

SEX DIFFERENCES IN REPRODUCTIVE EFFORT
AND THE POTENTIAL FOR A MIXED
REPRODUCTIVE STRATEGY IN THE
ATLANTIC PUFFIN (*FRATERCULA ARCTICA*)

CENTRE FOR NEWFOUNDLAND STUDIES

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ELIZABETH CREELMAN



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AND THE POTENTIAL FOR A MIXED REPRODUCTIVE STRATEGY
IN THE ATLANTIC PUFFIN (*Fratercula arctica*)

by

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ABSTRACT

Atlantic Puffins (*Fratercula arctica*) on Gull Island, Newfoundland were studied in order to compare the sexes in their patterns of parental activities during the breeding season. Time allocation was categorized as on the slope, in the burrow, and away from the colony. Compared to males, females spent more time in the burrow during pre-laying and incubation, and more time away during the chick-rearing period. With the exception of pre-laying, males spent more time on the slope throughout the season than females. Males were involved in a greater number of burrow maintenance activities and aggressive interactions than females, but because males spent more time on the slope, there were no differences in the rates of these activities. Females delivered more fish meals to chicks per season than did males. No sex differences occurred in the number, size or species of fish per meal, suggesting that the longer absence by females may have been due to greater time spent foraging for chick meals. Male and female Atlantic Puffins both perform all of the breeding activities to some extent, and probably contribute similar amounts of time and energy to reproductive effort. Although females may contribute more towards short-term breeding effort by investing more in current young, males may contribute more towards long-term breeding effort by investing slightly more in activities which serve burrow defense functions.

This study also attempted to determine whether extra-pair copulations and mate-guarding are important components of the Atlantic Puffins' reproductive strategy. Males apparently attempted to secure extra-pair copulations, as 39% of those observed on the water during the pre-laying stage solicited more than one female. Some of these males may have been mated as males spent more time away from mates during pre-laying and the early part of incubation, but this difference decreased as the number of females yet to lay eggs decreased. Female time away

did not show this pattern. Evidence of mate-guarding by males includes observations that mates spent more time paired, and were involved in a greater number of synchronous arrivals and departures, during the pre-laying stage than after. However, greater time paired indicates only greater mate proximity; it does not indicate whether one sex was more responsible than the other for maintaining proximity. In addition, there was no difference in which sex departed or arrived first when pairs arrived and departed together. Because successful copulations appeared to involve only paired birds, females may provide confidence of paternity by rejecting the solicitations of other males.

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INTRODUCTION

In this thesis, parental behaviour patterns and the potential for extra-pair copulations in the monogamously breeding Atlantic Puffin (*Fratercula arctica*) will be examined in an attempt to compare the reproductive strategies of males and females. Generally, males invest more in mating effort (securing mates), while females invest more in parental effort (caring for offspring). In monogamous species, however, offspring survival demands considerable parental care by both parents (Emlen and Oring 1977). The degree of equality in this contribution to parental care by the sexes is not fully known, and may differ among species.

According to Trivers (1972), females of monogamous species should invest slightly more than males. He argues that at any time the sex that has invested less than its mate should be more strongly selected to desert. This is based on the idea that the sex whose cumulative investment exceeds that of its mate is committed to greater future investment because its losses will be higher if unsuccessful. As a result of the female's initially larger gametic contribution, the male should be more strongly selected to desert, whereas the female should be more strongly selected to stay if deserted. Others have pointed out, however, that the amount of future investment a parent provides an offspring may not be determined by that already invested, but rather by the amount that will be required by the offspring in the future in relation to the cost of its replacement (Dawkins and Carlisle 1976; Boucher 1977). The amount previously invested is only important in that it determines how much more is required; it is not important which sex did the investing. Thus, it would not necessarily follow that females of monogamous species should be less likely to desert; or should invest slightly more than males in parental care. This would be especially true for a species which lays a single egg per year, and for which a replacement egg is only possible early in the season. It may be less costly for both sexes to complete investment in the first offspring than to attempt to replace it, and risk raising no offspring that year.

Trivers (1972) defines parental investment as "Any investment by the parent in an offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Because this definition includes only those activities which affect the survival chances of the current young, it has been argued that an appropriate comparison of male and female investments cannot be made without also taking into account activities such as increased aggression in defense of the nest-site and mate (Montevecchi and Kirkham 1980; Burger 1981a). Montevecchi and Kirkham suggest that for marine birds in particular, investment may be equal due to the costs resulting from site-related activities which are more often performed by males.

In order to compare the entire investment patterns of breeding males and females, it may be preferable to consider 'reproductive effort' as comprised of: 1) short-term effort - those activities which influence an individual's immediate reproductive success, such as incubating the egg(s) and provisioning the chick(s); and 2) long-term effort - those activities which may benefit the individual in the long term, such as establishing and maintaining a pair-bond and nest-site in those species which retain the same mate and breeding site for several years.

Sex differences in the parental effort of monogamous species may also be less than Trivers suggests if the species is long-lived and shows strong mate fidelity (Emlen and Oring 1977). Pairs breeding together over consecutive years often show greater synchronization and efficiency, resulting in higher reproductive success (Coulson 1966; Penney 1968; Mills 1973; Davis 1976). Thus purely selfish interactions should not be expected between monogamous mates as it may be to the advantage of both sexes that neither becomes so energetically taxed as to increase the risk of mortality (Lazarus and Inglis 1978; Montevecchi and Porter 1980).

In monogamous species, sex differences occur not only in the amount of time spent in parental activities, but in the stage in the breeding cycle at which these

differences occur. In Gannets (*Sula bassanus*) (Kirkham 1980), Herring Gulls (*Larus argentatus*) (Burger 1981b), and Northern Mockingbirds (*Mimus polyglottos*) (Breitwisch *et al.* 1986), both parents contributed to chick feeding but the roles of the sexes changed with the age of the young. In Ring-billed Gulls (*Larus delawarensis*), males were more aggressive in defense of the territory and brood (Southern 1981), and in Laughing Gulls (*Larus atricilla*) both sexes exhibited aggression, but there were sex differences in the frequency of different aggressive behaviour patterns (Burger and Beer 1975). Male Black Skimmers (*Rynchops niger*) did more incubation and brooding of young, and were more aggressive prior to hatching, whereas females delivered more chick meals and were more aggressive following hatching (Burger 1981a). In Western Gulls (*Larus occidentalis*), males fed chicks more often and were responsible for most of the territorial defense throughout the breeding season (Pierotti 1981); in Great Black-backed Gulls (*Larus marinus*), females did more of the incubation and males exhibited more agonistic behaviour during the incubation period (Butler and Janes-Butler 1983). The results from many of these studies indicate different patterns of parental time investment, but an equal, if not greater, investment by males than females. In order to compare the reproductive effort of males and females in a monogamous species, emphasis should therefore be made on the overall pattern of parental activities throughout the breeding season.

