



Mate rotation by female choice and coercive divorce in Nazca boobies, *Sula granti*

TERRI J. MANESS & DAVID J. ANDERSON

Department of Biology, Wake Forest University, Winston-Salem, North Carolina

(Received 27 December 2007; initial acceptance 14 February 2008;
final acceptance 7 April 2008; published online 18 July 2008; MS. number: A08-00004R)

The formation and dissolution of mating pair bonds have been fruitful areas of investigation for evolutionary biologists. Adaptive mate choice has been the focus of most research on pair dissolution. However, recent work has shown that an important cause of pair dissolution can be involuntary forced divorce, where intruder(s) oust one or both partners. Previously, we presented evidence that, in a male-biased population, females exchanged a reproductively depleted male for a new 'refreshed' mate. This 'mate rotation' model of divorce could be driven by female choice, forced divorce by unpaired males, or by males forgoing reproduction to recover condition. Here, we examine these alternatives with behavioural and demographic data from our long-term study of banded Nazca boobies. The mate rotation pattern of divorce appears to be driven by a combination of two circumstances involving a female's abandonment of a previous partnership. In some cases, the female appeared to cooperate with a male intruder, causing her former partner to leave the nest. In other cases, the female abandoned her former mate and joined a new male at another nest site. Recent studies that have disentangled age and breeding experience from pair bond length have shown that an initial increase in reproductive output correlated with pair bond length, but after a period of time together the reproductive success of the pair declined. Given the assumed ubiquity of the cost of reproduction, divorce after a lengthy pair bond would seem to be advantageous for one or both mates when fresh potential partners are available.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: cost of reproduction; divorce; mate choice; mate rotation; Nazca booby; pair bond; serial monogamy; sex ratio bias; *Sula granti*

The variability observed in bird mating systems, especially the prominence of monogamy and extended pair bonds (Black 1996), has long been a focus of interest to evolutionary biologists (Lack 1968). Recent work has emphasized the termination of mating partnerships, providing a complement to the older and larger literature on pair formation (reviewed in Andersson 1994). Divorce, the disruption of the pair bond without death, gives insight into important evolutionary topics including sexual selection and mate choice. The frequency of divorce varies considerably between species, from 0% in waved albatrosses, *Diomedea irrorata* (Harris 1973) to 98% in greater

flamingos, *Phoenicopterus ruber roseus* (Cézilly & Johnson 1995), as well as between different populations of the same species (reviewed in Ens et al. 1996).

Divorce may be imposed on the pair and so be non- or maladaptive; possibilities include chance events leading partners to lose contact (Choudhury 1995; Ens et al. 1996), asynchronous arrival at the breeding area (Dhondt & Adriaensen 1994; Naves et al. 2006), and intruder(s) forcing divorce by ousting one or both partners (Taborsky & Taborsky 1999; Jeschke et al. 2007). Alternatively, divorce may reflect adaptive abandonment by either partner to undo its previous mate choice. Most adaptive hypotheses fall under the 'better option' model (reviewed in: Choudhury 1995; Ens et al. 1996), whereby a partner leaves because of incompatibility (Coulson 1972), to obtain a higher-quality mate (Ens et al. 1993), to correct

Correspondence: T. J. Maness, Department of Biology, Wake Forest University, Winston-Salem, NC 27109, U.S.A. (email: manetj2@wfu.edu).

errors in mate choice (Johnston & Ryder 1987), or to obtain a mate whose condition has not been impaired by recent reproductive effort (Cézilly & Johnson 1995; Maness & Anderson 2007). Adaptive divorce could also result from one pair member, but not both, resting to recover breeding condition. This pattern of divorce might be expected in species with frequent 'time-outs', such as long-lived birds (e.g. Jouventin & Dobson 2002; Dobson & Jouventin 2007), or among low-quality individuals (Mougin et al. 1997; Cam et al. 1998; Bradley et al. 2000). These hypotheses have been evaluated at the ultimate level (Heg 2003; Jeschke et al. 2007 reviewed in: Choudhury 1995; Ens 1996), but few have added a proximate perspective by also investigating the behaviours leading to the divorce event.

The probability of divorce may be conditioned by the operational sex ratio (OSR; Emlen & Oring 1977) of the population of interest (Choudhury 1995). Considering a male-biased population, males (the abundant sex) have fewer breeding opportunities than females do and so should be less likely than females to divorce voluntarily; a female has a pool of unpaired males available, facilitating mate switching if her mate's condition declines below that of members of the nonbreeding pool (Cézilly & Johnson 1995; Maness & Anderson 2007); and pairs may be more likely to be victims of forced divorce imposed by unpaired males (López-Sepulcre & Kokko 2005). Our previous work on a male-biased population (Maness et al. 2007; Townsend & Anderson 2007) of Nazca boobies showed that divorce was common and that males enter and exit the breeding pool more frequently than females do (Maness & Anderson 2007). Those results and others indicated a female mating preference based on costs of reproduction and enabled by the ready availability of unpaired, high-condition males, consistent with a model of adaptive 'mate rotation' that maximized the physiological condition of the female's current mate (Maness & Anderson 2007).

Many studies have suggested that females are the predominant initiators of divorce in birds (reviewed in Cézilly et al. 2000). Our previous study suggested that female Nazca boobies drive divorce and that males are involuntarily rotated out of pairings by female choice; however, we could not rule out some other mechanisms underlying the divorce patterns we observed (Maness & Anderson 2007). Here, we test divorce hypotheses using data on pre-breeding behaviours, pairing histories, and reproductive consequences of pairing history of our study population. Divorce in Nazca boobies could be driven by adaptive mate rotation involving female choice, by males choosing nonbreeding status to recover condition, or by forced divorce imposed on the pair by one of the many nonbreeding males in our population (approximately one-third of all adult males lack mates at a given moment; Maness & Anderson 2007). Jeschke et al. (2007) found evidence that forced divorce may be more common than previously thought.

If the adaptive mate rotation model operates in our population, then (1) prior to divorce, a female choosing to leave her former partner should sample the behaviour of her old mate, plus that of one or more other males before

opting for a new mate, (2) the reproductive success (RS) of divorcing females should be high prior to, and not decline after, divorce, (3) divorced males should attempt to retain their mate or to attract a new one because they divorced involuntarily and (4) the RS of male 'victims' of female choice should be high prior to, and decline after, divorce. The prediction that divorce should follow a successful breeding attempt contrasts with a meta-analysis showing a negative association between breeding success and mate retention (Dubois & Cézilly 2002). We do not suggest that unsuccessful males should be retained preferentially under mate rotation; successful and unsuccessful males should be retained if a better alternative is not available. However, successful breeders are more likely to be in poorer condition than recently nonbreeding males, given the survival costs of reproduction (Townsend & Anderson 2007) and mass loss during breeding (Apanius et al. 2008) in this species, and females should select against these successful breeders (i.e. upgrade mates). Previously, we tested the prediction that male victims of divorce have higher RS than do retained males in the year preceding divorce and found no difference in these estimates (Maness & Anderson 2007). However, the operation of more than one factor causing divorce could have confounded this test conducted at the population level. Accordingly, a more specific prediction of the mate rotation model regarding male RS, replacing (4) above, is that (4) RS of males divorced 'due to female choice' should be high prior to, and decline after, divorce.

