Notornis, 2002, Vol. 49: 145-152
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The influence of experience, pair bond duration, and partner change on breeding frequency and success in southern Buller's mollymawk (*Thalassarche bulleri bulleri*)

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Abstract We investigated whether breeding frequency and breeding success of southern Buller's mollymawks (*Thalassarche bulleri bulleri*) were influenced by breeding experience and pair bond duration, using data from annual checks at 3 study colonies at The Snares from 1992 to 2001. Most pairs bred annually irrespective of the experience and length of the pair bond, although the proportions that did so varied with pair type. Thus, breeding frequency (% breeding in consecutive years) was lowest among pairs of 1st-time breeders (77%). Breeding frequency of those pairs after their 2nd attempt (89%) became similar to that of established pairs together for at least 1 previous breeding attempt (88%), or newly formed pairs in which one or both birds had previous breeding experience (91%). Overall breeding success was 71% and, in established pairs, breeding failure (loss of egg or chick) was associated with reduced breeding frequency (83% compared to 91% when successful). Lowest breeding success (58%) was associated with the attempts of 1st-time breeders. Performance of these pairs improved until the 3rd attempt (81%), when it became similar to that of established pairs (73%) and newly formed pairs in which one or both birds had previous breeding experience (77%). Divorce was rare (1.1-3.5% annually). First-time and former breeders mated more frequently with birds of similar status (85% and 58% respectively) than expected assuming random pairings. When changing partner, as a result of divorce or death, the average interval before breeding again was 2.1 years for males and 2.6 years for females, and so, on average, each change of partner resulted in the loss of 1 breeding attempt. Thus, the time taken to obtain a new partner has a lifetime reproductive cost.

Sagar, P.M.; Stahl, J.-C.; Molloy, J. 2002. The influence of experience, pair bond duration, and partner change on breeding frequency and success in southern Buller's mollymawk (*Thalassarche bulleri bulleri*). *Notornis 49(3)*: 145-152.

Keywords: Procellariiformes; albatrosses; population; breeding experience; pair bond; The Snares

INTRODUCTION

Delayed onset of breeding, extended breeding life span and high mate fidelity are traits shared by many long-lived birds, and breeding performance of such birds has been shown to be affected by both age or breeding experience (or both) and pair-bond duration. Age-related improvement in breeding success has been attributed to an increase in skill and efficiency in feeding (Lack 1968), increased reproductive effort (Pugesek 1981), or higher survival of high quality breeders (Curio 1983). However, breeding performance among birds of similar age usually improves with breeding experience, suggesting that after the 1st breeding attempt the effects of experience override those of age *per se* (Saether 1990). Long-term pair bonds also improve reproductive success in birds (Rowley 1983; Mock & Fujioka 1990). In many species with long-term pair bonds, experienced adults in pairs newly formed because of divorce or death of a mate have reduced reproductive success (Fowler 1995).

Albatrosses are extreme among long-lived birds in terms of delayed maturity, adult survival, mate fidelity, and length of breeding life. Influence of age, experience or pair bond or both on breeding success and breeding frequency were studied in the wandering albatross *Diomedea exulans* (Weimerskirch 1992; Jouventin *et al.* 1999) and Laysan albatross *Phoebastria immutabilis* (Fisher

Received 26 May 2001; accepted 4 October 2001

1976), although none of these studies examined all of these aspects simultaneously. In both these species of albatross, breeding frequency was substantially reduced when changing partner as it took between 2 and 6 years to breed again with a new partner (Fisher 1976; Jouventin *et al.* 1999). For example, in a population of Laysan albatrosses studied for 13 consecutive years, breeding frequency per year decreased from 0.82 in stable pairs to 0.71 and 0.64 with 1 and 2 partner changes respectively (Fisher 1976). The costs of changing partner on lifetime reproduction may be further increased if both breeding success and breeding frequency are lower in newly formed pairs than in stable pairs. In Laysan albatrosses, breeding frequency increased with pair-bond duration among newly formed pairs of 1st-time breeders, but not in newly formed pairs in which one or both birds had former breeding experience (Fisher 1976). Breeding success of wandering albatrosses increased with breeding experience at the Crozet Islands (Weimerskirch 1992), but not at South Georgia (Croxall 1991), although the effects of re-mating and pair-bond duration were not taken into account. Relationships between breeding success and experience or pair bond duration have not been studied in other albatross species.

