Better stay together: pair bond duration increases individual fitness independent of age-related variation

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Prolonged pair bonds have the potential to improve reproductive performance of socially monogamous animals by increasing pair familiarity and enhancing coordination and cooperation between pair members. However, this has proved very difficult to test robustly because of important confounds such as age and reproductive experience. Here, we address limitations of previous studies and provide a rigorous test of the mate familiarity effect in the socially monogamous blue-footed booby, Sula nebouxii, a long-lived marine bird with a high divorce rate. Taking advantage of a natural disassociation between age and pair bond duration in this species, and applying a novel analytical approach to a 24 year database, we found that those pairs which have been together for longer establish their clutches five weeks earlier in the season, hatch more of their eggs and produce 35% more fledglings, regardless of age and reproductive experience. Our results demonstrate that pair bond duration increases individual fitness and further suggest that synergistic effects between a male and female’s behaviour are likely to be involved in generating a mate familiarity effect. These findings help to explain the age- and experience-independent benefits of remating and their role in life-history evolution.

1. Introduction

A variety of animals, from crustaceans to humans, form socially monogamous pair bonds that are maintained during reproduction [1]. This is particularly common in birds, where most species breed exclusively with one partner at a time [2]. However, socially monogamous animals often breed multiple times throughout their lifespan, and some partnerships can extend for several reproductive events [1,3]. Theoretically, bonded breeders repeatedly face the choice of whether to retain their current mate or divorce and switch to a different one [4]. To understand adaptiveness of this behaviour, costs and benefits of both remating and divorce should be considered. Although long-lasting pair bonds have fascinated naturalists for centuries, in recent decades it is exploitation of partners and sexual conflict that have preoccupied theoreticians and empiricists [5–8], and the potential individual benefits of monogamous bonds have been largely overlooked. Current research on monogamy is notoriously focused on conflict and pair bond dissolution, and a plethora of functional hypotheses have been proposed to explain avian divorce [4,9–11]. Consequently, there is little theory to explain remating with the same partner over prolonged pair bonds, and few studies have attempted to test the long-claimed fitness benefits of persistent partnerships in birds [3].

Remating can potentially reduce time and energy costs associated to mate sampling and bond formation, enabling earlier breeding [12–14], which in birds is generally more successful [15]. Remaining with the same partner could also facilitate the adjustment of within-pair behaviour by increasing pair familiarity and enhancing coordination in shared breeding activities such as territory acquisition, anti-predator defence, breeding site preparation, and offspring attendance and provisioning [16–21]. These synergistic advantages...
bring mutual benefits to individuals in a long-term partnership and may lead to improved reproductive success, but this is yet to be demonstrated [22].

Although a number of avian studies report an improvement in reproductive performance over successive breeding events with the same partner (the ‘mate familiarity effect’) [3] [23–28], most fail to rule out important confounds owing to intercorrelational issues that have made it difficult, if not impossible, to reliably separate the effects of bond duration from those of age and reproductive experience—which also tend to covary [25,29]. To address this problem, many studies have used multiple regression analyses in an attempt to disentangle the statistical contribution of pair bond duration (reviewed in [24,30]). Unfortunately, owing to heavy multicollinearity this statistical approach often lacks power and thus requires larger samples than can usually be obtained [28,31]. On the other hand, cross-sectional approaches are generally unable to discount the possibility of a systematic bias in the phenotypic quality of individuals of different bond durations [28]. For instance, selective divorce or mortality of low-quality breeders could result in long-bonded pairs being of higher quality [25].

To our knowledge, two studies have attempted to explicitly address these limitations under natural conditions. Black’s [32] investigation of the effect of pair bond duration on reproductive success of the barnacle goose, Branta leucopsis, addressed the age-related variation that comes with longitudinal approaches by using the cumulative number of offspring as a single, lifetime measure of reproductive performance. This allowed him to demonstrate a positive association between stable, sustained bonds and fitness, while attempting to statistically control for the confounding effect of individual quality and its potential association with longer lifespan [28,32]. van de Pol et al. [28] found that lay date, egg survival and fledgling production of pairs of oystercatchers, Haematopus ostralegus, improved over the natural duration of their pair bond, but only up to a point, after which they declined. This quadratic effect was interpreted as being statistically independent of age-related variation, although only 16% of the population was of known age and collinearity issues precluded including variables other than reproductive experience in the analyses [28]. Nevertheless, at least one positive age- and experience-independent effect of bond duration was validated by experimentally inducing some birds to bond with a new mate and finding that newly formed pairs progressively advanced their timing of egg laying over the following years [28].

