulation activity. This might appear paradoxical as a female left alone would be open to the advances of extra-pair males. However, it is possible that only low quality females were left alone for long periods by their partners and such females may have been less attractive to extra-pair males, given the constraints of sperm production (Petrie & Hunter 1994).

Males maintained a higher level of attendance throughout the pre-laying period and seldom left their female partners unaccompanied during the presumed fertile period. Consequently, it appears that males attend the colony in an attempt to prevent their partners from engaging in EPCs. Many studies have assumed that mate guarding, or mate defence, involves a male attempting to prevent any extra-pair male from copulating with his passive mate. The emphasis has been on the pair male responding to the extra-pair male's behaviour. However, this study shows that the threat to a male's paternity may come not from the extra-pair male but from the female instead. Female Northern Fulmars play an active role in securing EPCs; 11% (4/36) of females in the present study went to the breeding sites of extra-pair males to engage in EPC attempts and for an EPC attempt to be successful the female must co-operate with the extra-pair male (pers. obs.). Males might benefit more from attempting to impede their pair female's EPC attempts than from terminating an extra-pair male's advances.

Male and female Northern Fulmars appear to be in conflict over female participation in EPC attempts. Females seek EPCs whereas males attempt to minimise their partner's opportunities for engaging in them. Females seem to be winning the conflict, as males that never left their partners

unaccompanied did not reduce their chances of being cuckolded. The partners of these males still engaged in EPCs, in some cases by going to the sites of other males. However, in their study of paternity in Northern Fulmars, Hunter *et al.* (1992) found no evidence that EPCs resulted in extra-pair paternity. So the question arises, why do females actively seek EPCs if they never result in extra-pair paternity. There are a number of possible reasons: (1) although Hunter *et al.* (1992) found no evidence for EPCs resulting in offspring, their effective sample size meant a level of extra-pair paternity of less than 4.6% could have gone undetected (95% confidence limits, $n = 85$). Extra-pair behaviour could be maintained in the population if even a low level of extra-pair paternity occurred. (2) Females may seek EPCs as insurance against their partner being infertile (Hatch 1987; Westneat *et al.* 1990), (3) females may use EPCs to promote sperm competition and test their males, or (4) there may be some non-genetic benefit to engaging in EPCs. Perhaps the most likely non-genetic benefit for Northern Fulmars is that by engaging in EPCs, long term extra-pair bonds may be maintained, then if a partner dies there will be an alternative mate to take over (Hatch 1987).

Two main forms of paternity assurance have been identified: mate protection, and frequent copulation (Birkhead & Møller 1992). The most commonly described form of mate protection is mate guarding by close following, in which the male actively maintains close contact with the female throughout her fertile period, following her wherever she goes (Birkhead 1979; Lumpkin *et al.* 1982). This strategy is appropriate for territorial birds (Birkhead *et al.* 1987), who remain in a more or less discrete area throughout the female's fertile period, where copulation can occur anywhere within that area and where the habitat gives rise to opportunities for EPCs (Björklund and Westman 1986). For some species however, resources such as food, water or nesting material may be distant from breeding sites, making it difficult for a male to maintain contact with his female (Frederick 1987; Mineau & Cooke 1979; Werschkul 1982). For species that copulate only at the breeding site, including the majority of seabirds, the pair male can still defend his female from the EPC attempts of other males if he ensures that he is at the colony whenever she is present (Birkhead *et al.* 1985; Hatchwell 1988). This form of mate protection is unlike mate guarding in that the male maintains contact passively, by being at the site of copulation, rather than following the female. Male Northern Fulmars appear to use passive mate defence to protect their paternity.

Møller & Birkhead (1991) have shown that mate guarding and frequent copulation are alternative strategies and that colonial species tend not

to protect their mate but instead rely solely on frequent copulation to ensure their paternity. This stems from the finding that in most colonial species one member of the pair must defend the nest site while the other is foraging so there will be times when the female cannot be guarded and must be left alone (Birkhead *et al.* 1987). Male Northern Fulmars appear to employ both mate defence and frequent copulation to protect their paternity (Hatch 1987; Hunter *et al.* 1992; this study). For Northern Fulmars there is no evidence that nest defence acts as a behavioural constraint, so males can forage at the same time as their partners and be present at the breeding site when their partners are present and available for EPCs. However, it appears that male Northern Fulmars cannot rely solely on passive mate defence to protect paternity as females in the present study engaged in extra-pair copulation attempts despite their male's presence. This may explain why male Northern Fulmars use frequent copulation in addition to mate defence to protect their paternity (Hunter *et al.* 1992). The low incidence of extra-pair paternity in this species would suggest that the use of multiple paternity protection strategies is largely successful.

Females participate in EPCs despite their partner's presence at the colony so the final question remains, why do males bother to attempt to prevent their mates from engaging in EPCs if their attempts are unsuccessful? There are two possible reasons. (1) It may be that mate defence behaviour reduces the overall frequency of EPCs and that only the most persistent or the most opportunistic females can overcome their partner's protective behaviour. (2) Males that are present and aware of their female's EPC attempts may be in a better position to respond to these by increasing their copulation rate.

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SAMENVATTING

Noordse Stormvogels brengen veel tijd door op de broedplaatsen in de maanden voorafgaande aan de eileg. In het hier gepresenteerde onderzoek werd de functie van dit verblijf onderzocht. Verondersteld werd dat de aanwezigheid in de kolonie gunstig zou kunnen zijn voor (1) een effectieve verdediging van de nestplaats (het territorium), (2) de extra mogelijkheden voor copulaties met de partner of met andere individuen op de kolonie (EPCs, *extra pair copulations*), of (3) juist ter verdediging van de partner tegen ongewenste intimiteiten van andere Noordse Stormvogels op de kolonie. Er werden geen aanwijzingen gevonden dat de aanwezigheid een rol speelde bij de verdediging van het nest. De nestplaats bleef vaak langdurig onbezet en kon vervolgens weer gewoon door dezelfde vogels worden ingenomen. Evenmin kon worden geconstateerd dat de aanwezige broedparen zich bijzonder actief bezighielden met copulaties. Er werden wel aanwijzingen verzameld dat de op de kolonie aanwezige

wijfjes zich bezighielden met *extra-pair* copulaties (paringen met niet-partners) en er bestond een positief verband tussen de duur van het verblijf op de kolonie en het aantal paringen met niet-partners. Het blijft mogelijk dat de vogels om andere redenen op de kolonie verbleven en dat de *extra-pair* copulaties niet het doel op zich waren, maar plaatsvonden omdat de vogels daar nu eenmaal zaten. De aanwezigheid van mannetjes op de broedplaatsen leek samen te hangen met hun pogingen om deze 'ontrouw' van de partner te voorkomen. Mannetjes waren gemiddeld veel langduriger aanwezig dan wijfjes en in de (verondersteld) vruchtbare periode van de wijfjes weken zij vrijwel niet van de zijde van de partners.

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