Incidental mortality of albatrosses during fishing operations is well documented (see review in Gales 1998) and suspected to have contributed to recent declines of several albatross populations (e.g., Jouventin & Weimerskirch 1988; Croxall & Prince 1990; de la Mere & Kerry 1994; Prince *et al.* 1994). However, when considering subsequent changes to breeding population size, most studies consider only changes in mortality rates of the birds and do not take into account effects such as the time taken for the surviving partner to obtain a new mate and subsequent effects on breeding success (e.g., Croxall & Prince 1990; de la Mere & Kerry 1994). In the New Zealand region, albatross mortality has been documented for trawl (Bartle 1991) and longline (Murray *et al.* 1993) fisheries. The southern Buller's mollymawk (*T. b. bulleri*) is one of the endemic New Zealand species most frequently reported in this incidental mortality. Breeding southern Buller's mollymawks are confined to the Solander Islands (46° 35'S, 166° 54'E) and The Snares (48° 02'S, 166° 36'E). At the Solander Islands, there was an estimated 2625 occupied nests in 1996 whereas at The Snares an estimated 8877 nests were occupied during 1997 (Sagar *et al.* 1999). The species is a long-lived annual breeder, laying a single egg during January-February, with most fledglings departing the islands during September (Sagar & Warham 1998; Sagar *et al.* 2000). Mate and nest-site fidelity are high (Sagar & Warham 1998), consequently, providing an opportunity to test whether frequency and success of breeding are related to the status of the pair bond.

Within the framework of modelling the interactions between this albatross and New Zealand fisheries, the main objectives of this study were to determine: (1) changes in breeding success and breeding frequency during the early attempts of newly recruited pairs; (2) the time taken to breed again with a new partner after death or divorce; and (3) effects of change in partner on breeding frequency and success. In this way we tested the hypothesis that breeding frequency and breeding success were influenced by length of the pair bond and breeding experience.

METHODS

The study was carried out at The Snares (48° 02'S, 166° 36'E) during visits in February-March (just after completion of laying) and July-August (just before the start of fledging) from 1992 to 2000, and in February-March 2001. During the 1992 breeding season, all occupied nests, in 2 study colonies, were marked with numbered stakes and 143 of the associated birds were banded. Nests in a 3rd study colony were marked in 1993. In addition, all birds breeding in this 3rd colony and all unbanded birds breeding in the 2 study colonies established during 1992 were banded. In 2 of these colonies some breeding birds had been banded since 1969, during a study of the basic breeding biology (Sagar & Warham 1998). These birds provided an opportunity to detect changes in breeding frequency and success against breeding experience (minimum number of years since they were banded as birds of unknown breeding experience). This earlier study of breeding biology was completed during 1969-1977. Subsequently, some birds were recaptured during the 1983 to 1986 breeding seasons and these data were used in an analysis of survival (Sagar *et al.* 2000). No visits were made to the study colonies during the 1987 to 1991 inclusive breeding seasons. The timing of recaptures, access to all nests and the discrete nature of the colonies enabled 99-100% of breeding birds to be recaptured each year. During the period 1992-1997 annual survival of breeding birds was a relatively constant 95.5% (Sagar *et al.* 2000).

Identification of first time breeders

First time breeders could not be identified directly, as only 1 cohort of chicks (1972) was banded before 1992, and most of these had started breeding by 1992. However, as breeding adults have never been recorded as changing colonies (Sagar & Warham 1998; P.M. Sagar & J. Molloy unpub. data), we assumed that new breeders banded after 1993 were either 1st-time breeders or pre-1992 breeders returning after 1 or more years of not breeding. An analysis of returns of the 1992 and 1993 breeding cohorts up to the 2000 breeding season showed that the latest birds to

Table 1 Time (years) to next breeding attempt by breeding southern Buller's mollymawks (*Thalassarche bulleri bulleri*) banded in 1992 and 1993.

