

## SEX DIFFERENCES IN REPRODUCTIVE BEHAVIOR OF ATLANTIC PUFFINS<sup>1</sup>

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**Abstract.** Female Atlantic Puffins (*Fratercula arctica*) incubated eggs longer and fed chicks more often than males, whereas males spent more time maintaining and defending the nesting burrow. Although time together was greatest during the pre-laying period, pair members were apart most of the time, suggesting limited mate guarding. Males attempt extra-pair copulations, but because copulations occurred on the water where females can dive to escape, copulations were never forced and may have been successful only between mates. These data suggest that the paired female's ability and willingness to prevent mating with additional males may be important in the evolution of mate guarding. Sex differences in time budgets and male mating attempts were consistent with suggestions that even with shared parental care in monogamous species, females invest more in direct care of the young (parental effort), while males invest more in territorial defense and attempted extra matings (mating effort).

**Key words:** Atlantic Puffin; parental investment; monogamy; extra-pair copulation; *Fratercula arctica*.

### INTRODUCTION

Males and females often differ in the extent to which reproductive effort is channeled into parental effort and mating effort. Parental effort involves investment in particular offspring; mating effort involves the securing of both mates and resources to attract mates (Low 1978), including territorial maintenance and securing extra-pair copulations (EPCs). Particularly in monogamous seabirds, male investment in procuring and defending a territory, gathering nest material, feeding the female, as well as parental effort, may make total reproductive effort nearly equivalent to that of females. Although the sexes may provide equal investment, they may differ in the degree to which they engage in specific activities (Montevocchi and Porter 1980, Burger 1981). This paper documents time budgets for male and female Atlantic Puffins (*Fratercula arctica*) from pre-laying through chick feeding, and examines whether males invest less than females in direct parental effort, while investing more in mating effort.

Atlantic Puffins are long lived, sexually monomorphic seabirds. They are one of the 22 species of the family Alcidae, a group primarily restrict-

ed to the oceanic regions of the Northern Hemisphere. Atlantic Puffins usually breed colonially on offshore islands, and their nest-site consists of a burrow or crevice in the rocks. Birds first breed at 4-5 years and they have a single-egg clutch. Puffins typically show high levels of mate and burrow fidelity (Harris 1984, Taylor 1984).

The requirements for biparental care have probably been an important determinant of monogamy in colonial seabirds such as the Atlantic Puffin (Montevocchi and Porter 1980, Wittenberger and Tilson 1980). The seabird species that rear only a single young per year apparently do so because, on average, that is the maximum production that can be maintained (Lack 1968). Atlantic Puffin chicks had higher mortality and slower growth when they were fed by only one parent (Harris 1978). Similarly in other seabirds with one-egg clutches, twinning experiments indicate that pairs cannot usually raise more than one chick (reviewed in Wittenberger and Tilson 1980).

An important factor related to the evolution of monogamy is the degree to which males can monopolize females (Emlen and Oring 1977). Given that burrow defense and maintenance result in males only being able to have one mate, females should be able to accurately assess male mating status by the absence of another female and egg at the burrow. Therefore males can only increase reproductive success during the pre-laying period by adopting a "mixed" reproductive

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strategy of a monogamous pairing while also attempting to gain extra pair copulations (Trivers 1972). Extra pair copulations (EPCs) have been observed in a number of supposedly monogamous species of birds (Gladstone 1979, Birkhead et al. 1985).

EPCs and male mating tactics have been documented in another alcid, the Common Murre (*Uria aalge*, Birkhead et al. 1985). Common Murres show high frequencies of extra pair copulations: males mounted all females returning to the colony in the week before egg-laying. In most cases (85%), copulations were forced (FEPCs), and frequently several males attempted to mount a returning female. All copulations occurred on cliff ledges where females were usually unable to escape from the males. Males spent most of their time on the ledges in the period just before their mates laid eggs, and they attempted to defend their mates from other males. Females arriving when their mates were absent were significantly more likely to be subjected to FEPCs. Puffins and murres feed at similar distances from these breeding colonies (Schneider et al. 1990). With similar foraging ranges, the two species should not differ in time available for being in the colony. Therefore, we examined whether the behavioral profile of frequent FEPCs, mate guarding, and males attempting to repel competitors also occurs in Atlantic Puffins.

