

# Mate replacement entails a fitness cost for a socially monogamous seabird

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**Abstract** Studies of the selective advantages of divorce in socially monogamous bird species have unravelled extensive variation among different lineages with diverse ecologies. We quantified the reproductive correlates of mate retention, mate loss and divorce in a highly philopatric, colonially breeding biparental seabird, the Australasian gannet *Morus serrator*. Estimates of annual divorce rates varied between 40–43% for *M. serrator* and were high in comparison with both the closely related *Morus bassanus* and the range of divorce rates reported across monogamous avian breeding systems. Mate retention across seasons was related to consistently higher reproductive success compared with mate replacement, while divorce per se contributed significantly to lower reproductive output only in one of two breeding seasons. Prior reproductive success was not predictive of mate replacement overall or divorce in particular. These patterns are in accordance with the musical chairs hypothesis of adaptive divorce theory, which operates in systems characterised by asynchronous territorial establishment.

**Keywords** Divorce rate · Divorce theory · Monogamy · *Morus serrator* · Reproductive success

## Introduction

The evolutionary causes and consequences of divorce in socially monogamous, biparental mating systems continue to generate new theory and data (Ens et al. 1996; Dubois and Cézilly 2002; Jeschke et al. 2007). The retention of the social mate within and across breeding seasons often entails a reproductive advantage (Taborsky and Taborsky 1999), even when the offspring is fathered by an individual other than the social mate (Young et al. 2008). This leads to the prediction of increased reproductive success for those birds that retain their mates across consecutive seasons. Yet, rates of mate retention vary greatly across long-lived biparental taxa, including diverse avian lineages (Choudhury 1995; Cézilly et al. 2000a).

Individuals in most bird species breed with more than one mate during their reproductive career (Dubois et al. 1998, 2004). Mate replacement can be the result of death of a member of the pair (mortality constraint hypothesis: Owen et al. 1988) or owing to asynchronous territorial settlement (musical chairs hypothesis: Dhondt and Adriaensen 1994; Dhondt et al. 1996). Divorce can also be caused by the dispersal of one or both members of the pair, resulting from a decision to pair with another individual at the same breeding site, or the outcome of the ousting of one of the social mates by an intruder (Taborsky and Taborsky 1999). Mate loss and/or divorce may hence hold an adaptive advantage for both mates involved through improving their parental coordination (the incompatibility hypothesis: Coulson 1966, 1972), or eliminating the cost of inbreeding (inbreeding avoidance hypothesis: Hatchwell et

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al. 2000) and, thus, benefit both or only one of the mates (better option hypothesis: Ens et al. 1993) or be detrimental (the mortality constraint and the ousting hypotheses; Taborsky and Taborsky 1999). The musical chairs scenario, in contrast, is related to the pattern and sequence of territorial establishment (Dhondt and Adriaensen 1994), predicting a reproductive advantage to early-settling breeders without any immediate consequences of divorce or mate retention per se on reproductive success.

The Australasian gannet *Morus serrator* is a long-living, philopatric, colonially breeding seabird, which is highly territorial and aggressive at its nest site (Nelson 1978). As in the Northern gannet *Morus bassanus* (Nelson 2002), males of *M. serrator* arrive at the colony first during the breeding cycle (SMHI et al. unpublished data) and establish territory by occupying, defending and displaying at a nest site. Australasian gannets are reported as socially monogamous (Nelson 1978), with the suggestion of mate retention for life (Stein 1971). In contrast, evidence for genetic similarity of mates and detectable levels of extra-pair parentage (Daniel 2007) both predict potential benefits for extra-pair fertilisation and/or divorce between seasons in accordance with the inbreeding avoidance hypotheses for this species (Macedo et al. 2008). These hypotheses of adaptive divorce theory would thus predict increased reproductive success for those birds and/or pairs that divorce their mates between seasons compared with those that retain their mates, contrary to the predictions made under adaptive mate-retention scenarios, as described above. To test these alternatives, we here assess, for the first time, the extent and the reproductive correlates of mate loss and divorce in known-sexed individuals of the Australasian gannet.

