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Incest avoidance, extrapair paternity, and territory quality drive divorce in a year-round territorial bird

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Divorce can be an important behavioral strategy to improve fitness. This is particularly relevant for species that are territorial year-round with continuous partnerships, where individuals face constraints on partner choice due to limited vacancies and dispersal opportunities. We tested several hypotheses for divorce in such a species, the cooperatively breeding bird *Malurus coronatus*. Based on 9 years of detailed information on dispersal and survival of 317 breeding pairs, we tested whether divorce is driven by inbreeding avoidance, by a better partner or territory, or by social variables (number of subordinates and fidelity of partners). We found that divorce is important to escape incest: incestuous pairs were substantially more likely to divorce (64%) than non-incestuous pairs (14%). However, incestuous pair bonds lasted up to a year, highlighting constraints on breeder dispersal. Non-incestuous pairs also divorced, but here the only predictor for divorce was the presence of extrapair offspring in a previous brood. Although reproductive failure did not trigger divorce, and reproductive success did not improve in the year following divorce, females that dispersed after divorce obtained higher quality territories, unlike females that dispersed after their partner died. Thus, divorce may be a strategy to improve long-term benefits associated with better territories. Some divorces appeared to be forced evictions by older females, although direct evidence for this is limited. Taken together, our findings demonstrate the complexity of factors that affect the occurrence of divorce when partner choice is constrained.

Key words: **breeder dispersal, inbreeding, infidelity, long-term pair bond, monogamy, cooperative breeding**

INTRODUCTION

In pair-breeding animals, optimal choice of a breeding partner has major fitness benefits (Andersson 1994, Black 1996). Additionally, there is ample evidence that mate familiarity results in higher fitness over time, especially in species that establish long-term monogamous pair bonds and have biparental care (Black 1996, van de Pol et al. 2006). Nonetheless, divorce, the dissolution of a pair bond in which both individuals remain alive and one or both have re-paired, occurs in 92% of socially monogamous birds (Choudhury 1995, Black 1996, Ens et al.1996, Culina et al. 2014).

It is therefore expected that changing social partners and remating should be an adaptive decision, with benefits greater than costs (Culina et al. 2014). In species where partners separate between breeding seasons, the benefits of fidelity and the costs of finding a new partner are relatively easily surpassed by the costs of waiting for the former partner who might not return (Ludwig and Becker 2006). However, in species that form year-round pair bonds, there is no uncertainty over the fate of the partner. In such species, re-pairing after divorce requires eviction of another breeder or opportunistic dispersal into a vacancy created by mortality or dispersal of territory owners (Ens et al. 1993, Dubois et al.1998). Thus, in such systems, divorce is expected to represent a balance between abandoning a breeding position (i.e., cost) and the relative benefits that are associated with doing so.

Several adaptive hypotheses for causes of divorce have been proposed (reviewed by Choudhury 1995). For species with year-round bonds they can be grouped in three main categories: 1) the "Better-Option" Hypothesis (Davies 1989; Ens et al. 1993; Desrochers and Magrath 1996) predicts that individuals with low prior breeding success, a low-quality partner, or in a low-quality territory might move to opportunistically take a better option. This hypothesis predicts that at least 1 member of the divorced pair will benefit by increasing their reproductive success with a new partner. This could be achieved by obtaining a more compatible or higher quality partner or a better breeding territory. 2) The Inbreeding Avoidance Hypothesis (Koenig and Haydock 1998; Hatchwell et al. 2000; Cockburn et al. 2003) predicts that divorce is more likely when partners are closely related, which is particularly relevant for species with kin-structured populations, in which such pair bonds are relatively common due to inheritance of a breeding position. If so, most likely both, but at least one, members of the pair will re-pair with an unrelated individual after divorce. 3) The Forced-Divorce Hypothesis (Taborsky and Taborsky 1999) predicts that divorce is not initiated by either partner but caused by an intruder that displaces a member of the same sex, and fitness benefits are accrued by the intruder and no improvement will be evident for former pair members after divorce. These hypotheses are not exclusive, and multiple mechanisms may occur within one species. Therefore, hypotheses should be considered simultaneously when assessing the underlying causes of divorce (Choudhury 1995).

A recent meta-analysis (Culina et al. 2014) confirmed that divorce is an adaptive strategy to increase reproductive success, rather than an unselected, nonadaptive event or a by-product of another strategy (Choudhury 1995). This same study also showed that the social and ecological factors driving divorce remain elusive (Culina et al. 2014). A contributing aspect may be that factors driving divorce are often studied independently of factors driving dispersal, yet the two processes are usually inextricably linked. In year-round territorial species, divorce is not just about changing partners but requires one individual to disperse—with all the associated costs and benefits. Limited understanding of dispersal patterns can lead to a failure to distinguish emigration and mortality, with nonbreeding individuals that dispersed to outside the study site assumed dead (Culina et al. 2015). In such cases, the observed divorces are a subset of true divorces. A related limitation frequently encountered is the inability to differentiate between two re-pairing categories: divorced and widowed (Culina et al. 2014). For example, 11 of the 16 studies in Culina et al. (2014, Supplementary Table S1) considered both categories as one: birds that changed partners. However, fitness benefits should be most evident when contrasting re-paired divorced with re-paired widowed individuals (Ens et al. 1993, Culina et al. 2014), to distinguish between the actual outcomes of divorce versus partner change. Moreover, other life-history strategies like mating outside the pair bond (i.e., extrapair [EP] mating) might affect selection pressures to divorce. EP mating and divorce can be alternative or complementary strategies for mate choice, both with a common target, which is to improve reproductive success (Birkhead and Møller 1992; Cézilly and Nager 1995; Ramsay et al. 2000). Thus, in order to understand the adaptiveness of divorce, studies should consider the incidence of alternative mating strategies, in a species with reliable longitudinal information on survival, post-divorce dispersal, and new pairing status. This will allow to differentiate between divorced, widowed, and faithful pairs (as in Ens et al. 1993; Dhondt and Adriaensen 1994; Orell et al. 1994; Jeschke et al. 2007; Culina et al. 2014). Our study of divorce in a species with continuous partnerships and year-round territoriality fulfills these criteria.

Here, we investigate factors underlying divorce and its consequences in the purple-crowned fairy-wren (*Malurus coronatus*), a year-round territorial cooperatively breeding passerine. We test which predictions of the major hypotheses for divorce (Table 1) are supported in this species that forms long-term pair bonds, can breed year-round, and lives in kin-based social groups in saturated habitats with constraints on pairing opportunities (Kingma et al. 2009). We show that occurrence of divorce cannot be explained by a single hypothesis, and several predictions were supported.

