

AGGRESSIVE NEST INTRUSIONS BY MALE HUMBOLDT PENGUINS

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SHORT COMMUNICATIONS

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EXTRA-PAIR PATERNITY IN THE COMMON MURRE¹

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Abstract. Multi-locus DNA fingerprinting was used to estimate the frequency of extra-pair paternity in the Common Murre (*Uria aalge*), a colonial, sexually monomorphic seabird that breeds at very high densities and in which extra-pair copulation is frequent. Common Murres produce a single chick. We detected 6 cases of extra-pair paternity in 77 families (7.8%). This value was higher than the proportion of successful extra-pair copulations (1.6%) estimated from behavioral data from an earlier study of the same population.

Key words: *Common Guillemot, Common Murre, extra-pair paternity, sperm competition, Uria aalge.*

The Common Murre (*Uria aalge*; Common Guillemot in Europe) is a colonial, socially monogamous seabird. Common Murres typically breed in physical contact with one or more neighbors at densities of up to 70 pairs m⁻² (Gaston and Jones 1998). The Common Murre was among the first bird species in which routine extra-pair copulation behavior was observed and described (Norrevang 1958). Subsequent studies of this species showed that extra-pair copulations can occur in two ways: they can be either forced on females by males, or more rarely they can be initiated by females (Birkhead et al. 1985, 1987, Hatchwell 1988). Forced extra-pair copulation attempts were much less likely to result in cloacal contact than extra-pair copulations solicited by females, most of which were successful (Hatchwell 1988). In two previous studies, the proportion of all successful copulations that were extra-pair was 2–5% (Birkhead et al. 1985, Hatchwell 1988). Hatchwell (1988) also showed that the likeli-

hood of either a female or a male Common Murre being involved in an extra-pair copulation increased with local breeding density. In addition to breeding at high densities, Common Murres are typical of many marine birds in that they have enduring pair bonds (Gaston and Jones 1998) and biparental care that is essential for successful breeding; each partner takes on an almost equal share of incubation, brooding, and chick-feeding (Gaston and Jones 1998). The levels of extra-pair paternity in bird species where the combined efforts of each parent are essential for chick-rearing are typically rather low (Birkhead and Møller 1996).

The aim of this study was to determine the level of extra-pair paternity of Common Murres at the same colony at which behavioral observations of extra-pair copulation had previously been conducted (Birkhead 1978, Hatchwell 1988).

METHODS

The study was conducted at Skomer Island, Wales (51°45'N, 5°17'W) during three breeding seasons (1996–1998). At a single subcolony known as the Amos, we caught a sample of adult birds and their single chick and individually marked them with Darvic bands engraved with large numbers and a British Trust for Ornithology metal band. From each bird captured, we took a sample of blood for paternity analysis. Blood was stored in 96% ethanol for later analysis. Common Murres do not build a nest and chicks are relatively mobile, so for several successive days after marking chicks we observed them from a distance of 50 m using a telescope in order to match adults with their chicks. Chicks seen with the same adults, or fed by the same adults on two or more days were assumed to be the offspring of those adults. This criterion was necessary because Common Murre chicks are occasionally brooded (but rarely fed) by other adults, re-

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ferred to as alloparents (Birkhead and Nettleship 1984). We obtained data for 42 chicks with both putative parents, and 45 chicks with one parent (35 with the putative father, 10 with the putative mother). In 21 instances, chicks from the same putative male parent were analyzed in successive years (16 in two years, 5 in all three years of the study). Common Murres are sexually monomorphic, and color marked adults were sexed either by observing copulation early in the season, or by molecular methods, as follows.