## Materials and methods

### Study site and individual identification

Presence records of individually banded Australasian gannets were established three to four times daily over 7 weeks of field observation at the Plateau Colony of Cape Kidnappers gannetry, New Zealand (39°38'S, 177°05'E), during the 2007–2008 and 2008–2009 austral breeding seasons (August–February, Stephenson (2005)). Bands were identified using 8×40 Nikon binoculars from the circumference of the colony, without recapturing the individual birds. Following Daniel et al. (2007), sex was determined for banded birds in this study by polymerase chain reaction (PCR) from blood samples and, as all pairs, except one in the 2005–2006 samples, were heterosexual,

the opposite sex of its PCR-sexed mate was presumed for two unsampled individuals.

Previously banded individuals were reported as missing from the colony only if absent from all presence record sessions collected across the respective breeding season. Additionally, only two of over 300 birds banded on the Plateau subcolony were sighted at a different subcolony of the same gannetry across these years of observation (SMHI personal observations), neither of these from earlier pair-bonding records, and there are no reports of sightings of Cape Kidnappers birds from other gannetries (Department of Conservation records, Wellington, New Zealand). Resighting likelihood within our records can thus be presumed to approximate 1.

### Observation of pair-bonds and reproductive success

For 57 in 2007–2008 (and 54 in 2008–2009) of the observed birds, previous pair-bonding behaviours and breeding records from the 2005–2006 breeding season were also available for comparison. Socially pair-bonded birds were identified as non-fighting adults interacting at a nest site (Fig. 1). These included 22 individuals with unbanded new mates in 2007–2008 and 27 unbanded new mates in 2008–2009.

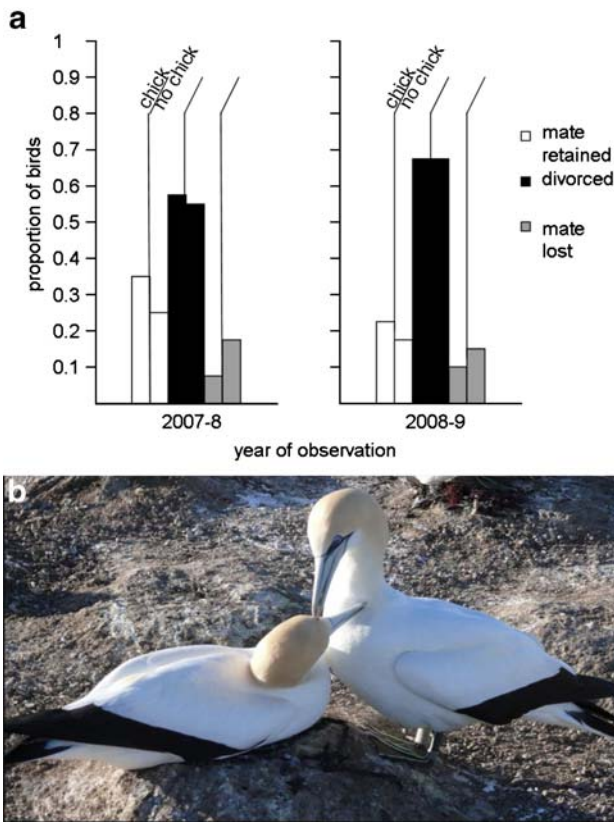
Breeding in the 2005–2006 season was assessed during the incubation stage (October) by recording the presence/absence of an egg for each banded individual and during parental care (December) by recording the presence of chicks (i.e. successful more than 1 month prior to expected fledging) attended by the adults. Pairs with an egg in October, but no members of the pair sighted with a chick in December, were listed as uncertain reproductive success. No comparable breeding data were collected in the 2006–2007 breeding season. Six of the pairs including two banded mates were observed in both 2007–2008 and 2008–2009 records.

### Retention or change of pair-bonds

Based on the published literature, we assigned individuals into mate retention versus mate changed categories, with the mate change category subdivided into divorce, when a focal bird was paired with a different individual while the previous mate was sighted (Ens et al. 1993; Choudhury 1995) and mate loss, when breeding with a new mate while the previous mate was absent from the colony (Coulson 1966).