METHODS

Study species

A population of *M. coronatus* was monitored at Mornington Wildlife Sanctuary, North West Australia (17°31′S, 126°6′E) from July 2005 until June 2014. The core study area is located along ~15 km of river length between Annie Creek and the Adcock River. Cooperative groups—a dominant breeding pair accompanied by a variable number of male and female subordinates—defend year-round territories linearly aligned along creeks and rivers in vegetation dominated by *Pandanus aquaticus*, an evergreen palm-like medium-sized tree (Rowley and Russell 1997; Kingma et al. 2009). Only the dominant pair performs duets and reproduces, and male and female subordinates can help raise offspring, improving productivity, and survival of dominants (Hall and Peters 2008; Kingma et al. 2010). Breeding can occur in every month of the year, with a peak during the wet season (December–March) and often, but not always, a peak during the dry season (September–October; Rowley and Russell 1997; Peters et al. 2013). Although the population-wide incidence of EP paternity (EPP) is only 5%, incestuous pairs have a much higher rate of EPP (46%) compared with 3.3% among non-incestuous pairs (Kingma et al. 2013). Some subordinates might be unrelated to one or both members of the dominant pair (Kingma et al. 2011b), but the majority (>60%) are retained offspring, and incestuous pairs result from subordinates inheriting a breeding vacancy after the disappearance of the same-sex breeder (Kingma et al. 2011b). Overall, natal dispersal is female biased, with most subordinate males remaining in their natal territory or moving nearby, whereas females generally disperse farther; however, some subordinate females also show natal philopatry (Kingma et al. 2010, 2013).

Field data collection

Territory boundaries were recorded from repeated observations of the birds' movements and the location of agonistic interactions between groups. Most boundaries remained stable through the years, but occasional shifts were recorded. *Pandanus* cover was quantified as an index of territory quality. Birds do not occupy stretches of river vegetation without *Pandanus*, and they depend strongly on this vegetation (51% daytime spent in *Pandanus* and 95% of nests built in *Pandanus*; Kingma et al. 2011a). Territories with greater *Pandanus* cover have more subordinates (Kingma et al. 2011a), indicating that these territories are more productive or more attractive for subordinates. Because subordinates increase breeder survival and fledgling recruitment (Kingma et al. 2010), territories with greater *Pandanus* cover thus provide benefits to breeders. Also, higher *Pandanus* cover reduces the likelihood of nest predation, which is the most important source of reproductive failure (Hidalgo Aranzamendi et al., unpublished data). Thus, we assume that a territory with greater *Pandanus* cover reflect the quality of a breeding

Table 1

Overview of main hypotheses proposed to explain divorce in year-round territorial species with continuous partnerships and their support in *Malurus coronatus*

Hypothesis	Assumption	Predicted drivers of divorce	Support in *M. coronatus*	Predicted outcomes of divorce	Support in *M. coronatus*
Better option[a,b]	Divorce occurs when one member is able to obtain a better partner or territory	Low breeding success	No (for non-incestuous pairs)	Improved reproductive success for one of the former members of a pair	No
		High within-pair relatedness	No (for non-incestuous pairs)	Improvement of genetic relatedness for both ex-partners after repairing	No
		Inferior territory or partner	No—territory quality No—group size	The dispersing pair member obtains: better territory larger group One of the ex-partners finds a partner of higher quality	Yes No No[f]
Inbreeding avoidance[c]	Partners divorce and one disperses to avoid breeding with philopatric offspring	Incest	Yes (for incestuous pairs)	Improvement of genetic relatedness for both ex-partners after repairing Improvement of reproductive success for both ex-partners	Yes No
Forced divorce[d]	Divorce caused by intrusion of a third individual	Traits of third individual (new partner)	Some evidence for eviction by older females [g]	Intruder benefits Evicted bird suffers	No Some evidence, some females obtain worse territories
Alternative mating strategy [e]	Infidelity associated with divorce	EPP	Yes (for non-incestuous pairs)	Female pairs with EP father Males evicts unfaithful female	No No

[a]See also Choudhury (1995) for detailed descriptions of hypotheses, and other hypotheses with overlapping assumptions or not applicable to year-round territorial species with continuous partnerships.
[b]Davies (1989), Ens et al. (1993), and Desrochers and Magrath (1996)
[c]Koenig and Haydock (1998), Hatchwell et al. (2000), and Cockburn et al. (2003).
[d]Taborsky and Taborsky (1999).
[e]Birkhead and Moller (1992).
[f]Males re-pairing with an older female is presumed indication of eviction of the ex-partner by new female, because males do not disperse to mate with an older female.
[g]Definitive evidence requires direct behavioral observations of the process of divorce.

territory. *Pandanus* cover was quantified along the territory by one observer assigning a score between 1 and 10, every 50 m (10 each river side, with maximum total 20). An average of all points was calculated for territories longer than 50 m.

Since 2005, all birds in the core study area were individually color-banded and group composition, dispersal, and survival documented. Between 2005 and 2010, territories were monitored weekly year-round and all breeding attempts followed. From 2010 onward, the population was monitored in 2 censuses per year: in May–June and in November, following the reproductive peaks. During this period, all new unbanded birds were banded, and a blood sample was taken for parentage analysis. All banded birds that survived were resighted and social status (subordinate or dominant) recorded.

From 2007 onward, intensive yearly censuses along the tributaries that join the study site were conducted to find birds that had dispersed outside the core area (emigrants). These censuses covered almost all suitable habitat within 20 km of the core area, and some up to 60 km away, covering a total of 95 km of river length (including Adcock, Hann, Fitzroy rivers and Throssell, Roy and Spider creeks). To locate birds during these censuses, a 90-s song playback was used at intervals of not more than 100 m to attract the resident birds. The accuracy of this technique is high, because 90% of dominant birds respond to on-territory playback (Hall and Peters 2008). During these censuses, 8 divorced breeders were found (plus 22 other banded birds from the core area). Additionally, no bird from our population was resighted during censuses conducted at a landscape scale in the surrounding potential habitat, and dispersal outside the river vegetation has never been recorded for this species (Skroblin and Legge 2010; Skroblin et al. 2014).

Between 2005 and 2010, no dominants were resighted after being declared dead on the basis of failure to sight them in intensive surveys. After 2010, 3.2% of breeders were initially assumed dead in one census but then found during a subsequent census in a different territory within the core area ($n = 10$ birds). Given that no birds were resighted outside the core area after being declared dead, it can be assumed that very few pair bonds classified as ended by death actually were divorces.