	No. (%) of birds next breeding		
Year	1992 (n = 143 birds)	1993 (n = 356 birds)	1992 + 1993 (n = 499 birds)
Yr+1	128 (89.5)	283 (79.5)	411 (82.4)
Yr+2	9 (6.3)	56 (15.7)	65 (13.0)
Yr+3	5 (3.5)	12 (3.4)	17 (3.4)
Yr+4	0 (0)	4 (1.1)	4 (0.8)
Yr+5	0 (0)	0 (0)	0 (0)
Yr+6	1 (0.7)	1 (0.3)	2 (0.4)

Table 2 Estimated proportion (%) of first time breeders among newly banded southern Buller's mollymawks (*Thalassarche bulleri bulleri*) at The Snares, 1993-1998. Pre-1992, estimated as the no. of pre-1992 breeders returning; new, no. of new breeders banded; first time, estimated % of first time breeders among newly banded breeders.

Year	Pre-1992	New	First time
1993	63	251	75.0
1994	16	40	60.0
1995	4	56	92.9
1996	1	42	97.6
1997	1	30	96.7
1998	0	39	100.0

return and breed again did so in year (n+6) (1999). We assumed that this was the maximum span of non-breeding years, and used the combined 1992 and 1993 cohorts of breeders to calculate overall percentages of birds returning for their next breeding attempt in years (n+1) to (n+6) (Table 1). These data showed that 98.8% of birds bred again within 3 years of their previous breeding attempt. Using the values for time taken to the next breeding attempt and assuming a breeding population of 356 birds (1993 total) in each of 1987-1991 (i.e. up to 6 years before banding in this study), we calculated the number of unbanded former breeders returning each year (Table 2). For example, of 251 birds newly banded in 1993 we estimated that about 63 would have bred previously; these birds comprised 46.3 (356 × 0.13) that bred last in 1991, 12.1 (356 × 0.034) that last bred in 1990, 2.84 (356 × 0.008) that last bred in 1989, 0 from the 1988 cohort, and 1.42 (356 × 0.004) that bred last in 1987. Based on these estimates, the proportion of 1st-time breeders among new breeders banded in each year increased from 60.0-75.0% in 1993-1994, to 92.9% in 1995, and 96.7-97.6% in 1996-1997. We selected 1995 as the threshold year and assumed that all birds banded as breeders from 1995 onwards were making their first breeding attempt.

Breeding success and breeding frequency

A bird was recorded as breeding when seen incubating an egg or occupying a nest containing egg fragments in February-March and a breeding attempt was considered successful when a chick was recorded during July or August. Pairs were categorised as newly formed when breeding together for the 1st time, and as established when maintained for 2 or more breeding attempts. Divorce was assumed where both birds of a pair were recaptured, but at least 1 member of the former pair was mated with another bird. Inexperienced birds were those that had no known previous breeding experience. After a single breeding attempt (i.e. production of an egg), whether successful or not, birds were considered experienced breeders.

To segregate the effects of pair bond duration and experience from those of pair disruption, only pairs that made subsequent breeding attempts together were used for calculation of breeding frequency. The relationships of breeding frequency to pair-type, breeding attempt number, and breeding outcome were analysed using returns of 1995-1998 breeding cohorts through to 2001. For 1996-1998 cohorts followed for less than 6 years, this will have introduced a slight (<2%, Table 1) bias in the percentages breeding again in years (n+1) through (n+3) by not taking into account all or part of later returns in years (n+4) to (n+6), but we consider the bias to be inconsequential.

The gender of birds was determined from measurements of bill and tarsus, using the formula developed by Sagar *et al.* (1998).

We compared means and standard errors using Student's t tests after the data were arcsine transformed to correct for any deviation from normal distributions; Bartlett's tests of homogeneity of variances were used before t tests were applied (Zar 1984). Where appropriate, Yates' correction was applied to calculations of χ^2.

RESULTS

Breeding frequency

On average (± SD), 88.4% ± 1.4% (n = 553 pair-years) of experienced breeders in established pairs bred in successive seasons, irrespective of breeding outcome, during the years 1995-1998. The breeding frequency of newly-formed pairs after their 1st breeding attempt varied according to the experience of the birds involved (Table 3). Thus, the proportion breeding again in consecutive years was 100% where both birds had previous breeding experience (n = 12 pairs), 90.9% where one bird was an experienced breeder and the other a presumed 1st-time breeder (n = 22 pairs), and 76.7% where both birds were presumed 1st-time breeders (n = 60 pairs). In pairs of 1st-time breeders, breeding frequency after the 2nd attempt increased to 89.7% (n = 34 pairs),

Table 3 Time (years) to next breeding attempt by established and newly formed pairs of southern Buller's mollymawks (*Thalassarche bulleri bulleri*), at The Snares. *n*, number of breeding pairs.