If males choose temporary nonbreeding status, then these males (1) should not attempt to breed and (2) might abandon their nest sites.

If divorce is forced upon a Nazca booby pair by a nonbreeding male, then (1) one or both members of the pair should resist (with aggression against the incomer) the take-over, (2) aggressive behaviour of the current male in a pair should predict his success in mate retention, (3) RS of males that lose their nest site should be high prior to divorce (leading to poor condition and thus poor fighting ability) and low after divorce and (4) the RS of only the incomer should improve postdivorce (Jeschke et al. 2007) and the RS of the female victim of forced divorce may decline.

METHODS

Behavioural Observations

Nazca boobies are socially and genetically monogamous (Anderson & Boag 2006), long-lived pelagic seabirds (Anderson & Apanius 2003) with biparental care and similar parental roles (Anderson & Ricklefs 1992; Apanius et al. 2008). The population breeds seasonally at our study site at Punta Cevallos, Isla Española, Galápagos Islands, with most egg laying between October and January, and most fledging completed by June. At the beginning of each breeding season, male Nazca boobies defend nest sites, where they exclude other males and perform mate attraction behaviours (Nelson 1978). To determine behaviours preceding divorce (or mate retention) and to

identify behaviours females could use to assess potential mates, all resident birds (defined below) in a subsection of the colony known as the ‘mini-area’ were observed during the prebreeding season, starting 30 August 2003, through the egg-laying period of 2003. The mini-area is the northern third of the study area, which is the northern half of subcolony 1 (Huyvaert & Anderson 2004; see detailed description in Apanius et al. 2008). Egg laying began in mid-October and continued until February of 2004, but observations ended on 21 December 2003, when 95% of all clutches had been established. Since most birds vacate the colony during the heat of midday (Anderson & Ricklefs 1992; Anderson et al. 2004), birds were observed from 0600 to 0900 hours and 1500 to 1800 hours. All resident birds in the mini-area were fitted with metal as well as numbered plastic bands. The sex of adult Nazca boobies can be determined easily by voice (Nelson 1978). Males were given black plastic leg bands, while females had grey bands. The numbering on each plastic band was large enough to read easily by eye or with binoculars from approximately 20 m (the maximum distance that observers were from the birds). We noted 26 specific behaviours (see Electronic Supplementary Material) of males and females at the beginning of the 2003–2004 breeding season. Our treatment of behaviour types followed those of Van Tets (1965) and Nelson (1978), except as noted in the Electronic Supplementary Material.

The mini-area was divided into four observation subsections (A, B, C and D), each of which contained approximately 75 birds that were present regularly. Each subsection was observed on a 6-day rotating schedule: on

day 1, section A was observed from 0600 to 0900 hours and section B from 1500 to 1800 hours; on day 2, section C was observed from 0600 to 0900 hours and section D from 1500 to 1800 hours; no observations were performed on day 3; on day 4, section B was observed from 0600 to 0900 hours and section A from 1500 to 1800 hours; on day 5, section D was observed from 0600 to 0900 hours and section C from 1500 to 1800 hours; no observations were performed on day 6; then the cycle started over again at day 1. The same two observers performed every observation session. The first observer dictated a bird’s behaviour, its plastic identification number, its location (nest number; every nest site in this area has a permanent metal identification number), and the identity of any birds it interacted with; the second observer recorded the dictated information and noted the time. The observers sat on natural rock formations (see Fig. 1 of Apanius et al. 2008) or a raised wooden platform, both of which afforded a clear view of most birds in the observation area and were one or more metres from the nearest nest site. If the view of a bird or its nest site was continuously obstructed by the rocky terrain, the bird’s observable behaviours were noted (particularly its interactions with neighbours), but these birds were omitted from all analyses. Given that individuals in our population are indifferent to humans, we assumed that our presence caused no disturbance to the birds. As a precaution, the observers were in position 15 min before each observation period began to allow the birds any necessary acclimation to their presence. The observers performed one 6-day practice rotation prior to beginning actual data collection

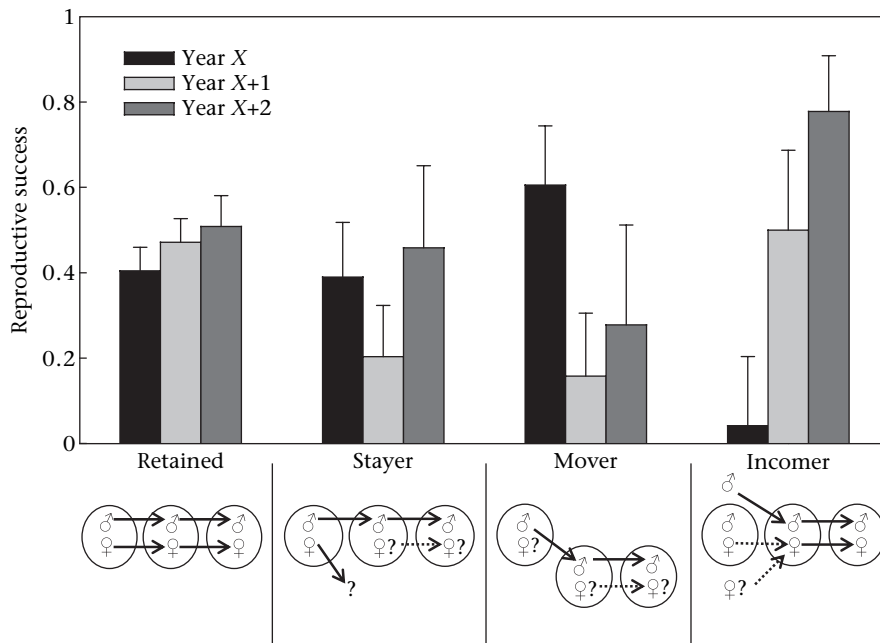


Figure 1. Male reproductive success by partnership category over a 3-year period. Year X was the year prior to the divorce (or no divorce if retained), year X + 1 was the year immediately after divorce, and year X + 2 was the final year that we followed the fate of pairs. Error bars represent 95% CI. The flow diagram illustrates the partnership categories; circles indicate nest sites and arrows represent yearly transitions. Individuals that stayed at the same nest site between years are linked by horizontal arrows, while birds that changed nest sites are linked by diagonal arrows. Solid arrows indicate transitions that must occur in a particular category, while dotted arrows represent transitions that may occur.

and had no knowledge of the previous pairing patterns of the birds. Approximately 2 weeks after data collection began the observation hours were reduced to 0600 to 0800 hours and 1600 to 1800 hours because most birds vacated the colony before 0900 hours and did not return until after 1600 hours. The observation hours were further reduced to 0600 to 0700 hours and 1700 to 1800 hours after 6 December 2003 since most clutches had been established by that date and interactions of interest were largely restricted to these hours. We were also present in the mini-area for several additional hours each day in the course of conducting other demographic studies and opportunistically noted aggressive interactions between individuals and injuries sustained from fights. These behaviours were not included in the factor analysis described below.