Associated with Trivers' model is the idea that, due to greater investment by females, males are provided with opportunities to attempt extra-pair copulations. Males should pursue a mixed reproductive strategy whereby they contribute heavily to parental care with one female while attempting to mate with females to whose offspring they contribute no care. Because the potential for extra-pair copulations in a population also increases the risk that males may invest in unrelated offspring, it has been argued that certain male behaviour patterns occurring prior to egg-laying (e.g. mate-guarding) are counter-adaptations to cuckoldry.

Behaviour patterns interpreted as evidence of mate-guarding during the female's fertile period include males following and remaining close to their mates (Horn 1970; Birkhead 1979; Birkhead *et al.* 1985), increased aggression and territoriality (Barash 1976; Burger 1981a; Morris and Bidochka 1982), and higher incidences of synchronous arrivals and departures of pairs (Hoogland and Sherman 1976). A male may also protect his paternity by being capable of recognizing and rejecting a female which has already been inseminated (Erikson and Zenone 1976), and by copulating with a mate immediately after an extra-pair copulation, as there is evidence that the last male to copulate with a female will fertilize the most eggs (Compton *et al.* 1978; Cheng *et al.* 1983).

The female's role and her propensity to participate in extra-pair copulations have generally been overlooked. Fitch and Shugart (1984) suggest that it may be erroneous to assume that increased male attendance during the fertile period is evidence of mate-guarding or of the necessity for mate-guarding. They found no increase in male Herring Gull aggression during this period compared to the pre-fertile period, although Morris and Bidochka (1982) found a higher frequency of aggression in Herring Gulls during the fertile period than during incubation. More importantly, however, Fitch and Shugart found that extra-pair copulations occurred with unpaired females who appeared to participate willingly; paired females neither copulated with nor solicited other males. Fitch and Shugart suggest that strongly-bonded females may provide confidence of paternity simply by rejecting the solicitations of other males.

Confidence of paternity provided by females may be expected to occur particularly in long-lived, monogamous species in which females are physically capable of resisting the mating attempts of other males. In some species, the necessity for mate-guarding may be real if inseminations by other males are successful despite the female's unwillingness. In Common Murres (*Uria aalge*) extra-pair copulations occur on densely-populated nesting ledges where females may have limited opportunities to escape, especially if more than one male is

involved (Birkhead *et al.* 1985). Thus the risk of cuckoldry, as well as the selection for mate-guarding, should be considered in terms of the ecological constraints on the potential for extra-pair copulations in a given species.

Atlantic Puffins are long-lived, monogamous, sexually monomorphic seabirds belonging to the Alcidae, a family comprising 22 species restricted primarily to oceanic regions of the northern hemisphere. Atlantic Puffins breed throughout the North Atlantic on offshore islands, and more rarely on undisturbed coastlines, to which they ~~come only to breed~~. The nest-site is a burrow or crevice among rocks in which a single egg is laid. Birds first breed at 4-5 years, and show strong mate and burrow site fidelity. They probably disperse widely over the open sea during the winter months, although their distribution at this time is largely unknown.

The bulk of scientific knowledge on Atlantic Puffins comes from research conducted in Great Britain. The first complete investigation of this species was made by Lockley (1934, 1953) in Wales. Since then, comprehensive work has been carried out by several others, including Corkhill (1972, 1973), Ashcroft (1976, 1979), and Harris (e.g., 1982, 1983, 1984). Information from the west Atlantic comes largely from Nettleship (1972), Pierotti (1983), and Rice (1985). Most research on Atlantic Puffins has occurred during the breeding season, and much of that has concentrated on feeding ecology, patterns of growth, fledging success, and gull-puffin interactions.

Much less work has been done on the patterns of sex differences in behaviour in relation to differential reproductive investments. Lockley (1934) found that females incubated more, and data collected by Corkhill (1973) suggest that females feed chicks slightly more frequently than do males. Most of the behaviour patterns associated with courtship, and burrow maintenance and defense, are shared by the sexes, but to what extent they are shared has not been documented.

Objectives

This study documents the patterns of parental investment behaviour in Atlantic Puffins throughout four stages of the breeding season: pre-laying, incubation, brooding, and chick-rearing. The following components of breeding activities are considered:

1. Time that males and females spend on the slope, in the burrow, and away.
2. Time that the male spends on the slope while the female is in the burrow and vice versa.
3. Number and rate of burrow-maintenance and aggressive behaviour in males and females.
4. Number, size, and species of fish delivered per meal, and number of meals delivered over the season, by males and females.
5. The relationship of nest-site tenacity with the reproductive strategies of males and females.

Because males of monogamous species may adopt a mixed reproductive strategy in which they invest slightly less than their mates while attempting to secure extra-pair copulations, attention is given to the potential for such matings and to evidence of mate-guarding. It is predicted that males should spend more time away than females early in the season when other females are fertile. In order to assure certainty of paternity by preventing access to mates by other males, it is also predicted that males should spend greater time paired with mates prior to egg-laying than after, and that males should depart and arrive after

mates more often than vice versa when pairs depart and arrive together. The necessity for mate-guarding in terms of the female's role is also discussed. The following objectives are considered:

1. A comparison of the proportion of time that males and females are away until the estimated date that most females have laid.
2. The proportion of time that mates are together throughout the reproductive cycle.
3. The number of synchronous arrivals and departures of mates throughout the reproductive cycle.
4. A comparison of which sex departs first when pairs do so together during the pre-laying stage.
5. Solicitation behaviour of males on the water during the pre-laying stage.

METHODS

Fieldwork was conducted on Gull Island, Witless Bay, Newfoundland ($47^{\circ}15' \text{ N.}$, $52^{\circ}46' \text{ W.}$), one of three islands comprising the Witless Bay Seabird Sanctuary (Figure 1). Gull Island is located 1.6 km from the nearest point of land, and is approximately 1.6 km long and 0.8 km wide. Most of the island is densely wooded with the exception of open grassy areas around the perimeter where Atlantic Puffins nest. The study site was located near the southeast corner of the island on a 28° grass-hummocked slope. A total of 16 pairs of puffins were observed from a canvas blind ($0.9 \times 0.9 \times 1.2 \text{ m}$) situated 8 meters from the nearest study burrow. The study burrows encompassed an area of 40 m^2 .

