IS MALE UNPREDICTABILITY A PATERNITY ASSURANCE STRATEGY?

by

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Summary

In socially monogamous birds, levels of extra-pair paternity vary widely across species. A possible explanation for this variation is that the costs to both sexes of pursuing extra-pair copulations (EPCs) varies widely, which may substantially depend upon the effectiveness of the paternity assurance tactics employed by pair males. Given the prevalence of extra-pair paternity, an enigma exists in non-mate-guarding species in which males have no apparent means of assuring their paternity and yet rarely or never lose paternity. We propose that males in some species may pursue a subtle but effective paternity assurance tactic consisting of unpredictable behaviour. By departing and returning to and from their mates at unpredictable intervals males may be able to deter other males and their mates from attempting EPCs. Consistent with this idea, we found in the monogamous kittiwake *Rissa tridactyla* that the absences of males became decreasingly predictable in duration as their mates' fertile periods approached. Moreover, the durations of 80% of male absences were shorter than the minimum duration of copulations, creating a high probability of pair males returning in time to prevent EPCs. Factors other than male unpredictability may explain the lack of extra-pair paternity in kittiwakes. Nevertheless, the unpredictable male hypothesis is testable in the many species with variable levels of EPP. Furthermore, we suggest that unpredictability may comprise a general strategy by which animals of both sexes protect various reproductive assets such as food, mates and territories.

Introduction

In socially monogamous birds extra-pair paternity (EPP) is highly variable, ranging from zero to 80% of offspring across species (Petrie & Kempenaers, 1998; Griffith *et al.*, 2002). One potential source of variation is in the costs and opportunities of males and females to pursue EPCs (Birkhead & Møller, 1992; Stutchbury *et al.*, 1997; Stutchbury, 1998) which may substantially depend upon the effectiveness of the paternity assurance tactics employed by pair males. The intense interest in mixed mating strategies of monogamous species has led to the focus on two male tactics to reduce the risk of losing paternity: mate guarding and frequent copulation (Birkhead & Møller, 1992). In many species, males mate-guard by escorting their mates throughout the female's fertile period. Mate-guarding may deter extra-pair males from attempting EPCs (Westneat, 1994; Sundberg, 1994) and may also prevent females from engaging in EPCs, especially when combined with male retaliation (Clutton-Brock & Parker, 1995; Dixon *et al.*, 1994; Valera *et al.*, 2003). In many species, however, such as colonial and courtship feeding species, males are ecologically constrained from mate-guarding by the need to forage away from their fertile mates (Birkhead *et al.*, 1987). An enigma thus exists for species in which males do not mate-guard, do not copulate frequently, and yet obtain almost complete paternity (*e.g.* western gull *Larus occidentalis*, Gilbert *et al.*, 1998; purple sandpiper *Calidris maritima*, Pierce & Lifjeld, 1998; long-eared owl *Asio otus*, Marks *et al.*, 1999; Wilson's storm-petrel *Oceanites oceanicus*, Quillfeldt *et al.*, 2001; capricorn silvereye *Zosterops lateralis chlorocephalus*, Robertson *et al.*, 2001; ringed plover *Charadrius hiaticula*, Wallander *et al.*, 2001; flammulated owl *Otus flammeolus*, Arsenault *et al.*, 2002; burrowing parrots *Cyanoliseus patagonus*, Masello *et al.*, 2002). In these species, males generally provide high levels of parental care and it is assumed that male confidence of paternity and subsequent investment in the offspring may be reduced by witnessing a single extra-pair copulation (Fitch & Shugart, 1984). However, non-mate-guarding males have no clear means of assessing their paternity. Moreover, females may prevent their mates from witnessing EPCs by timing their attempts soon after their partners have departed on often lengthy foraging trips. This leads to the question of whether additional, unidentified paternity assurance tactics exist.

