

# FIDELITY TO NEST SITE AND MATE IN FIORDLAND CRESTED PENGUINS

## *EUDYPTES PACHYRHYNCHUS*

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### SUMMARY

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Fiordland Crested Penguins *Eudyptes pachyrhynchus* are the least gregarious of the crested penguins, breeding in caves, burrows, and under dense vegetation along the coast of Fiordland, New Zealand. A population on Open Bay Island was monitored, with varying degrees of intensity, from 1988 to 1995. During this period, 175 adults were banded in three semi-contiguous areas and their returns to 46 mapped nest sites were recorded. In 1989, reproductive success to the crèche stage was also known. Return rates (used here as minimum annual survival estimates) ranged from 53–83% with means of 71% for both sexes. Mean nest fidelity averaged 76% for males and 72% for females with slightly lower values for mate fidelity (64% for males, 62% for females). Neither of these parameters differed significantly between the sexes. In 1989, penguins of both sexes that returned to a 1988 nest site exhibited higher reproductive success than those that nested at a new site. A similar, but non-significant, trend was apparent for mate fidelity. By contrast, reproductive success in 1989 did not result in a higher likelihood of returning to the same nest or mate in 1990. Females were more likely to 'separate' (i.e. mate infidelity when both members of the previous pair were present) than males (33% vs. 13%) and both sexes were more likely to separate if they had previously failed to raise a chick. Fifteen cases of mate switching occurred within years and all but one involved two females and a single male. Three of these followed the return of a male's previous mate. We compare these patterns to similar published data for other bird species and discuss their conservation implications.

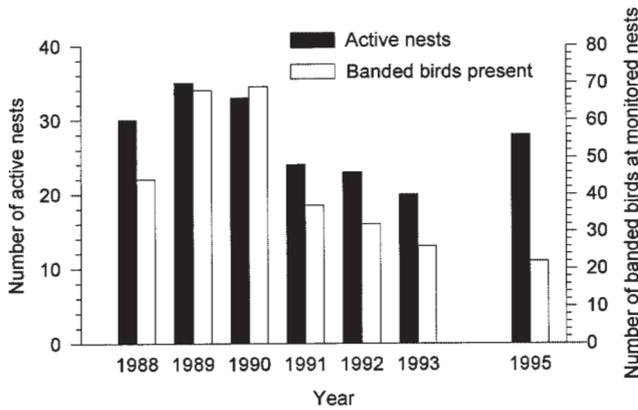
### INTRODUCTION

Among birds, already notable for strong tendencies to philopatry and mate fidelity, penguins are viewed as a quintessentially monogamous group. Life-history characteristics of longevity, low reproductive output and bi-parental care may contribute to the fidelity to nest and mate that is characteristic of penguins and many other seabirds. Benefits accrued by inter-annual fidelity (see Rowley 1983, Mock & Fujioka 1990 for reviews) may include increased reproductive synchrony, reduced costs of acquiring a territory and mate, and assurance of a mate's previous reproductive experience or success. Together these advantages and others may heighten the reproductive success of individuals that return to a previous partner and nest (reviewed by Rowley 1983, Choudhury 1995), although not all species studied show such clear benefits (e.g. Freed 1987, Haig & Oring 1988). Conversely, mate fidelity may stem secondarily from strong site philopatry in both sexes, have no immediate advantages of its own, and may actually have costs if, for example, it limits opportunities for extra-pair parentage by males (Birkhead & Møller 1992).

Although penguins exhibit strong social monogamy and both sexes are philopatric, substantial variation exists in the degree to which adults are faithful to nest and mate, both within and

among species (Williams & Rodwell 1992). Adélie Penguins *Pygoscelis adeliae* typically re-pair with their old partner if it is present (Ainley *et al.* 1983), but abandonment of one mate in order to relay earlier with another is likely more common in the unusual 14-month breeding season of King Penguins *Aptenodytes patagonicus* (Cooper *et al.* 1992). Anecdotal reports suggest that mate and nest fidelity are high in crested penguins *Eudyptes* spp. (Richdale 1950, Warham 1963, Carrick & Ingham 1970) and quantitative work on Macaroni Penguins indicates between-year rates of mate fidelity ranging from 71–79% (Williams & Rodwell 1992).

Some data exist on rates of fidelity in penguins, but less is known about its causes and consequences. In Adélie Penguins, re-pairing is less likely following asynchronous returns to the colony, although late-returning females may drive off the new partners of their mates (Davis & Speirs 1990). Although asynchronous returns in other bird species may promote mate switching both within and among seasons (e.g. Coulson & Thomas 1983), inter-annual mate switching seems often to stem from previous reproductive failure (Choudhury 1995). Such a link has also been observed in Little Penguins *Eudyptula minor* and Macaroni Penguins *Eudyptes chrysolophus* (Reilly & Cullen 1981, Williams & Rodwell 1992).



