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ANNUAL VARIATION IN RETURN RATE, MATE AND NEST-SITE FIDELITY IN BREEDING GENTOO AND MACARONI PENGUINS[1]

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Abstract. Annual variation in return rate of breeding birds, mate and nest-site fidelity was studied in the resident Gentoo (*Pygoscelis papua*) and migratory Macaroni (*Eudyptes chrysolophus*) Penguin from 1986 to 1990 at Bird Island, South Georgia (54°S, 38°W). Return rates (proportion of birds breeding in year x which returned to breed in year $x + 1$) varied significantly between years: 20–79% and 35–73% in Gentoo and Macaroni Penguins, respectively. Lowest values in both species (in 1987) followed a severe, prolonged winter and were associated with delayed onset of breeding and decreased breeding population size. Decreased return rate was caused by (a) extensive non-breeding in adult birds: 25% of Gentoo and 14% of Macaroni Penguins which bred in 1986 were alive but failed to breed in 1987, and (b) increased adult mortality. Mate fidelity also varied between years in Gentoo Penguins (0–89%) with no birds retaining the same mate in 1987. In contrast, in Macaroni Penguins mate fidelity was high (71–79%) in all three years. This difference may be due to the shorter pre-breeding period, greater synchrony of arrival and pattern of continuous nest attendance in Macaroni Penguins. Failed breeders were more likely to change mate in Macaroni, but not Gentoo, Penguins but there was no difference in subsequent breeding success or mean laying date between new and established pairs in either species. Both species showed a high degree of nest-site fidelity in all years (Gentoo, 89–100%; Macaroni 69–87%). Females were more likely than males to change nest-site following mate change. Intra-season pair fidelity was high in Macaroni Penguins (74–78%) between breeding and the post-nuptial molt. However, the post-nuptial molt was also an important period for formation of new pair-bonds in this species. Despite marked differences in breeding chronology and life-history patterns in these two species, return rates, mate and site fidelity were only markedly dissimilar in one of the three years studied.

Key words: *Penguins;* Eudyptes chrysolophus; Pygoscelis papua; *return rates; mate and nest-site fidelity.*

INTRODUCTION

Mate fidelity, i.e., mating for a subsequent breeding attempt with the same partner, is an important component of reproductive success in many long-lived, monogamous birds (Rowley 1983). Numerous studies have shown that reproductive success is greater in pairs which re-unite in successive seasons than in newly established pairs (e.g., Mills 1973, Coulson and Thomas 1983, Ollason and Dunnet 1988, Bradley et al. 1990). Advantages of maintaining the pair-bond between breeding seasons may include mate familiarity (Bradley et al. 1990), better coordination of the breeding effort (Chardine 1987, Davis 1988) and simply avoiding the cost of having to compete again for a new mate (Ainley et al. 1983). Despite the importance of mate fidelity to reproductive success, however, little attention has been given to factors which act against maintenance of pair bonds between years, e.g., asynchrony of return, habitat stability and high adult mortality (Rowley 1983). Furthermore, there are few published data for any species on the extent, cause or effect, of inter-annual variation in reproductive parameters such as mate or site fidelity (Boekelheide and Ainley 1989).

All penguin (Spheniscidae) species are long-lived and monogamous (Croxall 1984), but they appear to show marked inter- and intra-species variation in mate and site fidelity which may be related to variation in the environmental conditions each population experiences (Richdale 1957, Ainley et al. 1983, Trivelpiece and Trivelpiece 1990). In this paper we present data on annual variation in return rate, and mate and site fidelity in two sympatric penguin species—the Gentoo Penguin (*Pygoscelis papua*) and Macaroni Penguin (*Eudyptes chrysolophus*)—over a four-year period. Inter-annual and inter-specific differences are interpreted in terms of the species'

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life-history strategies and population dynamics. Gentoo Penguins are resident at South Georgia throughout the year and show high but variable seasonal reproductive success, whereas Macaroni Penguins are migratory and show lower but less variable seasonal reproductive success (Croxall et al. 1988).