Male kittiwakes must forage outside the colony to provision their mates during the two weeks preceding egg-laying (Neuman *et al.*, 1998; Helfenstein *et al.*, 2003b). During these long foraging trips fertile females are left

unattended in dense colonies containing large numbers of sexually active males. Females were never observed pursuing EPCs in over 25,000 nest-hours of observation of 313 copulations (Helfenstein *et al.*, 2004) and no EPCs were reported in another colour-marked population (Chardine, 1986). These behavioural observations were consistent with our genetic analyses which found no clear cases of extra-pair paternity in 119 offspring (Tirard *et al.*, 2002; Helfenstein *et al.*, 2004). Males did occasionally attempt EPCs with unguarded females and in two cases appeared to achieve insemination, despite apparent female resistance (Helfenstein *et al.*, 2004). However given the apparently abundant opportunities to attempt such potentially successful EPCs, male attempts were rare (six EPC attempts out of 313 copulations, Helfenstein *et al.*, 2004). One possible explanation for the uncommon occurrence of male EPC attempts is the frequency with which intruders are met with aggressive attacks by residents. During multiple years of field observations (Danchin, 1987, 1991; Cadiou, 1993; Danchin *et al.*, 1998; Helfenstein *et al.*, 2003b, 2004) we and our colleagues have observed numerous cases of residents returning to their nests and attacking intruders, resulting in visible injuries (our unpublished data).

While studying the sexual behaviour of kittiwakes (Helfenstein *et al.*, 2003a, b), we noticed that after copulating with or feeding their mates at the nest, males departed but often returned within several minutes. These rapid returns were unexpected because foraging trips between the breeding colony and the ocean feeding grounds tend to be lengthy, often spanning several hours and, indeed, males never returned with food or nest material after these short absences. We hypothesized that males may employ a subtle paternity assurance strategy compatible with the necessity of leaving their mates unattended. By returning to their nests frequently and unpredictably, they may be able to deter neighbouring males and their mates from attempting EPCs.

Our aim in this paper is to propose that a previously undetected paternity assurance tactic may be employed by males in certain species and to use our field study of kittiwakes to suggest ways of examining it. We examine whether the temporal patterns of male kittiwake nest attendance is consistent with the prediction that males behave unpredictably to prevent extra-pair copulations. If males employ a strategy of unpredictability we expect that they: (1) make frequent, short trips during their mates' fertile period but not during other periods of the nesting cycle; (2) make trips of durations

that are less than or equal to the durations of most copulations in order to maximise their chance of disrupting an EPC attempt; (3) are unpredictable in the durations of their absences, and (4) become increasingly unpredictable as females are approaching egg-laying and fertilization. Here we report that these expectations are met and discuss the implications for kittiwake paternity. After the field study was completed, our genetic study revealed a lack of EPP in the population (Helfenstein *et al.*, 2004). This lack of variation therefore prevented us from examining a predicted relationship between paternity and predictability. We suggest however that our findings are useful by proposing the unpredictable male hypothesis and illustrating methods to test it. Additionally, we discuss how animals of both sexes may behave unpredictably as an economical strategy to protect various kinds of resources such as territories, food and mates.

Methods

This work was part of a broader study on the sexual behaviour of kittiwakes (Helfenstein *et al.*, 2003a, b; Wagner *et al.*, 2004) conducted in the colonies of Cap Sizun (Brittany, western France), where more than 15,000 individuals have been colour-ringed since 1979 (Danchin & Monnat, 1992; Danchin *et al.*, 1998; Cam *et al.*, 2002, 2003; Helfenstein *et al.*, 2003a, b). In years 1999, 2000 and 2001, from mid-April to the end of the incubation period (ca. early-June), we observed at one cliff respectively 44, 68 and 85 pairs in which either the male, the female or both mates were colour-ringed. The position of the open, vertical cliff allowed us to observe all the nests from the same observation point, *ca* 30 m away from the opposite cliff. Laying dates were determined by daily inspection of the nests with a telescope. No licences or permissions were required to conduct this study.

Male and female attendance

Male and female attendance at the nest was recorded by daily scanning of the nests every two to three hours (3 to 6 scans per day), in a fixed order. During scans, the presence or absence of the male, female or both was recorded. This method provides a 'snapshot' of which individuals were present on their nests at a given moment. The percentage of time that individuals were in daily attendance at the nest was estimated as the number of times a bird was seen on its nest out of the total number of scans per day.