**Fig. 1.** The number of banded Fiordland Crested Penguins and active nests recorded at 46 nest sites monitored on Open Bay Island between 1988 and 1995.

Almost nothing is known about fidelity patterns in Fiordland Crested Penguins *E. pachyrhynchus*, a secretive species inhabiting the southwest coast and associated islands of Fiordland, New Zealand. Here we compile data pertaining to mate and site fidelity in this species collected over seven seasons on Open Bay Island (43°50'S, 168°53'E). With these data, we attempt to:

1. determine average rates of mate and nest site fidelity for both sexes;
2. assess the relationships between mate or nest site fidelity and reproductive success; and
3. identify the conditions associated with intra-annual mate-switching.

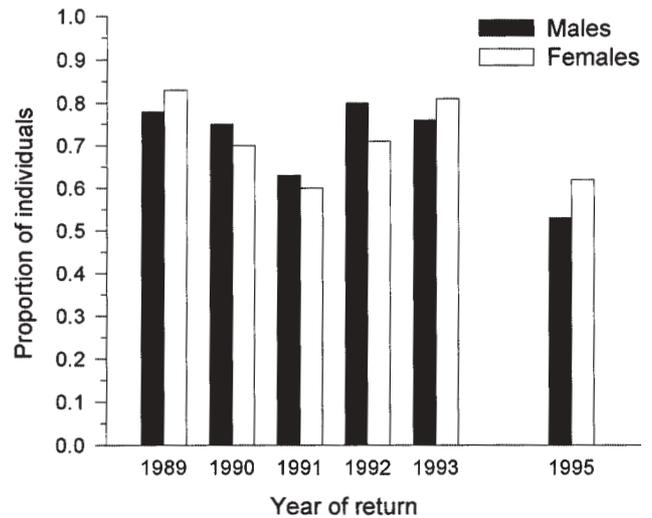
## METHODS

### Censuses

Fiordland Crested Penguins on Open Bay Island breed in caves, burrows, or beneath dense vegetation, generally at lower densities than their congeners. As part of other studies (Phillipson 1991, Murie *et al.* 1991, St Clair 1992, Studholme 1994) we banded 175 adults at or near their nests between 1988 and 1995 and counted variable numbers of mapped nests. Nests were visited daily during egg laying and early chick rearing in 1988 and 1989 (late July to early October), and sporadically during that time period in 1990 through 1995, except in 1994. During censuses, band numbers and nest contents were recorded when possible, although risk of predation by Weka *Gallirallus australis* (St Clair & St Clair 1992) sometimes precluded close approach. Forty-six nests were monitored during all seven seasons and the following results are restricted to these nests.

### Terminology

For the purposes of the analyses that follow, we consider *return rate* to be the proportion of banded birds associated with one of the monitored nests known to be alive in year  $x$  that is also known to be alive in year  $x + 1$ . For example, a bird that was banded at a nest in 1990 and next observed in 1995, is assumed to have 'returned' in the intervening years, even if it did not appear at one of the monitored nests. Thus, return rates reflect minimum survival estimates rather than nest occupancy. We use *mate fidelity* to be the proportion of birds observed in a given year that paired again with the partner with



**Fig. 2.** Annual return rates (the proportion of banded birds that were known to be alive in the year indicated that were also known to be alive in the preceding year) for male and female Fiordland Crested Penguins.

whom they were last observed to nest. Similarly, *nest fidelity* is the proportion that returned to their previous nest site, and *mate-switching* refers to changes in mates either within or between successive years. *Separation* is used to describe mate switches that occurred between years when the previous partner was also observed in the year of the change. We consider pairs to be birds that were observed together at a nest site, whether or not they had laid eggs. For 1989, reproductive success is defined as the production of a chick that reached crèche age (usually about 20 days old).