During the summer of 1984, fieldwork was directed primarily towards capturing and marking birds. In 1985, watches ranged in length from 4 to 17 hours, and occurred on 80 days between 18 May and 14 September for a total of 960 observation hours. During incubation, watches were generally from dawn to dusk for two to three consecutive days followed by a one to two day break; during the chick-rearing period, watches lasted one to two consecutive days followed by a one to two day break. In 1986, a two week visit was made in early May to observe pre-laying behaviour patterns as a means of confirming the sexes of marked birds.

Birds were either caught in the burrow, or with 0.5-m squares of chicken-wire attached with nylon line nooses. These were placed at burrow entrances and snared birds as they walked over them. Birds were banded with one or two plastic color-bands and standard numbered aluminum bands supplied by the Canadian Wildlife Service. The identification of color-bands is difficult during the chick-rearing period as the arrival and departure of parents delivering food to chicks is rapid. Therefore, in 1985 adults were re-caught eight to nine days

following chick-hatching, and their breasts marked with picric acid, Malachite Green dye, or Rhodamine B Extra dye. The two dyes were combined with 1% Tergitol, a wetting agent. Due to the possibility that the behaviour patterns of birds were affected by this treatment, individuals were excluded from data analyses until three days following handling. Personal observations indicated that three days was an adequate length of time.

Sexing Technique

Study birds were sexed using both morphological and behavioural differences. Male Atlantic Puffins are on average slightly larger and heavier than females. In particular, males have significantly larger and deeper bills (Corkhill 1972). In a previous study a discriminant function was calculated from three bill measurements taken from birds of known sex and used to sex birds caught at Scottish breeding colonies (Harris 1979). A similar endeavor was made in this study using 112 birds caught accidentally in fishing nets around the colonies. Since puffins develop grooves on the outer portion of their bills as they age and probably do not breed until they have acquired at least two grooves (Harris 1981), only birds with two or more grooves were included in the sample. Birds were sexed by dissection, and culmen length, depth, and gape (Figure 2) were measured with Vernier calipers (estimation to 0.1 mm) and used to calculate a discriminant function. The same three bill measurements were taken from study birds and the function was used to predict sex.

Copulation in puffins generally occurs on the water, making observations of this behaviour a difficult means of sexing study birds. Males, however, often perform a pre-copulatory display on the slope consisting of a distinctive head-flick and wing-flutter directed towards another individual, presumably a female (Taylor 1984). Observations of this behaviour were recorded and, in combination with the discriminant function calculated from bill measurements, used to sex study birds.

Breeding Stages

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

1) Pre-laying - This covered the period prior to egg-laying, and ranged from five to ten observation days depending on the time of egg-laying in individual burrows. Due to the extreme sensitivity of puffins during this period (Lockley 1934; Ashcroft 1979), burrows were not inspected for eggs. Instead, egg-laying dates were estimated by subtracting 41 days from hatching dates. Because incubation ranges from 39 to 43 days (Harris 1984), estimates of laying dates are accurate within ± 2 days. Fourteen pairs were observed during this period.

2) Incubation - This covered the period from egg-laying to chick-hatching. Hatching dates equal 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). Fourteen pairs were observed during this period.

3) Brooding - This covered the period from chick-hatching until chicks were present alone in the burrow for more than 50% of total time. The end of brooding was defined by percent time the chick was attended because the length of intensive brooding was variable among pairs ($X \pm SD = 8.17 \pm 2.59$ days, range = 4 - 12). Only 12 pairs were observed during this period because one pair lost its egg just prior to hatching, and one lost its chick just after hatching.

4) Chick-rearing - This covered the time from the end of brooding to the departure of chicks. One pair failed at the start of this stage, and two new pairs were added. Thus 13 pairs were observed during this period.

Data Collection and Analyses

Reproductive Effort

1. The arrival and departure of marked birds from the slope, and their

entrance and exit from burrows, were recorded and used to compute time (hr) that each bird spent on the slope near the burrow entrance, in the burrow, and away for each breeding stage. Time that males and females spent in these three categories for each stage were compared using the Wilcoxon matched-pairs signed-ranks test.

2. Time on the slope, time away, and time in the burrow were compared over the four stages for each sex using Friedman 2-way tests. Because observation time differed between breeding stages, the proportions of time spent in each activity per total time observed were used.

3. Time spent on the slope and in the burrow were totalled for each bird for the entire breeding season. A comparison of time spent by the male on the slope while its mate was in the burrow, with time spent by the female on the slope while its mate was in the burrow, was made, using the Wilcoxon matched-pairs signed-ranks test.

4. Throughout pre-laying and incubation, instances of burrow-maintenance activities were recorded. During pre-laying these consisted primarily of digging and expelling dirt from the burrow; during incubation it consisted of a bird pulling grass from the slope and carrying it into the burrow where its mate was incubating. The Wilcoxon matched-pairs signed-ranks test was used to test for a sex difference in both the number and rate of bouts of burrow-maintenance activities.

5. An attempt was made to record aggressive behaviour throughout the breeding season. Aggressive interactions usually resulted from a bird wandering near another's burrow. The burrow owner chased and/or attacked the intruder, who occasionally retaliated, and a full grapple resulted. The Wilcoxon matched-pairs signed-ranks test was used to test for a sex difference in both the number and rate of aggressive interactions.

6. During the brooding and chick-rearing periods, data were also collected on the times of food deliveries and the sex of the parent delivering the meal. The species and length of fish, and the number per meal, were determined through observation when possible. Length was estimated by comparison of the fish with the depth of the bird's bill. Wilcoxon matched-pairs signed-ranks tests were performed to compare sexes in the total number of chick meals delivered per season, the mean number of fish per meal, the mean length of fish, and the number of Capelin (*Mallotus villosus*) per total number of fish.

7. For the period 1984 to 1986, the mate-changing rate for 50 pair-years is reported, as well as information on the nest-site tenacity of males and females when mate-changing occurred.

Mate-guarding and Extra-pair Copulations

1. Percent time away for each sex was plotted against date for the pre-laying and incubation stages in order to compare the sexes in their patterns of time away. Note was made of when most females in the population should have finished laying. To establish a rough estimate of when this would have occurred on Gull Island, seven days were subtracted from 8 June, the date of the first observation of a puffin carrying fish. This number was arrived at by taking the maximum incubation length (43 days, Harris 1984), from the spread of laying dates recorded for Newfoundland (35 days, Harris and Birkhead 1985). Because not all pairs were represented on all days, the mean proportion of time away in three to four day periods was used.