STUDY AREA AND METHODS

Fieldwork was carried out between October 1986 and March 1990 at Bird Island, South Georgia (54°00'S, 38°02'W). Austral summers are referred to by the year in which they commence. Detailed studies were carried out at the Johnson Cove Gentoo Penguin colony (3,777–5,532 breeding pairs depending on year) and the Fairy Point Macaroni Penguin colony (946–1,174 breeding pairs). Study nests of Gentoo Penguins were distributed throughout the whole colony area. Those of Macaroni Penguins were mostly within 3 m of the colony edge. This was a potential source of bias because an "edge effect" has been reported in colonies of other species of penguins (Tenaza 1971, Spurr 1975, Ainley et al. 1983, but see Oelke 1975). However, 65% of nests used to collect data in this study were "central" as defined by Ainley et al. (1983) and Oelke (1975), i.e., with at least one nest between them and the periphery.

Breeding adults were marked with numbered flipper bands during incubation, and were sexed using a combination of (1) bill size measurements, (2) comparison of bill and body size between birds of a pair, males being larger, heavier billed birds, and (3) in Macaroni Penguins, the pattern of incubation shifts (Downes et al. 1959, Williams 1990, Williams and Croxall 1991). Study nests were visited every 2–3 days during egg-laying, incubation and chick-rearing to obtain data on laying date, band numbers of the pair, nest location and breeding success. Birds which laid eggs were described as "breeders." Due to the difficulty of following large numbers of chicks after creching, breeding success was defined as rearing one or more chicks to creching age (29 days in Gentoo Penguins and 23 days in Macaroni Penguins). Creching was defined as the first day that neither parent was in attendance at the nest guarding the chick.

Breeding population estimates for the study colonies were obtained as described in Williams (1990) and Williams and Croxall (1991). In addition, the breeding population for the adjacent large (main) Macaroni colony was estimated in each year as described in Croxall and Prince (1979).

The return rate of previous-breeders was defined as the proportion of birds breeding in year x which returned and bred in year $x + 1$. Birds were considered to be nest-site faithful if they nested within 1 m of the previous years' nest-site. Non-breeding Macaroni Penguins returning to the colony were faithful to their old nest-site, remained in attendance for several days and were therefore likely to be recorded in their non-breeding year. In contrast, non-breeding Gentoo Penguins only attended the colony at night, spending the day at sea, and were unlikely to be recorded in their non-breeding year (T. D. Williams, pers. observ.). Therefore, "non-breeders" included any breeding bird banded in one year (year x) which was recorded alive in year $x + 2$, but which was not recorded in year $x + 1$. As some non-breeders alive but not recorded in year $x + 1$ may have died before year $x + 2$ the estimate of non-breeders will represent a minimum figure. In 1988 and 1989, Macaroni Penguin study nests were also visited regularly during the post-nuptial molting period and band numbers, sex and nest location of molting birds recorded. This was not possible for Gentoo Penguins because they have a less synchronous period of post-nuptial molt and show low nest-site fidelity between breeding and molt (T. D. Williams, pers. observ.). The estimated rate of band loss (see Williams (1991) for details of methods) in Gentoo Penguins over one year was 6.1% ($n = 147$) and in two years in Macaroni Penguins was 2.6% ($n = 38$) and 0% ($n = 39$).