A daily index of mate-guarding potential was derived from male and female attendance as the amount of time a female was observed on her nest with her mate divided by the total amount of time she was on the nest (alone or with her mate) (Fitch & Shugart, 1984).

In 2001, we recorded male departures and arrivals from and to their nests every other day during observation sessions of 7.5 to 10 hours (from 08:30 to 19:30 hours). Since simultaneous observations of departures and arrivals of different males are difficult, we reduced our sample to 21 central pairs in which both mates were colour-ringed. The time of each departure and arrival of males from or to their nests was recorded to the nearest second. We then

calculated the duration, in seconds, of males' absences from their nests and computed daily time series of absence duration for each male. Daily frequencies of departures from the nest were estimated for each male as the number of trips observed divided by the duration of the observation session.

Copulations

Copulation behaviour was recorded by a second observer in three consecutive years from 1999 to 2001. We focussed on a total of 84 nests where both birds were colour-ringed. Daily observations ranged from 1 to 10 h for a total of 99 h in 1999, 100 h in 2000 and 512 h in 2001, and were made opportunistically throughout the day, from 08:30 hours to 19:30 hours. Copulation frequency did not vary throughout the day (Helfenstein unpublished data). Copulation commenced after the male mounted his mate and ended at the last cloacal contact, and its duration was recorded to the nearest second.

The mean sperm storage duration in birds varies widely (Birkhead & Møller, 1992). As it is the case in wild species generally, the amount of time that female kittiwakes can store sperm is unknown. However, copulation frequency markedly increases between 21 and five days before egg-laying, when it reaches a peak (Helfenstein *et al.*, 2004). We therefore defined the pre-laying period as the period from 20 before egg-laying to the day the last egg was laid (day $+ 2$). We assumed, as in other studies (Birkhead & Møller, 1992), that female kittiwakes became increasingly likely to be fertilized as egg-laying approached.

Time series analyses

We examined the degree to which male absences from their nests were predictable within a day, *i.e.* whether neighbouring males and mates can predict when a male will return. This predictability can be estimated by analyses of daily series of male absence durations (Box & Jenkins, 1976). The derived predictability indexes can be plotted against the date relative to egg-laying to test whether males change the predictability of their behaviour as their mates approach egg-laying and fertilization.

A time series may exhibit different forms of temporal structure, which may be estimated through different statistics (Box & Jenkins, 1976). We thus used two different methods to measure the predictability of the series of absences. We first used the autocorrelation coefficient ρ (Box & Jenkins, 1976) at one time interval $\tau = 1$, for each series. This statistic measures the correlation between the durations of two consecutive absences ($\tau = 1$). It indicates how predictable an absence will be in duration based on the previous one. The smaller the absolute value of the coefficient, the less predictable is an absence compared to the previous one. As an example, let us imagine a series of absences lasting 1 second followed by 100 seconds, 1 second, 100 seconds, and so forth. This series would have a correlation coefficient, at one time interval, of -0.75, meaning it is highly predictable. Note that, for a series of 20 durations, the probability of generating this autocorrelation coefficient by a random process is $p < 0.0001$. Thus, a high absolute value of ρ indicates a high degree of autocorrelation in the series.

We then applied a non-parametric method derived from the runs test for dichotomised data (Sokal & Rohlf, 1995) which is used to test whether binary events occur at random or non-random sequences. This statistic measures the general degree of autocorrelation in a series of events. The method is as follows. For a given series of time durations, starting with the