2. Time that mates were paired on the slope and in the burrow was taken for each breeding stage, and divided by the total observation time. It was not possible to know whether or not birds were together when both were away, although it is likely that the majority of time was spent foraging at sea, and that mates were unable to remain in contact with each other over such long periods. Thus, the time that both birds were absent was not included as time paired. The

Friedman 2-way test was performed to test whether a significant difference occurred between breeding stage and the proportion of time paired.

3. For each pair, the number of times that mates arrived and departed together was totalled for each breeding stage. These were divided by the total number of arrivals and departures of birds (both singly and with mates) for each breeding stage to insure that any changes in the synchronous arrivals and departures of mates did not simply reflect seasonal changes in the total number of arrivals and departures. The Friedman 2-way test was then used to compare the proportion of synchronous arrivals and departures between the four periods.

4. The Wilcoxon matched-pairs signed-ranks test was used to test whether one sex departed first more often than the other when pairs did so together. These data were taken from only the pre-laying stage when protection of paternity by mate-guarding is expected to occur.

5. During the pre-laying period, 56 males were observed on the water in 10-minute watches. Males were identified by head-flicking and wing-fluttering displays directed at other birds, indicating soliciting behaviour (Taylor 1984). The number of birds solicited, of attempts to mount by the male, and of apparently successful copulations, were recorded. Apparently successful copulations were those in which the female did not immediately dive or swim away, and which lasted more than several seconds.

All analyses were made using *Statistical Package for the Social Sciences, Tenth Edition* (Nie et al. 1983).

RESULTS

Sexing of Study Birds

Of the 16 pairs observed, 14 were sexed using behavioural observations of male pre-copulatory displays at the burrow entrance. Discriminant function predictions were in accordance with these observations in all but one case where both individuals were predicted as female. For the remaining two pairs behavioural observations were not available and birds were sexed using the discriminant function. In these cases the discriminant scores and probability levels were reliable.

Reproductive Effort

1. Males spent significantly more time on the slope than females during incubation (Wilcoxon matched-pairs signed-ranks test, $Z = -3.23$, $n = 14$, $P < 0.01$), brooding ($Z = -2.98$, $n = 12$, $P < 0.01$), and chick-rearing ($Z = -3.04$, $n = 13$, $P < 0.01$), but no significant difference occurred during pre-laying (Figure 3). For the stages combined, however, females spent only 2% of their total time on the slope, and males only 4%.

2. Females were present in the burrow significantly more than males during pre-laying (Wilcoxon matched-pairs signed-ranks test, $Z = 2.51$, $n = 14$, $P < 0.05$) and incubation ($Z = 2.35$, $n = 14$, $P < 0.05$). Throughout brooding and chick-rearing there were no sex differences in time in the burrow (Figure 4). For the stages combined, females spent 33% and males 30% of their total time in the burrow.

3. During pre-laying males spent more time away from the colony than

females (Wilcoxon matched-pairs signed-ranks test, $Z=-2.48$, $n=14$, $P<0.05$), 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 (Figure 5). For the stages combined, females spent 65% and males 66% of their total time away.

4. For the sexes combined, a significant relationship occurred between breeding stage and time on slope (Friedman two-way test, $X^2=32.78$, $df=3$, $P<0.001$), time in burrow (Friedman two-way test, $X^2=51.11$, $df=3$, $P<0.001$), and time away (Friedman two-way test, $X^2=48.00$, $df=3$, $P<0.001$). Figures 6 and 7 show the seasonal pattern of time spent in these activities for each sex. During incubation, time away and time in the burrow comprised the majority of time allocation in similar proportions (46% and 51%, respectively), whereas during pre-laying and chick-rearing the majority of time was spent away (73% and 92%, respectively). Time on the slope comprised a relatively small proportion throughout (range = 2 - 11%).

5. For the breeding stages combined, time spent by the male on the slope while the female was in the burrow was greater than time spent by the female on the slope while the male was in the burrow (Wilcoxon matched-pairs signed-ranks test, $Z=-3.31$, $n=16$; $P<0.001$; Figure 8). This was especially true during incubation.

6. Males performed a greater number of bouts of burrow-maintenance activities during the pre-laying and incubation stages than females (Wilcoxon matched-pairs signed-ranks test, $Z=-2.55$, $n=14$, $P<0.05$). However, there was no significant sex difference in the number of bouts per time on slope (Table 1).

7. Males were involved in a higher frequency of aggressive interactions throughout the breeding season than were females (Wilcoxon matched-pairs signed-ranks test, $Z=-3.3$, $n=14$, $P<0.001$), whereas there was no significant sex difference in the number of aggressive interactions per time on slope (Table 2).

The numbers recorded per individual are low, probably because some interactions were missed. However, it is possible that males were involved in a greater number of grapples, which occur primarily during burrow establishment. Since grapples are more obvious than other aggressive behaviour, a greater number of female aggressive behaviour may have been overlooked than male. More data are therefore required in order to accurately establish sex roles differences in these interactions.

8. Females delivered more fish meals per season than did males (Wilcoxon matched-pairs, signed-ranks, $Z = -2.13$, $n = 14$, $P < 0.05$). Of the 1,488 fish meals delivered, males were responsible for 43%, with an average (\pm SD) of 1.89 ± 1.93 meals delivered per day, whereas females were responsible for 57%, with an average (\pm SD) of 2.55 ± 2.34 meals delivered per day. Of the 1,689 individual fish delivered, males and females delivered 44% and 56%, respectively. Capelin comprised the major fish species, with females delivering 56% and males 42% of this species (Table 3). There were no sex differences in the mean number of fish per meal, the mean length of fish, or the number of capelin per total number of fish (Table 4). 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 was due to birds entering burrows rapidly, presumably in order to avoid attacks by Herring Gulls, thus making identification of fish species often difficult.

9. Mate-changing occurred in 22% (11/50 pair-years) of the cases where both birds were banded. 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 of the males and two of the females retained their burrows. When considering only those cases where both birds were accounted for, the 'divorce-rate' was 9.3% (4/43). In two of these cases, the male retained the burrow while the female re-mated at a nearby site; neither of these pairs had failed the year before. 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, whereas 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. Although the sample size for separated pairs is small, males retained burrows 71% (5/7) of the time, whereas females retained burrows 25% (2/8) of the time, and only when the male had disappeared.

Mate-guarding and Extra-pair Copulations

1. Figure 9 shows the patterns of male and female time away through incubation. Males were absent more than females through the first two weeks of incubation, although it was during pre-laying and the earliest part of incubation that this difference was greatest. Male and female patterns of time away were similar thereafter.