RESULTS

RETURN RATE AND MATE FIDELITY OF PREVIOUS BREEDERS

There was significant variation in return rate between years in both Gentoo ($\chi^2 = 100.7$, $P < 0.001$) and Macaroni ($\chi^2 = 49.7$, $P < 0.001$) Penguins (Table 1). In 1988 and 1989, 79% and 59% of Gentoo Penguins, and 70% and 73% of Macaroni Penguins, that had bred in the previous year returned and bred. In contrast, in 1987 only 20% and 35% of previously-breeding Gentoo and Macaroni Penguins respectively returned and bred. In 1987, 25% of previously-breeding Gentoo Penguins were non-breeders compared to only 3% and 2% respectively in 1988 and 1989. For Macaroni Penguins, 14% of

TABLE 1. Number and percentage of Gentoo and Macaroni Penguins breeding in one year (year x) which returned as breeders (Br) or non-breeders (NBr) in the following year (year $x + 1$), in relation to the percentage change in breeding population size (remaining birds were not recorded in year $x + 1$).

	Gentoo Penguin				Macaroni Penguin			
		n (%) returning as				n (%) returning as		
	n (year x)	Br	NBr	% popn. change	n (year x)	Br	NBr	% popn. change
1987	101	20 (20)	25 (25)	−19	94	33 (35)	13 (14)	−19[1] −18[2]
1988	222	175 (79)	7 (3)	+50	335	235 (70)	27 (8)	+22[1] +10[2]
1989	300	177 (59)	6[3] (2)	−7	301	220 (73)	6 (2)	−14[1] +7[2]

[1] Calculated for the study colony.
[2] Calculated for the Main colony.
[3] Minimum estimate because birds may still have been alive but not recorded after the end of the study.

previously-breeding birds returned as non-breeders in 1987 compared to 8% and 2% in 1988 and 1989 respectively.

Of 101 Gentoo Penguins breeding in 1986, 25 (25%) bred in 1988 but not in 1987, i.e., they missed one year. In contrast, of 222 breeders in 1987 only 6 (3%) missed one year, breeding in 1989 but not in 1988. Two birds (2%) which bred in 1986 failed to breed in 1987 and 1988 but bred again in 1989, i.e., they missed two years. In Macaroni Penguins, 9 of 94 (10%) birds breeding in 1986 missed one year (1987), breeding again in 1988, 4 (4%) missed two years, breeding again in 1989, and 3 (3%) did not breed for at least three years.

In 1988 and 1989, 89% and 72% respectively of Gentoo Penguins retained the same breeding partner as in the previous year but in 1987, no bird retained the same partner (Table 2). In Macaroni Penguins, the proportion of birds which retained the same breeding partner was 75, 71 and 79% in the three years. No Gentoo Penguin bred with the same partner in all four years (because all partnerships changed between 1986 and 1987). Of 28 Macaroni Penguins recorded in all four years, six (21%) bred with the same partner in each year. Over three years (1987–1989), 36% of Gentoo Penguins (n = 99) and 52% of Macaroni Penguins (n = 124) retained the same breeding partner.

"Separation" (i.e., where the partner of the previous year was known still to be alive) accounted for 3–38% of mate changes in Gentoo Penguins and 4–13% of mate changes in Macaroni Penguins (Table 2). In both species the highest value was recorded in 1987. Of 18 separations

TABLE 2. Mate fidelity and cause of mate change in Gentoo and Macaroni Penguins.

Species unknown	Year	n (pairs)	No change of mate from previous year n (%)	Mate change following		
				Separation (%)	Mate death (%)	(%)
Gentoo	1987	13	0 (0)	38	54	8
	1988	146	130 (89)	3	8	1
	1989	126	91 (72)	12	—[1]	16
Macaroni	1987	24	18 (75)	13	13	0
	1988	160	114 (71)	11	14	5
	1989	183	145 (79)	4	—[1]	17

[1] Not known because partner could still have been alive but not recorded after end of study.

TABLE 3. Reproductive success in previous year (year $x - 1$) for Gentoo and Macaroni Penguins which (a) returned as breeders, non-breeders, or were not recorded in the following year (year x), and which (b) paired with the same or a new partner in the following year.