first value, if the following duration is greater, one notes a plus sign; if the following duration is smaller, one notes a minus sign. The same process is repeated for the whole series until obtaining N-1 signs where N is the size of the series. One then obtains several successions of consecutive '+' or '−', termed runs and denoted r. When the number of runs equals the number of pluses and minuses, each duration in the series is either smaller or greater than the previous one and the series oscillates with a 'period' of one time interval. When there is only one run of either pluses or minuses, the series comprises either continuously increasing or decreasing durations. Between these two extreme values, the number of runs indicates that the series may be generated by a random process (intermediate number of runs) or by a more or less oscillating process (very small or very high number of runs). The general degree of autocorrelation of a given time series depends on the number of runs, the number of pluses and the number of minuses. Using these three values one can compute a variable that is normally distributed (Sokal & Rohlf, 1995) and allows comparison between time series of different sizes. The obtained variable z measures the general degree of autocorrelation of the series: the higher the absolute value of z, the more autocorrelated the series is, *i.e.* the more predictable. Conversely, a low absolute value of z indicates a random, unpredictable time series. To illustrate how this method works, let us take the same example as previously and imagine a series of absence durations of 1 second then 100 seconds, repeated 10 times to have a 20-point series. When a duration goes from 1 to 100 seconds, we code a '+'; when a duration goes from 100 to 1 second we code a '−'. Our example counts ten '+', nine '−' and 19 'runs' of consecutive identical signs. According to the formula provided by Sokal & Rohlf (1995), this gives a z-value of 4.04. Note that, for this highly predictable series the obtained z-value has a $p < 0.0001$ probability of being produced by a random process.

Time series analyses rely on a mimimum series length to allow accurate estimation of autocorrelation. We therefore selected time series comprising at least ten consecutive absences (mean $\pm$ SD size of the time series: 16.86 ± 7.20, range 10-34, $N = 42$ male-series). Recordings of males' trips were made every other day and we thus obtained several series of absence durations per male at different dates relative to egg laying. To avoid pseudoreplication and have a single series per male, we selected the series recorded on the first day of observation for each male.

Results

Male and female nest attendance and mate-guarding potential

The mean $\pm$ SD percentage of time that nests were left unattended during the pre-laying period was only 3.6% $\pm$ 5.2% ($N = 174$ nests). It was necessary for at least one mate to attend the nest to prevent the theft of nest material by neighbours which we found may reduce reproductive success; the mean reproductive success per pair over the three years (*i.e.* the number of offspring fledged, ranging from zero to two) was negatively correlated with the mean percentage of time their nests were left unattended (regression with log-transformed data: $F_{1,124} = 10.34$, $p = 0.002$).

Females spent an increasing percentage of time on their nests as egg-laying approached and as EPCs were more likely to successfully fertilize the eggs (Birkhead & Møller, 1992) (Fig. 1). Female nest attendance peaked in the week before laying when they spent up to 89% of the time on their nests. This period also corresponds to the peak in copulation frequency (Helfenstein *et al.*, 2004) and is likely to correspond with female fertility. In contrast, male nest attendance tended to decline during that period. Mate-guarding potential, estimated as the percentage of time mates were together on their nests, varied between 9.1% and 26.7% (mean $\pm$ SD = 16.4 $\pm$ 4.1%) throughout the pre-laying period. Females spent up to 76.2% (mean $\pm$ SD = 56.2 $\pm$ 12.3%) of the time in the absence of their mates when presumably fertile (Fig. 1).

Copulation duration and male absences

Males' daily frequency of trips significantly increased when egg-laying approached and significantly decreased during the incubation period (Fig. 2) (ANCOVA with quadratic date relative to egg-laying, male identity as a co-variate and log-transformed frequencies: $F_{42,170} = 2, 36, p < 0.0001$; date
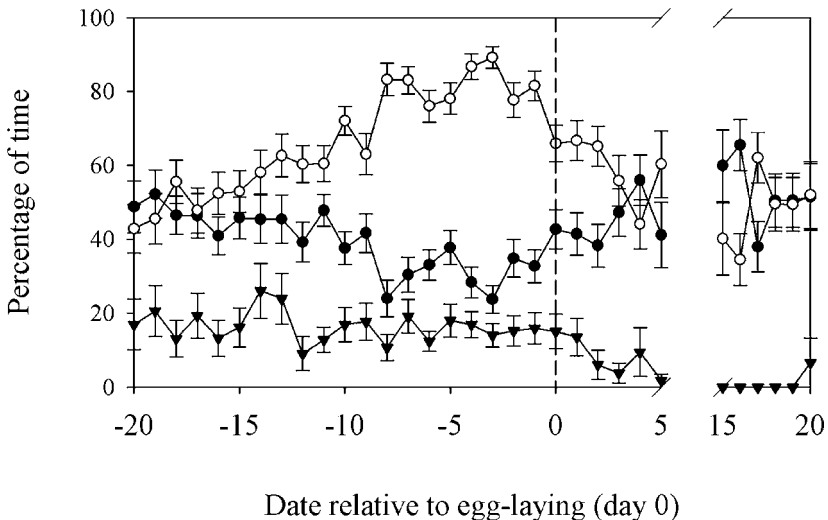