#### STUDY SITE AND MATERIALS

We observed Atlantic Puffins on Gull Island, Witless Bay Seabird Sanctuary, Newfoundland (47°15'N, 52°46'W). The island is densely wooded with the exception of open grassy areas along the perimeter where Atlantic Puffins nest. The study site was 40 m<sup>2</sup> of grass-hummocks, sloping at 28°. Time budgets were derived from sixteen pairs of color-banded puffins observed from a blind located 8 m from the nearest study burrow. Birds were also banded with Canadian Wildlife Service bands.

Birds were sexed using both morphological and behavioral differences. Copulation in puffins generally occurs on the water, making observations of this behaviour a difficult means of sexing banded birds. Instead we observed which bird performed the male pre-copulatory display on the slope. This display consists of a distinctive head-flick and wing-flutter directed towards another individual, presumably a female (Taylor 1984).

Male Atlantic Puffins have, on average, significantly larger and deeper bills than females (Corkhill 1972), and these differences have been successfully used to sex birds (Harris 1979). We measured culmen length, depth, and gape on 112 puffins that had drowned in fishing gear near the colony and had been sexed by dissection. These data were used to calculate a discriminant function, which was then used to sex study birds from which the same three bill measurements had been taken.

Fourteen of the 16 study pairs were sexed from observations of the pre-copulatory display. Discriminant function predictions were in accordance with these observations in all but one case (27/28 individuals correct), where both individuals were predicted to be female, and in this case birds were sexed behaviorally. For the remaining two pairs, birds were sexed using the discriminant function. In these last two cases the discriminant scores and probability levels allowed us to determine which birds were the males and females in the two pairs (probability of accurate assignment: pair 1; female .83, male .95; pair 2; female .72, male .93).

Dawn-to-dusk watches were conducted between 18 May and 14 September 1985 for a total of 960 observation hours. Prior to chick hatching, watches were generally made on two to three consecutive days followed by a one to two day break; thereafter, watches were made on one to two consecutive days followed by a one- to two-day break. The burrows were close enough together that all burrows could be observed at the same time. We recorded the following data: (1) The time of each arrival and departure of marked birds from the slope, and their entrance to, and exit from, burrows were noted. These observations were used to compute total time (hr) that each bird spent, either alone or with its mate, on the slope near the burrow entrance, in the burrow, and away for each breeding stage. (2) Burrow-maintenance activities, such as digging and carrying nest material, were recorded throughout pre-laying and incubation. (3) Aggressive interactions, which usually resulted from a bird wandering near another's burrow. The burrow owner chased and/or attacked the intruder, who occasionally retaliated, resulting in a fight. (4) The times of food deliveries, the species and length of fish, and meal size (the number of fish per trip) were recorded. Fish length was estimated by comparison of the fish with the depth of the bird's

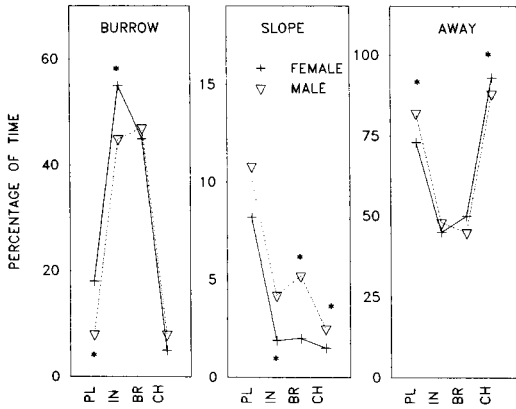


FIGURE 1. Percent time in burrow (1a, left), on the slope (1b, middle), and away from the colony (1c, right) for male and female puffins during pre-laying (PL), incubation (IN), brooding (BR), and chick rearing (CH). \* indicates sex differences,  $P < 0.05$ .

bill. (5) Mate and burrow site changes among study birds were recorded for 1985 and 1986.