Throughout the study, 317 different breeding pairs were recorded, totaling 507 pair-years (179 dominant males and 192 dominant females). Average group size (breeders plus subordinates) was stable around a mean of 3.6. Annual survival of dominants was on average 81%, and average sex-ratio of adults was 1.2 males per female (Kingma et al. 2009). On average, 7.3 (range 6–10) new immigrant females entered the study site per year. Most (70%) of these settled as dominant breeders, totaling 6.9% of immigrant breeders per year of the study period (no. of immigrant birds × 100/no. of breeding adults). The proportion of immigrants did not differ between sampling periods (mean before 2010 = 7.8 and mean after 2010 = 8.0 immigrants/year). The number of fledglings detected per year did not differ between the two study periods (mean before 2010 = 0.55 fle/pair/year, mean after 2010 = 0.57 fle/pair/year, *t*-test $\chi^2 = -0.18$, df = 1, $P = 0.43$)

Data analysis

Pair-bond duration and frequency of divorce
Divorce was defined as the failure to maintain a pair bond when both partners were still alive and observed with new social partners and/or in new locations. Annual divorce rate was calculated for July–June by dividing the total number of divorces by the total number of pairs present in that year.

Until 2010, pair-bond duration (PBD) was calculated as the time (days) between the first and last date a pair was seen together. After 2010, the start date of a partnership was estimated as the midpoint date between two censuses when birds were first seen paired and the previous census; the end date of a partnership was estimated as the midpoint date between the last census birds were seen paired and the subsequent census. To assess how accurate our estimates after 2010 were, we recalculated PBD for pairs that started and ended between 2005 and 2010 using the same methods as 2010–2015, by simulating two censuses per year and assigning midpoint dates as the start and end of the relationships. Following this method, we would have missed 15 relationships that lasted less than 6 months (5 divorces and 10 deaths), of the 195 relationships in total (7.7%). The simulated estimates of PBD closely resemble the PBD based on weekly censuses ($r = 0.98$), with a mean difference of 43 days (median = 38). Considering that the mean PBD for all relationships before 2010 was 370 days (median = 201), we believe that the less intensive sampling after 2010 does not alter our conclusions markedly.

Paternity analysis
DNA was extracted following Barrett et al. (2012). Paternity was assigned using Cervus 3.0.3 (Marshall et al. 1998; Kalinowski et al. 2007). Throughout the study, 1111 individuals were genetically screened by 2 commercial suppliers using 6 or 9 microsatellites (as in Kingma et al. 2009, 2013). Until 2010, we sampled nestlings, and these could be unambiguously assigned genetically to the local breeding female. The sires of EP offspring were identified by repeating the analysis including as possible fathers all dominant and subordinate males present at the time of capture. Less than 5.7% offspring were sired by an EP father (Kingma et al. 2009, 2013). After 2010, nestlings were no longer sampled and instead we assigned paternity to unbanded birds found at each census (these could be fledglings, subordinates, or immigrants). First, all unbanded birds were tested as offspring of the local breeding pair (i.e., the dominant pair of the territory in which they were captured). If the local breeding pair did not match as genetic parents, we tested whether the unbanded birds were subordinates that had already moved from their natal territory; we did this by testing as potential parents all breeding pairs present at the time of capture or last seen in the previous census (i.e., each pair in the population was tested as putative parents to previously unassigned birds). We also tested EP fathers as indicated above. Unbanded birds were considered immigrants if they could not be assigned to the local breeding pair or to other breeding pairs. The two periods with different methods of assigning parentage yielded comparable results: 2011–2014, the percentage of EPP remained similar (6.1%) compared with during 2005–2010 (5.7%; Kingma et al. 2013).

Incest and relatedness
Information about the occurrence of incest was extracted from a genetic pedigree containing all known parent–offspring relationships. Twenty-nine socially bonded pairs were thus identified as first-degree relatives (mother–son, father–daughter, and brother–sister) and categorized as "incestuous." One brother–sister pair was excluded from all analyses because they were unfamiliar with one another (hatched in different years and never concurrently resident on their natal territory). All other pairs were categorized as "non-incestuous"; according to the pedigree, 5 of those pairs consisted of second- and third-degree relatives. In addition, pairwise genetic relatedness of pair members [Lynch and Ritland (LR) estimator;

Lynch and Ritland 1999] was calculated using 6 microsatellites (as in Kingma et al. 2013) with GenAlEx 6.5 (Peakall and Smouse 2012).

Statistical analyses

Design of analyses

The hypotheses explaining adaptive divorce make several different predictions (see Table 1; adapted from Choudhury 1995). The Inbreeding Avoidance hypothesis predicts that divorce is more likely when partners are related. We define inbreeding avoidance here as avoiding mating with first-order relatives (i.e., incest avoidance; Koenig and Haydock 1998). This hypothesis predicts that one or most likely both partners should show reduced relatedness to their new partner after divorce. The Better Option hypothesis predicts that individuals with low prior breeding success, a low-quality partner, or in a low-quality territory might move to opportunistically take a better option. The benefits of divorce should be evident in the outcome after divorce for one of the former partners, if they achieve greater reproductive success, obtain a better territory or a better partner than previously. Additionally, divorce can also be associated with infidelity (EP mating). In this case, it is predicted that either females will divorce and subsequently pair with a former EP mate or males will evict unfaithful females. The predictions of the Forced Divorce hypothesis are clear: The only partner characteristics that might be identified as drivers of divorce would be lower competitive ability than the replacement individual (age or size). After divorce, neither ex-partner is expected to benefit, only the intruder. In this case, previous reproductive success does not affect the probability of divorce, and there is no change in breeding success after divorce.

To test these predictions, 1) we first compared the pattern of pair-bond persistence for incestuous and non-incestuous pairs. Divorce affected those two groups differently to such an extent that they could not be analyzed in a single statistical model (all incestuous pairs divorced within a year; see Results); so, for all subsequent analyses, incestuous and non-incestuous pairs were analyzed separately. 2) We analyzed the possible drivers of divorce and pair-bond duration, and 3) we analyzed the outcomes of divorces to test whether divorce led to improvements of breeding success or reduced relatedness to partners in either sex. Finally, we explored whether any of the patterns found were consistent with forced divorces.

Samples sizes vary for each analysis due to missing parameters, see Tables 1–3 for sample sizes and text for details.

1. Pair-bond persistence: the importance of incest avoidance

To investigate to what extent inbreeding avoidance is a driver of divorce, we tested whether the probability of divorce depended on the type of relationship (incestuous or not; independent variable) using a survival analysis. This allows inclusion of pairs in which an individual died and persisting pairs at the end of the study (as right-censored cases). This analysis expresses the probability that relationships lasting any given length will be terminated by divorce (Cox 1972; Cockburn et al. 2003). First, the persistence over time of all incestuous and non-incestuous pairs in each of the three classes (divorced, widowed, and ongoing) was plotted using Kaplan–Meier graphs with the *survdiff* function of the survival package (Diez 2012). Second, a Cox's proportional hazard analysis was performed comparing pair-bond persistence in both groups (using *coxph* in the same package).