Several different Nazca booby behaviours appear to convey similar messages to a receiver. For example, yes/no head wagging, wing flailing and jabbing are all used in territoriality (Van Tets 1965; Nelson 1978). Therefore, many behaviours were expected to correlate with one another. We used factor analysis to reduce the 26 recorded behaviours to a smaller set of factors for use in later analyses. We used principal components analysis (PCA; SPSS, ver.15.0; SPSS, Inc., Chicago, IL, U.S.A.) for this data reduction, using a covariance matrix as input, rather than a correlation matrix, because we wanted to compare factor structures between different groups of birds (Kim & Mueller 1978). Logistic regressions compared factor structures between different groups of males (breeders versus nonbreeders and retained versus divorced males). Akaike's information criterion corrected for small sample sizes (AICc) was used for logistic regression model selection and ranking (Burnham & Anderson 2002). Since AICc converges to AIC with large sample sizes, AICc should be employed regardless of sample size (Burnham & Anderson 2002). We also report Bayesian information criterion (BIC) values as an alternative model selection tool. The BIC penalizes free parameters more strongly than does AIC (Schwarz 1978).

We recorded the behaviours of 160 resident males and 107 resident females, over a total of 318 h. Birds present during observation periods for more than 500 min (2 SD from the mean) were considered resident birds; birds present less than the cutoff time were considered visitors and were excluded from all analyses. Two resident females did not breed in 2003–2004, but did form exclusive bonds with a social partner. These females and their social partners were excluded from all analyses that determined predictors of mating success. Only the behaviours that males performed prior to the subpopulation's initiation of breeding (the first egg was laid in the mini-area on 16 October 2003) were considered for factor analysis, because an unpaired male's behaviour may change as the likelihood of obtaining a mate diminishes as fewer females remain available for breeding. We calculated the frequency of each of the 26 behaviours that a male performed and the total time that a male was present over the truncated observation period. The 26 recorded behaviours were likely to factor well (KMO test = 0.784; Bartlett's approximate $\chi^2_{325} = 2768.95$, $P < 0.0001$). Five components, explaining 85.0% of the variance in the data set, were extracted. A varimax rotation with Kaiser normalization was used to determine component loadings.

We named the five components Mate, Territorial, Prospecting, Aggression and Advertising, based on the behaviours that loaded onto them (see Table 1 for the behaviours and their component loading scores). Two behaviours, displaced and fight, did not load highly onto any factor, probably because they were relatively rare behaviours. These behaviours were left in the analysis because removing them did not appreciably change the outcome of the PCA and they were subsequently assigned to the factors that they correlated with most. Two other behaviours, garden and circle flight, loaded onto two factors each. Garden correlated with Advertising and Territorial components, reflecting the dual nature of this behaviour. Males may garden to make their symbolic nests more attractive to females (Advertising) and they also pick

Table 1. Components and component loading scores from a principal components analysis of the 26 different behaviours (described in Electronic Supplementary Material) performed by male Nazca boobies during the pre-egg-laying period in 2003

| Component loading score | | | | | | | | | |
|-------------------------|-------|---------------|-------|-------------|-------|------------|-------|-------------|-------|
| Mate | | Territorial | | Prospecting | | Aggression | | Advertising | |
| Behaviour | Score | Behaviour | Score | Behaviour | Score | Behaviour | Score | Behaviour | Score |
| Gift | 0.908 | Yes/no | 0.864 | Roaming | 0.675 | Squabble | 0.841 | Skypoint | 0.842 |
| Mutual jab | 0.882 | Garden | 0.699 | Roam flight | 0.661 | Bill clash | 0.732 | Garden | 0.660 |
| Mutual gift | 0.811 | Vocal | 0.651 | Returned | 0.633 | | | Parade | 0.426 |
| Allopreen | 0.748 | Wing flail | 0.613 | Left | 0.604 | | | | |
| Bill touch | 0.704 | Jab | 0.477 | Flee | 0.587 | | | | |
| Copulation | 0.619 | Circle flight | 0.432 | | | | | | |
| Cop. attempt | 0.553 | Fight | 0.296 | | | | | | |
| Roam | 0.496 | | | | | | | | |
| Chased | 0.478 | | | | | | | | |
| Circle flight | 0.457 | | | | | | | | |
| Displaced | 0.198 | | | | | | | | |

The behaviours reduced to five components and were named by the main behaviours that loaded onto them.

up and rearrange nest material during conflicts with neighbours (Territorial). Circle flight correlated with Mate and Territorial components. Males perform circle flights to establish and maintain territories (Nelson 1978). In this study, males also performed circle flights repeatedly to bring gifts to potential mates or preceding mutual jabs with a potential mate.

The five behavioural components and total minutes present were used as fixed effects in a logistic regression ('R' open-source software by R-project, ver.2.6.1; <http://www.r-project.org>) with mating success (105 breeding and 53 nonbreeding males) as the binary outcome variable. All predictors were entered using a block entry method. The omnibus test of model coefficients was significant ($\chi^2_6 = 76.55$, $P < 0.0001$) and the model was a good fit ($-2LL = 125.043$; Hosmer & Lemeshow $\chi^2_8 = 1.71$, $P = 0.99$; AICc = 139.79; BIC = 160.48); however, total minutes present was not a significant predictor ($P = 0.91$) and was dropped from the model. The final model correctly classified 80.4% of males ($-2LL = 125.044$; Hosmer and Lemeshow $\chi^2_8 = 1.71$, $P = 0.99$; AICc = 137.60; BIC = 155.42). Significant positive predictors of male mating success were Mate, Territorial and Advertising behaviours, while Prospecting behaviour was a significant negative predictor and Aggression was not significant (Table 2). All males were used in this analysis, including those retained as mates from the previous season.

Females who retain their mate may use different behavioural criteria than do divorcing females when deciding with whom to mate because they have prior experience with the male (Dubois et al. 2004); therefore, a second logistic regression was performed with retained males left out of the model. As in the previous logistic regression, the five behavioural components and total

minutes present were used as fixed effects with mating success (43 breeding and 53 nonbreeding males) as the binary dependent variable. Again, total minutes present was not a significant predictor ($P = 0.90$; AICc = 107.43; BIC = 124.10) and was dropped from the model. The omnibus test of model coefficients was significant ($\chi^2_5 = 36.87$, $P < 0.0001$) and the model was a good fit ($-2LL = 92.174$; Hosmer & Lemeshow $\chi^2_7 = 8.77$, $P = 0.27$; AICc = 105.28; BIC = 119.56) and correctly classified 80.2% of males. Thus, the two regression approaches produced nearly identical results with significant positive predictors of mating success being Mate, Territorial and Advertising behaviours, Prospecting was a significant negative predictor, and Aggressive behaviours were not significant (Table 2). We used these aggregating behavioural components to test predictions of various divorce models below.

Reproductive Success of Male and Female Categories

To examine predictions regarding pre- and postdivorce RS, we categorized male and female Nazca boobies using a modification of the partnership categorization of Jeschke et al. (2007): retained (partnership remains intact); stayer (focal bird divorces and retains its nest site); mover (focal bird divorces and leaves its nest site); incomer (focal bird acquires both a nest site and a new partner). Pairs in which one member died were not divorces and were omitted from all analyses. We calculated RS in the years prior to and after divorce, or in years without divorce (see flow diagrams in Figs 1 and 2). To separate males and females into the four partnership categories, we examined our database of reproductive histories of 469 banded adults in the study area (see above). Nest sites in this area have been marked with permanent nest numbers since 1995. We restricted our investigation to the breeding seasons beginning in 2000 through 2004 because (1) we could not track nest take-overs prior to 1995, (2) many adults became nonbreeders for several years after the strong El Niño-Southern Oscillation event of 1997–1998 (Maness & Anderson 2007) and (3) the size of the banded population was larger during these years than during earlier years of our work, facilitating the tracing of mating patterns of recognizable birds. The proportion of birds banded in the study area was higher than in the rest of our study site, avoiding analytical problems associated with pairs including an unbanded (and so unidentifiable) bird.