2. A comparison between breeding stages of the proportion of time paired both on the slope and in the burrow (which does not include time that both were away) was significant (Friedman two-way test, $\chi^2=21.98$, $df=3$, $P<0.001$). Figure 10 shows that the pre-laying stage was highest in this measure, followed by a decline through the breeding season. For all stages, however, time together accounted for only a small proportion of total time. This is due in part to the large proportion of time that one or both birds were away (Figure 11, and pp. 45-46).

3. There was a significant relationship between breeding stage and percent arrivals and departures of mates together (Friedman two-way test, $\chi^2=15.66$, $df=3$, $P<0.01$). Figure 12 shows the breakdown into arrivals and departures, with the pre-laying stage similarly high for both relative to other stages with the exception of brooding, during which the number of departures together increased. However, the arrivals and departures of mates together represented only a small proportion of the total number of arrivals and departures, with the highest during pre-laying equalling only 21%.

4. Neither sex showed a tendency to depart first significantly more often when pairs left the slope together (Wilcoxon matched-pairs signed-ranks test, $Z=-0.47$, $n=14$, $P=0.64$; Figure 13).

5. Of 56 males observed on the water during the pre-laying stage, 39% (22) solicited more than one female throughout a 10-minute watch (Table 5). In total, 100 females were solicited; mounting attempts occurred in 34 of these cases, 26% (9) of which appeared to lead to successful copulations (Table 6). The mean length of 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.

DISCUSSION

Puffins were sexed on the basis of sexual behaviour patterns and a discriminant function taken from bill measurements. This method proved successful in all cases, and serves as the basis for the following discussion of reproductive effort and the potential for extra-pair copulations in Atlantic Puffins.

Reproductive Effort

Female puffins spent significantly more time than males incubating the egg and feeding the chick. Throughout most of the breeding season males spent more time on the slope and were involved in a greater number, but not rate, of site-related activities. However, despite the significant levels of these sex differences, both sexes contributed substantially to reproductive effort at all stages of the breeding cycle.

Although the female spent more time in incubation, this may not have necessarily resulted in a dramatically greater energetic contribution. Incubation requires heat, which comes from the parent bird's body and at some point from embryonic metabolism. However, there is evidence that the energetic requirements of an incubating bird do not exceed the resting metabolic level (Mertens 1977; Walsberg and King 1978). 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. The fact that incubating birds often desert the egg for short periods (Harris 1984; pers. obs.) further indicates that heat loss is not a major problem, and that the energy requirements for incubation may not be considerable.

The greater female time away during the chick stage may reflect greater time and energy spent foraging. Females delivered more meals, but the quality of meals did not appear to differ between the sexes. Higher rates of chick feeding by females has been observed in other species. Burger (1981a) found that female Black Skimmers brought back more fish to young. Male Northern Gannets fed chicks more often during the first four weeks, but a reversed trend occurred during the remaining nine weeks (Montevecchi and Porter 1980).

It is possible that the greater time spent incubating is energetically taxing to the female in that it is time not available for foraging. The greater female time away during the chick-rearing period may then be in part due to the need to forage more for herself in order to make up for supplies depleted (relative to males) during her more burrow-attentive incubation period. However, Barrett *et al.* (1985) found that, although both male and female puffins lost considerable weight during incubation, these losses occurred at similar rates, suggesting that energy expenditure is relatively equal for males and females during incubation. Further, males spent significantly greater time on the slope while the female was in the burrow than vice versa. Although it was not as great as the difference in time spent incubating, it was time that the male could have otherwise spent foraging, and may be costly to the male in terms of predation risks.

Although not measured in this study, one cost to female puffins which males do not share is that resulting from egg production. Generally, the eggs of precocial species are comparatively large, with larger yolks and higher energy levels than those of altricial species. The egg of the altricial Gannet is relatively small with a small yolk and low energy level (Montevecchi and Porter 1980). In comparison, the egg of the precocial Leach's Storm-petrel (*Oceanodroma leucorhoa*) is relatively large with a large yolk and high energy content (Montevecchi *et al.* 1983). However, on the basis of metabolic rate estimates, it appears that for both species the egg is energetically inexpensive to produce. Because puffin chicks develop semi-precocially and are intermediate of gannets

and petrels in terms of egg and yolk size (Birkhead and Nettleship 1984); it is possible that the single egg does not represent a large energetic investment. However, measurements of adult metabolic rates and egg energy levels are required in order to better estimate the cost of egg production to female puffins.

Although it comprised only a minor proportion of their time, males were on the slope overall twice as much as females. This accounts for the fact that males were involved in a greater number, but not rate, of site-related activities. 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. Most non-breeders have returned to the colony by the chick-rearing period; and being unassociated with a specific site, spend time wandering over the slope investigating burrows. It may be advantageous to a male in the short term if his presence at or near the burrow entrance discourages these prospectors from entering the burrow, as they may either drive out a chick, or the chick, if hungry and expecting a parent with food, may be stimulated to come to the burrow entrance. Both of these responses could easily result in predation by Herring Gulls.

The greater time present near the burrow may also benefit the male in the maintenance of burrow ownership, both within and between breeding seasons. Nettleship (1972) suggests that male puffins secure and defend burrows whereas females choose among unpaired males with burrows. Observations from the present study confirm this. Five females were observed visiting unpaired males who occupied burrows. The male initiated bill-clapping and encouraged the female to enter the burrow by looking down the hole and periodically raising his head, activities associated with pair-bond formation (Taylor 1984). If the female wandered to another burrow, the male did not follow. Further, Ashcroft (1979) found that birds without burrows showed no signs of being paired. Thus it is likely that a sex difference occurs in the obtainment of burrows and that pairs are not permanently formed each year until a burrow site is established. A similar

situation occurs in Manx Shearwaters (*Puffinus puffinus*), in which males spent more time at the burrow during the pre-laying period when they may be visited by females (Brooke 1978).

That the burrow-site may be more important to males is further supported by data on mate-changing. Although the sample size was small, where mate-changing occurred males retained the burrow more often than did females. 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 (Brooke 1978) and Leach's Storm-petrel (Lien *et al.* 1977).

Higher reproductive success, as a result of nest-site tenacity has been recorded in Adelie Penguins (*Pygoscelis adeliae*) (Penney 1968) and Leach's Storm-petrels (Lien *et al.* 1977). Although not yet documented for Atlantic Puffins, it is possible that retention of a suitable burrow over consecutive years leads to greater reproductive success in this species as well. This is supported in part by evidence that most of the higher quality nest-sites are occupied (Ashcroft 1979; Birkhead 1985). This may be because 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).

If burrow-site tenacity is an important factor in long-term puffin breeding success, it may in part explain the male's greater time spent on the slope. A female may be able to mate with another male and thereby acquire a new burrow, whereas a male may have to either displace a male from another burrow, acquire an empty one, or dig a new one. In those cases where burrows are suitable, maintenance of ownership throughout the season may therefore be advantageous to male puffins in the long term if it helps to insure ownership the following year.