2a. Drivers of divorce: What determines the likelihood of pair-bond dissolution?

To investigate which factors are drivers of the likelihood of divorce in non-incestuous pairs, we scored for each year of study (July–June) whether pairs present on 1st July of each year were still together or ended in divorce (binomial response variable). This data set ($n = 126$ pairs) excluded relationships ending due to death of one of the pair members, because these could have divorced before death, if both had survived. For this, a generalized linear mixed model (GLMM) was constructed including male ID and female ID as random factors, to account for multiple entries for males and females that stay together longer than a year or that were in more than one pair over the study. Predictor variables were genetic relatedness (LR estimator), reproductive success, territory quality, and group size; we also controlled for female origin (local/immigrant; all males are residents). Group size (on 1st July of each year) was included, because breeders derive reproductive and survival benefits from living in larger groups (Kingma et al. 2011b). Similarly, a territory of high or low quality could be an asset that influences divorce (see Field Data Collection, for details). Reproductive success (number of fledglings, range 0–8) was the number of offspring that survived at least 6 weeks during the calendar year (July–June). Annual variation in fledgling production is larger (range 16–37 fle/year) than the variation between the two study periods (see Field Data Collection), therefore year was included as a random factor.

We built a second GLMM with the predictor and random variables of the first model adding another predictor variable: whether any previous broods of the pair contained EP offspring (as a proxy of infidelity in the pair). For this analysis, only pairs that reproduced and for which offspring had been genotyped could provide this information, so sample size was much reduced ($n = 53$ pairs).

Because the number of fledglings produced has a large degree of stochasticity (e.g., nests often fail due to predation and flooding, Hidalgo Aranzamendi et al. unpublished data), this reduces the likelihood of detecting breeding failure as a driver of divorce (Culina et al. 2014). For this reason, and because birds can use hatching success as an indicator of within-pair compatibility, another model was built using hatching success (proportion of eggs that hatched from each clutch for all nests found in a calendar year) instead of number of fledglings. Hatching success data were available only for 2005–2010, when all nesting attempts were followed in detail. Presence of EP offspring was not included, due to insufficient sample size (we did not know paternity for a large number of nestlings that were depredated or nests flooded before sampling).

Although clutch size and timing of breeding may be important determinants of fitness in general (Culina et al. 2014), we did not test whether these factors affected the likelihood of divorce in *M. coronatus*. Clutch size is extremely consistent (2.93 ± 0.05 SE eggs, Kingma et al. 2012) and birds breed year-round, thus the definition of timing of the onset of breeding would be arbitrary, and but more importantly, its meaning would be unclear in terms of fitness, as we have no indication that there are distinct seasonal differences in success.

2b. Pair-bond duration in divorced pairs

To test whether any factor predicted pair-bond duration (number of days, log-transformed, dependent variable) for pairs that eventually divorced, we built linear models (LMs) with genetic relatedness, territory quality, and group size as independent variables. We

constructed separate models for incestuous and non-incestuous pairs. Genetic relatedness was not included in the model of incestuous pairs. Group size at the start of the pair bond was used to avoid problems distinguishing cause and effect (pairs that were together longer had more time to breed and produce helpers).

3. Outcomes of divorce

Individuals may divorce in order to obtain a less related partner, or a partner of higher quality, and/or, if an individual disperses, better quality of the new territory. Those changes can only be detected by comparing partners and territories (former vs. new) and by comparing individuals that have experienced partner change: divorcees vs. widows (individuals whose partner died). Three approaches were used to test whether divorce resulted in improvements in partner or territory quality: 1) within-bird comparison between the new partner and the ex-partner (paired comparison); 2) comparison post-divorce between ex-partners and their new partners (paired comparison); and 3) comparison of changes in divorcees compared with changes for widows.

Predictor variables were genetic relatedness, reproductive estimates, age and size of partners, territory quality, and group size. For analyses of reproductive estimates, we included the offspring produced during the last year with the ex-partner versus the offspring of the first year with the new partner. Pairs that were together less than 6 months or associated only through the dry season were excluded, because the wet season is the time when most pairs reproduce. Age and size were used as measures of individual quality or competitive ability. Age has been reported as an important factor in divorce for other species (e.g., older partners may be preferred after divorce or older birds may be less likely to divorce; McNamara and Forslund 1996; Green et al. 2004; Cockburn et al. 2008; García-Navas and Sanz 2011). Similarly, size is often regarded as an important signal of quality in small songbirds (Cardoso 2011); larger purple-crowned fairy-wrens males are able to produce lower pitched low-frequency songs, suggesting that size is important in sexual competition (Hall et al. 2013). Tarsus length ($\pm 0.1\,$mm) was used as measure of body size. Finally, changes in territory quality and group size are relevant only for individuals that dispersed (i.e., changed territories).

1) Within-bird comparisons were performed with the difference between the characteristics of the new partner minus the old partner as a dependent variable in mixed models, with bird ID as random factor. There is a significant difference between partners if the intercept in these models differs from 0 (Varian-Ramos and Webster 2012). We tested whether new partners were less related, larger than previous partners or were older (including only birds with known hatch date, age [in months] at the time of divorce vs. age of new partner at first date seen together) and whether new pairs had higher reproductive success. To test whether post-divorce dispersal resulted in the acquisition of a higher quality territory (*Pandanus* cover), or a larger group size, all female dispersers were grouped (incestuous and non-incestuous) and the differences between the old and new (post-divorce) territory were compared, adding bird ID as random factor. For males dispersing post-divorce, a paired *t*-test (due to low sample size $n = 7$) was used to compare territory quality and group size between the old and new territory. 2) For post-divorce comparisons between ex-partners and their new partners (divorced female and new partner vs. divorced male and new partner), we compared the differences in reproductive output between both new pairs using a GLMM with: (number of fledglings produced by divorced female + new partner) − (number of fledglings produced by divorced male + new partner) as dependent variable and both male and female ID as random terms. No other characteristic was compared between ex-partners and their new relationships, because changes will be determined only by who dispersed or stayed (analyzed in previous section). 3) We compared changes in divorcees with changes for widows, as a control group, to test costs of partner change. Genetic relatedness and reproductive success of new pairs were compared between divorcees and widows. Similarly, characteristics of new partners (age and size) were compared between divorcees and widows. We used these variables as dependent terms in GLMMs with maximum likelihood (ML) and Poisson distribution or restricted ML models for continuous variables, in which divorce and death were independent variables and bird ID a random factor. Sample sizes for widowed incestuous pairs were small, so we only compared non-incestuous pairs. To test whether post-widowhood dispersal resulted in changes in territory quality or group size, we compared the differences between the old and new (post-widowhood) territory, this analysis was restricted to dispersing females (paired *t*-test). Information of territory quality for males dispersing post-widowhood was incomplete ($n = 5$ of 9 males dispersed to outside the area for which we had territory quality estimates), so they were not analyzed.