### Limitations

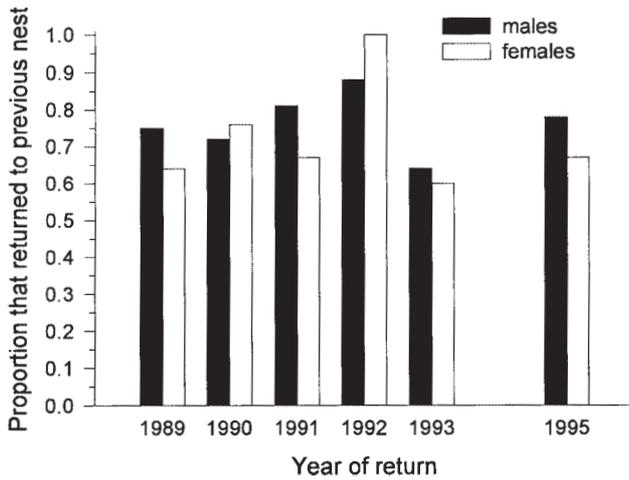
We monitored only three areas in every year of the study (hut, knoll, and penguin gut) and did not systematically search nearby areas for banded birds. Combined with differences in banding and census intensity across years, it is likely that some banded birds were not observed, so values describing return rates and mate fidelity are minimum estimates.

### Statistics

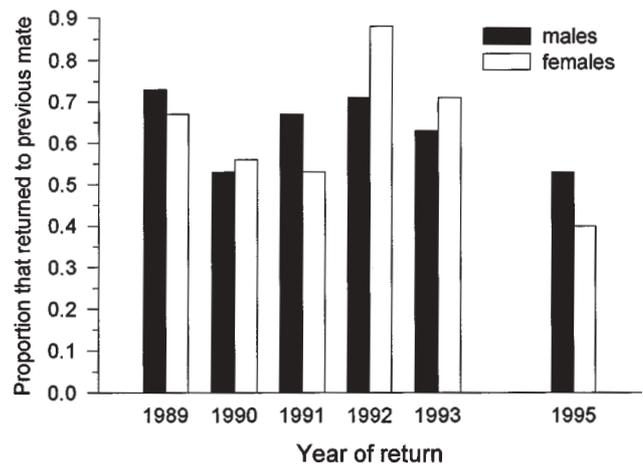
Comparisons of data with pooled years (between sexes and fidelity types) are based on paired *t*-tests of arcsine-transformed proportions. Within-year comparisons consist of *G*-tests of  $2 \times 2$  contingency tables. Means are followed by standard deviations where appropriate. Due to the small sample sizes involved and associated loss of statistical power (Cohen 1988), we consider relationships to have potential biological significance when  $P \leq 0.10$ .

## RESULTS

Banding effort was concentrated in the early years (1988–1990) and, along with differences in the number of active nests (Fig. 1) and intensity of sampling, produces variation in the sample sizes that follow. Among the 46 monitored nest sites, the number that was active decreased by 20% between 1989 and 1995. Return rates, based on the known survival of banded birds from these focal nests ranged from 0.53 to 0.83 (Fig. 2) and were remarkably similar for males (mean  $\pm$  SD =



**Fig. 3.** Annual rates of return to the previous nest site for male and female Fiordland Crested Penguins at 46 monitored nest sites.



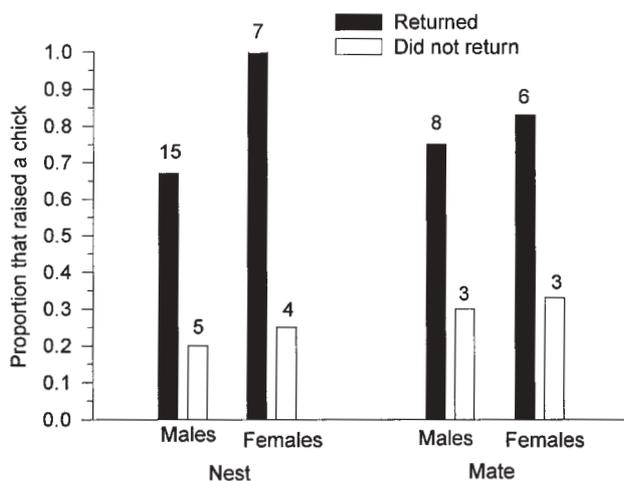
**Fig. 4.** Annual rates of return to the previous mate for male and female Fiordland Crested Penguins at 46 monitored nest sites.

0.71±0.11) and females (mean = 0.71±0.09;  $t = 0.11$ ,  $df = 5$ ,  $P = 0.92$ ). Males and females also exhibited similar nest fidelity (Fig. 3; males = 76±0.08%; females = 72±0.15%;  $t = 0.16$ ,  $df = 5$ ,  $P = 0.88$ ) and mate fidelity (Fig. 4; males = 64±0.11%; females = 62±0.17%;  $t = 0.18$ ,  $df = 5$ ,  $P = 0.87$ ). Mate infidelity stemming from separation was higher for females (mean = 0.33±0.18) than for males (mean = 0.13±0.21;  $t = 2.41$ ,  $df = 5$ ,  $P = 0.061$ ).