Pair type	Breeding outcome Year n	*n*	Next breeding attempt (%) Year (n + 1)	Year (n + 2)	Year (n + 3)	Year (n + 4)	χ^2	*df*	*P*
Established									
Experienced × experienced	Successful	401	90.5	8.7	0.8	0	6.89	1	<0.05
	Unsuccessful	152	82.9	16.4	0	0.7			
Newly formed									
Experienced × experienced	Successful	8	100	0	0	0	0.00	1	>0.05
	Unsuccessful	4	100	0	0	0			
Experienced × 1st-time	Successful	18	88.9	11.1	0	0	2.08	1	>0.05
	Unsuccessful	4	100	0	0	0			
1st-time × 1 st-time	Successful	34	79.4	20.6	0	0	0.24	1	>0.05
	Unsuccessful	26	73.1	23.1	0	3.8			

a figure comparable to that of all other pair types. In most instances, both established and newly formed pairs that did not breed in year (n+1) did so in year (n+2) (Table 3).

Breeding frequency of the breeding birds banded in 1969 showed no further consistent change during the first 24 years of breeding experience. Thus, the proportion breeding in consecutive years was 84.5% (n = 58 pairs) among pairs with 1-4 years breeding experience; 74.2% (n = 26 pairs) for those pairs where at least one bird had a minimum breeding experience of 16 years; and 86.9% (n = 14 pairs) where at least one bird had a minimum of 24 years breeding experience.

Breeding frequency was related to breeding outcome in established pairs of experienced breeders, where pairs that raised a chick were significantly ($P<0.05$) more likely to lay an egg the following year (Table 3). A similar trend was recorded among newly formed pairs of first-time breeders, although the difference was not significant (Table 3).

Breeding success

The average (± SD) breeding success pooled for all 3 study colonies over the 4 years (1995-1998) was 70.8% ± 3.2% per year (range 67.9-76.1%, n = 859 pairs). Breeding success among established pairs during these 4 years averaged 72.5% ± 2.0% per year (range 70.4-75.2%, n = 553 pairs) when the 2 birds were the same as in the previous season. Pairs of presumed 1st-time breeders were less successful at raising a chick than established pairs during their 1st 2 attempts, but their breeding success increased to a comparable level by their 3rd attempt (Table 4). Newly formed pairs in which one bird had former breeding experience were as successful from their 1st attempt onwards as established pairs. In fact, breeding success of those pairs during their 1st 3 attempts was higher than that of when both birds were experienced. However, sample size of the latter pair type was small (Table 4), and so we do not have high confidence in the result.

Table 4 Breeding success (%) during the first 3 breeding attempts of newly formed pairs of southern Buller's mollymawks (*Thalassarche bulleri bulleri*) at The Snares; first attempts 1995-1998, breeding records to 2000 season. *n*, number of pairs.

Pair type	Attempt 1	2	3
Experienced × experienced	66.7 (12)	63.6 (11)	37.5 (8)
Experienced × 1st-time	81.8 (22)	89.5 (19)	82.4 (17)
1st-time × 1st-time	57.7 (71)	63.3 (60)	81.1 (37)

In established pairs, breeding success may be affected by the length of breeding experience. Breeding success was 69.3 ± 23.7% (n = 26 pairs) where at least 1 bird of the pair had a minimum breeding experience of 16 years. This declined to 56.6 ± 36.2% (n = 14 pairs) in pairs where at least 1 bird had a minimum of 24 years breeding experience; however, the lower breeding success was not significant (t = 1.30, $P > 0.05$, d.f. = 38).

Mate fidelity

During the period 1992 to 1998, 76 to 179 pairs of banded birds bred in the study colonies each year, for a total of 858 pair-years. Divorce ranged from 1.1% to 3.5% annually, with a mean (± SD) of 2.1 ± 0.9% (n = 7 years). However, of the 18 instances of divorce 4 involved birds that re-paired with their original partner after one or several breeding attempts with another partner, and so such divorce could be termed temporary. If these cases are removed then the annual divorce rate averaged 1.7 ± 0.5%. None of the instances of divorce involved birds banded before 1992, and so no information is available to determine whether the length of breeding experience (years) affects divorce rate.