		Gentoo Penguin		Macaroni Penguin	
Year	Status	n in year x	% breeding successfully in year $x - 1$	n in year x	% breeding successfully in year $x - 1$
1987	Not recorded	47	96	31	80
	Non-breeder	—	—	13	38
	Breeder	9	89	27	67
1988	Not recorded	40	48[1]	51	35[1]
	Non-breeder	—	—	18	22[1]
	Breeder	144	74	155	52
	Same ptnr.	110	76	88	64[2]
	New ptnr.	13	77	41	32
1989	Not recorded	82	52	55	38
	Non-breeder	—	—	—	—
	Breeder	153	63	174	50
	Same ptnr.	87	60	132	58[2]
	New ptnr.	31	71	32	19

[1] Significant difference between breeders and birds not recorded, and between breeders and non-breeders, χ^2-test, $P < 0.01$.
[2] Significant difference between birds which bred with the same partner and those which changed mate, χ^2-test, $P < 0.01$.

recorded for Macaroni Penguins, where complete subsequent histories were known, 11 males (61%) and 17 females (94%) bred in the year following separation (Fisher's-exact, $\chi^2 = 5.79$, $P < 0.05$), i.e., females were more likely to breed immediately following separation than males. The seven remaining males bred two years ($n = 4$), three years ($n = 3$) and more than three years ($n = 1$) after separation. In Gentoo Penguins ($n = 14$ divorces), all 14 males (100%) bred the year following separation but only 9 of 14 females (64%) did so.

RELATIONSHIP BETWEEN BREEDING SUCCESS, RETURN RATE AND MATE FIDELITY

Between birds which returned to breed and those which did not return (in year $x + 1$), there was no difference in reproductive success in the previous year (year x) for either Gentoo or Macaroni Penguins in 1987 and 1989 (Table 3). However, in 1988, for both species, previous breeders which did not return were significantly more likely to have failed the previous year than were birds which returned to breed (Gentoo, $\chi^2 = 9.80$, $P < 0.01$, Macaroni, $\chi^2 = 7.98$, $P < 0.01$).

Macaroni Penguins which retained the same partner between years were significantly more likely to have bred successfully the previous year compared to birds which changed mate, both in 1988 ($\chi^2 = 9.62$, $P < 0.01$) and 1989 ($\chi^2 = 16.15$, $P < 0.01$, Table 3). In Gentoo Penguins there was no difference in breeding success the previous year between birds which retained the same mate and those which changed mate (Table 3).

In the one year for which there were data (1988), there was no significant difference in breeding success following mate change compared to birds which retained the same mate (Table 4). Similarly, there was no difference in mean egg-laying date (relative to the population mean) for birds breeding with the same or a new partner, in Gentoo Penguins in 1988 (26.9 vs. 27.3 Nov., $t = 0.34$, $P > 0.50$) or in Macaroni Penguins in 1987 (24.8 vs. 25.1 Nov., $t = 0.22$, $P > 0.50$) and 1988 (22.0 vs. 22.8 Nov., $t = 0.66$, $P > 0.50$).

PAIR FIDELITY BETWEEN BREEDING AND MOLT IN MACARONI PENGUINS

Birds which bred in year x but failed to return to breed in year $x + 1$ were significantly less likely to have been recorded at molt in year x than

TABLE 4. Effect of change of mate on breeding success in Gentoo and Macaroni Penguins in 1988.

	Gentoo Penguin		Macaroni Penguin	
	Total n	n (%) breeding successfully	Total n	n (%) breeding successfully
Same mate	111	67 (60)	101	43 (43)
Different mate	13	5 (42)	41	21 (51)

TABLE 5. Number and percentage of (previously-breeding) Macaroni Penguins breeding or not recorded in one year (year x) which were recorded during molt in the previous year (year $x - 1$), and their status during molt.