SEX IDENTIFICATION

Sex identification is based on the amplification of a portion of two sex-linked genes (Griffiths et al. 1998). The first gene is CHD-Z and is located on the Z chromosome (Griffiths and Korn 1997), is common to both sexes (male ZZ; female WZ), and forms a positive control. The second gene, CHD-W, is from the female-specific W chromosome and is used to identify sex. The polymerase chain reaction (PCR) amplification was carried out in a volume of 10 μ l where the final reaction conditions were 50 mM KCl, 10 mM Tris.Cl pH9 (25°C), 1.5 mM MgCl₂, 0.1% Triton X-100, 200 μ M of each dNTP, 1 μ g of each primer, and 0.15 units Taq polymerase (Promega, Madison, Wisconsin). Between 50 and 250 ng of genomic DNA was used as template and the PCR was performed in a Biometra thermal cycler. An initial denaturation step at 94°C for 1 min 30 sec was followed by 30 cycles at 48°C for 45 sec, 72°C for 45 sec, and 94°C for 30 sec. A final cycle of 48°C for 1 min and 72°C for 5 min finished the program. The PCR products were separated by electrophoresis in a 3% agarose gel stained with ethidium bromide. Although this method has been comprehensively tested (Griffiths et al. 1998), we confirmed its specific accuracy by correctly sexing all 20 females and 22 males which we had previously sexed by observation of copulations.

PATERNITY ANALYSES

Five to ten μ g of purified Hae III-digested DNA was loaded on to 20 \times 40 cm 0.8% agarose gels in 1 \times TBE buffer. The gels were electrophoresed at 1.2 V cm⁻¹ for about 40 hr and blotted onto Nfp (Amersham Pharmacia, Uppsala, Sweden) nylon membranes (Burke and Bruford 1987, Bjørnstad and Lifjeld 1997). The minisatellite probe per (Shin et al. 1985) was radioactively labelled with Redivue α dCTP using the Prime-a-Gene labeling kit (Promega). The hybridization procedure followed the Amersham protocol for multilocus probes that is supplied with the membrane. Filters were autoradiographed with one intensifying screen at -80°C for 1-4 days using Kodak BioMax MS film.

Fingerprint profiles were scored by marking each band in the chicks on an acetate overlay with specific colors according to whether there was a matching band in one parent, in both parents, or in neither. Band-sharing was calculated using the following equation (Wetton et al. 1987): $B_s = 2NAB/(NA + NB)$ where NAB corresponds to the number of bands shared by individuals A and B combined; NA and NB denote the number of scored bands in A and B, respectively. This index theoretically ranges between 0 (no bands shared) and 1 (all bands shared) and should be around 0.5 for

first-order relatives. In reality the index is always slightly higher because background band-sharing between unrelated individuals is normally about 0.2 and therefore average band-sharing between first-order relatives can also be expected to be higher than 0.5. We assumed that offspring with three or more novel bands and with band-sharing of 0.3 or less with the putative father were extra-pair offspring (see below). Values presented are means \pm SE.

RESULTS

The mean band-sharing coefficient for social partners, which were assumed to be unrelated individuals, was 0.213 ± 0.014 (maximum = 0.359). The mean band-sharing coefficient for siblings from consecutive years (because clutch and brood-size were one) was 0.643 ± 0.047 (minimum = 0.433).

For the 42 cases where a chick could be compared with both putative parents, the number of novel fragments per offspring showed a discontinuous and bimodal distribution with offspring having either three or fewer, or five or more novel fragments. Twenty-three chicks had at least one novel fragment: 19 had between one and three and 4 had five or more novel bands.

The mutation rate was estimated to be 0.019 (calculated using Westneat's 1990 method), and the probability of scoring a mutated fragment was estimated to be 0.597. Assuming that mutations occur independently of each other, the probability of scoring n novel fragments = p^n ; the probability of scoring five or more novel fragments due to mutation was therefore $P \leq 0.076$.