We should generalize only with caution from the studies reporting a mate familiarity effect because the best support comes from studies of two species where pairs generally stay together for most of their lives (annual divorce rate is approximately 2% for barnacle geese [32] and approximately 8% for oystercatchers [33]). Several authors have noted that studies which failed to detect an effect of bond duration were mostly of species with high divorce rates (approximately 19% annually [25,28]), whereas the clearest effects were observed in species where pairs maintain long, continuous bonds that sometimes extend into the non-breeding season [25,32]. Long-lived species with high divorce rates demand further exploration and may provide the most promising context for measuring and explaining the benefits of persistent pair bonds, if potential confounds can be controlled.

Here, we used long-term data on the socially monogamous blue-footed booby, Sula nebouxii, a long-lived marine bird with a particularly high annual divorce rate (approximately 50%), to test whether duration of the pair bond affects onset of breeding and reproductive output, independently of age-related variation. Taking advantage of an unprecedentedly large sample, we were able to address most concerns over previous pair bond analyses by exploiting the natural disassociation between age and bond duration in this species, and by controlling for the separate effects of age and reproductive experience without the constraints of multivariate statistical approaches. Additionally, we were able to test whether an association between pair bond duration and reproductive performance is due to superior phenotypic quality of longer bonded individuals.

2. Material and methods

(a) Study species

Blue-footed boobies are colonial marine birds that nest seasonally on islands in the eastern tropical Pacific [34]. We studied an individually ringed population on Isla Isabel, Mexico, where males and females exhibit lifelong fidelity to their natal neighbourhood and rarely disperse to other breeding colonies (mean breeding dispersal is 13.1 and 15.6 m for males and females, respectively [35]). Early in the seven-month breeding season, males obtain territories in which they spend a few hours each day displaying to conspecifics. After several days, females arrive and pair with males on their territories and, as laying approaches, both pair members progressively increase their site attendance, perform courtship displays and copulate until the female lays a clutch [36,37]. The pre-laying period lasts from a few days to several weeks [36] and individuals occasionally switch mates during this stage [38]. Female boobies lay one to three eggs at intervals of roughly 4 days. Both parents share all parental duties during 41–49 days of incubation and three to four months of chick rearing but females, the larger sex, provide more food to the young while males invest more in territory defence [39,40].

This booby can live for 20 years or more and males and females usually start reproducing at the age of 3–5 years [41]. Most recruits breed yearly, taking an average of 1.9 sabbaticals over the lifespan (estimated from 208 birds that lived more than 16 years), and in any single season only approximately 12% of birds attempt to breed twice, mostly to replace lost clutches (estimated from seasons 1994 to 2012). On Isla Isabel, although roughly half of breeding pairs split in the following season [35,42], pair bond durations can extend for up to nine consecutive years (on average 1.7 years [35]). Both males and females commonly engage in extra-pair behaviour and nearly 11% of the broods sampled in 2011 contained extra-pair young (Ramos et al. [43]). In this population, adult survivorship, breeding participation, onset of breeding and nest success all vary between years and are strongly related to the El Niño Southern Oscillation [44,45]. Breeding conditions at Isla Isabel deteriorate as the season progresses and chicks from clutches laid late in the season have lower survival and are less likely to fledge and recruit into the breeding population [41,46].

(b) Population monitoring and sampling

Between 1988 and 2012, reproduction was monitored annually in two plots (26889 m²) roughly 400 m apart containing 65% of all breeding pairs on the island. Each season, usually from February to July, all nests in these plots were marked, breeders were identified and observers recorded nest contents every 3–6 days until clutches or broods failed or chicks were ringed as fledglings at the age of 70 days (details in [41]). Nests within 20 m of the plots were also monitored if at least one of the breeders was ringed. Identities of most breeders were confirmed by three independent ring readings, and pair members were reliably sexed by...
voice (males whistle and females grunt [34]). When not observed, laying dates of clutches were inferred from hatching dates or estimated using chick growth curves for beak and ulna [47].