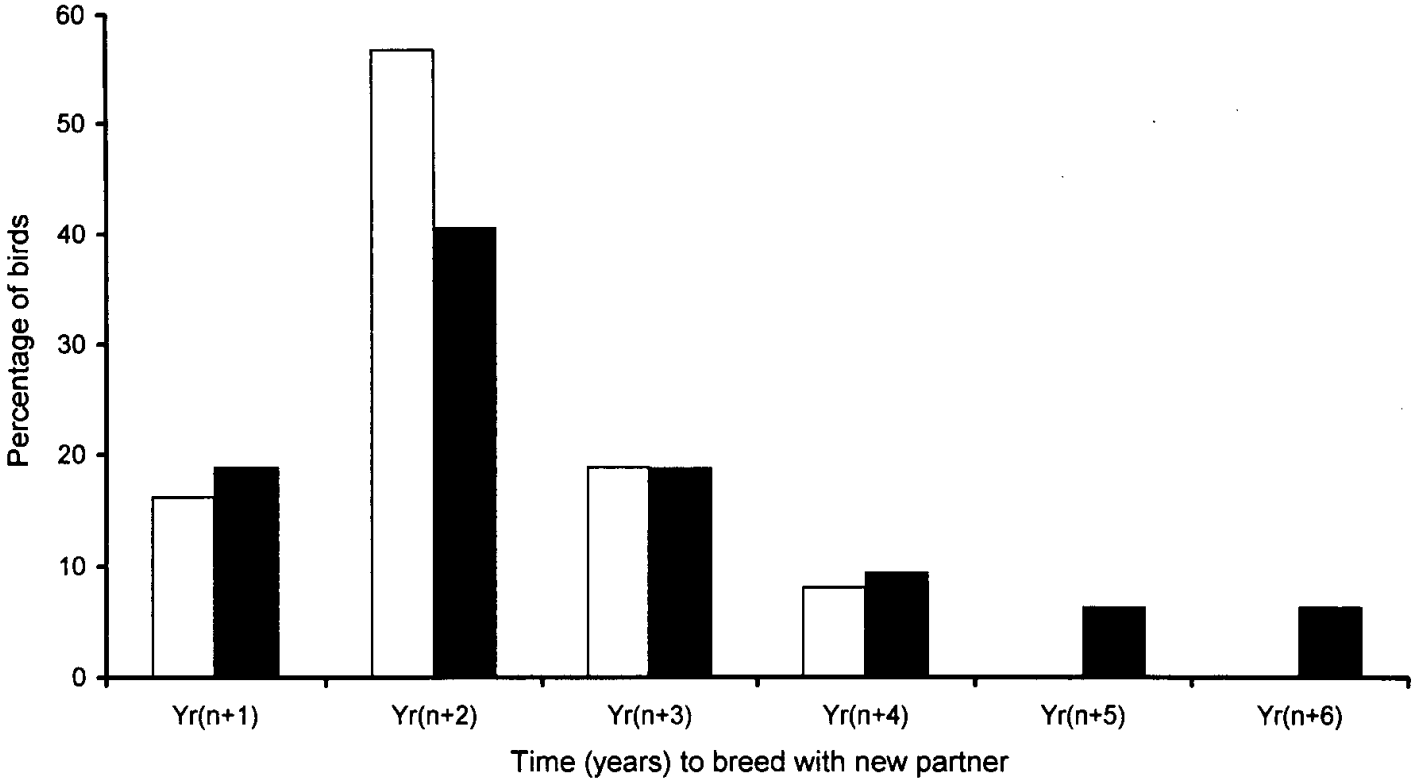

Fig. 1 Time (years) taken by widowed/divorced southern Buller's mollymawks (*Thalassarche bulleri bulleri*) to breed with a new partner. Open, males, $n = 37$; filled, females, $n = 32$.

Time taken to obtain new mate

The average (± SD) time taken for 69 experienced breeders to obtain a new mate and breed again following divorce or the death of a previous mate was 2.39 ± 1.14 years (Figure 1). The interval between consecutive breeding attempts with different partners was shorter for males (2.11 ± 0.65 years, $n = 37$) than females (2.63 ± 1.41 years, $n = 32$), and the difference approached significance ($t = 1.958$, $P > 0.05$, $df = 67$).