	Status in year x			
	1988		1989	
	Breeder (n = 162)	Not seen (n = 45)	Breeder (n = 220)	Not seen (n = 78)
n (%) recorded molting in year $x - 1$	113 (70)	17[1] (38)	163 (74)	27[1] (35)
Status at molt in year $x - 1$				
with breeding partner of same year (%)	74		78	
with different partner (%)	12		12	
molting alone (%)	14		11	

[1] Significant difference between breeders and birds not subsequently seen, χ^2-test, $P < 0.01$.

birds which returned and bred (Table 5, 1988, $\chi^2 = 16.0$, $P < 0.01$; 1989, $\chi^2 = 37.8$, $P < 0.01$).

In 1987 and 1988, 74% and 78% of birds, respectively, were recorded molting with their breeding partner of that year, 11% and 14% respectively of breeding birds molted alone and the remainder molted with a different partner (Table 5). Of a total of 53 breeding birds which molted alone or with a different partner, 28 (53%) bred with a new bird, 14 (26%) bred with their old partner and 11 (21%) were non-breeders the following year (data pooled for 1987 and 1988). Of a total of 27 birds which molted with a new partner, 7 (26%) bred with that bird in the following year.

NEST-SITE FAITHFULNESS

The proportion of Gentoo Penguins which returned to breed at the same nest-site in successive years was 100% (n = 19), 96% (n = 169) and 89% (n = 163) in 1987–1989 respectively. For Macaroni Penguins the same values were 69% (n = 26), 87% (n = 158) and 81% (n = 142) in 1987–1989 respectively. Over all three years, of 23 Gentoo Penguins which changed nest-site in successive seasons, 11 were male and 12 female ($\chi^2 = 0.14$, ns). Of 56 Macaroni Penguins which changed nest-site between years, 17 were male and 39 female ($\chi^2 = 7.01$, $P < 0.01$).

Following separation, 10 of 10 male Macaroni Penguins bred at the same nest-site but only one of 12 females did so. Four females bred at adjacent nest-sites (1–2 m from the old nest) and seven moved 2–5 m. Similarly in Gentoo Penguins, 11 of 11 males bred at the same nest-site following separation but no females did so. Instead, seven females used adjacent nest-sites and two moved 2–5 m.

DISCUSSION

CAUSES OF ANNUAL VARIATION IN RETURN RATE

Both Gentoo and Macaroni Penguins showed significant inter-annual variation in the return rate of breeding birds between 1987 and 1990. In particular, the proportion of birds breeding in 1986 which returned and bred in 1987 was very low: 20% and 35% in Gentoo and Macaroni Penguins respectively, compared to 60–80% in other years. At South Georgia, 1987 was anomalously cold (at least during the early part of the season), the winter was severe, late and persistent, with an extreme northern limit of pack ice, and snow and ice accumulation remaining on breeding areas until early November (Duck 1990, Williams 1990). The low return rate of previously-breeding penguins was associated, in both species, with a decrease in the size of the breeding population (by 18–19%, Table 1) and with significantly delayed onset of breeding (Williams 1990, Williams and Croxall 1991). This low rate of return may have been due to (1) non-breeding by adult birds, (2) movement of birds to other breeding colonies, or (3) increased adult mortality. The observed rate of band loss was too low to account for the decrease.

Non-breeding by adult birds was an important cause of this low return rate of breeding birds: 25% and 14% of Gentoo and Macaroni Penguins respectively which bred in 1986 were alive but did not breed in 1987. This suggests that a major component of the marked annual variation in breeding population size in Gentoo and Macaroni Penguins (Croxall et al. 1988), in addition to variation in recruitment of first-time breeders (Williams 1990), is the frequency of non-breed-