Burrow maintenance activities and aggressive behavior were quantified in terms of frequency, as well as rate per unit time that the bird was on the slope.

Thirty ten-minute watches were also conducted (three per observation day) on unmarked birds on the water near the colony to observe the frequency and success of attempted EPCs. During the ten-minute watches a total of 56 males were observed attempting to copulate on the water. Males were identified by head-flicking and wing-fluttering displays directed at other birds, indicating soliciting behavior (Taylor 1984). The lack of proximity to other puffins made it clear which bird was the recipient of the courting behavior. We recorded the number of birds solicited, numbers of attempts to mount by the male, and numbers of apparently successful copulations (i.e., those in which the female did not dive or swim away, and were long enough for cloacal contact to have occurred).

The breeding season was divided into the following four stages for analyses:

(1) Pre-laying period ranged from five to ten observation days depending on the time of egg-laying in individual burrows ( $n = 14$  pairs). Because puffins are extremely sensitive to human disturbance during the pre-laying period (Lockley 1934, Ashcroft 1979), egg-laying dates were estimated by subtracting 41 days from hatching

dates. Incubation ranges from 39–43 days (Harris 1984) so estimates of laying dates are accurate within  $\pm 2$  days,

(2) Incubation was the period from egg-laying to chick-hatching ( $n = 14$  pairs). Hatching date was counted as the date of the first arrival of a parent with fish to the burrow less one day, as the chick is often not fed during its first day (Harris 1984),

(3) Brooding period varied in length among pairs ( $\bar{x} \pm SE = 8.17 \pm 0.78$  days, range = 4–12,  $n = 12$  pairs), and was defined as the period from chick-hatching until chicks were present alone in the burrow for more than 50% of total time. Sample size was reduced because one pair lost its egg just prior to hatching, and one lost its chick just after hatching,

(4) Chick-rearing was the period from the end of brooding to the departure of chicks ( $n = 13$  pairs). One pair failed at the start of this stage, and two new pairs were added.

Comparisons of sex differences in reproductive effort within each breeding stage were made using the Wilcoxon matched-pairs signed-ranked test ( $Z$ ). The Friedman two-way test ( $\chi^2$ ) was used to test for changes in mate relationships across the breeding season, that is in time spent together, and departures and arrivals together ( $\chi^2$ ). Percentage data, the change in sample size across breeding stages, and the non-independence of male and female activities prevented analysis with repeated measures ANOVA.

## RESULTS

### SEX DIFFERENCES IN TIME ALLOCATION

Overall, females spent 33% of their time in the burrow, 2% on the slope, and 65% away from the colony. Males spent 31% of their time in the burrow, 4% on the slope, and the remaining 66% of their time away.

Time in the burrow was greatest for both sexes during incubation and brooding, and lowest during pre-laying (Fig. 1, left). Females were present in the burrow significantly more than males during pre-laying (Wilcoxon  $Z = -2.51$ ,  $n = 14$ ,  $P < 0.05$ ) and incubation (Wilcoxon  $Z = -2.35$ ,  $n = 14$ ,  $P < 0.05$ ), whereas throughout brooding and chick-rearing there were no sex differences in time in the burrow.

For both sexes, time on the slope was greatest during pre-laying, and it decreased thereafter (Fig. 1, middle). Males spent significantly more time

TABLE 1. Total frequency, mean frequency per pair ( $\pm$ SE), and mean rate per hr on slope ( $\pm$ SE) of burrow maintenance activities and aggressive interactions for 14 pairs.