Fig. 1.   The percentage of time males (black circles) and females (open circles) spent at the nest relative to the timing of egg-laying (day 0, verticle dashed line). Mate-guarding potential (black triangles) was estimated as the percentage of time females are on their nests in the presence of their mates.
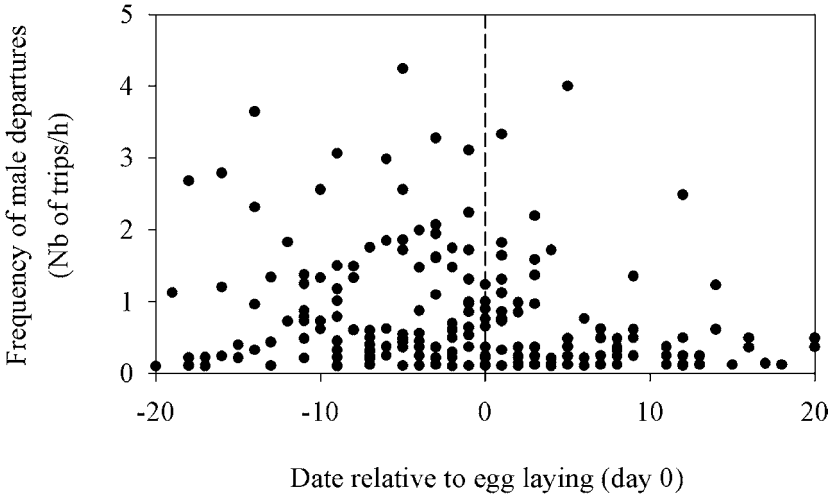
Fig. 2.   The daily frequency of male departures from their nests (number of trips/h) varied according to the date relative to egg-laying (day 0, vertical dashed line).

relative to egg-laying: $F_{1,170} = 17.90$, $p < 0.0001$; squared-date: $F_{1,170} = 20.21$, $p < 0.0001$; male identity: $F_{20,170} = 2.65$, $p = 0.0004$; interaction between male identity and squared-date: $F_{20,170} = 2.19$, $p = 0.004$; all probabilities are two-tailed). The significant interaction between the squared-date and individual males may suggest that all males may not have changed their daily absence frequencies the same way, *i.e.* either they did not make more frequent trips during the pre-laying period or did not decrease the frequency of their absences during incubation.

On average, males were away from their nests (mean $\pm$ SD) 65.9$\pm$28.2% of the time (total absence duration divided by the observation session duration, $N = 147$ individual-days) which was consistent with male attendance pattern estimated by the scan method. Absence durations ranged from 3 to 30,897 seconds (mean $\pm$ SD: 1265.2 $\pm$ 3710.8 s, $N = 845$ departures) with some very long absences of several hours possibly corresponding to lengthy foraging trips (Fig. 3). Very short absences (*e.g.* less than 10 s), during which males might have remained in the sight of their mates and neighbours, represented less than 2%. By contrast, trips lasting 10 seconds to 10 minutes represented 78.5% of their absences.