Pairs of birds were followed for 3 years (the mean breeding bout length for males; Maness & Anderson 2007). Year X was the year prior to the divorce (or no divorce if retained), year $X + 1$ was the year immediately after divorce, and year $X + 2$ was the final year that we followed the fate of pairs. The RS of each bird was determined for each of these points in a breeding sequence. Since the extrapair fertilization rate of Nazca boobies is estimated as 0% (Anderson & Boag 2006) and RS is binary for Nazca boobies (they rear at most, one offspring per year; Humphries et al. 2006), within-year RS between

Table 2. Logistic regression coefficients, standard error, statistical significance, odds ratio and 95% confidence intervals of odds ratios of behavioural predictors of male mating success in Nazca boobies

| Predictor | β | SE | P | Odds ratio | 95% CI for OR | |
|-------------------------------|---------|-------|--------|------------|---------------|-------|
| | | | | | Lower | Upper |
| All males* | | | | | | |
| Constant | 1.434 | 0.302 | <0.001 | | | |
| Mate | 2.159 | 0.403 | <0.001 | 8.67 | 3.94 | 19.10 |
| Prospecting | -1.303 | 0.334 | <0.001 | 0.27 | 0.14 | 0.52 |
| Territorial | 0.615 | 0.290 | 0.034 | 1.85 | 1.05 | 3.26 |
| Advertising | 0.465 | 0.238 | 0.050 | 1.59 | 1.00 | 2.54 |
| Aggression | 0.149 | 0.234 | 0.525 | 1.16 | 0.73 | 1.84 |
| Nonbreeders/New males† | | | | | | |
| Constant | 0.551 | 0.335 | 0.100 | | | |
| Mate | 1.635 | 0.437 | <0.001 | 5.13 | 2.18 | 12.08 |
| Prospecting | -0.949 | 0.338 | 0.005 | 0.39 | 0.20 | 0.75 |
| Territorial | 0.775 | 0.321 | 0.016 | 2.17 | 1.16 | 4.07 |
| Advertising | 0.651 | 0.262 | 0.013 | 1.92 | 1.15 | 3.20 |
| Aggression | 0.252 | 0.241 | 0.297 | 1.29 | 0.80 | 2.06 |

*All males, including those retained by their previous mates, were used in this analysis.

†Only nonbreeding and males breeding with a new mate (retained males excluded) were used in this analysis.

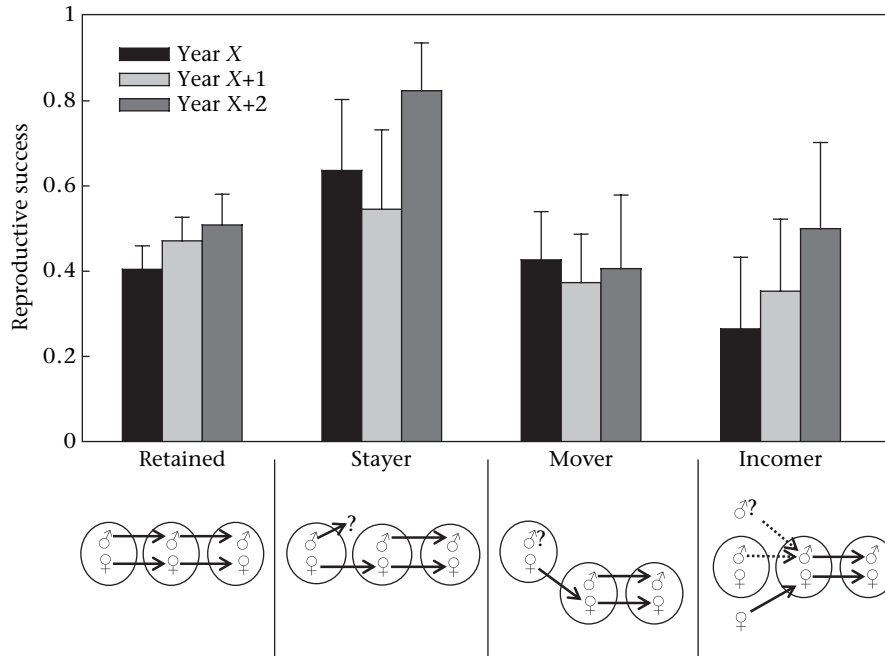


Figure 2. Female reproductive success by partnership category over a 3-year period. Year X was the year prior to the divorce (or no divorce if retained), year $X + 1$ was the year immediately after divorce, and year $X + 2$ was the final year that we followed the fate of pairs. Error bars represent 95% CI. The flow diagram illustrates the partnership categories; circles indicate nest sites and arrows represent yearly transitions. Individuals that stayed at the same nest site between years are linked by horizontal arrows, while birds that change nest sites are linked by diagonal arrows. Solid arrows indicate transitions that must occur in a particular category, while dotted arrows represent transitions that may occur.

categories was compared using log-linear analysis of frequency tables (Statistica, v. 6.1; Statsoft, Inc., Tulsa, OK, U.S.A.). Repeated measures log-linear analyses (SPSS, ver.15.0; SPSS, Inc., Chicago, IL, U.S.A.) were used to assess whether within-category RS improved or declined after year X . To avoid pseudoreplication, RS was considered separately by sex and partnership category.

To minimize the number of statistical tests performed, omnibus log-linear analyses of partnership category (four levels) by RS_{yrX} (two levels) by RS_{yrX+1} (two levels) frequency tables were analysed separately by sex to test for category by RS_{yrX} , and category by RS_{yrX+1} , interactions. Tabulations of category by RS_{yrX} by RS_{yrX+2} (two levels) were analysed similarly. If the model fit was adequate and the maximum likelihood (ML) chi-square value of two-way interactions was significant, then individual contrasts of interest were examined. Effect sizes were determined by odds ratios. The false discovery method (Benjamini & Hochberg 1995; Curran-Everett 2000) was used to adjust the critical value when multiple comparisons were performed. All hypotheses tested below were directional, so one-tailed tests were performed in all cases.

RESULTS

Mate Rotation Predictions

Twenty-four of the 87 males (27.6%) that bred the year before (2002–2003) the behavioural observations were conducted were divorced at the beginning of the 2003–2004 breeding season. Fourteen (58.3%) of these

divorces involved pairs that successfully fledged a chick in 2002–2003.