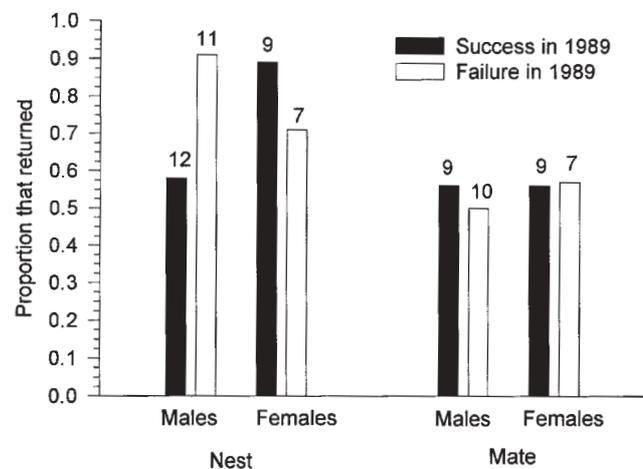
There were some apparent relationships between fidelity and reproductive success. Penguins that returned to their previous nest in 1989 were more likely to raise a chick to the crèche stage than those that did not (Fig. 5) among both females ( $G = 7.59$ ,  $df = 1$ ,  $P = 0.006$ ) and, to a lesser extent, males ( $G = 3.43$ ,  $df = 1$ ,  $P = 0.064$ ). Mate fidelity in 1989 appeared to be less important in determining later reproductive success for both sexes (Fig. 5; females,  $G = 2.23$ ,  $P = 0.14$ ; males,  $G = 1.60$ ,  $P = 0.21$ ). By contrast, reproductive success in 1989 did not result in higher fidelity for either sex in 1990 (Fig. 6). Indeed, males appeared to be more likely to return to their

previous nest site if they failed in 1989 ( $G = 3.40$ ,  $P = 0.065$ ) although the other contrasts were almost equal in proportions ( $G < 0.79$ ,  $P > 0.37$  for each). When causes of infidelity (i.e. non-return vs. separation) were separated, a different pattern emerged: both sexes were more likely to separate from a previous partner in 1990 if they had failed to produce a chick in 1989, although this effect was more pronounced for females ( $G = 9.56$ ,  $P = 0.002$ ) than for males ( $G = 3.45$ ,  $P = 0.06$ ). Thus, prior reproductive success seemed to influence mate fidelity, but only when there was a choice of repairing with a previous partner that had also returned.

Fifteen cases of intra-annual mate switching were observed. In all but one of these, one female was apparently displaced by another (two females and one male were observed at the nest). In three of these cases, the second female was reclaiming a previous mate and site, in four cases the second female was unbanded (and thus of unknown history) and she displaced a former neighbour of the resident male, in one case an unknown bird replaced a former female resident, and in the



**Fig. 5.** The relationship between fidelity to a 1988 nest or mate and reproductive success in 1989 for male and female Fiordland Crested Penguins. The number of individuals is indicated above each bar.



**Fig. 6.** The relationship between 1989 reproductive success and 1990 fidelity to nest site and mate for male and female Fiordland Crested Penguins. The number of individuals is indicated above each bar.

other seven cases we did not know the circumstances of the switch. In seven of 15 cases where the timing of the switch was known, all occurred well prior to egg-laying except for a single case that occurred two days before the displaced female laid an egg at another site. Of the 15 displaced females, only four were known to have bred later at another site.

## DISCUSSION

### Patterns of return, fidelity, and reproductive success

Rates of nest occupancy across the seven seasons of the study reflect the downward population trend suspected by individual researchers. Four new nests were observed among the 46 monitored sites in 1995, suggesting that the population may be stabilizing. Estimated return rates of 71% were similar to the 75% reported for Macaroni Penguins (Williams & Rodwell 1992). Our estimate of the proportion of birds that were alive but failed to return was also similar for both females (18%) and males (19%) to the estimate of 14% for Macaroni Penguins. Thus, in both species, it appears that mature adults sometimes miss one or more years between breeding attempts, though the causes of these breaks are unclear.