Although we never observed females seeking EPCs, males occasionally attempted forced EPCs, which comprised less than 1% of all copulations
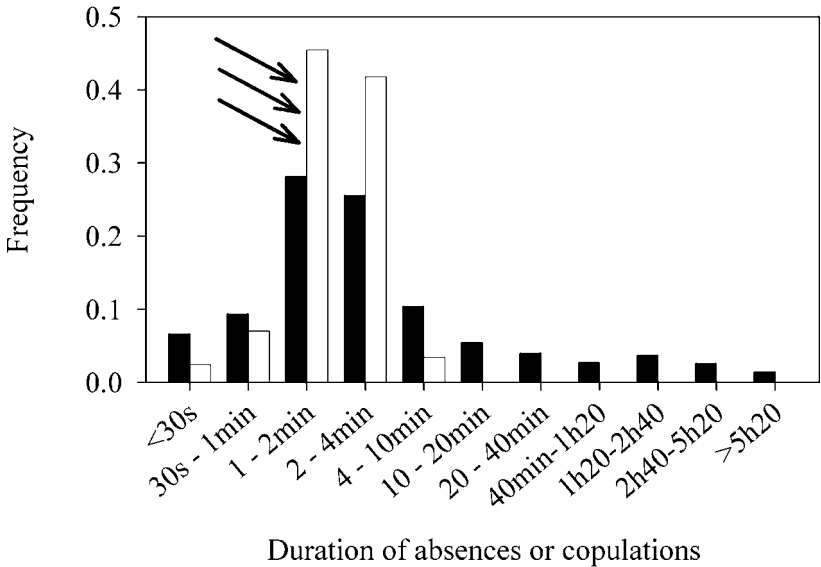
Fig. 3.   Distribution of male absence (black bars) and copulation (white bars) duration. The arrows indicate the durations corresponding to the three extra-pair copulations we timed.

(Helfenstein *et al.*, 2004). Because extra-pair copulations are rare, we were unable to directly compare the durations of EPC and male absences. Instead, we used the minimum amount of time required to achieve insemination during within-pair copulations as an estimate of the minimum duration of an EPC. Because of the position of nest sites on narrow ledges, copulation requires careful balance and coordination by both partners (Danchin & Nelson, 1991). In order to be able to mount and achieve cloacal contact (*i.e.* insemination) males must first position themselves next to the female and then remain balanced on her back. These constraints may help explain the relatively long durations of copulations in kittiwakes and should also exist for extra-pair copulations. To be conservative, we considered the minimum time necessary to achieve insemination, which is the actual mounting minus the pre-copulation sequence. Copulation duration from the mounting to the last cloacal contact lasted from 6 to 436 seconds (mean $\pm$ SD: 117.8 ± 51.9 s, $N = 274$ copulations). We recorded three extra-pair copulations which lasted 85, 93 and 100 seconds, and found that their durations were within the range of within-pair copulation durations (Fig. 3). 80.1% of the durations of male absences corresponded to the copulation duration from the mounting to the last cloacal contact (Fig. 3).

Male unpredictability

We obtained 42 daily series of absence durations for 21 males. However, some series were too short to allow the computation of an autocorrelation index. In addition, to avoid pseudoreplication, we used only the first time series for each male leading to a 13-male sample. The autocorrelation coefficient, which measures the correlation between the duration of two consecutive trips, significantly decreased as egg-laying approached ($F_{1,11} = 6.16$, $p = 0.03$, two-tailed, Fig. 4), indicating that males returned more unpredictably as egg-laying approached. The z-value, which is a measure of the general degree of autocorrelation of the series, decreased with the date relative to egg-laying: $F_{1,11} = 4.41$, $p = 0.06$, two-tailed. This lack of significance may be due to a lack of power in the non-parametric method we used to estimate temporal predictability or to our small sample size. These two methods measure different forms of temporal organisation. In our sample the two measures of predictability were not correlated in a given time series ($F_{1,11} = 1.88$, $p = 0.20$, two-tailed) and the two methods thus provide
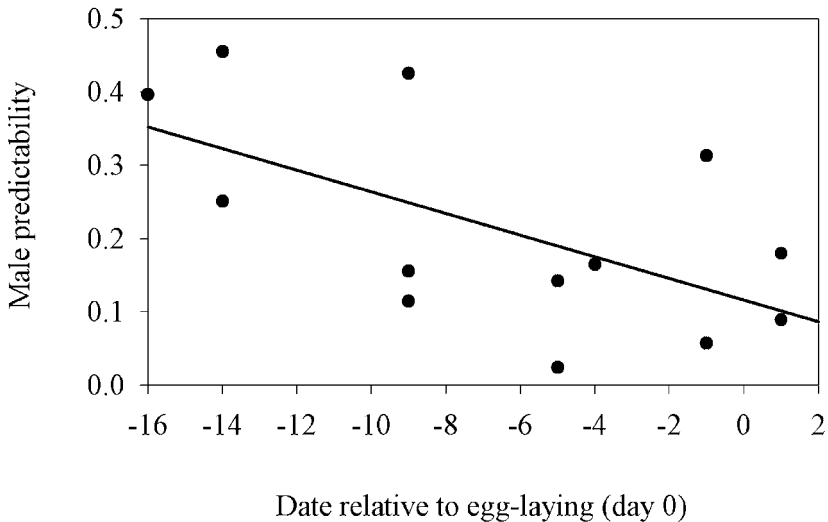