All offspring ($n = 38$) with up to three novel fragments had a band-sharing coefficient of 0.35 or higher with both putative parents (Fig. 1: mother-offspring mean band-sharing coefficient = 0.59 ± 0.01 , range 0.41-0.76; father-offspring mean band-sharing coefficient = 0.53 ± 0.01 , range 0.358-0.737). We assumed that these chicks were all related to their putative parents. Four offspring with more than three novel fragments shared a similar proportion of bands with their putative mother (mean band-sharing coefficient = 0.627 ± 0.06 , range 0.46-0.70) as those with fewer novel fragments, suggesting that they were related to their social mother. However, band-sharing with the putative father was much lower in this group of four offspring (mean band-sharing coefficient = 0.22 ± 0.04 , range 0.14-0.31; Fig. 1) and similar to the band-sharing coefficient between pair members (above). We therefore assumed that these were extra-pair offspring, genetically unrelated to their social father.

For those cases ($n = 45$) where only one of the putative parents was known, band-sharing coefficients were used to assign parentage. Where parentage could be assigned with certainty (complete families with ≤ 3 novel fragments), the lowest recorded band-sharing coefficient was 0.358 ($n = 38$). We therefore defined chick-parent band-sharing values of below 0.35 as mismatched parentage. In all 10 cases where we established the degree of band-sharing between offspring and the putative mother, the values were above this limit. Of the 35 cases where offspring were compared with putative fathers, there were 2 (band-sharing co-

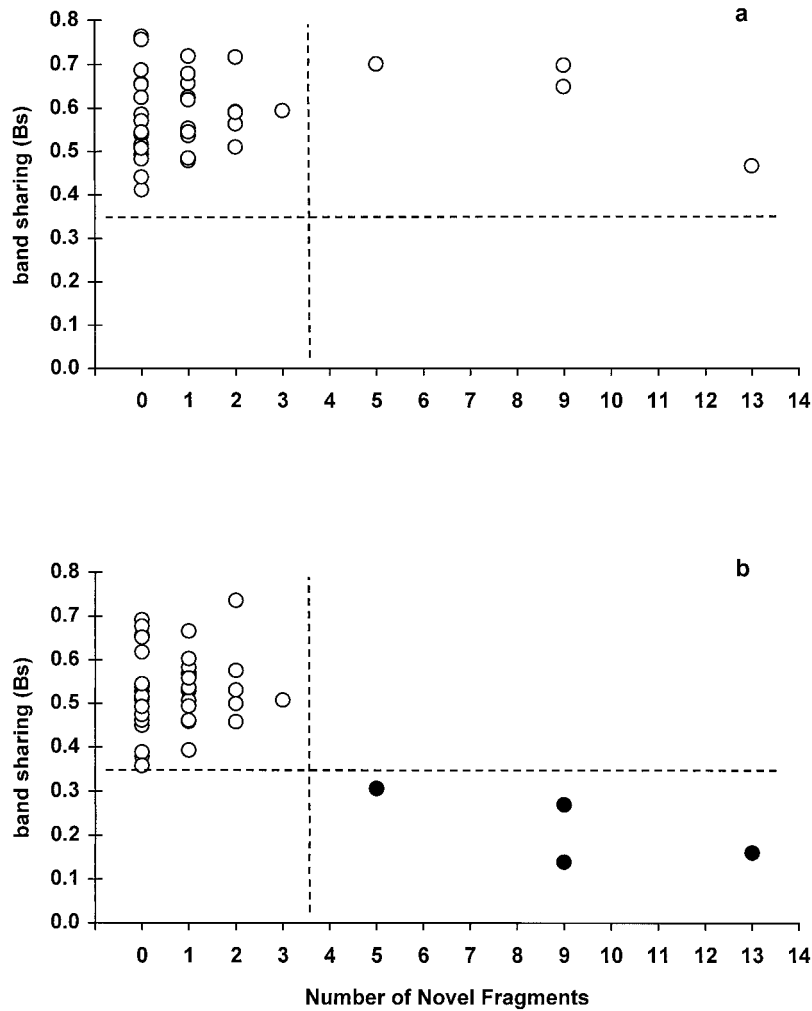


FIGURE 1. Relationship between the number of novel fragments and band-sharing coefficients with (a) the social mother and (b) the social father. The dashed lines indicate the criteria for excluding parentage, and solid circles indicate cases where parentage was excluded.

efficients of 0.25) where the band-sharing coefficient was lower than 0.35, which we also considered to be cases of extra-pair paternity.