The male appears to spend slightly more time in site-related activities which may be beneficial in both the short and long-term, whereas the female's greater time spent incubating and feeding the chick contribute to her short-term breeding effort as they benefit her immediate reproductive success. However, if males are chiefly responsible for obtainment of burrows there is the possibility that the quality of a female's egg and chick-related behaviour one year may influence a male's readiness to mate with her the following year. Assuming the burrow is suitable, those activities which affect a female's short-term success could therefore affect her long-term success as well.

Mate-guarding and Extra-pair Copulations

Behavioural observations of birds on the water indicated that some males solicit and attempt to mount several females, but that females may reject males that are not their mates. It is possible that some of these soliciting males were unpaired, as four-year-old non-breeders return to colonies at the start of the season and three-year-old non-breeders return during the laying period (Harris and Birkhead 1985). Males generally spent more time away than females during pre-laying and the early part of incubation, but this difference decreased as the estimated number of fertile females in the colony decreased. It is possible that the absence of mated-males at this time may have been due to their attempts to secure extra-pair copulations.

Regardless of whether the majority of males seeking extra-pair copulations are breeders or non-breeders, the potential for extra-pair copulations by mated females, and therefore the risk of cuckoldry to males, appears to exist. Thus counter-adaptations by mated males should be expected. However, not all the results are consistent with what is generally considered evidence of mate-guarding. The greater time paired on the slope and in the burrow, and the greater number of synchronous arrivals and departures of pairs during pre-laying, indicate that pairs remain in closer proximity during this period than during those following. However, time paired represented only a small proportion of total time even

during pre-laying. In addition, females did not depart first more often than males, which would be expected if males were safeguarding paternity by following and remaining close to females. The increase in departures of mates together during brooding may reflect the start of Herring Gull harassment resulting from kleptoparasitism. Because harassment by gulls often results in a mass exodus of puffins from the slope (Nettleship 1972; pers. obs.), pairs in, or at the entrance to, the burrow may have exited and taken flight simultaneously.

There are several reasons why it may be to the advantage of the female, as well as the male, to maintain proximity, and why mate-guarding may not be as necessary a means of securing confidence of paternity for male puffins as it is in some species. The advantages accruing to a strongly-bonded female who participates in extra-pair copulations are questionable. It has been suggested that females who have extra-pair copulations produce genetically diverse offspring (Williams 1975; Gladstone 1979). This explanation may not be as applicable to a species such as the Atlantic Puffin which raises only a single young per year. It is also possible that a female may benefit from extra-pair copulations by being fertilized by a genetically superior male (Trivers 1972; Mineau and Cooke 1979), or that she may be insured of laying fertile eggs in case her mate is sterile (Buitron 1983). However, because copulation occurs on the water, it may be difficult for a female puffin to assess the quality of other males and their burrows.

It has been suggested that participation by females in extra-pair copulations may function as an anti-infanticide adaptation (Crook and Shields 1985). A female who copulates with several males, and whose mate dies, may benefit if one of those males has fathered some of the offspring and assists in raising them rather than killing them. Given that copulation occurs on the water, such adaptations are unlikely in puffins, as it is probable that a male who secures an extra-pair copulation with a mated female has no association with that female's burrow.

It has also been proposed that females engaging in extra-pair copulations may risk desertion by mates (Trivers 1972; Dawkins 1976). In Ring Doves

(*Streptopelia risoria*), males showed less courtship and more aggression towards females that had prior exposure to other males than towards females that had no exposure (Erikson and Zenone 1976). Desertion by the male could be disadvantageous to a female puffin's long-term as well as short-term success, if, as discussed above, it is possible that by retaining the same mate she will retain the same burrow. This assumes that the burrow is a suitable one. It should be noted, however, that there is no direct evidence that participation by female puffins in extra-pair copulations may result in desertion by mates.

In terms of the ability of female puffins to provide confidence of paternity by successfully rejecting other males, those who are unwilling to participate in extra-pair-copulations are probably capable of resisting such attempts. Copulation occurs on the water while the male stands upright on the female's back; an unwilling female can simply dive or swim away. Often a male was rejected several times and then turned his attention to another female or drifted away. When apparently successful copulations did occur, the birds were paired throughout the observation period and the female appeared to be responsive. This would indicate that although extra-pair copulations are attempted, they are rarely successful. Thus female puffins may provide confidence of paternity by rejecting the solicitations of other males, in which case selection for mate-guarding in male puffins should be fairly weak.

When present at the colony during pre-laying, pairs of puffins alternate between time on the slope where courtship, resting, maintenance and defense of the burrow occurs, and time on the water where resting, feeding, courtship, and copulation occurs. In order for mates to remain in contact once they leave the slope, they should depart together, whereas their synchronous arrivals may indicate that they had been paired on the water. The fact that neither sex showed a greater propensity to follow the other during the pre-laying period when the arrival and departure of mates together was most frequent, suggests that they may be equally interested in maintaining proximity. This may be due to relaxed

mate-guarding in the male as well as an attempt by the female to contribute to pair-bond maintenance. Such an attempt by the female may be advantageous if retention of a mate guarantees retention of a burrow site. For the same reason, females may provide confidence of paternity by successfully avoiding other males.

Conclusions

Differences in time allocation to parentally related behaviour do not appear to be very great in male and female Atlantic Puffins. However, there is a difference in the patterns of parental care, and in the roles of the sexes towards the young. Females spent greater time in egg and chick related activities, while males spent greater time in burrow-site related activities. In terms of reproductive effort, the female performed slightly more incubation and provided more chick meals, parental activities which constitute short-term breeding effort. These may also represent long-term effort if the quality of investment a female provides one year influences a male's tendency to remate with her. The greater time spent on the slope by the male may represent both short and long-term breeding efforts. Providing nest-material and protecting the chick may increase his immediate reproductive success, whereas maintenance and defense of the burrow site may increase his future reproductive success. Although male behaviour patterns on the slope may help explain his greater time there, time on the slope comprised only a small proportion of total time.

In terms of Triver's model that females should invest slightly more than males, it is possible that the greater time that males spent on the slope and in site-related activities offsets the greater time that females spent in chick-related activities. However, direct measurements of the energetic costs of each activity are required in order to adequately compare male and female parental investments.

Successful extra-pair copulations appear to be uncommon in puffins. Mate-guarding may be less developed than it is in other species because females may provide confidence of paternity by successfully rejecting the solicitations of other

males. It is suggested that the development of mate-guarding in a given species should be considered in terms of the ecological constraints on the potential for extra-pair copulations. It may be adaptive for female puffins to reject other males if it helps to maintain the pair-bond and reduces the risk of desertion by the male.