	Burrow maintenance		Aggressive interactions	
	Females	Males	Females	Males
Total frequency	248	412	33	123
Mean frequency	17.7 $\pm$ 2.3	29.4 $\pm$ 3.2	2.4 $\pm$ 0.7	8.8 $\pm$ 1.4
Rate	1.9 $\pm$ 0.3	1.2 $\pm$ 0.2	0.14 $\pm$ 0.04	0.23 $\pm$ 0.04

on the slope than females during incubation ( $Z = -3.23$ ,  $n = 14$ ,  $P < 0.01$ ), brooding ( $Z = -2.98$ ,  $n = 12$ ,  $P < 0.01$ ), and chick-rearing ( $Z = -3.04$ ,  $n = 13$ ,  $P < 0.01$ ), but there was no significant difference during the pre-laying period.

During pre-laying and chick-rearing both sexes spent the majority of time away (73% and 92%, respectively Fig. 1, right), whereas during incubation, time was almost equally divided between time away and time in the burrow (46% and 51%, respectively). Males spent more time away from the colony during pre-laying than females ( $Z = -2.48$ ,  $n = 14$ ,  $P < 0.05$ ), whereas females spent significantly more time away during chick-rearing ( $Z = -2.34$ ,  $n = 13$ ,  $P < 0.05$ ). Throughout incubation and brooding there were no sex differences in time away.

#### BEHAVIORAL DIFFERENCES IN BURROW MAINTENANCE AND CHICK FEEDING

Males performed more bouts of burrow-maintenance activity during the pre-laying and incubation stages than females ( $Z = -2.55$ ,  $n = 14$ ,  $P < 0.05$ , Table 1). However, there were no significant sex differences in the rate (number/hr

on the slope). Males were involved in a higher number of aggressive interactions throughout the breeding season than were females ( $Z = -3.3$ ,  $n = 12$ ,  $P < 0.001$ ), but again there were no significant sex differences in the rate of aggressive interactions (Table 1).

Females delivered more meals per season than did males ( $Z = -2.13$ ,  $n = 13$ ,  $P < 0.05$ ) in all pairs in the study sample (Table 2). Of the 1,488 meals delivered, females were responsible for 57% of the meals delivered per day, whereas males were responsible for 43%. Of the 1,689 individual fish delivered, females and males delivered 56% and 44%, respectively. Capelin (*Mallotus villosus*) were the commonest prey (1,029 out of 1,689 fish, 61%). There were no sex differences in the mean number of fish per meal delivered, the mean length of fish, or the number of capelin per total number of fish (Table 2). This suggests that no sex differences occurred in the method of fishing or quality of fish meals delivered to chicks. The high number of unidentified fish species (19% for both sexes, see Table 2) was due to birds entering burrows rapidly, presumably in order to avoid attacks by Herring Gulls, thus often making it difficult to identify fish species.

TABLE 2. Mean ( $\pm$ SE) frequency and composition of meals (fish delivered in one trip) delivered by each sex ( $n = 13$  pairs).

	Males	Females
Number of meals per day	1.9 $\pm$ 0.5	2.6 $\pm$ 0.7*
Length of fish (cm)	10.6 $\pm$ 0.8	10.5 $\pm$ 0.8
Number of fish per meal	1.6 $\pm$ 0.4	1.6 $\pm$ 0.4
Number of <i>Mallotus villosus</i> per meal	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1
Composition of chick feeds		
Capelin ( <i>Mallotus villosus</i> )	435 (58.9%)	594 (62.5%)
Cod ( <i>Gadus morhua</i> )	162 (21.9%)	152 (16.0%)
Other identified	11 (1.4%)	16 (1.6%)
Species unknown	131 (17.7%)	189 (19.8%)
Total	739	950

\*  $P < 0.05$ .

TABLE 3. Summary of burrow changes: number of burrows retained by males and females.

	Males	Females
Burrow reused, male present	6/6 (100%)	0/2 (0%) <sup>a</sup>
Burrow reused, total	6/6 (100%)	2/5 (40%) <sup>b</sup>
Total burrows, with non-reused	6/8 (75%)	2/7 (29%) <sup>c</sup>

Fisher Exact Test: <sup>a</sup>  $P < 0.05$ ; <sup>b</sup>  $P = 0.06$ ; <sup>c</sup>  $P = 0.10$ .