Experience-related mate choice

Of 94 newly formed pairs, 60 (63.8%) consisted of 2 presumed first-time breeders, 22 (23.4%) comprised 1 experienced bird and 1 presumed 1st-time breeder, and 12 (12.8%) comprised 2 experienced birds. Thus, 84.5% of presumed 1st-time breeders and 52.2% of experienced birds paired with birds of similar status. Pairings between birds of similar status were significantly more frequent than expected from random pairings among unmated birds ($\chi^2_1 = 19.66$, $P < 0.001$).

DISCUSSION

Effects of breeding success on breeding frequency

The results of our study show that established pairs that raised a chick were more likely than pairs that failed to raise a chick to breed again the following year. Both breeding success and breeding frequency could be influenced by the foraging efficiency of the parents. Although no links have been identified, better foragers are likely to be more able to feed their chick and, therefore, to have higher breeding success (Fowler 1995).

Studies that have measured individual effects on breeding performance in birds suggest that quality may be one of the most important factors influencing reproductive success over the whole lifetime (Coulson & Porter 1985; Coulson & Thomas 1985; Ollason & Dunnet 1988; Croxall *et al.* 1992, Cobley *et al.* 1998). In wandering albatrosses, Croxall *et al.* (1992) showed that although age influenced egg size, and so hatching success, it accounted for only about 6% of the variation compared with 50% that was attributable to individual effects. Cobley *et al.* (1998) examined individual quality effects and reproductive performance in the grey-headed albatross (*T. chrysostoma*). They found that pairs that had breed successfully consistently arrived back at the colony significantly earlier, had significantly shorter 1st and 2nd incubation shifts, and hatched larger chicks that grew significantly faster than in pairs where breeding attempts consistently failed. Earlier return to the breeding colony, shorter incubation shifts and faster growing chicks are all factors that indicate more efficient foraging by the parents.

Effects of breeding experience on breeding frequency and breeding success

Following the second breeding attempt, breeding experience had no discernible effect on the breeding frequency of southern Buller's mollymawks, even within those pairs where at least one bird had over 24 years of breeding experience. This indicates a similar situation to that reported from a long-term study of Cory's shearwaters (*Calonectris diomedea*) where breeding frequency also increased during the early breeding years, but showed little variation later (Mougin *et al.* 1997). However, when the pattern of breeding frequency stabilises is not reported for Cory's shearwater.

Rowley (1983) extensively documented the improvement in breeding success with breeding age and the results of our study supports his conclusions, with breeding success increasing during the 1st 3 years of a pair bond between 1st-time breeders. This improvement in breeding success is attributed to familiarity with the mate and such species are generally characterised by the long duration of their pair bonds (Ens *et al.* 1996). However, as with some other species of seabirds (Wooller *et al.* 1989) those southern Buller's mollymawks with the greatest breeding experience, while maintaining a similar breeding frequency to birds with less breeding experience, had lower breeding success. A similar situation was determined for long-lived short-tailed shearwaters *Puffinus tenuirostris*, which Wooller *et al.* (1989) interpreted in terms of 2 processes. First, early in their life, higher quality individuals may have better breeding success than lower quality birds, which also die sooner. Second, for those individuals that survive beyond average life expectancy, the greater reproductive effort may result in reduced survival. In southern Buller's mollymawks survival of the oldest birds is reduced (Sagar *et al.* 2000) and this may well result from the greater reproductive efforts of these birds.

Mating between individuals with similar breeding experience occurs in many seabirds (e.g., Coulson & Thomas 1983; Bradley *et al.* 1995; Jouventin *et al.* 1999). This may indicate non-random selection of mates on the basis of age or experience, as implicated by population modelling (Shaw 1985; Reid 1988). However, this may be related more to the behaviour of seabirds, where experienced birds have been observed to return to their breeding colonies earlier than inexperienced birds (Bradley *et al.* 1995), with individuals simply taking the next available partner if their previous mate fails to return or divorce has occurred.