Fig. 4.   Temporal predictability of males' daily series of trips in relation to the relative date (the first egg of the clutch was laid on day 0). The autocorrelation coefficient measures the correlation between the duration of two consecutive trips. The greater this coefficient, the more predictable a male is in the duration of his absences. Each point represents one male's predictability index on a day relative to his mate's egg-laying. No male was used more than once in the analysis.

independent measures of different aspects of the series' temporal structure. Together, these two results suggest that males' reappearances at the nest became increasingly unpredictable as egg-laying approached and when EPCs would have been more likely to achieve fertilization.

Discussion

Colonial and courtship-feeding species are generally unable to guard their mates (Birkhead *et al.*, 1987; Birkhead & Møller, 1992), as we found to be the case in kittiwakes. During their presumed fertile period females were left unattended approximately 70% of the time. Despite the presence in the breeding colony of numerous sexually active males, neighbouring males rarely attempted EPCs during the pair males' absences even though such attempts were occasionally successful (Helfenstein *et al.*, 2004). In a genetic analysis we were unable to detect any cases of extra-pair paternity (Helfenstein *et al.*, 2004). Thus, despite the lack of mate-guarding and a relatively low frequency of within-pair copulations (mean = 0.042 copulation/hour; Helfenstein *et al.*, 2004), male kittiwakes appear to achieve complete paternity. These findings raise the question of how, without apparent paternity guards, male kittiwakes do not suffer paternity losses.

We propose that one factor may be that male kittiwakes employ a previously unrecognised strategy to prevent EPCs. During their mate's fertile period, males make trips of various durations, some of which are very short and do not involve food delivery. The majority of the durations of male absences corresponded to the minimum amount of time that an extra-pair male may need to achieve insemination (*i.e.* from mounting to the last cloacal contact). Hence, males may be able to disrupt extra-pair copulations that would have begun soon after they had departed from their nest. Moreover, by making a number of short non-foraging trips males may disguise the lengths of their absences during longer foraging trips. It may be difficult for an extra-pair male to optimally time his EPC attempts to match the social males' absences if (1) a male does not always leave his nests for long periods, and (2) if, at the moment a male leaves his nest, the duration of his absence is unpredictable.

If male unpredictability is timed according to female fertility we would expect the rate of departures from the nest to increase as laying approached and to decrease after laying, which was the case (Fig. 2). Perhaps more significantly, males returned with decreasing predictability as their mates' likely

fertility peak approached. Male unpredictability may prevent females and neighbouring males from engaging in EPCs because, even if a male departs for a several-hour foraging trip, they can't predit when he will return. Our numerous (unpublished) observations of residents aggressively attacking intruders suggest that the risk of being caught may deter males from attempting EPCs with the unattended mates of their neighbours.

Male trips do not necessarily involve only mate-guarding. Males make regular trips to collect nest material and find food for their mates. However, the fact that all these trips are unpreditable in their durations at the moment the males depart from their nests may discourage EPC attempts. Sexual selection may have shaped male organization and timing of their various activities, such as foraging and nest-building, during their mates' fertile period, selecting against predictable males whose mates may be more likely to be receptive to EPCs.