We retrieved the breeding histories of ringed individuals from a database detailing all breeding attempts involving at least a clutch and analysed the effect of pair bond duration, computed as the number of consecutive years breeding with the current mate, on the reproductive performance of 752 focal breeders during their fourth breeding event in life. This centred cross-sectional design allowed us to separate bond duration effects from age-related confounds by holding reproductive experience constant and statistically controlling for the effect of age. Our sample comprised all 378 males and 374 females from the cohorts 1988–2003 that bred for the first time by the age of 6 years and then bred annually for four consecutive seasons. We excluded birds that recruited after the age of 6 years because most boobies that manage to recruit afterwards breed only once [48]. Age varied from 5 to 9 years and was not correlated with pair bond duration (r_s = 0.05, n = 752, p = 0.14); age composition was similar among the four bond duration categories: 1 year (the current year): 6.9 ± 0.98 years; 2 years: 6.9 ± 1.01 years; 3 years: 7.1 ± 1.02 years; 4 years: 7.1 ± 0.94 years. As measures of reproductive performance for each focal bird, we used the lay date of its first-laid egg (expressed as a proportional rank among all breeding pairs in each year), clutch size, hatching success (proportion of eggs that hatched), brood size, fledging success (proportion of chicks that fledged) and number of fledglings produced.

To test whether breeders of the four pair bond duration categories differed in phenotypic quality (e.g. owing to high-quality pairs staying together for longer), we compared the four categories for the following indicators of quality: hatch date and body mass at fledging (measured to the nearest 20 g at the age of 70 days) in the natal year, age, partner quality and reproductive performance during their recruiting event, and, for a subsample of all 255 focal males and 246 focal females that switched to a new partner for their fifth breeding event in life, age-related confounds by holding reproductive experience constant and statistically controlling for the effect of age. Our sample comprised all 378 males and 374 females from the cohorts 1988–2003 that bred for the first time by the age of 6 years and then bred annually for four consecutive seasons. We excluded birds that recruited after the age of 6 years because most boobies that manage to recruit afterwards breed only once [48]. Age varied from 5 to 9 years and was not correlated with pair bond duration (r_s = 0.05, n = 752, p = 0.14); age composition was similar among the four bond duration categories: 1 year (the current year): 6.9 ± 0.98 years; 2 years: 6.9 ± 1.01 years; 3 years: 7.1 ± 1.02 years; 4 years: 7.1 ± 0.94 years. As measures of reproductive performance for each focal bird, we used the lay date of its first-laid egg (expressed as a proportional rank among all breeding pairs in each year), clutch size, hatching success (proportion of eggs that hatched), brood size, fledging success (proportion of chicks that fledged) and number of fledglings produced.

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(c) Statistical procedures

To test the effect of pair bond duration on lay date, we fitted a generalized linear model (GLM) with normal error distribution. In addition to bond duration, explanatory variables in the initial model included year of observation (to control for inter-annual variation), sex, age and age^2 of the focal bird, partner age and all two-way interactions with pair bond duration. To test for effects of pair bond duration on clutch size, brood size and number of fledglings (count data), we used GLMs with negative binomial error distributions; for effects on hatching success and fledging success (proportional data), we used GLMs with quasi-binomial error distributions to account for overdispersion [49]. Explanatory variables in these last five models included pair bond duration, year of observation, sex, age and age^2 of the focal bird, age of the partner and all two-way interactions with pair bond duration. By including a quadratic term for age and its interaction with pair bond duration, we were able to explicitly test for a potentially confounding effect of early senescent decline.

To examine whether phenotypic quality varied among pair bond duration categories in our sample, we built several GLMs testing for differences in each of the indicators of quality (listed in the electronic supplementary material, table S1). Explanatory variables in these models included bond category at the fourth breeding event in life, year of observation, sex of the focal bird, and, where appropriate, age and age^2 of the focal bird and partner age, as well as two-way interactions.

We simplified all models by sequentially dropping non-significant interactions and main terms (α ≤ 0.05). The reported significance of each term was assessed using two-tailed F or likelihood ratio (L. ratio) tests comparing the simplified minimal adequate model with the model including a non-significant term or with the model excluding a significant term [49]. Analyses were carried out using R v. 3.0.1 [50]. Inconsistencies in sample sizes are owing to exclusion of individuals whose lay date was unknown or whose body mass could not be registered. We report means ± s.d. throughout the paper, unless otherwise stated.