### Statistical analyses

We assumed that a constant proportion of pairs remain stable across consecutive years, as seen in other avian taxa, including



**Fig. 1** **a** Proportions of mate retention, divorce and mate loss groups in 2007–2008 and 2008–2009 for successful (=chick) and unsuccessful =no chick breeders in 2005–2006 in *M. serrator*; **b** socially interacting (allopreening) Australasian gannets on nest at the Cape Kidnappers Plateau Colony, New Zealand. Photo credit: S. Ismar

seabirds (Aebischer et al. 1995; Cézilly and Johnson 1995; Bradley et al. 1990), and supported for *M. serrator* from our dataset. Divorce, as a reproductive choice and a compliment of mate retention, was therefore assessed as:

$$\text{divorce rate}_{2007-2008} = 1 - \left[ \frac{\text{no. birds with mates retained}}{\text{no. birds with mates retained}_{2007-8} + \text{no. of birds with mates} + \text{divorced}_{2007-8}} \right]^{(1/2)}$$

For the 2008–2009 data, the cubic root was applied accordingly relative to the 2005–2006 records. Mate loss was defined as breeding with a new mate in 2007–2008 or 2008–2009 in the absence of the old mate from sighting records,

$$\text{mate loss rate}_{2007-2008} = \frac{\text{no. of birds with mates absent from the colony}_{2007-2008}}{\text{total no. of birds assessed}_{2007-2008}} / 2$$

For 2008–2009, the total proportion of birds with mates lost from the breeding site was divided by three, accordingly.

We first applied univariate  $\chi^2$  tests to compare reproductive success between the mate retention, divorce and mate loss subgroups within the respective observational years. We then used a multivariate, nominal logistic analysis to account for repeated measures on individuals in our dataset.

To further assess patterns within the 2007–2008 data, we employed a nominal logistic regression analysis with the mate choices of mate retention, overall mate changed, divorce and mate loss as independent variables, and breeding success as the dependent variable. We also ran this regression with the predictor term of divorce nested within the mate changed term, which, as divorce is a subcategory of mate change, served to more conservatively address the effects of divorce per se on reproductive success. Because our predictions were non-directional from the different adaptive divorce and mate-retention hypotheses. All statistical tests, using Statview5.0.1 and JMP®7.0, were two-tailed with  $\alpha=0.05$ .

**Results**

Annual estimates of divorce rates

Overall, annual divorce rate estimates were calculated between 43% (from 2007–2008 against 2005–2006 data) and 40% (form 2008–2009). Fourteen out of 35 known individuals observed breeding with another banded bird in

**Table 1** Reproductive success for mate retention, divorce and mate loss groups in *M. serrator* compared between 2005–2006 and 2007–2008 and 2008–2009 breeding seasons at Cape Kidnappers gannetry, New Zealand

Seasons	Total	Mate retained	Mate changed	
			Divorced	Mate absent
<b>2007–2008</b>				
Number	57	16	33	8
Chick 2007	23	10	12	1
No chick 2007	34	6	21	7
Chick 2005	32	11	19	2
No chick 2005	21	5	12	4
Unknown 2005	4	0	2	2
<b>2008–2009</b>				
Number	54	10	36	8
Chick 2008	16	8	7	1
No chick 2008	38	2	29	7
Chick 2005	39	8	27	4
No chick 2005	13	2	9	2
Unknown 2005	2	0	0	2

2007–2008 retained their mates in 2008–2009, while nine divorced their 2007–2008 mates; nine other birds changed to a new, banded mate, but it could not be determined if they fell in the mate loss or in the divorce category because their 2007–2008 mates were unbanded. The divorce rate between the consecutive seasons of 2007–2008 and 2008–2009 thus comprised both the above estimates, falling between 36% and 56%. In turn, annual mate loss estimates fell between 7% (from 2007–2008 data) and 5% (from 2008–2009 data; Table 1).