#### MATE AND BURROW CHANGES

Mate-changing occurred in 22% (11/50 pair-years) of the cases where both birds were banded (Table 3). In seven cases this may have resulted from the death of one of the pair, as it was not seen the following spring. Three males and four females disappeared; of the returning mates, all four males and two of three females retained their burrows. The mate-changing rate was 9.3% (4/43) of those cases where both birds were present the following year. In two of these four cases, the male retained the burrow while the female re-mated at a nearby site; both of these pairs had reared a chick the previous year. In the remaining two cases both individuals moved to nearby burrows where they re-mated. This relocation may have been related to low quality nesting sites, as one pair had bred in an extremely short burrow and had failed the year before, and the other pair had bred in a burrow located at the edge of the colony on more level slope and had failed for two years prior. Their new burrows were more similar to those used by successful pairs in terms of slope and drainage. Overall it appears that males were more likely to retain the burrow than females (Table 3).

#### MATE GUARDING AND MATE FIDELITY

The proportion of time that pair members were together on the slope differed significantly among the various stages of the breeding cycle ( $\chi^2 = 22.0$ ,  $P < 0.001$ ). Birds were together in the colony more during the pre-laying stage (8%), while time together declined throughout the rest of the breeding season (<3% in all other phases). Females were alone in the colony for about 18% of the observation time during the pre-laying period. For all stages, however, time together in the colony accounted for only a small proportion of total time, but increased for both sexes towards the end of the pre-laying period.

Pairs arrived and departed together more often

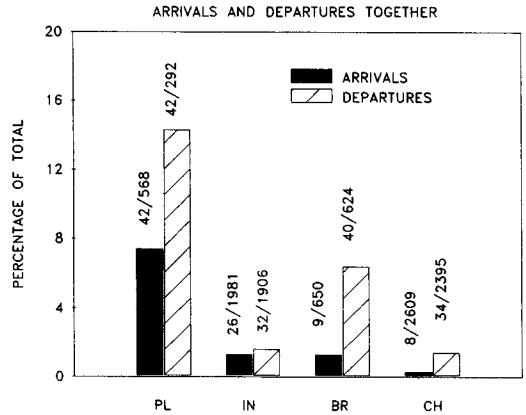


FIGURE 2. Percent arrivals and departures of mates together during pre-laying (PL), incubation (IN), brooding (BR), and chick rearing (CH). Fractions at the top of columns indicate the number for mates together divided by the total number of arrivals and departures.

during the pre-laying stage relative to other stages except for the increased number of departures together during brooding ( $\chi^2 = 15.66$ ,  $P < 0.01$ , Fig. 2). However, the arrivals and departures of mates together represented only a small proportion of the total number of arrivals and departures, with greatest proportion during pre-laying equalling only 14%. Neither sex showed a tendency to depart first significantly more often when pairs left the slope together ( $Z = -0.47$ ,  $n = 14$ ,  $P = 0.64$ ).

Each successful copulation occurred on the water while the male stood upright on the female's back. Males solicited females by rapidly swimming towards them while performing "head-flick displays." The male "wing-fluttered" as he attempted to mount the female. Unreceptive females simply dove or swam away from the male. Often a male was rejected several times and then turned his attention to another female or drifted away. Of the 56 males observed on the water during the pre-laying stage, 39% (22) solicited more than one female during a particular 10-min watch (Table 4). In total, 100 females were solicited; mounting attempts occurred in 34 of these cases, and 26% (9) of these attempts appeared to lead to successful copulations. The mean length of these successful copulations was 24.5 sec (range = 5–35 sec). In all apparently successful copulations the male solicited only one female and the two birds did not separate throughout the observation period, suggesting that they may have

been paired individuals. This may not be a valid conclusion, but it is supported by various differences in the mating sequences between puffins and murres. There were no cases in which female puffins were unsuccessful in attempts to repel males (thus, no FEPCs); puffins interfered with copulation; or where a successful copulation was followed by a copulation attempt from another male (promoting sperm competition in favor of the mate). There were also no cases where marked females were seen following unmarked males from the slope to the water. Brief mounts were frequently observed on the slope, particularly at sunset, and when they involved marked individuals, the mounts always occurred between paired birds.