3. Results

Timing of egg laying was significantly affected by pair bond duration (GLM: F_3,678 = 17.75, p < 0.001; figure 1), independently of the breeder’s age (GLM: F_1,658 = 0.004, p = 0.95), age^2 (GLM: F_1,657 = 0.138, p = 0.71), sex (GLM: F_1,659 = 0.003, p = 0.96), reproductive experience (held constant at four events; see Material and methods), partner age (GLM: F_1,660 = 0.203, p = 0.65) and year of observation (GLM: F_17,663 = 1.55, p = 0.07). Boobies laid their first egg on average 11.6 days earlier for each year of bond duration. Interestingly, the greatest difference between sample means was between familiar and unfamiliar pairs: on average, pairs in their second year together laid 18.6 days earlier than newly formed pairs, while pairs in their fourth year together, the longest bonded in our sample, laid only 4.8 days earlier than third-year pairs and 16.2 days earlier than pairs in their second year (figure 1).

All four bond duration categories established clutches of similar size (1.91 ± 0.63 eggs; GLM: L. ratio_{1,670} = 0.677, p = 0.88; figure 2a), but longer bonded pairs hatched a greater proportion of their eggs (GLM: F_{3,729} = 5.51, p = 0.001) and consequently raised larger broods (GLM: L. ratio_{3,731} = 8.82, p = 0.03; figure 2b). Pair bond duration was further associated with higher fledging success (GLM: F_{3,542} = 2.78, p = 0.04), so longer bonded breeders ultimately produced more fledglings than newly paired birds (GLM: L. ratio_{3,731} = 13.30, p = 0.004; figure 2c). For none of these five reproductive parameters did we find a statistically significant effect of breeder’s age (in all GLMs: p ≥ 0.09), age^2 (in all GLMs: p ≥ 0.10), sex (in all GLMs: p ≥ 0.22), reproductive experience (held constant at four events), partner age (in all GLMs: p ≥ 0.33) or any of the interactions included in the initial models (in all GLMs: p ≥ 0.14). As expected, all reproductive parameters, except...
4. Discussion

The results of this study show important benefits of long-term pair bonding in the blue-footed booby and demonstrate a mate familiarity effect in a species with a high divorce rate. Boobies that were together for longer: (i) established their clutches earlier in the season, (ii) hatched more of their eggs, and (iii) produced more fledglings, independent of their age and reproductive experience. This suite of benefits is consistent with descriptive observations of other avian species suggesting that reproductive output improves over the natural pair bond as a result of a progressive advance in the onset of breeding [24,27,28]. Bringing egg laying forward can greatly increase egg survival [51,52], which in turn can increase reproductive success. For example, in van de Pol’s et al. [28] observational study of oystercatchers, increased fledgling production with greater pair bond duration may have been owing to higher survival of earlier-laid eggs, because chick survival was not itself influenced by bond length. It seems likely that the reproductive improvement we observed over the blue-footed booby’s pair bond was also at least partly the result of earlier laying and its association with higher hatching and fledging success [41,46,51].

Boobies with longest pair bonds were able to establish their clutches more than a month earlier than newly bonded pairs. This is a substantial advance and represents roughly 25% of the duration of a typical five-month laying season [46]. Several studies of other avian species have reported an advance in onset of breeding with continuing pair bonds [reviewed in [24]], and at least three experimental studies provide support for a causal association between mate retention and timing of egg laying [14,19,28]. Nevertheless, the mechanisms enabling earlier breeding of remated pairs remain uncertain. In the short-lived zebra finch, *Taeniopygia guttata*, captive individuals that were allowed to remate with the same partner were able to initiate their next clutch earlier than others that were forced to bond with a different mate [14]. This suggests that reduction of pair-formation time is the mechanism behind the earlier laying of remated pairs [14]. However, in the longer lived oystercatcher this mechanism did not seem to explain late laying in the season following experimental pair bond disruption because most individuals replaced their removed partners within a week of disruption, almost a year before the start of the next breeding season [28]. Whether remated pairs of the long lived, blue footed booby advance the onset of breeding by devoting less time to pair formation remains to be tested.

In our cross-sectional data, the greatest improvement in onset of breeding and reproductive output occurred on the first remating (figures 1 and 2). Similarly, in other birds reproductive performance strongly improves on the first remating, then tends to stabilize, although in exceptional cases it declines towards the end of long bonds [26–28]. The steep reproductive improvement on the booby’s first remating could be owing to familiarity with the mate’s traits and behaviour acquired during their first breeding event together. Beyond this event,
there is probably less scope for annual increments in familiarity, although progressive improvement of pair coordination in specific parental tasks could explain the gradual increment in reproductive performance observed up to at least the fourth year of the booby’s pair bond (but see [22]). A complementary explanation could be that in their first breeding attempt with a novel partner boobies invest with restraint [28] (e.g. attempting to reduce their own share of parental investment [5,53,54]).