Overall, our findings are consistent with the idea that male unpredictability is employed as a paternity assurance tactic in kittiwakes. However, due to the lack of variation in EPC and EPP in this species we were unable to falsify the unpredictable male hypothesis in kittiwakes. Doing so would entail examining the unpredictability of individual males against the frequency of EPC attempts with their mates or against their paternity losses. Nevertheless, kittiwakes have stimulated an idea that may be testable in the other numerous species in which EPC and EPP does vary. We propose that it may be fruitful to investigate both intra- and inter-specific variation in male unpredictability as a potential source of variation in EPP.

Given the prevalence of EPP in socially monogamous species, it is interesting to consider why EPP is low or non-existent in some species (Griffith *et al.*, 2002). One possibility is that females in certain species never evolved receptivity to EPCs (Bennett & Owens, 2002). This might be expected in species in which male care is crucial (Møller & Cuervo, 2000; Griffith *et al.*, 2002) such that the costs of EPCs to females are outweighed by the risks of reduced male parental care (Fitch & Shugart, 1984; Xia, 1992; Dixon *et al.*, 1994; Gowaty, 1996; Lifjeld *et al.*, 1998). However, even in some gulls and other long-lived, biparental waterbirds, EPP frequency can be substantial (reviewed in Birkhead *et al.*, 2001; see also the Adélie Penguin *Pygoscelis adeliae*, Pilastro *et al.*, 2001, the waved albatross *Phoebastria irrorata*, Huyvaert *et al.*, 2000, and the shag *Phalacrocorax aristotelis*, Graves *et al.*, 1993), making it interesting to consider why EPP varies widely even in

such species. We expect that male unpredictability varies among species and could therefore be a source of variation in EPP. In species that defend all-purpose territories in open habitat, males can maintain visual surveillance over their mates (*e.g.* Valera *et al.*, 2003) and therefore may lack both the need and ability to pursue a strategy of unpredictability. In contrast, males in many colonial species forage out of visual range of their mates and are thereby able to return at unpredictable intervals. In colonial species with no EPP such as kittiwakes it is possible that male unpredictability is an evolutionarily old trait that has contributed to the low receptivity to EPCs by females. Testing this idea would entail the measurement of male unpredictability in many species and correlating it with EPP and the degree to which females allow or actively pursue extra-pair copulations. Male unpredictability and EPP levels may covary across species, either positively or negatively depending on the ecological context and the existence of other forms of paternity assurance strategies. In such a comparative analysis kittiwakes would represent an extreme case of low EPP and possibly of high unpredictability.

Male unpredictability may be most likely in species like kittiwakes in which males must leave the female unattended to forage and are therefore unable to mate guard. However, even in species without such constraints, mate-guarding is often the best-of-a-bad-job (Kempenaers *et al.*, 1995; Wagner *et al.*, 1996). Male unpredictability therefore may provide an additive benefit to mate guarding, in which case it may occur widely. More generally, unpredictable behaviour in many species may guard against territorial intrusion, thereby lowering the risk of mate switching, brood parasitism or nest-material stealing,

We also suggest performing experiments to determine whether unpredictability effects paternity. For example, one could manipulate male predictability in a songbird in which males sing from various song posts in their territories. Males can be detained and playbacks of their songs broadcast at consistent (predictable) intervals from a rotating set of posts. Another group of males can have their song broadcast randomly (unpredictably) from the same configuration of posts. The intrusion rates of neighbouring males would then be compared to determine whether unpredictable males are more effective in preventing intrusions. Such an experiment can be applied specifically to the question of predictability and paternity, or more generally to whether unpredictablity is an overall strategy of territorial defence. In this

context, it would also be interesting to examine whether females also be-
have unpredictably when it would appear adaptive to do so. For example, fe-
males as well as males suffer from intra-specific brood parasitism (reviewed
in Arnold & Owens, 2002) and other forms of intra-sexual competition. It
would be interesting to examine whether the frequency of female intrusions
covaries with the predictability of female nest attendance.

In summary, our study of kittiwakes stimulated the idea that male unpre-
dictability may be an overlooked paternity assurance tactic in certain species.
This idea can be tested experimentally and by inter-specific comparative
studies. More generally, we suggest that behaving unpredictability may be
a subtle but widespread and effective tactic to defend a variety of resources.

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