ing in experienced, previously-breeding birds. A marked decrease in breeding population size (>20%) and/or late onset of breeding in Gentoo Penguins has occurred at least three times (1979, 1987, 1990) in 14 years at South Georgia (data from 1977–1990, Croxall et al. 1988, British Antarctic Survey, unpubl. data). This suggests that extensive non-breeding by adult birds may be a fairly frequent event, at least in this species. Coulson (1984) presented evidence of extensive non-breeding in adult Eider Ducks, *Somateria mollissima,* and suggested that it may be widespread in long-lived birds. Recent studies in Northern Fulmars (*Fulmarus glacialis,* Ollason and Dunnet 1988), European Shags (*Phalacrocorax aristotelis,* Aebischer 1986), Short-tailed Shearwaters (*Puffinus tenuirostris,* Wooller et al. 1990) and several alcid and cormorant species at the Farallon Islands, California (Ainley and Boekelheide 1990) have confirmed this, with between 25–100% of birds with previous-breeding experience failing to breed in any given year. The cause of this failure to breed by adult birds is not known (Newton 1989), although it is most likely related to low food availability (Aebischer 1986, Ainley and Boekelheide 1990). There is evidence for both long- and short-term variation in food availability around South Georgia (Croxall et al. 1988; Priddle et al. 1988; Kato et al., in press). However, with our current state of knowledge, variation in early breeding season events (including return rate of adult birds) does not appear to be consistently related to variation in food availability, or to other local environmental conditions, e.g., presence of snow and ice (Croxall et al. 1988, Williams 1990).

Breeding success was significantly related to the likelihood of a bird returning in the subsequent season in only one year, 1988, when, in both species, failed breeders were less likely to return. Birds may fail to return to the colony to breed either through emigration or mortality. Emigration of large numbers of birds to other breeding colonies is unlikely in these two species at South Georgia. In three years no adult Gentoo Penguin banded as a breeding bird at the study colony was recorded breeding subsequently at any of the five other colonies on Bird Island (T. D. Williams, unpubl. data). Although similar data are not available for Macaroni Penguins, other *Eudyptes* species show a high degree of philopatry following breeding (Carrick 1972; Warham 1974a, 1974b). This suggests that there was increased mortality of breeding birds in 1987, possibly as a cost of reproduction (review, Partridge 1989). Only 3%, or less, of 1986-breeding birds known still to be alive had failed to breed again after three years. Year-to-year variation in adult survival has been demonstrated in a number of other bird species (e.g., Dunnet and Ollason 1978, Coulson 1984, Safriel et al. 1984).

RE-MATING, MATE CHOICE AND THE TIMING OF PAIR FORMATION

In addition to variation in return rate of breeding adults, Gentoo Penguins also showed significant variation in the degree of mate fidelity between years. In 1987, when return rates were low, no bird retained the same partner whereas in 1988 and 1989 mate fidelity was high: 72% and 89%, respectively. In contrast, in the Macaroni Penguin mate fidelity was high in all three years (71–79%). Rowley (1983) has pointed out that there is no clear relationship between "lifestyle" (i.e., resident or migratory status) and mate fidelity in long-lived species. Gentoo Penguins are resident at South Georgia and at least some pairs are recorded together in the colony throughout the winter (T. D. Williams, unpubl. data). Conversely, Macaroni Penguins are migratory, spending the winter at sea, and are unlikely to maintain pair-bonds during this period. It would therefore be predicted that Gentoo Penguins would show higher mate fidelity, the opposite of the observed pattern (at least in 1987). A possible reason for this is that in years of delayed breeding Gentoo Penguins have a protracted pre-breeding period and continue to forage at sea during the day. This would minimize the time a pair may spend together at the nest and increase the chance of a male mating with a new female. Macaroni Penguins remain in the colony following arrival at the beginning of the season, and arrival is highly synchronized even in years when breeding is late (Williams and Croxall 1991). Therefore, both members of a pair will return to the colony over a short period and there is a high probability they will meet and re-unite before either bird mates with a new partner. In both species, the high degree of nest-site fidelity will increase the probability of pairs re-uniting if both birds return (see below). The level of mate fidelity recorded in this study for Gentoo Penguins (0–89%, average 54% over three years) is less than the value of 90% given by Trivelpiece and Trivelpiece (1990, average of four-years data) for the South

Shetland Islands, but similar to that for Gentoos at the northern limit of their range at Crozet Island (49%, Bost and Jouventin 1991). No previous data are available on mate fidelity for Macaroni Penguins.