All analyses were done in R 3.2.0 (R Core Team 2015). A mixed-modeling approach (GLMM) was used when data had repeated measures from the same individual(s) (as random term(s)) using the *lmerTest* and *lme4* package (Kuznetsova et al. 2014; Bates et al. 2015). Generalized LMs were run first without random terms and quasi-binomial distributions to estimate dispersion. All models indicated that data were not overdispersed ($x = 1.02$), so GLMMs were appropriate (Quinn and Keough 2002). R^2 values (Nakagawa and Schielzeth 2013; Johnson 2014) were calculated using the *MuMIn* package (Barton 2014). For models with random terms, individual-level repeatability was calculated following Nakagawa and Schielzeth (2010). Models had values of repeatability close to 0 unless reported. For model analyses without random effects, LMs and *t*-tests were used. Residuals for models with continuous variables were checked for normality and variables log-transformed if necessary; all independent variables were checked for collinearity (all $r < 0.56$).

RESULTS
Constraints on acquisition of first and subsequent partners

Almost 15% of males and 7% of females acquired their first partner by inheriting the breeding position on their natal territory, and such inheritance generally resulted in the formation of incestuous pairs (detailed information on routes to formation of first and subsequent partners are provided in Supplementary Tables S1 and S2). In total, 28 incestuous pairs formed during our study (first and subsequent partners): 15 males paired with their mother, 6 females with their father, and 7 pairings were between full siblings. However, most individuals acquired their first partner by natal dispersal: 60% females and 58% males.

Subsequent partners were obtained after a partnership ended in divorce (19% of 317 pairs recorded) or due to the death of one pair member (53% of 317 pairs); the remaining partnerships ended when both partners died, 6% or were ongoing, 22%. Eleven males and 8 females divorced more than once. The average annual rate

of divorce was 8%, fluctuating between 5% and 13%. Divorce occurred in any month of the year, although never when pairs had dependent young.

Individuals that divorced and dispersed obtained an unrelated partner (except 1 unusual case of pairing between unfamiliar relatives; Supplementary Table S2). After divorce, in 88% of 50 cases, it was the female that dispersed much more frequently than males (binomial test $P < 0.001$). In contrast to divorcees, the majority of widowed individuals did not disperse (83%), and this was similar for females (61 of 77) and males (78 of 87, binomial test $P = 0.32$). The risk of pairing incestuously for birds that remained as breeder in the territory following divorce or widowhood was higher for females (25% of 67) compared with males (8% of 119; $\chi^2 = 9.88$, df = 1, $P = 0.001$).

Divorce in incestuous pairs

Divorce occurred more often in pairs formed by first-order relatives (incestuous: 64% of 28) compared with non-incestuous pairs (14% of 285; Cox PH $\chi^2 = 18.50$, df = 1, $P < 0.001$, Figure 1). All incestuous pairs divorced ($n = 18$, median = 107, range 7–364 days) or ended by partner death ($n = 10$, median = 60, range 29–188 days) within a year. The duration of incestuous pair bonds was not explained by territory quality ($R^2 = 0.21$, $F_{2,16} = 2.09$, $z = 0.05 \pm 0.06$, $P = 0.43$), and although incestuous pairs in larger groups tended to stay together longer than pairs in smaller groups, the effect size was small ($z = 0.34 \pm 0.17$, $t = 1.97$, $P = 0.06$).

Divorce in non-incestuous pairs

One driver of the likelihood of divorce was identified: non-incestuous pairs that previously had EP offspring had a higher likelihood of divorce ($z = 2.56 \pm 1.11$, $P = 0.02$, Table 2). EP offspring occurred in 21% of divorcing pairs (3 of 14 reproducing pairs, Fig. 2) compared with 8% in pairs that did not divorce (3 of 39, Figure 2). Neither genetic relatedness between partners nor previous reproductive success predicted whether pairs divorced (Table 2). Pair-bond duration for non-incestuous pairs that divorced was extremely variable and sometimes very long ($n = 40$, median = 224 days, range 7–1824, Figure 1). However, no variable predicted pair-bond duration ($R^2 = 0.24$, $F_{3,26} = 2.67$, group size $z = 0.30 \pm 0.17$, $t = 1.72$, $P = 0.10$, territory quality $z = 0.07 \pm 0.05$, $P = 0.18$, and relatedness $z = 2.70 \pm 2.10$, $P = 0.21$).

Outcomes of divorce

When incestuous pairs divorced, both pair members subsequently paired with a less related individual (LR estimator for females: $x = -0.50$, males: $x = -0.54$, both $P = 0.01$, Table 3). Genetic relatedness between the bird that dispersed and the new partner were not different from the average genetic relatedness between the same dispersing bird and any other dominant bird of the opposite sex in the population (paired t-test for divorced females that dispersed, $n = 15$, $t = -0.09 \pm 0.01$, df = 10, $P = 0.47$). For non-incestuous birds, there was no evidence of an effect of divorce on the genetic relatedness with their new partner (Table 3, females $t = 0.02$, df = 31.99, $P = 0.59$; males $t = -0.03$, df = 26.74, $P = 0.33$). No improvement in reproductive success followed divorce in either incestuous or non-incestuous pairs (Table 3). Males that were divorced by a non-incestuous partner ended up with a partner that was older than the previous one ($x = 17$ months older; df = 9.95, $P = 0.02$, Table 3). No other partner quality attributes differed before and after divorce (Table 3). Annual reproductive success of divorcees with their new partners was not significantly different between the sexes ($n = 45$ pairs, $x = 0.57 \pm 0.98$ and 0.27 ± 0.65 fledgling/year for female and male respectively, $z = 0.41$, df = 32.90, $P = 0.07$), regardless of whether females or males stayed.