Nineteen (79.2%) divorces were attributable to female choice. Fourteen of these 19 involved mover females. Eight of the 14 movers performed Mate behaviours (see [Methods](#)) with their old mate and one or more other males before settling with a new mate at a new nest site, consistent with prediction 1; six of these fledged a chick in the previous year. Six mover females did not interact with their previous partners and spent no time at their old nests; instead, these females performed Mate behaviours with one or more males before settling at a new site with a new male. Only one of these six movers produced a fledgling with her old mate in the previous year. The remaining five of the 19 divorces were all preceded by successful breeding in the previous year and involved stayer females. In two of these five cases, the female only interacted aggressively towards her old mate and assisted the incoming male in defending their nest site from the previous year from her old partner. One of these incoming males was defeated and driven away by the old male, but then the female joined with the incoming male to defeat and drive away her old partner. In the remaining three cases, the female performed Mate behaviours with her old mate and with the incoming male while her original mate was absent, presumably foraging. The female then became aggressive towards her old mate and assisted the incoming male in defending the nest site from her old partner.

Five of the 24 divorces (20.8%) could not be attributed exclusively to female choice. Two of these divorces had no

clear instigator and were perhaps cases of mutual divorce because neither member of the pair spent time at their old nest sites, the pair members did not interact (except for one brief aggressive encounter), and no incoming birds took over their old sites. All males and both females in these two divorce cases obtained new mates in 2003–2004. One of these five divorces appeared to be due to asynchronous arrival of the pair members because the original male remated before his old mate returned from nonbreeding absence; she was unusually late, arriving 60 days later than the median arrival date for females. One of the five divorces could have been due to chance events or forced divorce because the pair's nest site was occupied by a new pair before either member of the old pair returned from nonbreeding absence, and both former residents had aggressive encounters with the incoming pair. The last of these five divorces was consistent with a forced divorce because an incoming male defeated and chased away the original male before the original female returned from nonbreeding absence. The female paired with the incomer and so this divorce could arguably be attributed to female choice because she could have chosen to pair with her old mate (a nonbreeder in 2003–2004) at his new nest or to pair with a new male at a new site rather than staying with the incomer. However, we did not treat this divorce as a case of female choice.

Inconsistent with prediction 2 of mate rotation, females divorcing in 2003–2004 were not more likely to have fledged a chick ($RS = 0.63$, 95% CI = 0.41–0.81) in the preceding year than females that retained their mates ($RS = 0.48$, 95% CI = 0.36–0.61, $\chi^2_1 = 1.22$, $P = 0.14$), but the statistical power of this test was low (0.304) because of the small number of females divorcing in the 1-year analysis. Prediction 2 received partial support in the larger multiyear log-linear analysis. The female category by RS_{yrX} by RS_{yrX+1} frequency table produced a well-fit model ($\chi^2_4 = 5.14$, $P = 0.27$) with significant two-way interactions ($\chi^2_7 = 15.77$, $P = 0.027$). Female stayers had significantly higher RS_{yrX} than did retained females ($\chi^2_1 = 4.54$, $P = 0.016$, adjusted $\alpha_{crit} = 0.017$, odds ratio = 1.19; Fig. 2), but female movers did not have higher RS_{yrX} than did retained females ($\chi^2_1 = 0.12$, $P = 0.36$; Fig. 2). The RS_{yrX} of stayer and mover females combined (all divorcing females, $RS_{yrX} = 0.47$, 95% CI = 0.38–0.57) was not different from the RS_{yrX} of retained females ($RS_{yrX} = 0.40$, 95% CI = 0.35–0.46; $\chi^2_1 = 1.48$, $P = 0.11$). No difference was found in the RS_{yrX+1} between any of the female categories ($\chi^2_3 = 3.76$, $P = 0.29$). The log-linear analysis of female category by RS_{yrX} by RS_{yrX+2} frequency table produced a well-fit model ($\chi^2_4 = 2.30$, $P = 0.68$) with marginally significant two-way interactions ($\chi^2_7 = 13.89$, $P = 0.053$). Stayer females had marginally higher RS_{yrX+2} than retained females ($\chi^2_1 = 4.10$, $P = 0.022$, adjusted $\alpha_{crit} = 0.017$, odds ratio = 3.16; Fig. 2), but mover females did not have higher RS_{yrX+2} than retained females ($\chi^2_1 = 1.13$, $P = 0.144$). All divorced females (movers and stayers; $RS_{yrX+2} = 0.53$, 95% CI = 0.39–0.66) did not have higher RS_{yrX+2} than retained females ($RS_{yrX+2} = 0.51$, 95% CI = 0.44–0.58; $\chi^2_1 = 0.08$, $P = 0.39$). Repeated measures log-linear analysis revealed that RS did not change for any female category across either time span ($LR_1 < 3.14$, $P > 0.04$, adjusted $\alpha_{crit} = 0.006$). As

predicted, some (stayer), but not all, divorced females had higher RS prior to divorce than those females choosing to retain their partners. Also, the RS of divorcing females did not decline postdivorce.

All of the divorced males performed Advertising behaviours during the prebreeding period; those that attracted a female to their nests performed Mate behaviours with them; none willingly abandoned their old sites, and none appeared to try to drive their old mate (or potential new mates) from their nest site, supporting prediction 3. The RS values for male 'victims' of divorce in 2003–2004 were the same as those reported above for female choice, inconsistent with prediction 4, because these male victims were not more likely than retained males to have fledged a chick the prior year (but see analysis of larger sample size below).

No divorces that occurred during the observation year could be attributed exclusively to male choice, and only two divorces could not be attributed at least partly to female choice (a female arriving late, and a pair displaced by another pair), so we made the simplifying assumption that all divorces in the multiyear analysis were results of female choice. Inevitably, without behavioural observations in all years, a small minority of divorces will be classified incorrectly with this assumption. The multiyear log-linear analysis of male category by RS_{yrX} by RS_{yrX+1} frequency table produced a well-fit model ($\chi^2_4 = 5.89$, $P = 0.21$) with significant two-way interactions ($\chi^2_7 = 50.93$, $P < 0.0001$). Mover males had significantly higher RS_{yrX} than retained males ($\chi^2_1 = 5.59$, $P = 0.009$, odds ratio = 2.26; Fig. 1), but stayer males did not ($\chi^2_1 = 0.04$, $P = 0.42$). All divorced males combined (movers and stayers) had similar RS_{yrX} ($RS = 0.47$, 95% CI = 0.38–0.57) to retained males ($\chi^2_1 = 1.48$, $P = 0.11$). Repeated measures log-linear analysis revealed that the RS of mover and stayer males was significantly reduced 1 year after divorce (movers: $LR_1 = 14.07$, $P < 0.001$, odds ratio = 0.12; stayers: $LR_1 = 6.06$, $P = 0.007$, odds ratio = 0.40), but not reduced 2 years after divorce with respect to year X ($LR_1 = 1.159$, $P = 0.28$ and $LR_1 = 0.111$, $P = 0.74$, respectively). Prediction 4 received mixed support because some, but not all, divorced males had higher RS in the previous year than retained males and the RS of divorced males was significantly reduced the year after divorcing.

Male Time-Out Predictions

All males that were divorced at the beginning of the 2003–2004 breeding season established nest site territories and performed Advertising behaviours during the prebreeding season inconsistent with prediction 1. Only two males appeared to willingly give up their previous nest sites and both of these males obtained new mates at new sites, inconsistent with prediction 2. Moreover, 58.3% of divorced males obtained new mates in 2003–2004.