In all 52 cases where genetic relatedness of putative mothers and offspring was assessed (42 cases with both putative parents and 10 with putative mothers only), the genetic and social parentage matched. Of the total of 77 cases where paternity was analyzed, we found 6 (7.8%) instances where the social father did not match the genetic father. The 95% confidence interval on this estimate was 1.1–19.3% (Rohlf and Sokal 1981).

DISCUSSION

The level of extra-pair paternity in the Common Murre on Skomer Island, 7.8%, is similar to the values reported for several other socially monogamous marine

birds (Table 1). These results are consistent with an emerging pattern suggesting that extra-pair paternity is generally much lower in seabirds and other non-passerines than in passerine birds (Westneat and Sherman 1997).

The extra-pair offspring in the Common Murre could arise from either forced or unforced extra-pair copulations, that is, extra-pair copulations solicited by females. Hatchwell (1988) showed that during the presumed fertile period, 89.5% of 1,316 copulation attempts were pair copulations, whereas 9.9% were forced extra-pair copulations, and 0.6% were unforced extra-pair copulations. The proportions of these that appeared to be successful (resulted in cloacal contact, and we presume, insemination) were 80%, 6%, and 100%, respectively. Therefore, of every 100 successful copulations, 98.4 are likely to be successful pair cop-

TABLE 1. Levels of extra-pair paternity (% EPP) in seabirds. Confidence intervals are calculated from sample sizes (n = number of families) following Rohlf and Sokal (1981).

Species	%EPP (n)	95% CI	Reference
Humbolt Penguin <i>Spheniscus humboldti</i>	0 (49)	0–15.5	Schwartz et al. (1999)
Northern Fulmar <i>Fulmarus glacialis</i>	0 (85)	0–4.6	Hunter et al. (1992)
Short-tailed Shearwater <i>Puffinus tenuirostris</i>	11 (83)	5.3–19.7	Austin and Parkin (1996)
Leach's Storm-petrel <i>Oceanodroma leucorhoa</i>	0 (48)	?	Mauck et al. (1995)
Shag <i>Phalacrocorax aristotelis</i>	18 (28)	7.7–45.6	Graves et al. (1992)
Brown Skua <i>Catharacta lonnbergi</i>	0 (45)	0–14.2	Millar et al. (1994)
Common Gull <i>Larus canus</i>	5 (55)	0.6–13.0	Bukacinska et al. (1998)
Western Gull <i>Larus occidentalis</i>	0 (33)	0–10.4	Gilbert et al. (1998)
Common Murre <i>Uria aalge</i>	8 (77)	1.1–19.3	This study

ulations and just 1.6 successful extra-pair copulations. We found that 7.8% of all offspring were extra-pair, suggesting that extra-pair copulations were disproportionately successful. However, the confidence intervals on our estimate of extra-pair paternity are such that the apparent disparity between incidence of extra-pair copulations and extra-pair paternity must be treated with caution. If the disparity is genuine, there are two explanations. First, although there was no significant difference in the overall timing of pair copulations and extra-pair copulations relative to the day of egg-laying (Hatchwell 1988), forced extra-pair copulations did appear to be better timed (Colegrave et al. 1995), occurring significantly closer to egg-laying and hence ovulation (day -9.13 ± 1.5 , $n = 8$) than unforced extra-pair copulations (day -16.00 ± 2.3 , $n = 8$; Mann-Whitney U -test, $P = 0.04$). Second, because males that forced extra-pair copulations tended to be those whose partners were absent from the colony (Hatchwell 1988), they may have had fewer recent pair copulations and hence inseminated more sperm than paired males (Birkhead et al. 1995). However, a critical test of the relative success of forced and unforced extra-pair copulations would require considerably larger sample sizes than we obtained in the present study.