Correlates of breeding success with mate retention vs. divorce vs. mate loss

Reproductive success (Table 1) both in 2007–2008 and 2008–2009 was significantly higher for individuals with mates retained ( $\chi_{07}^2=4.53$ ,  $p_{07}=0.033$ ;  $\chi_{08}^2=14.93$ ,  $p_{08}<0.001$ ), who in turn bred significantly more successfully than individuals with mates lost ( $\chi_{07}^2=5.37$ ,  $p_{07}=0.021$ ). The proportion of divorced birds fledging chicks was lower than for those birds who retained their mates in both 2008–2009 ( $\chi_{08}^2=13.06$ ,  $p_{08}=0.003$ ), with a similar, though non-significant pattern observed in 2007–2008 ( $\chi_{07}^2=2.98$ ,  $p_{07}=0.085$ ). Breeding success between confirmed divorced birds and birds breeding with mates lost was similar in both seasons ( $\chi_{07}^2=1.69$ ,  $p_{07}=0.19$ ;  $\chi_{08}^2=0.212$ ,  $p_{08}=0.645$ ).

The same statistical patterns persisted when analysing breeding success for complete pairs rather than individual breeders within the mate-retention group ( $\chi_{07}^2=2.73$ ,  $p_{07}=0.098$ ,  $\chi_{08}^2=9.278$ ,  $p_{08}=0.005$  against all breeders with different mates;  $\chi_{07}^2=1.81$ ,  $p_{07}=0.18$ ,  $\chi_{08}^2=8.201$ ,  $p_{08}=0.004$  against true divorces;  $\chi_{07}^2=4.27$ ,  $p_{07}=0.039$ ,  $\chi_{08}^2=5.923$ ,  $p_{08}=0.015$  against the mate loss group).

Multivariate analyses confirmed our results (overall model:  $\chi_{07}^2=6.49$ ,  $p_{07}=0.011$ ), with the divorce term ( $\chi_{07}^2=3.3$ ,  $p_{07}=0.070$ ) not statistically significant when nested within the mate changed term ( $\chi_{07}^2=4.1$ ,  $p_{07}=0.043$ ) in the model.

Prior breeding success as a predictor of mate retention

Similar proportions of birds that bred or did not breed successfully in 2005–2006 (Fig. 1) retained their mates in 2007–2008 ( $\chi_{07}^2=0.413$ ,  $p_{07}=0.672$ ) and 2008–2009 ( $\chi_{08}^2=0.165$ ,  $p_{08}=0.685$ ), respectively, and there were no statistical differences when limiting these analyses to individuals whose mates from 2005–2006 were also seen in 2007–2008 and/or 2008–2009 and did or did not breed successfully in 2005 ( $\chi_{07}^2=0.254$ ,  $p_{07}=0.614$ ;  $\chi_{08}^2=0.528$ ,  $p_{08}=0.467$ ). Hence, neither mate loss nor divorce versus mate retention was correlated with prior breeding success.

## Discussion

Our observations reveal that Australasian gannets known to have bred with the same mate in a prior breeding season were more likely to successfully reproduce than birds observed with new mates. This pattern of reproductive success implies a fitness benefit for social monogamy across breeding seasons for this long-living, breeding philopatric and socially monogamous species.

Yet, the estimated annual divorce rates of 40% and 43% are within the upper third of divorce rates reported throughout seabirds (Cézilly et al. 2000b) and their closely related taxa and are especially high in comparison with the 17% reported for the Northern gannet *M. bassanus* (Nelson 1978), while the mate loss rates we report are highly consistent with adult mortality estimates for the study species (Nelson 1978).

The data reported here are consistent with the musical chairs hypothesis (Dhondt and Adriaensen 1994) in that reproductive success was not greater following divorce. In contrast to predictions of the incompatibility and also the better option hypotheses, for neither member of the pair was prior reproductive success predictive of mate retention. Nonetheless, the assessment of the validity of this hypothesis warrants further investigation.

More research on the behavioural dynamics, identity, age, quality and experience of divorcing individuals is therefore needed to characterise potential sex-specificity in mate-retention decisions and to unravel the likely varied ecological and ethological precursors of these choices in gannets and other long-living seabirds with prolonged obligate biparental care.

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