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Table 1: Number of burrow maintenance activities, time(hr) on slope, and rate of burrow maintenance activities (number per hr on slope) by each sex for 14 pairs during the pre-laying and incubation stages.

Pair	Number		Time(hr) on slope		Number per hr on slope	
	Females	Males	Females	Males	Females	Males
1	16	13	4.8	27.2	3.4	0.5
2	18	31	9.8	21.4	1.8	1.4
3	41	50	10.9	33.4	3.7	1.5
4	14	44	19.3	18.2	0.7	2.4
5	18	46	12.9	18.9	1.4	2.4
6	8	25	6.5	13.4	1.2	1.9
7	12	20	11.4	22.3	1.0	0.9
8	14	27	5.2	22.1	2.7	1.2
9	16	26	13.4	40.0	1.2	0.6
10	27	13	22.1	32.7	1.2	0.4
11	18	18	4.9	28.1	3.7	0.6
12	15	34	10.7	41.4	1.4	0.8
13	23	36	10.4	21.8	2.2	1.6
14	8	29	12.4	26.6	0.6	1.1
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Total	248	412	154.7	367.5	26.4	17.3
X±SD	17.71±8.41	29.43±11.68	11.05±5.08	26.25±8.21	1.89±1.10	1.24±0.67

Table 2: Number of aggressive interactions, time(hr) on slope, and rate of aggressive interactions (number per hr on slope) by each sex for 14 pairs.

Pair	Number		Time(hr) on slope		No. per hr on slope	
	Females	Males	Females	Males	Females	Males
1	2	8	8.93	37.77	0.22	0.21
2	1	3	9.80	21.37	0.10	0.14
3	1	8	10.93	33.40	0.09	0.24
4	1	6	28.67	33.33	0.03	0.18
5	7	9	16.40	24.87	0.43	0.36
6	1	2	11.67	25.50	0.09	0.08
7	2	16	16.43	47.07	0.12	0.34
8	1	8	13.80	43.57	0.07	0.18
9	1	4	17.37	58.10	0.06	0.07
10	7	9	31.53	67.63	0.22	0.13
11	0	10	9.30	50.30	0.00	0.20
12	4	7	15.07	63.63	0.27	0.11
13	0	12	15.77	40.63	0.00	0.30
14	5	21	17.43	32.03	0.29	0.66
<hr/>						
Total	33	123	223.10	576.20	1.99	3.20
$\bar{x} \pm SD$	2.36 \pm 2.41	8.79 \pm 5.63	15.94 \pm 6.73	41.37 \pm 14.51	0.14 \pm 0.13	0.23 \pm 0.15

Table 3: Number (and percent) of each food type delivered by males and females.

	FOOD TYPE					
	<i>Mallotus villosus</i>	<i>Gadus morhua</i>	<i>Ammodytes</i> spp.	<i>Peronotus irianthus</i>	Unknown	Total
	# (%)	# (%)	# (%)	# (%)	# (%)	# (%)
Males	435 (42)	162 (52)	7 (35)	4 (57)	131 (41)	739 (44)
Females	594 (59)	152 (48)	13 (65)	3 (43)	189 (59)	950 (56)
Total	1029 (61)	313 (19)	20 (1)	7 (<1)	320 (19)	1689 (100)

Table 4. Mean number of meals per day, mean length and mean number of fish per meal, and mean number of *Mallotus villosus* per total number of fish delivered by each sex. Means are reported \pm S.D.

	\bar{X} no. of meals per day*	\bar{X} length of fish (cm)	\bar{X} no. of fish per meal	\bar{X} no. <i>Mallotus</i> <i>villosus</i> per total no. fish
Males	1.99 \pm 1.93	10.6 \pm 3.0	1.60 \pm 1.50	0.61 \pm 0.19
Females	2.55 \pm 2.34	10.5 \pm 2.8	1.60 \pm 1.40	0.64 \pm 0.17

* Includes data from dawn to dusk watches only.

Table 5. Number (and percent) of times males solicited
1 to 6 females during a 10-minute watch.

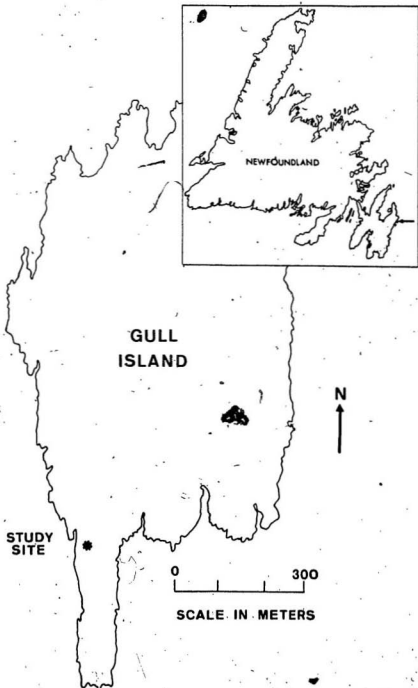
No. females solicited per 10-minute watch	No. (%)
1	34 (81)
2	11 (20)
3	5 (9)
4	2 (3)
5	3 (5)
6	1 (2)
Total	56 (100)

Table 6. Number (and percent of total) successful and unsuccessful mounting attempts when males solicited 1 to 6 females during a 10-minute watch.

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

Figure 1.

Map of Gull Island showing location of study site, and inset showing location of Gull Island in Newfoundland.



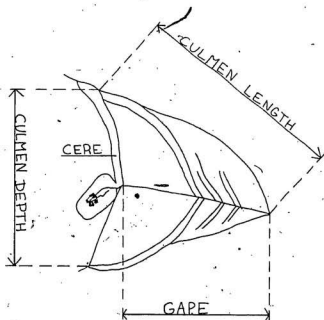


Figure 2.

Diagram of three bill measurements used to sex study birds. Gape was taken from the bill tip along the cutting edge of the mandibles to the anterior edge of the cere; culmen depth was taken from the dorsal edge of the bill anterior of the cere to the base of the bill; and culmen length was taken from the dorsal edge anterior of the cere to the bill tip.

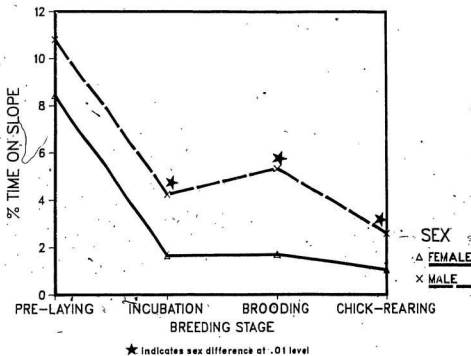


Figure 3.