Forced Divorce Predictions

Six divorced males lost their nest sites to an incoming male and one lost his nest to an incoming pair (described above) in 2003–2004. All seven of these males attempted to resist the nest take-over: they all had aggressive

encounters with the incoming male and/or their former mates prior to losing their nests, consistent with prediction 1. As described above, the six former partners of these males did not appear to resist the incoming males. Instead, these females were aggressive towards their former mates, indicating that males but not females were forced to divorce in these cases. Although Aggressive behaviour was not a significant predictor of male mating success, retained males had marginally higher component scores for Aggressive behaviours (Welch $F_{1,35.4} = 3.65$, $P = 0.032$, adjusted $\alpha_{\text{crit}} = 0.025$) than males that lost their nest sites, but retained males did not have higher component scores for Territorial behaviours (Welch $F_{1,7.9} = 1.53$, $P = 0.13$), providing mixed support for prediction 2 (Welch tests (SPSS, ver.15.0; SPSS, Inc., Chicago, IL, U.S.A.) were performed because the sample size (events per parameter) was too small to adequately estimate logistic regression coefficients of the PCA behavioural components (Peduzzi et al. 1996)). Males that lost their nests to incomers had significantly higher RS in 2002–2003 (RS = 1.0, 95% CI = 0.63–1.0) than did retained males (RS = 0.48, 95% CI = 0.36–0.61; $\chi^2_1 = 6.74$, $P = 0.009$, $\phi_2 = 0.31$; Cramer's coefficient (Zar 1999, Page 403) is reported here because the odds ratio cannot be calculated when a proportion = 1.0), consistent with prediction 3. Only one male that was forced from his former nest site obtained a new mate in 2003–2004, so RS declined for this group of males (RS = 0.14, 95% CI = 0.03–0.53; repeated measure analysis of contingency tables and effect size could not be calculated because of zeros in one column of the table), which is also consistent with prediction 3. Incomer males had significantly lower $RS_{\text{yr}X}$ than all other male categories ($\chi^2_1 > 12.69$, $P < 0.001$, odds ratio < 0.07 ; Fig. 1). The log-linear analysis of male category by $RS_{\text{yr}X}$ by $RS_{\text{yr}X+2}$ frequency table produced a well-fit model ($\chi^2_4 = 5.14$, $P = 0.27$) with significant two-way interactions ($\chi^2_7 = 21.06$, $P = 0.004$). Incomer males had significantly higher $RS_{\text{yr}X+2}$ than all other male categories ($\chi^2_1 > 3.99$, $P < 0.046$, odds ratio > 4.55 ; Fig. 1). The RS of incomer males significantly improved in both years after their partner's divorce (yr_X to yr_{X+1} : $LR_1 = 15.25$, $P < 0.001$, odds ratio = 36.85 and yr_X to yr_{X+2} : $LR_1 = 18.02$, $P < 0.001$, odds ratio = 77.50; Fig. 1). Incomer males were the only category, male or female, to significantly improve their RS postdivorce (or no divorce, if retained), which is consistent with prediction 4. However, the RS of stayer females did not decline after the forced divorce, which is inconsistent with prediction 4.

DISCUSSION

Empirical and theoretical assessments of pair formation, divorce and remating strategies have been fruitful areas of investigation for evolutionary biologists (reviewed in: Choudhury 1995; Ens et al. 1996), but the importance of involuntary forced divorce as a mechanism of pair dissolution has been overlooked and underinvestigated (Jeschke et al. 2007). Nonbreeding adults have been postulated to be a buffer against population fluctuation (Durell & Clarke 2004), but recent theoretical work has suggested that these 'unemployed' (Anderson et al. 2004)

individuals can reduce population growth, perhaps through harassment of breeders and disruption of established pair bonds (López-Sepulcre & Kokko 2005; Jeschke et al. 2007). In the case of Nazca boobies, nonbreeding adults regularly attack unattended chicks in our study colony and the resulting injuries can lead to substantial nestling mortality from subsequent blood feeding by landbirds (Anderson et al. 2004). Nonbreeding males in this study also harassed incubating females; sometimes the female stopped incubation to chase these males away (T.J.M., personal observation). Given the excess of adult males in our population and their interference with normal breeding activities, nonadaptive forced divorce is a plausible cause of pair disruption in addition to adaptive mate rotation, and instances of forced divorce have been reported in other species (Ens et al. 1993; Dhondt et al. 1996; Williams & McKinney 1996; Taborsky & Taborsky 1999; Heg et al. 2003; Jeschke et al. 2007). We know of no other study before ours that has systematically investigated the behaviour of pairs and nonbreeding adults prior to divorce to reveal the proximate cause(s).

Our behavioural observations provided evidence for chance events, forced divorce and female choice against successful (mate rotation) as well as unsuccessful (better option) males as likely causes of divorce in our population. Two instances of divorce could not be classified but were consistent with both parties instigating the divorce (error in mate choice or incompatibility). Individuals of differing quality or breeding status may pursue different divorce strategies (Choudhury 1995); therefore, it is likely that multiple causes of divorce exist within a population, as we have concluded in this study. This pattern could be fairly common, but only a few studies have documented this phenomenon to date (Ens et al. 1993; Cockburn et al. 2003; Heg et al. 2003).

We found marginal support for mate rotation predictions among stayer females, whose gain in RS compared to that of retained females approached significance. Mover females did not have higher RS prior to divorce than did retained females, inconsistent with prediction 2 of the mate rotation model, and behavioural observations suggested that these females divorced, as predicted by the better option model and not the mate rotation model. Mover females came largely from unsuccessful pairs, and most did not visit their old nest sites or interact with their old partners, suggesting that they had decided to avoid their old partners some time before we began our observations. Thus, reproductive histories and behavioural observations indicate that female choice against prior mates can follow the mate rotation model in the case of successful pairs and can follow the better option model in the case of failed pairs. It is possible that the male partner in unsuccessful pairs (all stayers in our observational study) could be the instigator of divorce. We find this unlikely because many divorced males became nonbreeders in the year following divorce, and RS of divorced males decreased significantly, at least in the year immediately following divorce, while mover females' RS did not. In divorces involving successful pairs, the females tended to interact (perform Mate behaviours) with their old mate and one or more other males before pairing with a new

male, perhaps indicating that the decision to upgrade mates required more time and information than in the case of previously unsuccessful pairings.

We found no evidence of adaptive departure of males from the breeding pool to recover condition because all divorced males advertised their availability to potential mates, none willingly gave up their nest sites (except for the two cases of mutual divorce) and none attempted to drive their old mate or potential new mates from their nest sites.

Divorced males that moved from their old nest sites defended their nest sites from the incoming male and former mate prior to being forced away, consistent with forced divorce by outside males in cooperation with pair females. Incoming males were the only category of males that improved their RS significantly after divorce (Fig. 1). This outcome is predicted by both the mate rotation model of divorce and the forced divorce scenario because females should switch to previously nonbreeding males under mate rotation and unemployed males should most easily oust depleted (=successfully breeding) males under forced divorce. Collectively, our results suggest that mate rotation was usually accomplished by forced divorce. Divorce generally had a negative effect on male RS, particularly in the year immediately following divorce, because many mover and stayer males failed to obtain a new mate that year. Most divorced males return to breeding status after one or two years of nonbreeding (Maness & Anderson 2007), and most mover males would then become incomers, so it could be argued that divorce benefits these males as well. However, in all seven cases (100%) of an incoming male taking a mover male's nest site, the males had aggressive interactions that led to bleeding lacerations for both males and often (five out of seven cases) the stayer female also had aggressive interactions with her former mate that occasionally led to injury to the stayer female (T.J.M., personal observation). Also, a male that did not have an established nest site was highly unlikely to obtain a mate, as indicated by the negative logistic regression coefficient of Prospecting behaviours. In summary, we found no evidence to support voluntary ceding of the breeding attempt by the mover male to the incomer.