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AGGRESSIVE NEST INTRUSIONS BY MALE HUMBOLDT PENGUINS¹

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Abstract. During observations at a breeding colony of Humboldt Penguins (*Spheniscus humboldti*), we noted five male penguins enter nests occupied by breeding pairs and engage in aggressive interactions with the resident adult. These nest intrusions resulted in egg loss or infanticide, and accounted for 11.1% of breeding failure in the colony. Two intruder males ultimately mated with respective resident females. This

behavior had not been observed previously in Humboldt Penguins and we suggest that it may occur when males are unable to obtain mates through advertising at the nest. Intrusion behavior may slow down population recovery in this endangered species.

Key words: *Humboldt Penguin, infanticide, mate usurpation, mating strategy, skewed sex ratio, Spheniscus humboldti.*

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Resumen. Durante observaciones a una colonia de Pingüinos de Humboldt, observamos cinco pingüinos machos entrar a nidos ya ocupados por parejas repro-

ductivas e interactuar agresivamente con los adultos residentes. Estas intrusiones a los nidos resultaron en la pérdida de huevos e infanticidio, y explicó 11.1% del fracaso reproductivo de la colonia. Dos machos intrusos formaron pareja con las respectivas hembras residentes. Este comportamiento no había sido observado antes en el Pinguino de Humboldt. Nosotros sugerimos que dicho comportamiento ocurre cuando los machos no logran atraer hembras a sus nidos. Este comportamiento de intrusión podría retardar la recuperación de esta especie en peligro de extinción.

Pair formation in long-lived, monogamous bird species can result in long term partnerships (Black 1996). However, pair bonds may be broken for a variety of reasons including asynchronous arrival at the breeding site, the availability of higher quality habitats or mates, mate death, and breeding failure (Black 1996, Dhondt et al. 1996). Pair bonds also may be broken when a single individual usurps a paired bird (Ens et al. 1996). Usurpation occurs in a variety of species including Mute Swans *Cygnus olor* (Minton 1968), African Black Ducks *Anas sparsa* (Ball et al. 1978), House Wrens *Troglodytes aedon* (Freed 1987), and Oystercatchers *Haematopus ostralegus* (Ens et al. 1993), and can be an important mechanism for mate change (Williams and McKinney 1996).

Here we describe five nest intrusions by unpaired, male Humboldt Penguins (*Spheniscus humboldti*) that resulted in two mate changes and one case of infanticide. We suggest that intrusion behavior is a usurpation strategy used to gain mates when nest advertisement is ineffective.

METHODS

The information for this study was collected during a larger study on parental investment in Humboldt Penguins at Punta San Juan, Peru (15°22'S, 75°12'W), between 21 May and 24 November 1999. The study colony consisted of 120 nests including 78 surface and 10 burrow nests excavated in guano, 9 crevice nests, and 23 artificial nests. Eggs were laid in 11 surface nests, 7 burrow nests, 2 crevice nests, and 2 artificial nests. Three pairs nested twice, one pair in a surface nest, the other two in burrows. From May to November, there was a total of 22 pairs that laid eggs at the colony, a total of 14 single males advertising at nests, and 4 single females that each eventually mated with one of the single males. Ten single males remained unmated. On average, 36 adults (range = 15–57) were present in the colony daily. This count included one or both members of breeding pairs (\bar{x} = 31, range = 11–50), single males (\bar{x} = 5, range 1–11), and transient females. We do not have a count for transient females because they were often passing through the colony investigating the males and/or their nests.

We conducted continuous daily observations between 06:00–18:00 from a study blind located approximately 30 m from an edge of the colony. Observations made for our larger study included identification and duration of attendance of individuals at the colony, 1-hr focal observations of all residents (individuals present in the colony for at least two weeks), and the number and fate of eggs laid by each pair. We identi-

fied individuals based on the unique spotting patterns on their breast (Scholten 1989). Birds were considered to be paired if all three of the following were observed: the pairs engaged in mutual vocalizations (Schwartz et al. 1999), copulated, and were present at a nest together for at least two weeks. These observations allowed us to assess individuals' status and reproductive success.