On average, females dispersing after divorce moved to territories with more *Pandanus* cover (i.e., to a higher quality territory; $n = 44$, $t = 2.20 \pm 1.06$, df = 34, $p = 0.01$; Figure 3), but males did not ($n = 7$, $x = -3.00$, $P = 0.98$). For both sexes, post-divorce dispersal did not lead to a change in group size and the direction of the effect was opposite from expected (i.e., individuals moved to smaller groups; females $x = -1.43$, df = 34, $P = 0.26$; males $x = -2.25$, $P = 0.10$). For three divorcing females, we observed fights between the replacing and the dispersing female, followed by the intruder female taking over the breeding position. The replacing females were an older dominant female, an immigrant of unknown age and a subordinate female and all of those three females were in neighboring territories before usurping the dominant position. Afterward, the evicted females were observed floating through several territories before taking new breeding positions. All three evicted females moved to an inferior territory, with lower *Pandanus* cover. More generally, when divorcing females moved to an inferior territory after divorce (an indication that they may have been evicted), 67% of the ex-partners (10 of 15) were joined by an older female. In contrast, when divorcing females moved to a better territory, 30% of the divorced
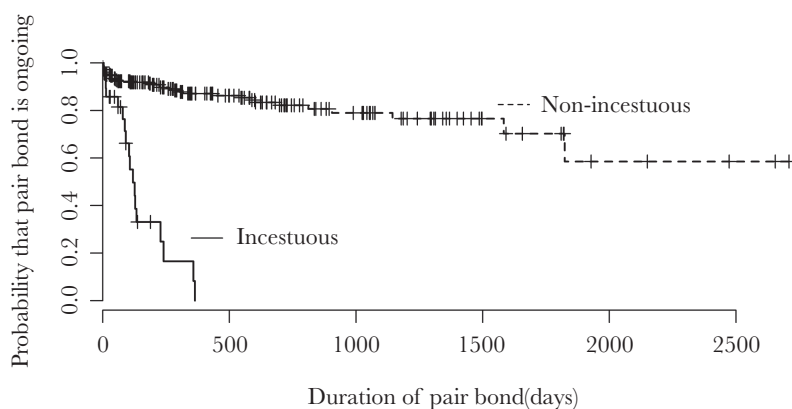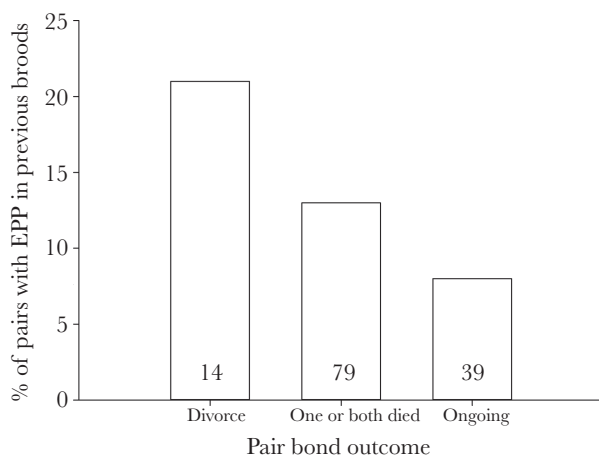

Figure 1
Pairs of first-degree relatives (incestuous; $n = 28$) divorced more often and had shorter pair bonds than non-incestuous pairs ($n = 285$; $\chi^2 = 18.50$, df = 1, $P < 0.001$). Shown is the probability that the pair bond is ongoing; vertical lines indicate pair bonds ending due to deaths; each step down indicates a divorce.

Table 2

Drivers of divorce in non-incestuous pairs: effects of relatedness, reproductive success (number of fledglings and hatching success), previous EP offspring, group size and territory quality, on the probability of divorce (binomial GLMMs; controlling for female origin). Model (a) tests whether the number of fledglings predicted the probability of divorce, including pairs that were never successful ($n = 126$ pairs, 220 observations); model (b) tests whether number of fledglings predicted the probability of divorce and included only pairs that produced at least one genotyped offspring so that information on EPP was available ($n = 53$ pairs, 81 observations); and model (c) tests whether reduced hatching success predicted the probability of divorce, and included only pairs for which hatching success data was available ($n = 24$ pairs, 44 observations). Random effects did not contribute to the variance explained by the models. Significant values in bold* ($P < 0.05$)

	Model (a)			Model (b)			Model (c)		
Explanatory variables	Estimate	SE	z Value	Estimate	SE	z Value	Estimate	SE	z Value
Within-pair relatedness (LR estimator)	2.03	2.51	0.81	4.97	5.03	0.99	3.54	4.84	0.73
Number of fledglings	0.01	0.19	0.03	0.11	0.23	0.48	n.a.	—	—
Hatching success	n.a	—	—	n.a.	—	—	−1.99	1.47	−1.35
EP offspring (y/n)	n.a.	—	—	**2.56**	**1.11**	**2.30***	n.a.	—	—
Group size	−0.03	0.18	−0.18	0.20	0.21	0.96	−0.10	0.18	−0.55
Territory quality	−0.01	0.06	−0.19	0.05	0.11	0.44	0.08	0.08	0.96
Female origin (immigrant y/n)	−1.58	0.90	−1.76	−1.09	1.21	−0.90	n.a.	—	—

n.a. = term not fitted in this model.

Figure 2
Pairs that divorced were more likely to have had EPP in previous broods compared with pairs in which one or both partners died or ongoing relationships ($z = 2.56 \pm 1.11$, $P = 0.02$). Bars show percentage of pairs with at least one EP offspring in previous broods; numbers indicate sample size (total number of pairs, non-incestuous pairs only).

males (8 of 27) obtained an older female, which is significantly less often (8/27 vs. 10/15, $\chi^2 = 5.40$, df = 1, $P = 0.02$). On average, the time to obtain a new breeding position after divorce was longer for females that moved to lower quality territories ($n = 8$, median = 42 days) than for females that moved to higher quality territories ($n = 12$, median = 6 days, data from 2005–2010 only), although those differences were not significant (t-test of log-transformed days to re-pair after divorce, $t = -1.76$, df = 18, $P = 0.09$). Widowed females that dispersed did not obtain territories of better quality (Figure 3, paired t-test, $n = 13$, $x = -0.38$, df = 12, $P = 0.24$) or experience a change in group size ($x = -0.83$, df = 12, $P = 0.28$). No other characteristic was different when comparing divorcees and widows (Supplementary Table S3).

DISCUSSION

We found support for several hypotheses for divorce in cooperatively breeding *M. coronatus* (Table 1). The Inbreeding Avoidance hypothesis was supported by the observation of high rates of divorce among incestuous pairs and that those individuals paired with less related partners after divorce. The Better Option hypothesis was supported by evidence that dispersing females obtained higher quality territories following divorce. We also directly observed a few evictions of breeding females by a usurper and some further indirect support for the Forced Divorce hypothesis. Finally, we found that the occurrence of infidelity (EPP) was a predictor of divorce, although its meaning is unclear in terms of long-term fitness for either sex.