## DISCUSSION

### SEX DIFFERENCES IN TIME BUDGETS

Female puffins spent significantly more time than males incubating eggs and feeding chicks. However, this difference does not necessarily translate to a greater energetic cost incurred by females. Barrett et al. (1985) found that, although both male and female puffins lost considerable weight during incubation, these losses occurred at similar rates, suggesting equivalent energy expenditures for males and females during incubation. Further, energetic requirements of incubating seabirds are lower than for other normal activities (Birt-Friesen et al. 1989). Puffins incubate only a single egg, and as compared to open nesters, also have the advantage of nesting in burrows where heat loss may be dramatically reduced (White et al. 1978). The fact that incubating birds often leave the egg for short periods (Harris 1984, pers. obs.) further suggests that heat loss within the burrow is not a major problem, and that the energy requirements for incubation may not be considerable.

Female puffins were away from their burrows more than males during the chick period, which reflects their greater contribution to feeding chicks. The quality of meals did not appear to differ between the sexes. Further, given that males and females lose weight at the same rate during incubation (Barrett et al. 1985), females are probably not foraging more during chick rearing to make up for greater depletions. Corkhill (1973) and Harris (1987) also noted that somewhat more female than male puffins were observed carrying fish.

TABLE 4. Frequency (and percent) of male solicitations, and number (and percent) successful and unsuccessful mounting attempts.

No. females solicited per 10-minute watch	No. male solicitations	Number of mounting attempts		
		Successful No. (%)	Unsuccessful No. (%)	Total No. (%)
1	34 (61)	9 (26)	9 (26)	18 (52)
2	11 (20)	0	6 (18)	6 (18)
3	5 (9)	0	3 (9)	3 (9)
4	3 (3)	0	3 (9)	3 (9)
5	3 (5)	0	2 (6)	2 (6)
6	1 (2)	0	2 (6)	2 (6)
Total	56 (100)	9 (26)	25 (74)	34 (100)

### BURROW MAINTENANCE AND DEFENSE

Male puffins secure and defend burrows, whereas females choose among unpaired males and burrows (Nettleship 1972), and birds without burrows show no signs of being paired (Ashcroft 1979). Burrows require a great deal of maintenance, and new ones probably take several years to establish, an observation which has also been made for the Manx Shearwater (Storey and Lien 1985).

Although it comprised only a minor proportion of total time, males were present on the slope overall twice as much as females. During this time on the slope, males were involved in a greater number, but not rate, of burrow-maintenance activities and aggressive behaviors. Because individuals spent most of their time in the immediate vicinity of their burrows when observed on the slope, any aggressive interactions probably serve burrow defense functions. Many non-breeders have returned to the colony by the chick-rearing period, and during this time they wander over the slope investigating burrows. The presence of breeding males in or near their burrows may help to prevent these prospecting non-breeders from entering the burrow, and either driving out a chick, or attracting a hungry chick to the burrow entrance. Both of these responses by chicks could result in predation by Herring Gulls (Nettleship 1972). Thus overall it appears that the male's contribution in defending the burrow, which can be considered both in terms of parental effort and mating effort, appears to balance the extra direct care that females provide to young.

The importance of the burrow site to both the

long- and short-term reproductive success of male puffins is further supported by data on mate-changing. Although the sample size was small, males retained the burrow more often than did females where mate-changing occurred. In the two cases where males moved, they did so only when the former burrows appeared to be of low quality, and when they had failed to fledge young the previous year. A higher rate of burrow movement following breeding failure, possibly as a result of the unsuitability of the burrow, has also been reported for the Manx Shearwater (*Puffinus puffinus*, Brooke 1978) and Leach's Storm-petrel (*Oceanodroma leucorhoa*, Lien et al. 1977).