Our results on the effect of pair bond duration were obtained for the fourth breeding event in the boobies’ lives, when they were approximately 7 years old. This is roughly the age when they attain maximum reproductive output, before males and females start to experience reproductive senescence beyond the age of 8–10 years [55,56]. A similar analysis of a sample of birds on their ninth breeding event revealed a similar mate familiarity effect at ages of 10–18 years, showing that pair bond duration effects also occur during the period of senescent decline (see the electronic supplementary material, table S2). Thus, the benefits of remating are similar in early and late adulthood (e.g. [57] and this study).

In theory, effects of pair bond duration on fitness could be complicated by effects on extra-pair paternity. However, cross-sectional analysis of a large sample in 2011 showed that probability of extra-pair paternity in a brood increases by only 1.9% from the first to the second (consecutive) pairing of two individuals, and regresses on subsequent pairings (H. Drummond, A. Ramos, O. Sánchez-Macouzet & C. Rodríguez 2014, unpublished data). This increase implies no cost to female fitness and only a trivial cost to males in comparison with their 27% increase in fledgling production on the second pairing.

The observed effects of pair bond duration on reproductive performance of the blue-footed booby were not caused by differential phenotypic quality of individuals of different bond durations. First, by limiting the analyses to breeders with the same reproductive experience, we avoided potential bias owing to differential mortality of low-quality birds. Second, comparisons among bond categories of their natal conditions and recruiting profiles, and their lay dates, clutch sizes, hatching success and brood sizes at first reproduction revealed no evidence of differences in phenotypic quality. Nonetheless, the fact that individuals in the 4 year category produced more fledglings at their very first breeding event (despite not breeding any earlier; figure 3) is puzzling because they showed no reproductive superiority after switching to a new mate for their fifth breeding event; they performed no better than individuals from the other categories (figure 3).

Synergistic effects between a male’s and a female’s behaviour are likely to be involved in generating mate familiarity effects. The behavioural mechanisms through which continuance of
the bond enhances within-pair coordination and cooperation could act across prelaying, egg incubation and chick rearing periods [28]; they could affect synchronized arrival at breeding sites [38], matching of readiness to breed [59], securing and defending territories [16,17] and turn-taking during incubation and brooding [18–21], as well as efficient division of the workload between the sexes [21]. Furthermore, improvements in coordination of highly ritualized within-pair displays could mediate bond maintenance [60] and even stimulate partners to increase their parental investment [61]. Such coordination and cooperation in avian pairs may have been overlooked by focusing on sexual conflict [17,20] and by overemphasizing the behaviour of domesticated captives displaying only a fraction of the cooperative repertoire observed in the wild [17,20,21].

Why boobies still divorce at a notably high rate given the demonstrated fitness benefits of persistent partnerships is not clear, and there could be more than one reason. Because early breeding is advantageous [41,46], when pair members fail to synchronize their arrival to the breeding site, the earlier individual may sometimes be unwilling to wait for a mate that may arrive late or not at all [4,62]. Mate rotation could be favoured when former mates are ‘depleted’ by previous reproduction (sense Maness & Anderson [63,64]) and also when genetic diversity among offspring over the lifetime is advantageous [65]. Divorce could also occur when the net benefit of pairing with a different individual exceeds that of remaining with a suboptimal partner [4,66,67], or even when it is imposed on both partners by the intrusion of a third party that ousts one or both of them [68].

In conclusion, our study offers robust evidence of the fitness benefits of extended pair bond durations in a socially monogamous animal and demonstrates for the first time, to our knowledge, that reproductive performance of a pair may depend not just on the phenotype of each individual but on the joint phenotype of the two working together. Joint reproductive investment over the duration of the bond yielded important age- and experience-independent fitness benefits to both individuals. Such benefits may have important life-history consequences and could have played a key role in the evolution of socially monogamous pair bonds. Our findings are an invitation to start looking at the potential adaptive benefits of social monogamy and demand further probing of the cognitive processes [69] and behavioural interactions between bonded monogamous partners.

Population monitoring was conducted in accordance with the ABS/ASAB guidelines for the ethical treatment of animals, with approval from the Secretaría de Medio Ambiente y Recursos Naturales.

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