Divorce to escape inbreeding in incestuous pairs

Divorce in *M. coronatus* is an important mechanism to escape incest (Figure 1). Incestuous pairs frequently resulted when birds did not disperse from their natal or breeding territories (Supplementary Tables S1 and S2), suggesting constraints on opportunities for dominant and subordinate birds dispersing to a breeding position. In line with this, many incestuous pairs persisted for a substantial amount of time (average = 107 days, max = 1 year). Since males are more philopatric than females, mother–son pairings were the most common form of incestuous pairs, and the risk of engaging in an incestuous relationship following death or dispersal of a partner was 3 times greater for females (25% females vs. 8% males). Females usually dispersed after divorce but were less likely to disperse after death of a partner (Supplementary Table S2), despite the high risk of incest. This lack of breeder dispersal after an unexpected event, such as partner death, implies that divorce in *M. coronatus* is usually an opportunistic stay-and-wait strategy, and breeder dispersal is triggered when a more attractive vacancy is created elsewhere by the death or divorce of a breeder.

Incest is costly for females but even more so for males: incestuous pairs have a 30% reduction in hatching success, and almost 37.5% of the surviving hatchlings are sired by an EP male (compared with 3.3% EPP in non-incestuous pairs, Kingma et al. 2013). Nonetheless, it was usually females that dispersed: 15/17 incestuously paired females dispersed. The fact that many incestuous pairings did not dissolve immediately (see above) suggests that females moved voluntarily, rather than being coerced or evicted by the male: if males were evicting an incestuous partner, given their low expectations of reproductive success (low hatching success and high EPP), we would have expected eviction to occur more rapidly.

Table 3

Paired comparisons between the new partner and the partner before divorce (within-bird comparison) to analyze whether divorce resulted in an improvement for divorced females and males. Shown are mean of the change from former to subsequent partners of divorced individuals and *P* values (significant in bold) for (a) incestuous and (b) non-incestuous pairs. Positive values indicate improvement after divorce; the opposite is true for genetic relatedness. GLMMs for variables with more than one entry per individual, random effects did not contribute to the variance explained by the model, *n* = number of individuals

(a) Incestuous	Females				Males			
	n	Mean		*P*	*n*	Mean		*P*
Genetic relatedness[a]	13	−0.50		**0.01**	13	−0.54		**0.01**
Reproductive success[a,c]	7	0.28		0.20	7	0.31		0.17
Partner age (months)[a,d]	6	11.43		0.31	6	6.28		0.99
Partner size (tarsus length, mm)[b]	13	−0.43		0.29	10	0.08		0.81

(b) Non-incestuous	Females				Males			
	n	Mean	SE	*P*	*n*	Mean	SE	*P*
Genetic relatedness	26	0.02	0.04	0.59	28	0.01	0.03	0.33
Reproductive success[a,c]	12	0.09	—	0.31	14	1.00	—	0.34
Partner age (months)[d]	15	3.31	5.14	0.53	11	13.25	4.90	**0.02**
Partner size (tarsus length, mm)	27	−0.18	0.14	0.35	26	−0.15	0.21	0.41

[a]Wilcoxon test or [b]*t*-tests for variables with reduced sample size.

[c]Reproductive success is the number of fledglings of the first year with the new partner minus number of fledglings produced during the last year with the previous partner.

[d]Only birds with known hatch date.
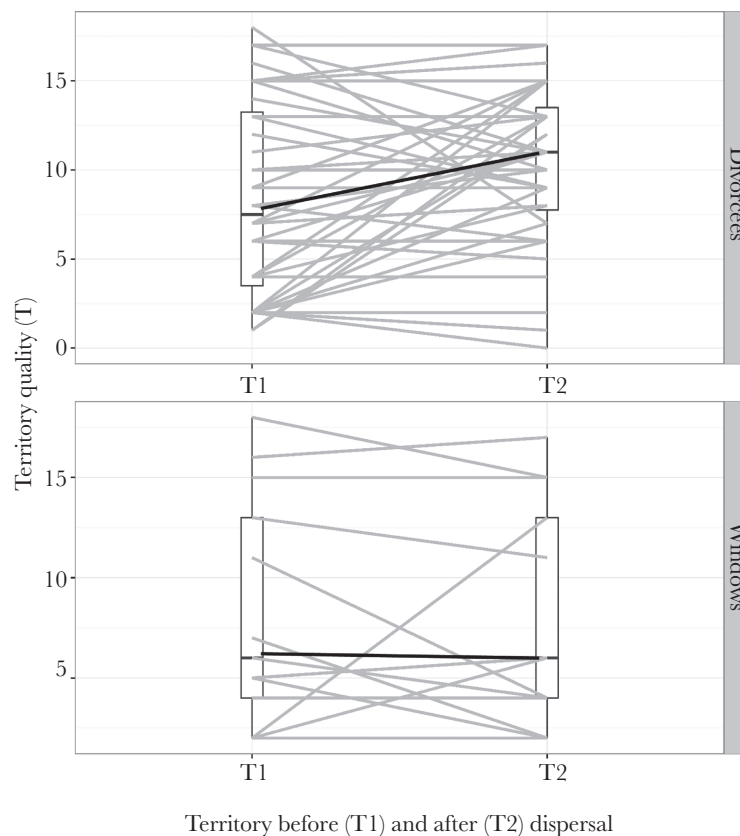
Figure 3

On average, females that dispersed after divorce (top panel; *n* = 44) moved to better quality territories (T2) than their initial territory (T1; *x* = 2.20, *P* = 0.01). This contrasts with widowed females that dispersed (bottom panel; *n* = 13): these did not obtain a better territory (*x* = −0.38, *P* = 0.24). Territory quality is expressed is an index of *Pandanus aquaticus* cover (1–20). Gray lines connect T1 and T2 for individual females, black lines connect medians. Box plots showing the interquartile range (box), medians, and SE.

Divorce driven by incest avoidance is not uncommon in cooperative breeders, as they are usually constrained by a social environment with a high density of relatives (Koenig and Haydock 1998; Daniels and Walters 2000; Hatchwell et al. 2000; Cockburn et al. 2003). In our study, divorce is a straightforward solution to end incest, and its outcome benefits both members: males and females paired with a less related individuals after divorce (Table 3). However, we found no evidence that dispersers actively sought unrelated partners, because the degree of relatedness among newly formed pairs could have been generated by random mating.