In some seabirds, breeding success depends both upon the breeding ages of the partners and the length of time they have bred together (e.g., Bradley *et al.* 1995). However, in southern Buller's mollymawks breeding success appears to depend more upon breeding experience, with the reproductive performance of newly formed pairs consisting of at least one experienced breeder being similar to that of established pairs and greater than that of pairs of 1st-time breeders. A similar situation occurred in Cory's shearwater, where the first breeding attempt of newly formed pairs of 1st-time breeders, first-time × experienced and experienced × experienced birds averaged 45%, 56%, and 65% breeding success, respectively (Mougin *et al.* 1993).

Effects of a change in partner on breeding

Establishing a new pair bond and remating has a substantial reproductive cost for southern Buller's mollymawks. In several other species of seabirds, such as Manx shearwater *Puffinus puffinus* (Brooke 1990), Cory's shearwater (Mougin *et al.* 2000), and fulmar *Fulmarus glacialis* (Ollason & Dunnet 1978) the immediate effect of mate change was unfavourable to breeding success. However, in southern Buller's mollymawks although the breeding success of newly formed pairs of experienced breeders was similar to that of established pairs, divorced and widowed birds required time to obtain a new partner. During the period 1992-1997, the annual survival rate of breeding birds was 0.955 (Sagar *et al.* 2000), and so southern Buller's mollymawks have a median period of 16 years available for reproduction. Consequently, assuming a breeding frequency of 88.4% per annum, each adult will average 14.1 breeding attempts during its life. On average, each experienced bird required 2.1 years (males) and 2.6 years (females) to acquire a new mate and attempt to breed; a loss of at least one breeding attempt per change in partner. Therefore, a single divorce or death of a partner has the potential to reduce the potential lifetime reproduction of an individual by 7.8% (males) and 11.3% (females). Consequently, any decline in the survival rate of adult southern Buller's mollymawk not only has an immediate effect on the size of the breeding population, but also a delayed effect by reduced breeding frequency, through the time taken to obtain a new mate by birds which have lost a partner. Such a high cost of changing partner appears typical among albatrosses, where potential reductions in lifetime reproduction of 10-20% have been calculated for wandering albatross (Jouventin *et al.* 1999) while among Laysan albatrosses females failed to breed for 1.9 seasons and males for 1.4 seasons (Fisher 1976).

Among the predominantly annual breeding southern Buller's mollymawks and Laysan albatrosses females took longer to breed again after changing partner than did males (Buller's 2.6 and 2.1 years, this study; Laysan 1.9 and 1.4 years, Fisher 1976). This contrasts with the biennial-breeding wandering albatross where males averaged 3.2 years and females 2.3 years to breed again

(Jouventin *et al.* 1999). Such gender-related differences in the time taken to breed again are difficult to explain. Presumably, males with breeding experience have already established a nest site, and so the time taken to obtain a new partner presumably mainly involves the finding of a suitable partner and completion of courtship behaviour.

In some species, mate fidelity may be a by-product of fidelity to the nest site (Ens *et al.* 1996). In southern Buller's mollymawks, 67% of intact pairs retained the same nest site in successive years (Sagar & Warham 1998). Where partnerships changed between years, 67% of males and 22% of females retained the same nest (Sagar & Warham 1998). Mate retention averaged 96.2-97.9% (Sagar & Warham 1998; this study). Therefore, the rate of nest-site retention is substantially less than that of mate retention, indicating that the former may not have such a strong influence on mate retention in this species. Consequently, mate fidelity in southern Buller's mollymawks may simply result from the time taken to obtain a new partner and subsequent loss of breeding potential. Thus, supporting Ens *et al.* (1996) who, in a review of mate fidelity and divorce in monogamous birds, concluded that in species with high mate fidelity, divorce may be constrained by the high costs of mate change.

In conclusion, the results of our study supports the hypothesis that, in southern Buller's mollymawks, breeding frequency and breeding success are influenced by partner change and breeding experience. We found that breeding experience exerts a greater influence on breeding success than change of partner. Following the 3rd breeding attempt, breeding frequency, and breeding success were similar irrespective of the length of the pair bond.

ACKNOWLEDGEMENTS

We thank the many field workers at The Snares who have helped with this project, particularly Sue Lake and Don Geddes. We also particularly appreciate the support of and interest in the project shown by staff of the Southland Conservancy, Department of Conservation. The project has been funded primarily by the Foundation for Research, Science and Technology (NZ) under contract CO1507, and the Department of Conservation and NIWA. We appreciate comments from Sandy Bartle and two anonymous reviewers that improved earlier versions of the manuscript.

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