During observations for our study, we also noticed and recorded interactions between resident pairs and males that were apparently unpaired, which we referred to as intruder males. We noted whether aggressive physical contact, including biting, pecking, and flipper slapping occurred between the intruder male and the resident male or female. We also noted whether any mutual vocalizations, flipper patting, bowing, head quivering or copulation occurred between the intruder male and the resident female. Periods of aggression separated by at least 1 min without physical contact were considered separate bouts. We also recorded the number of eggs broken or taken by gulls during interactions between the intruder male and resident adult and the number of chicks harassed (i.e., pecked, bitten, or shaken) or killed by intruder males. We considered an intruder male to be successful if he displaced the original male or mated with the resident female (criteria for pairs listed above).

Humboldt Penguins lay 1–2 eggs, so in burrow and crevice nests in which we could not see eggs or chicks from the blind (n = 4 nests), we assumed that the pair had 1 egg in order to conservatively calculate mortality due to intruder males.

RESULTS

In 2,256 hr of observation, we observed five intruder males enter the nests of five breeding pairs. Two of these five intruders ultimately paired with the resident female. The two successful males were unpaired colony residents at nests adjacent (<0.5 m) to the breeding pair. The other three intruders were unidentified males that were either unsuccessful in displacing the resident male during aggressive interactions or left before the resident male returned. In all intrusions, the females were initially alone when intruder males approached their nests. Females initially reacted aggressively to intruder males and resisted copulation attempts. Intrusions occurred at three surface nests and two burrow nests. Both successful intrusions occurred at surface nests.

In one of the successful intrusions, the intruder male entered the nest after the resident male had been absent for five days (the resident male never returned to the colony). The intruder male killed the chick and remained with the female during the remaining two months of observations. During this time the resident female and the intruder male engaged in pair behavior including flipper patting, mutual vocalizations, bowing, and head quivering.

In the second case, the intruder male entered the nest twice. The first time, the female was present and engaged in an aggressive interaction with the intruder male including biting, pecking, and flipper slapping. These interactions resulted in peck wounds to the female's face. Immediately following this interaction, the

intruder male remained within 0.5 m of the nest, made display calls, and attempted to copulate with the female. Two days later, the intruder male again entered the nest when the female was present. The resident male returned to the nest 20 min following the intrusion and engaged in three bouts of pecking, biting, and flipper slapping (bout length: \bar{x} = 5 min, range = 4–6 min) with the intruder over the next 2 hr 43 min. During these interactions, the resident male re-opened a flipper wound he sustained 13 days earlier, bled profusely, and then left the nest following the third bout. The resident male was not observed in the colony for the next three months but returned in the fourth month with a flipper deformation at the wound site. Throughout the second intrusion, the female engaged in mutual vocalizations, bowing, and head-quivering with the intruder male only. After the intrusion, the female stayed in the nest with the intruder male and fed the two chicks until they fledged 28 and 36 days later. The intruder male pecked and bit the resident chicks and demonstrated no parental care. Following fledging of the chicks, the female copulated with the intruder male and laid eggs.

At the time of the intrusions, two nests contained two eggs each and three nests contained chicks. The three nests with chicks contained one chick aged 13 days, one chick aged 19 days, and two chicks aged 41 and 44 days. Four chicks ultimately fledged from nests where intrusions occurred. Three eggs and one chick were destroyed during interactions between intruder males and residents. One egg was broken incidentally during an aggressive interaction between the female and intruder male, and the other two eggs were carried off by Band-tailed Gulls (*Larus belcheri*) during interactions with intruder males. All chicks exposed to intruder males were pecked, shaken and periodically driven from the nest by the intruder where they experienced similar harassment from neighboring penguins. When an intruder was present in the nest without the female, the chicks did not vocalize. Harassment by the intruder male appeared to occur haphazardly. The chick that died (19 days old) was killed by two shakes and five pecks from the intruder male.