Divorce and EPP: infidelity in non-incestuous pairs

Despite the apparent difficulties of changing breeding partners, divorce was not restricted to incestuous pairs. However, in non-incestuous pairs, genetic relatedness did not predict divorce. Rather, divorce was related to female infidelity: 21% of divorcing pairs had EPP in a previous brood compared with 8% in non-divorcing pairs (Figure 2). The link between divorce and previous occurrence of EPP in non-incestuous pairs might reflect 2 alternative scenarios: EP mating is used to prospect for future partners (i.e., looking for a better quality partner; Spoon et al. 2007; Pérez-Staples et al. 2013) or it reflects weak pair bonds (Forstmeier et al. 2014). Our available evidence provides no support for EP mating as a prospecting mechanism for a partner of better quality: only 1 EP father (of the 14) became the new partner after a divorce. In this instance, a female left a son and paired with a previous EP partner who was paired to his daughter until then. We suggest that the positive association between divorce and EP paternity indicates that divorce and EP mating serve—at least to some extent—the same purpose. This relationship reflects the intense limitations on social partner choice (Cézilly and Nager 1995; Ramsay et al. 2000), whereby EP mating is an interim solution for females to compensate for a suboptimal partnership until this can be rectified by acquiring a new social partner through divorce (as in Ramsay et al. 2000).

Reproductive success is not a driver or outcome of divorce

We expected divorce to lead to an increase in reproductive success or to occur as a response to reproductive failure (Ens et al. 1993; Dhondt and Adriaensen 1994; Black 1996; Culina et al. 2014). However, divorce in non-incestuous pairs of *M. coronatus* is not obviously driven by reproductive failure: neither number of fledglings nor hatching success predicted divorce (Table 2). Similarly, there was no change in reproductive success after divorce (Table 3). More importantly, divorcees did not obtain higher reproductive success compared with individuals that had changed partner due to partner death (Supplementary Table S3). These patterns could be due to the fact that fairy-wrens are fairly long-lived (Cockburn et al. 2003): improvements in reproduction for species with long-term permanent pair bonds often occur slowly with pair-bond duration, as a consequence of mate familiarity or breeding experience (Marzluff and Balda 1992; Cézilly et al. 2000; Van de Pol et al. 2006; Sánchez-Macouzet et al. 2014). Thus, benefits of divorce might become evident only after multiple breeding attempts: indeed, more generally, reproductive benefits of divorce in long-lived species are less evident (Culina et al. 2014). Additionally, environmental stochasticity (Culina et al. 2014), the proposed main explanation for why performance at later breeding stages does not predict divorce, could apply to breeding success as a whole for *M. coronatus*. Reproductive success

for this species is largely determined by predation and flooding events (Hidalgo Aranzamendi et al. unpublished data), as for many tropical species (Martin 2015). Such high environmental stochasticity reduces the potential for reproductive failure to be selected for as a driver of divorce as well as hampering detection of reproductive failure driving individual divorce decisions. Alternatively, divorce might function as a mechanism to obtain long-term benefits, rather than an immediate reproductive benefit, as we will discuss below.

Improvement after divorce: territory quality over partner quality?

Divorced females that dispersed usually obtained a territory of higher quality. This was independent of whether females divorced a related or unrelated partner or other potential benefits such as number of subordinates on the territory. Such an improvement in territory quality did not occur in dispersing widowed females (Figure 3), indicating that obtaining a better quality territory is a clear benefit associated with divorce rather than breeder dispersal *per se*. The timing of such divorces was most likely opportunistic, with dominant females seizing an opportunity to obtain a better breeding territory. This seems to be an important female strategy as a third of female breeding vacancies (41 of 119, Supplementary Table S2) were filled by another dominant female dispersing, despite the constant presence of subordinate females in the population. The quality of territories has long-term importance for species with site fidelity (Desrochers and Magrath 1996; Heg et al. 2003). This is especially true for *M. coronatus*, in which territories are defended year-round (Hall and Peters 2008) and breeding vacancies occur rarely. Furthermore, higher quality territories are associated with long-term benefits, because they experience greater nest success (Hidalgo Aranzamendi et al. unpublished data) and support larger social groups, with more subordinate helpers (Kingma et al. 2011a), and helpers over time have a positive effect on fledgling production and breeder' survival (Kingma et al. 2010). Although divorcing females did not immediately acquire a larger group—presumably because subordinates often disperse immediately after death of a related dominant (Hidalgo Aranzamendi unpublished data)—in the long run, a high-quality territory is important for reproductive success. Therefore, in species with site fidelity, territory quality could take priority over partner quality, and divorce could be considered indicative of territory choice rather than partner choice (Ens et al. 1993; Desrochers and Magrath 1996).

Divorce: mostly a female-driven strategy?

In agreement with comparative evidence (Otter and Ratcliffe 1996, Culina et al. 2014), our evidence shows that females benefit more from divorce. First, most commonly the female instigated divorce by leaving (88% of divorces, Supplementary Table S2) and this was beneficial: Divorcees that did not disperse were likely to end up in an incestuous partnership with a resident, former subordinate male (Supplementary Table S1). Moreover, females dispersing after divorce acquired a higher quality territory (Figure 3), but no male dispersed to a better territory ($n = 7$, $x = -3.00$, $P = 0.98$). Additionally, some divorces may have been triggered by female–female competition (i.e., forced divorce; Taborsky and Taborsky 1999; Jeschke et al. 2007), driven by older females evicting younger ones. Direct evidence for this hypothesis is limited: we observed that 3 divorces were preceded by fights with a usurper female, and afterward the evicted females dispersed to lower quality territories. More broadly, we found that those females that dispersed to a lower quality territory after divorce took longer to re-pair and were more

likely to be replaced by an older female than females dispersing to higher quality territories (Table 3). Nevertheless, we cannot discard the possibility that such patterns reflect an undetected process of partner choice by males accepting older females.

CONCLUSION

We found that several nonexclusive hypotheses simultaneously explained divorce in this tropical cooperative breeder (Table 1). By adding demographic covariates and differentiating pairs according to their degree of relatedness, we found that divorce is a strategy to escape inbreeding for incestuous pairs. For unrelated pairs, previous female infidelity (presence of EP paternity) predicted divorce even though this was not directly linked to future pairing with the EP sire. Additionally, females appear to use divorce as a strategy to acquire a better quality territory. The importance of the acquisition of a better quality territory is in agreement with the absence of immediate improvements in reproductive success and the species' slow life history: annual survival is high, annual reproductive success is generally low with a large stochastic component, and the benefits of a good territory are expected to accrue slowly over the long term. Our detailed longitudinal data and reliable information on survival and movement of all breeders allowed us to overcome the most common limitations that hamper the understanding of divorce (see introduction). Our study provides a clear illustration of the complexity of factors underlying divorce for species with continuous partnerships and year-round territoriality.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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