Mate fidelity appeared to be more variable and slightly lower than the 71–79% range that has been reported for Macaroni Penguins (Williams & Rodwell 1992). Most mate switches resulted from the failure of one member of a previous pair to appear in the subsequent season. The proportion of between-year mate switches stemming from separation fell within the range of 7–44% reported for other penguin species (see Rowley 1983 for a review, also Williams & Rodwell 1992). However, in Fiordland Crested Penguins, females were more likely to separate than males (33 vs. 13%), suggesting that females are more plastic in their returns to former mates. Nest fidelity tended to be slightly higher than mate fidelity for both sexes. This difference may stem from a tendency to return to the nest as a means of reuniting with a mate (*sensu* Rowley 1983). In Adélie Penguins, 90% of males appear to return to their previous site and court any female that happens by (Davis & Speirs 1990). Female Adélie Penguins, by contrast, were predicted to return to their old site, but to pair with a nearby male if their previous mate has failed to return (Davis & Speirs 1990). Fiordland Crested Penguin females may modify this rule by returning to their old site, but being less likely to stay if it is occupied by a partner with whom they were previously unsuccessful.

As for many other species, returning to a previous nest or mate appears to have reproductive advantages for Fiordland Crested Penguins. Individuals that returned to a 1988 mate or nest in 1989 had higher reproductive success than those that paired anew, although apparent differences were statistically significant only for nest fidelity. In this and other philopatric species, patterns of mate and nest fidelity are necessarily correlated and it is difficult to separate their effects on reproduction (but see Morse & Kress 1984 and Fairweather & Coulson 1995 for examples). Associations between mate fidelity and subsequent reproductive success have been reported for many other seabirds (e.g. Mills 1973, Coulson & Thomas 1983, Ollason & Dunnet 1988, Bradley *et al.* 1990, Harris *et al.* 1996). However, the apparent links between fidelity and reproductive success can be confounded by effects of age and experience (e.g. Coulson & Thomas 1983, Freed 1987). Moreover, fidelity and reproductive success may both depend on bird quality (Perrins & McCleery 1985). Clearly, more work is needed

to identify the causes of a relationship between fidelity and subsequent reproductive success in Fiordland Crested Penguins.

As a complementary causal relationship, previous reproductive success was a limited predictor of subsequent fidelity. Females and, to a lesser extent, males, were more likely to separate from a previous partner if they had experienced reproductive failure in 1989. Low reproductive success is among the most frequently cited causes of separation among diverse bird species (reviewed by Choudhury 1995) and females may often initiate the separation (Coulson & Thomas 1983). When low reproductive success promotes mate switching, separating birds may be merely incompatible (Rowley 1983) or one may be of markedly better quality than the other and seeks a better mate in subsequent seasons (Ens *et al.* 1993). Despite substantial reproductive consequences, inter-annual mate switching in colonial species may also stem from asynchronous departure (and thereby subsequent arrival) of failed breeders, rather than from reproductive failure *per se* (Coulson & Thomas 1983). Separation can also occur for reasons unrelated to reproductive success. At least one separation in 1990 appeared to be caused by the destruction of a nest during the preceding winter.

Within-year mate switching may occur when females usurp their previous site from a new female (Davis & Speirs 1990). Such displacement accompanied at least three of the 15 cases of intra-annual mate switches that we observed. Displaced females were generally unlikely to nest again elsewhere, suggesting that displacement is a costly setback for females. Later laying dates and attendant problems with breeding synchrony may limit opportunities to relay, but males may also resist pairing with previously-mated females to avoid cuckoldry. Of the four females that relaid, one laid an egg within two days of leaving her first nest. Because fertilization occurs three to six days before laying (St Clair *et al.* 1995), this switch may have resulted in an extra-pair offspring in the nest of the new male. Although no extra-pair parentage was detected among 24 fingerprinted families in Fiordland Crested Penguins (I.G. McLean unpubl. data), extra-pair fertilizations are likely when mate switches occur during the laying period.

### Conservation implications

The patterns of return, fidelity and reproductive success reported here have some potential implications for the conservation of this little-known, vulnerable species. First, the population on Open Bay Island appears to have decreased substantially although it may have stabilized slightly in 1995. Extensive surveys by McLean *et al.* (1997) suggest that the total annual breeding population of this species is probably about 2500–3000 pairs, mostly in discrete sub-populations on the offshore islands of Fiordland. It is important to know the extent and causes of this decrease, particularly because of the relative isolation of breeding populations. Identifying the factors that cause birds to miss breeding seasons deserves similar attention. Second, the high philopatry shown by both sexes indicates that local habitat disturbance is likely to severely curtail reproductive success because birds may lack the flexibility to breed elsewhere. For this reason, areas where nest predation may be concentrated (e.g. by introduced mammals on the mainland and introduced Weka on Open Bay Island) should be identified and protected. Finally, the negative effect of reduced nest and mate fidelity on reproductive success, combined with increased separation following breeding failure, attest to the importance and complexity of disturbance

factors. For example, egg loss stemming from introduced predators or human disturbance may reduce breeding success directly in the season of its occurrence and cause further problems in subsequent seasons through heightened mate separation.

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