Instead, our behavioural observations suggest that, in most cases, divorce appears to be a new type of forced divorce, one that is forced upon a successful male by his old mate and the incoming male in the context of adaptive mate rotation. Females have good reason to join with the incomer because the RS of the female stayers, the supposed 'victims' of forced divorce, was higher than any other female category prior to divorce and remained highest 2 years after the divorce (Fig. 2). Males that lost their nest sites to an incoming male were less aggressive in the prebreeding season than retained males were, although this behaviour was not a significant predictor of overall male mating success. Other behavioural criteria, such as Mate, Prospecting, Territorial and Advertising behaviours, may be used in females' mate choice decisions, perhaps because highly aggressive males tend to be poor parents (Wingfield et al. 1990; Forsgren 1997; Qvarnström & Forsgren 1998; Wong 2004).

Previous studies suggested that forced divorce may be important in populations that are at, or near, their carrying capacity and limited by high-quality nesting sites (Heg et al. 2003; Jeschke et al. 2007). Our population does not fit this pattern because nesting sites do not appear to be limited (Townsend et al. 2002) and nest site quality (microclimate, ease of flight initiation, substrate characteristics, etc.) does not explain variation in the number of fledglings produced at a particular site (D.J.A., unpublished data). In addition, if high-quality females (stayers) in our population selected preferred nest sites only, then they would have no reason to assist an incomer with the nest take-over. Instead, these females could settle for the winner of the male contest, but these stayer females were active participants in the take-over and we observed one female opt for an incomer that lost a fight with her former partner. So while site fidelity could contribute to mate fidelity in our system, it does not appear to be the driving force in mate rotation.

The mate rotation pattern of divorce appears to be due to a combination of two effects involving a female's abandonment of a previous partnership. In some cases, forced divorce included female collusion, and in other cases, the female chose another male at another nest site. Long-lived species with obligate biparental care, such as seabirds, are expected to divorce rarely because RS should improve as familiarity with a mate increases (Black 1996) and most seabirds form persistent pair bonds (Ens et al. 1996). We found no evidence supporting a mate familiarity effect because mover females and incomer males had higher RS than faithful pairs. Recent studies that have disentangled age and breeding experience from pair bond length have shown that pair bond length correlated with an initial increase in RS, which is then followed by a decrease (Lewis et al. 2006; van de Pol et al. 2006; Naves et al. 2007). Experimental removal of either pair member reversed this downward reproductive trend once the 'victim' of divorce paired with a new mate (van de Pol et al. 2006). If costs of reproduction are ubiquitous in iteroparous organisms, as suggested by life history theory (Stearns 1992), then divorce, after a period of time together, would seem advantageous for one or both members of a pair, particularly if nonbreeding partners are available. A logical line of future inquiry then becomes 'What constrains older pairs to stay together?'

Acknowledgments

We thank the Galápagos National Park Service for permission to work in the Park, the Charles Darwin Research Station and TAME Airline for logistical support, the National Geographic Society, the Oak Foundation, the Mead Foundation and Wake Forest University for research funding, our many competent assistants and colleagues for their work in producing our long-term databases, Tiffany Beachy for assistance with behavioural observations, V. Apanius and M. Müller for statistical guidance, and the members of the Anderson lab group and two anonymous referees for comments on an earlier draft. This material is based upon work supported by the National Science Foundation under grant nos DEB 93045679, DEB 9629539, DEB 98-06606 and DEB 0235818 to D.J.A.

Supplementary Material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.anbehav.2008.04.020](https://doi.org/10.1016/j.anbehav.2008.04.020).