#### MATE GUARDING AND EXTRA-PAIR COPULATIONS

Male and female puffins spent more time on the slope during the pre-laying period than at any other time in the breeding season. Further, pairs spent more time together in the colony, and arrived and departed together more often in the pre-laying period than during the rest of the breeding season. However, time paired in the colony represented only a small proportion of total time even during pre-laying (8%). Female puffins are thus left alone in the colony more than were female Common Murres, with male puffins spending much less time near the nest site than did male Common Murres throughout the pre-laying period (comparison of our data with Birkhead et al. 1985 and Wanless and Harris 1986). In addition, female puffins did not depart first more often than males, which would be expected if males were safeguarding paternity by following and remaining close to females. These data indicate that male puffins guard their mates less than do male Common Murres. Another alcid, the Razorbill (*Alca torda*), resembles the puffin in that it only shows an increase in male time in the colony at egg-laying rather than during the entire fertilization period, and in this species, like the puffin, extra-pair copulation has not been observed (Wanless and Harris 1986).

Individual male puffins attempted to mate with several different females, but females were able to resist these attempts by diving under water. The only successful copulations occurred for males that only solicited one female. In no cases did puffins attempt to interfere with copulations in progress, nor did groups of males attempt to copulate with a single female. In contrast, FEPCs occur frequently in Common Murres, and mates

attempt to repel the intruders (Birkhead et al. 1985). Given that murres copulate at their nest sites on cliff edges, female cannot usually prevent copulation attempts, particularly those involving groups of males (Birkhead et al. 1985). Thus, although we are not certain that all puffins with completed copulations were paired, it appears that the EPC rate is higher in murres than in puffins. It is certainly the case that forced copulations are rare in puffins than in murres: they are frequently observed in the latter, while we observed none in the puffins.

Low levels of mate guarding cannot be taken alone as evidence that EPCs do not occur. For example, Westneat (1987a, 1987b) found low levels of mate guarding in Indigo Buntings (*Passerina cyanea*), and yet 35% of young were not sired by the mate. Even in species where mate guarding is frequent, the extent to which males can mate guard must be balanced against time required for other activities. It may therefore be of particular interest to compare the male mating strategies of closely related species, whose foraging and nesting habits should result in similar amounts of time and energy being available for mate guarding and EPC. Taken together, the information on copulation sequences suggests that EPCs, particularly FEPCs are less common in puffins than in murres, and that, relative to puffins, male murres spend more time both guarding and copulating with their mates as anti-cuckoldry behavior patterns (comparison of our observations with those of Birkhead et al. 1985, Hatchwell 1988).

It is possible that a single factor, different copulation locations in the two species, has affected several aspects of male reproductive strategies. Copulating on water instead of at the nest site may have evolved for reasons unrelated to FEPCs, such as difficulty associated with copulating on slopes near puffin burrows. However, copulating on water means that female puffins must cooperate for mating to be successful, and this may have contributed to male puffins showing less mate guarding than Common Murres. None of the putative advantages of EPCs to females, such as production of genetically diverse offspring in a single breeding attempt (Williams 1975, Gladstone 1979) appear to apply to female puffins. In contrast, there are several potential disadvantages for females of EPCs including decreased courtship or desertion by the mate (Trivers 1972, Dawkins 1976, Erickson and Zenone 1976), or

reduced paternal care (Møller 1988). Strongly-bonded females may provide confidence of paternity simply by rejecting the solicitations of other males (Fitch and Shugart 1984). However even if paternity is uncertain, male puffins may have few other options for enhancing reproductive success besides caring for young. Wanless and Harris (1986) note the greatest investment in chicks by male than female common murres is unexpected, given the prevalence of EPCs, but this higher investment may reflect a lack of other options for the males.

In terms of time available for various activities, the foraging patterns of murres and puffins suggest that the two species should have the same constraints in terms of spending extensive time in or away from the colony, and after the pre-laying period members of the two species do spend comparable amounts of time in the colony (our data compared to Wanless and Harris 1986). It appears that for the murres, relative to puffins, that the inability of females to resist copulation attempts by other males may have dramatically increased the time and energy males devote to guarding and copulations with their mates.

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