Percent time on the slope for each sex for four stages of the breeding season.

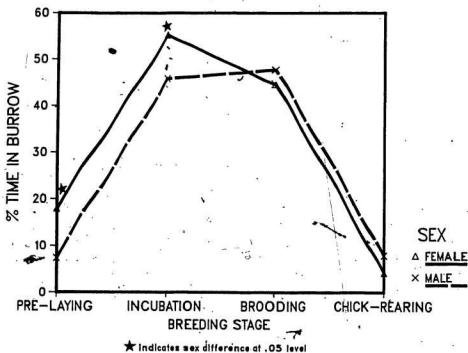


Figure 4.

Percent time in the burrow for each sex for four stages of the breeding season.

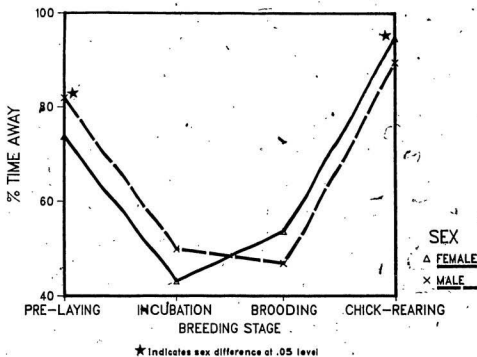


Figure 5.

Percent time away for each sex for four stages of the breeding season.

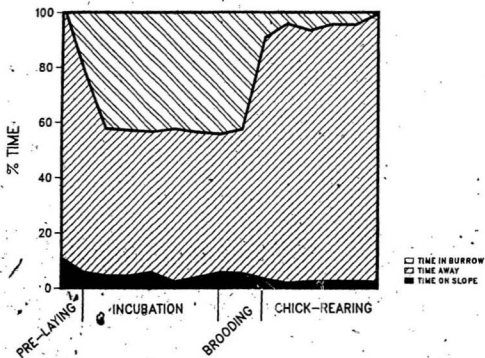
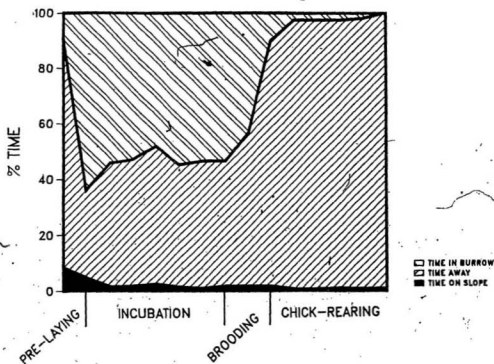


Figure 6.

Time budget for males for pre-laying through chick-rearing.



- Figure 7.

Time budget for females for pre-laying through chick-rearing.

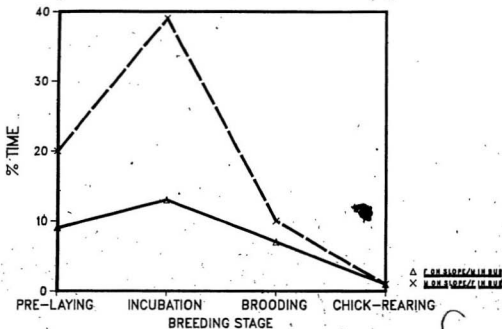


Figure 8.

Percent time the male spent on the slope while the female was in the burrow (broken line) and percent time the female spent on the slope while the male was in the burrow (solid line).

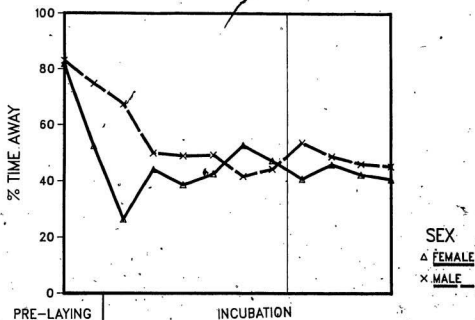


Figure 9.

Percent time that males (broken line) and females (solid line) were absent over three to four day periods during the pre-laying and incubation stages. Vertical reference line marks that time at which most females were estimated to have laid.

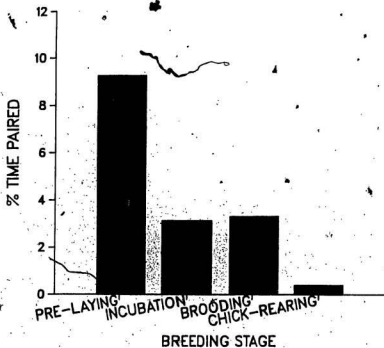


Figure 10.

Percent time mates were paired in the burrow and on the slope for four stages of the breeding season.

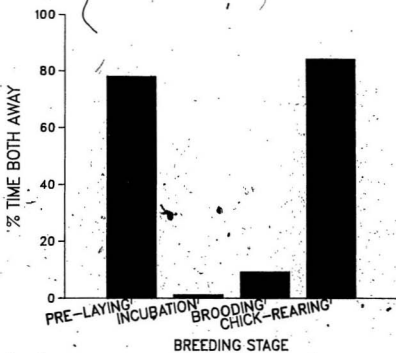


Figure 11.

Percent time both mates were away for four stages of the breeding season.

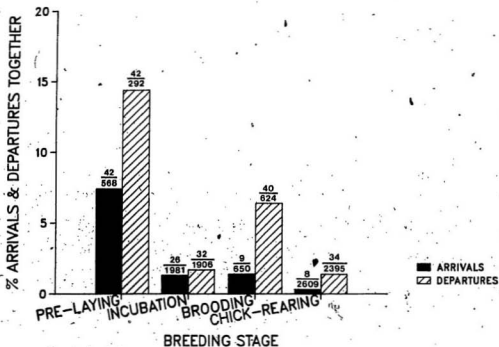
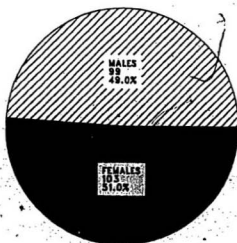


Figure 12.

Percent arrivals and departures of mates together for four stages of the breeding season. Fractions at top of columns indicate the number of arrivals and departures of mates together per total number of arrivals and departures of birds both singly and together.



FEMALE = 7.38 ± 2.44
MALE = 7.07 ± 2.89

Figure 13.

Number and percent of total that each sex arrived and departed first when mates arrived and departed together during the pre-laying stage.