References

- Anderson, D. J. & Apanius, V. A. 2003. Actuarial and reproductive senescence in a long-lived seabird: preliminary evidence. *Experimental Gerontology*, **38**, 757–760.
- Anderson, D. J. & Boag, P. T. 2006. No extra-pair fertilization observed in Nazca booby (*Sula granti*) broods. *Wilson Journal of Ornithology*, **118**, 244–247.
- Anderson, D. J. & Ricklefs, R. E. 1992. Brood size and food provisioning in masked and blue-footed boobies (*Sula* spp.). *Ecology*, **73**, 1363–1374.
- Anderson, D. J., Porter, E. T. & Ferree, E. D. 2004. Non-breeding Nazca boobies (*Sula granti*) show social and sexual interest in chicks: behavioural and ecological aspects. *Behaviour*, **141**, 959–977.
- Andersson, M. B. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Apanius, V. A., Westbrook, M. W. & Anderson, D. J. 2008. Reproduction and immune homeostasis in a long-lived seabird, the Nazca booby (*Sula granti*). *Ornithological Monographs*, **65**.
- Benjamini, Y. & Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B – Methodological*, **57**, 289–300.
- Black, J. M. 1996. Introduction: pair bonds and partnerships. In: *Partnerships in Birds: the Study of Monogamy* (Ed. by J. M. Black), pp. 3–20. Oxford: Oxford University Press.
- Bradley, J. S., Wooller, R. D. & Skira, I. J. 2000. Intermittent breeding in the short-tailed shearwater *Puffinus tenuirostris*. *Journal of Animal Ecology*, **69**, 639–650.
- Burnham, K. P. & Anderson, D. R. 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretical Approach*. 2nd edn. New York: Springer-Verlag.
- Cam, E., Hines, J. E., Monnat, J. Y., Nichols, J. D. & Danchin, E. 1998. Are adult nonbreeders prudent parents? The Kittiwake model. *Ecology*, **79**, 2917–2930.
- Cézilly, F. & Johnson, A. R. 1995. Re-mating between and within breeding seasons in the greater flamingo *Phoenicopterus ruber roseus*. *Ibis*, **137**, 543–546.
- Cézilly, F., Prévault, M., Dubois, F., Faivre, B. & Patris, B. 2000. Pair-bonding in birds and the active role of females: a critical review of empirical evidence. *Behavioral Processes*, **51**, 83–92.
- Choudhury, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behaviour*, **50**, 413–429.
- Cockburn, A., Osmond, H. L., Mulder, R. A., Green, D. J. & Double, M. C. 2003. Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus*. *Journal of Animal Ecology*, **72**, 189–202.
- Coulson, J. C. 1972. The significance of the pair-bond in the kittiwake. *Proceedings of the International Ornithological Congress*, **25**, 424–433.
- Curran-Everett, D. 2000. Multiple comparisons: philosophies and illustrations. *American Journal of Physiology Regulatory Integrative and Comparative Physiology*, **279**, R1–R8.
- Dhondt, A. A. & Adriaensen, F. 1994. Causes and effects of divorce in the blue tit *Parus caeruleus*. *Journal of Animal Ecology*, **63**, 979–987.
- Dhondt, A., Adriaensen, F. & Plompen, W. 1996. Between- and within-population variation in mate fidelity in the great tit. In: *Partnerships in Birds: the Study of Monogamy* (Ed. by J. M. Black), pp. 235–248. Oxford: Oxford University Press.
- Dobson, F. S. & Jouventin, P. 2007. How slow breeding can be selected in seabirds: testing Lack's hypothesis. *Proceedings of the Royal Society of London, Series B*, **274**, 275–279.
- Dubois, F. & Cézilly, F. 2002. Breeding success and mate retention in birds: a meta-analysis. *Behavioral Ecology and Sociobiology*, **52**, 357–364.
- Dubois, F., Wajnberg, É. & Cézilly, F. 2004. Optimal divorce and re-mating strategies for monogamous female birds: a simulation model. *Behavioral Ecology and Sociobiology*, **56**, 228–236.
- Durell, S. E. A. le V. dit & Clarke, R. T. 2004. The buffer effect of non-breeding birds and the timing of farmland bird declines. *Biological Conservation*, **120**, 375–382.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- Ens, B. J., Safriel, U. N. & Harris, M. P. 1993. Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behaviour*, **45**, 1199–1217.
- Ens, B. J., Choudhury, S. & Black, J. M. 1996. Mate fidelity and divorce in monogamous birds. In: *Partnerships in Birds: the Study of Monogamy* (Ed. by J. M. Black), pp. 344–401. Oxford: Oxford University Press.
- Forsgren, E. 1997. Female sand gobies prefer good fathers over dominant males. *Proceedings of the Royal Society of London, Series B*, **264**, 1283–1286.
- Harris, M. P. 1973. The biology of the waved albatross *Diomedea irrorata* of Hood Island, Galapagos. *Ibis*, **115**, 483–510.
- Heg, D., Bruinzeel, L. W. & Ens, B. J. 2003. Fitness consequences of divorce in the oystercatcher, *Haematopus ostralegus*. *Animal Behaviour*, **66**, 175–184.
- Humphries, C. A., Arevalo, V. D., Fischer, K. N. & Anderson, D. J. 2006. Contributions of marginal offspring to reproductive success of Nazca booby (*Sula granti*) parents: tests of multiple hypotheses. *Oecologia*, **147**, 379–390.
- Huyvaert, K. P. & Anderson, D. J. 2004. Limited dispersal by Nazca boobies (*Sula granti*). *Journal of Avian Biology*, **35**, 46–53.
- Jeschke, J. M., Wanless, S., Harris, M. P. & Kokko, H. 2007. How partnerships end in guillemots *Uria aalge*: chance events, adaptive change, or forced divorce? *Behavioral Ecology*, **18**, 460–466.
- Johnston, V. H. & Ryder, J. 1987. Divorce in larids: a review. *Colonial Waterbirds*, **10**, 16–26.
- Jouventin, P. & Dobson, F. S. 2002. Why breed every other year? The case of albatrosses. *Proceedings of the Royal Society of London, Series B*, **269**, 1955–1961.
- Kim, J. & Mueller, C. W. 1978. *Factor Analysis: Statistical Methods and Practical Issues*. Thousand Oaks, California: Sage Publications Quantitative Applications in the Social Sciences Series, No. 14.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Chapman & Hall.
- Lewis, S., Wanless, S., Elston, D. A., Schultz, M. D., Mackley, E., du Toit, M., Underhill, J. G. & Harris, M. P. 2006. Determinants of quality in a long-lived colonial species. *Journal of Animal Ecology*, **75**, 1304–1312.
- López-Sepulcre, A. & Kokko, H. 2005. Territorial defense, territory size, and population regulation. *American Naturalist*, **166**, 317–329.
- Maness, T. J. & Anderson, D. J. 2007. Serial monogamy and sex ratio bias in Nazca boobies. *Proceedings of the Royal Society of London, Series B*, **274**, 2047–2054.
- Maness, T. J., Westbrook, M. A. & Anderson, D. J. 2007. Ontogenetic sex ratio variation in Nazca boobies ends in male-biased adult sex ratio. *Waterbirds*, **30**, 10–16.

- Mougin, J. L., Jouanin, C. & Roux, F.** 1997. Intermittent breeding in Cory's shearwater *Calonectris diomedea* of Selvagem Grande, North Atlantic. *Ibis*, **139**, 40–44.
- Naves, L. C., Monnat, J. Y. & Cam, E.** 2006. Breeding performance, mate fidelity, and nest site fidelity in a long-lived seabird: behaving against the current? *Oikos*, **115**, 263–276.
- Naves, L. C., Cam, E. & Monnat, J. Y.** 2007. Pair duration, breeding success and divorce in a long-lived seabird: benefits of mate familiarity? *Animal Behaviour*, **73**, 433–444.
- Nelson, J. B.** 1978. *The Sulidae: Gannets and Boobies*. Oxford: Oxford University Press.
- Peduzzi, P., Concato, J., Kemper, E., Holford, T. R. & Feinstein, A.** 1996. A simulation of the number of events per variable in logistic regression analysis. *Journal of Clinical Epidemiology*, **99**, 1373–1379.
- van de Pol, M., Heg, D., Bruinzeel, L. W., Kuijper, B. & Verhulst, S.** 2006. Experimental evidence for a causal effect of pair-bond duration on reproductive performance in oystercatchers (*Haematopus ostralegus*). *Behavioral Ecology*, **17**, 982–991.
- Qvarnström, A. & Forsgren, E.** 1998. Should females prefer dominant males? *Trends in Ecology & Evolution*, **13**, 498–501.
- Schwarz, G.** 1978. Estimating dimension of a model. *Annals of Statistics*, **6**, 461–464.
- Stearns, S. C.** 1992. *The Evolution of Life Histories*. New York: Oxford University Press.
- Taborsky, B. & Taborsky, M.** 1999. The mating system and stability of pairs in kiwi *Apteryx* spp. *Journal of Avian Biology*, **30**, 143–151.
- Townsend, H. M. & Anderson, D. J.** 2007. Assessment of costs of reproduction using multi-state mark–recapture models. *Evolution*, **61**, 1956–1968.
- Townsend, H. M., Huyvaert, K. P., Hodum, P. J. & Anderson, D. J.** 2002. Nesting distributions of Galápagos boobies (Aves: Sulidae): an apparent case of amensalism. *Oecologia*, **132**, 419–427.
- Van Tets, G. F.** 1965. A comparative study of some social communication patterns in the Pelicaniformes. *Ornithological Monographs*, **2**, 1–88.
- Williams, M. & McKinney, F.** 1996. Long-term monogamy in a river specialist: the blue duck. In: *Partnerships in Birds: the Study of Monogamy* (Ed. by J. M. Black), pp. 73–90. Oxford: Oxford University Press.
- Wingfield, J. C., Hegner, R. E., Dufty, A. M. & Ball, G. F.** 1990. The challenge hypothesis: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, **136**, 829–846.
- Wong, B. B. M.** 2004. Superior fighters make mediocre fathers in the Pacific blue-eye fish. *Animal Behaviour*, **67**, 583–590.
- Zar, J. H.** 1999. *Biostatistical Analysis*. 4th edn. Upper Saddle River, New Jersey: Prentice Hall.