In Macaroni Penguins, birds which retained the same partner were significantly more likely to have bred successfully in the preceding year, compared to birds which re-mated with a new partner, whereas in Gentoo Penguins there was no difference. Higher separation rates following breeding failure have also been recorded in many other studies of long-lived seabird species (e.g., Coulson 1966, Brooke 1978) including penguins (Richdale 1957, Reilly and Cullen 1981). Davis (1988) has shown that in Adelie Penguins (*P. adeliae*) pairs which successfully coordinate their prolonged incubation shifts are more likely also to coordinate their arrival at the colony and to re-unite the following year. Macaroni Penguins have a similar (but more extreme) pattern of prolonged incubation shifts. Non-complementary pairs, which as a result fail to breed successfully, might similarly also be more likely to mate with a new partner the following year (but see Williams and Croxall 1991). In Gentoo Penguins, which have daily changeovers during incubation and brooding, it is presumably less important for birds to coordinate nest relief. Bost and Jouventin (1991) also reported no relationship between mate fidelity and the outcome of the previous year's breeding attempt in Gentoo Penguins on the Crozet Islands.

There was no difference in subsequent breeding success (or laying date) between pairs which reunited and those which changed mate in either Gentoo or Macaroni Penguins (Table 4). In many other studies breeding success fell markedly after a change of mate (e.g., Coulson 1966, Mills 1973, Brooke 1978, Bradley et al. 1990). However, Ainley et al. (1983) concluded that changing mates had little effect on reproductive success in Adelie Penguins at Cape Crozier, albeit in a population that shows much lower mate fidelity than in the present study. This suggests that mate familiarity may be less important in determining breeding success in penguins, at least in the first year after mate change, than in other seabird species.

If there is no difference in breeding success with change of mate why is mate fidelity so high in both species? Both Gentoo and Macaroni Penguins showed a high degree of nest-site faithfulness (69–100%), even in the year of low return rate. Many species that show high mate fidelity also show high site fidelity and the probability of re-uniting may often be a function of both mates returning to the same nest-site. For example, in Leach's Storm Petrel (*Oceanodroma leucorhoa,* Morse and Kress 1984) and Caspian Terns (*Sterna caspia,* Cuthbert 1985) mate retention between successive seasons is largely or totally dependent on site tenacity. However, Gentoo Penguins at South Georgia have, on average, lower mate fidelity than those at the South Shetland Islands even though they are more highly site-faithful (89–100% cf. 60%, Trivelpiece and Trivelpiece 1990). Trivelpiece and Trivelpiece (1990) suggested that year-round association and non-limiting nest-site availability might account for the low site- but high mate-fidelity at this breeding location. This also applies to the Gentoo Penguin population at South Georgia, however, and does not therefore explain the intraspecies differences. Instead, it is possible that the shorter breeding season (by 10–20 days) at the more southerly South Shetland Islands necessitates greater synchrony of breeding effort than at South Georgia thus increasing the likelihood of mate fidelity (cf. Macaroni Penguins, see above). This hypothesis contradicts Ainley et al.'s (1983) suggestion that the shorter breeding season experienced by Adelie penguins in the southern Ross Sea was the cause of very low mate fidelity, because there was a premium on re-mating rapidly rather than waiting for the previous partner.

Females were significantly more likely to change nest-site between successive seasons than males in Macaroni Penguins but there was no difference between sexes in Gentoo Penguins. Davis and Speirs (1990) have suggested that all male Adelie Penguins returning to breed should adopt a single strategy: return to last season's nest site, as early as possible, and court all females until paired. Females similarly should initially return to the old nest-site, but if their old mate is absent they should pair with the unattached male nearest to the old nest. This maximizes the chance of their successfully re-uniting with their previous mate should he return late (Davis and Speirs 1990). Macaroni Penguins appear to adopt the same strategy. Both sexes are highly site faithful, males arrive before females (Williams and Croxall 1991) and females that change mate pair with males adjacent, or close, to their old nest-site. Following separation all males retained the same nest-site suggesting that they had mated

TABLE 6. Comparison of return rates and mate and nest-site fidelity in Gentoo and Macaroni Penguins, South Georgia, 1988–1989.