Total colony mortality was calculated by dividing the total number of eggs and chicks that did not survive by the total number of eggs laid. Total colony mortality was 58.3% (21/36). Mortality caused by intruder males was calculated by dividing the number of eggs and chicks destroyed during intrusions by the total number of eggs laid. The loss of eggs and chicks due to intruder males represented 11.1% (4/36) of the total mortality in the colony.

DISCUSSION

We observed five intrusions in our study colony and consider them to be a type of usurpation behavior used to acquire mates. Usurpation has not been observed in Humboldt Penguins despite intensive observations (Schwartz et al. 1999; M. Schwartz, pers. comm.). Furthermore, incidents of usurpation have not been previously reported in penguins (Williams 1996), so to our knowledge, this is the first report of mate usurpation behavior in this group.

The two successful intruders were residents in the

colony and had been unpaired until the time of the intrusion. We assume that the other three intruder males also were unpaired, however, their identities were not confirmed so their status is unknown. It is possible in these cases that the males were paired and simply seeking extra-pair copulations. We consider this unlikely because the females they approached had eggs or chicks and were probably not reproductively receptive. Furthermore, males approached females in our observations, whereas in most reported cases of extra-pair copulations in Humboldt Penguins females approached males (Schwartz et al. 1999).

Overall, the number of intrusions by single males was low, which may have been a function of the risks associated with this strategy. The aggressive interactions that occurred following intrusions resulted in injuries to both males and females. Despite the potential risks of intrusions, males that fail to obtain a mate by advertising at a nest could experience complete breeding failure in the absence of intrusions. Moreover, because of high mate retention in penguins, a successful intruder may obtain a mate for several years. It is interesting that the two successful intruder males originally occupied nests adjacent to the ones they usurped. Intrusions may be more successful if single males are able to gauge their probability of success by assessing the condition of a paired male or the probability that a female has lost her mate.

It is not clear why this behavior has not been observed previously in Humboldt Penguins at Punta San Juan. One possible reason is that the extreme El Niño of 1997–1998 disrupted existing pair bonds through mate death or emigration. Approximately 75% of the penguins in this colony failed to return to Punta San Juan in 1999 following El Niño (P. Majluf, pers. comm.). Thus, it is likely that many pair bonds were broken and that males used usurpation to replace an absent partner. In Blue Ducks (*Hymenolaimus macrorhynchos*), territorial males who lose their mates usurp neighboring males to replace their partner (Williams and McKinney 1996). Moreover, usurpation in response to mate loss appears to be the most common reason for mate change in this species (Williams and McKinney 1996).

El Niño may also have created or exacerbated a male-biased sex ratio, which could also lead to usurpation behavior. Although a male-biased sex ratio may be typical for Humboldt Penguins (as in several penguin species, Davis and Speirs 1990), information from closely related Galápagos Penguins (*Spheniscus mendiculus*) suggests that female mortality was higher than male mortality during El Niño years (Boersma 1998). A surplus of males may have created competitive conditions so that males unable to obtain females through nest advertisement used aggressive mate usurpation and infanticide to acquire a mate.

One of the effects of intruder males was to reduce colony productivity by 11.1% through egg breakage, infanticide, and gull depredation during fights. This loss may be important for Humboldt Penguins, which are listed as threatened by the IUCN and endangered by CITES. Recently, the IUCN conducted a population viability analysis for Humboldt Penguins, and the probability of extinction was modeled using data in-

cluding reproductive success (Cheney 1998). However, reproductive success may be less than predicted following El Niño events if single males respond with mate usurpation. Slower population recovery as a result of skewed sex ratios has been recognized as having important conservation implications. In endangered Hawaiian monk seals (*Monachus schauinslandi*), for instance, skewed sex ratios are associated with "mobbing" behavior in which several males attempt to copulate with a single female or subadults of either sex. This behavior results in severe injuries and deaths and appears to retard population growth (Gilmartin and Eberhardt 1995, Starfield et al. 1995).

Nest intrusions by male Humboldt Penguins appear to be rare. We suggest that future observations be made at larger breeding colonies where it may be more likely to observe a larger number of these aggressive interactions.

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