	Gentoo Penguin	Macaroni Penguin
Return rate		
as breeders	59–79%	70–73%
as non-breeders	2–3%	2–8%
Mate fidelity	72–89%	71–79%
Mate change due to separation	3–12%	4–11%
Failed breeders more likely to change mate?	No	Yes
Nest-site fidelity	89–100%	69–87%
Change of nest-site by sex (all mate changes)	Females = males	Females > males
Change following separation	Females ≫ males	Females ≫ males

with a new female prior to the delayed arrival of their previous mate. These data suggest that in Macaroni Penguins males primarily aim to retain their old nest-site and, secondarily, aim to reunite with their old mate. This idea is supported by the observation that males whose old mate fails to return remain at their old nest-site rather than attempting to pair at a new site (T. D. Williams, unpubl. data). It also explains why following separation some males (40%) may not breed for 2–4 years whereas most females (94%) remate and breed immediately. Richdale (1957) similarly showed that male Yellow-eyed Penguins (*Megadyptes antipodes*) which had bred at least once were more likely than females to miss subsequent breeding attempts. Although Gentoo Penguins are more highly site faithful than Macaroni Penguins they showed greater variation in mate fidelity. Among pairs which failed to reunite, for any reason, males and females were equally likely to change nest-site between seasons but following separation males always retained the old nest-site. These differences may be related to this species' resident habit, the longer breeding season and a higher level of nest-site availability (Trivelpiece and Trivelpiece 1990).

Davis and Speirs' (1990) model for re-mating and mate choice in penguins only considered pair-formation during the pre-breeding courtship period. The present study has revealed the importance of the post-nuptial molt period for pair-bond formation, not just reinforcement of existing pair-bonds, at least in the migratory Macaroni Penguin (cf. the "reoccupation period" in Adelie Penguins, Ainley et al. 1983). For many birds which failed to reunite in successive breeding seasons, their mate had already failed to return to molt in the preceding year (Table 5). About half (46–52%) of the birds whose mate failed to return to molt paired with a new partner for molt in that same year, and 26% of these bred with their new mate in the following year. Pairing during the molting period (and associated nest-site establishment) might allow more rapid initiation of breeding the following year even in pairs which had not previously bred together.

INTER-SPECIES VARIATION IN BREEDING STRATEGIES

Differences in return rates and in mate and nest-site fidelity between Gentoo and Macaroni Penguins, at South Georgia, for the two years 1988 and 1989 are summarized in Table 6. These species have markedly different breeding chronologies and life-histories (Croxall et al. 1988, Williams 1990, Williams and Croxall 1991). The Gentoo Penguin is a resident species, first breeds at two years of age, has high but highly variable breeding success (mean 0.85, range 0.01–1.42 chicks/pair), and shows marked inter-annual variation in onset of egg-laying and in breeding population size. In contrast, Macaroni Penguins are migratory, defer breeding for 6–8 years, have lower, but less variable, breeding success (mean 0.45, range 0.09–0.61 chick/pair) and show highly synchronous onset of egg-laying and less annual variation in breeding population size. Despite these differences, and therefore rather surprisingly, this study has shown that return rate and mate and nest-site fidelity of breeding birds were in fact very similar in the two species, at least for the two 'normal' years of 1988 and 1989. The only major difference was that failed breeders were more likely to change mate in Macaroni, but not in Gentoo, Penguins. Only in the apparently anomalous 1987 season were inter-species differences marked: Gentoo Penguins showed a

much greater decrease in return rate and mate fidelity.

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