

Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus*

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Summary

1. Between 1988 and 2001, we studied social relationships in the superb fairy-wren *Malurus cyaneus* (Latham), a cooperative breeder with male helpers in which extra-group fertilizations are more common than within-pair fertilizations.
2. Unlike other fairy-wren species, females never bred on their natal territory. First-year females dispersed either directly from their natal territory to a breeding vacancy or to a foreign 'staging-post' territory where they spent their first winter as a subordinate. Females dispersing to a foreign territory settled in larger groups. Females on foreign territories inherited the territory if the dominant female died, and were sometimes able to split the territory into two by pairing with a helper male. However, most dispersed again to obtain a vacancy.
3. Females dispersing from a staging post usually gained a neighbouring vacancy, but females gaining a vacancy directly from their natal territory travelled further, perhaps to avoid pairing or mating with related males.
4. Females frequently divorced their partner, although the majority of relationships were terminated by the death of one of the pair. If death did not intervene, one-third of pairings were terminated by female-initiated divorce within 1000 days.
5. Three divorce syndromes were recognized. First, females that failed to obtain a preferred territory moved to territories with more helpers. Secondly, females that became paired to their sons when their partner died usually divorced away from them. Thirdly, females that have been in a long relationship divorce once a son has gained the senior helper position.
6. Dispersal to avoid pairing with sons is consistent with incest avoidance. However, there may be two additional benefits. Mothers do not mate with their sons, so dispersal by the mother liberates her sons to compete for within-group matings. Further, divorcing once their son has become a breeder or a senior helper allows the female to start sons in a queue for dominance on another territory. Females that do not take this option face constraints on their ability to recruit more sons into the local neighbourhood.

Key-words: breeding dispersal, cooperative breeding, divorce, incest avoidance, *Malurus*, natal dispersal.

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Introduction

Female birds can influence their reproductive prospects via initial choice of breeding site and partner through subsequent breeding dispersal and divorce to improve their territory or partner and through extra-

pair mating. The relative importance of these tactics will depend heavily on the social organization and demography of the species concerned, but their interaction remains poorly understood.

Comparative analysis suggests that divorce rates are highest in species with high extra-pair mating (Cezilly & Nager 1995). This could be because pair-bonds are broken more frequently by male retaliation, but many studies of divorce implicate female control (although see Cezilly *et al.* 2000a). An alternative possibility is that breeding dispersal and extra-pair mating are

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alternative paths towards a general tactic of improving the quality of mates (e.g. black-capped chickadees *Parus atricapillus* L. Otter & Ratcliffe 1996; Ramsay *et al.* 2000). Comparative studies suggest that divorce is correlated negatively with site fidelity in Cinconiiformes (Cezilly, Dubois & Pagel 2000b), and more likely in migratory species (Ens, Choudhury & Black 1996). Möller (1992) argued that extra-pair mating would be the primary option available to long-lived species that maintain year-round territories because the availability of breeding vacancies will be constrained, so birds will be forced to disperse to the first vacancy that becomes available. Theoretical analyses also suggest that divorce will be less common as life span increases (McNamara & Forslund 1996; McNamara, Forslund & Lang 1999), although comparative data are unconvincing on this point (Ens *et al.* 1996).

Because cooperative breeders are often long-lived and occur in stable philopatric populations (Cockburn 1996; Arnold & Owens 1998), some of these generalizations suggest that divorce should be rare in cooperative breeders (e.g. Rowley 1983; Marzluff *et al.* 1996; Russell & Rowley 1996). However, divorce occurs for more than one adaptive reason in red-cockaded woodpeckers *Picoides borealis* (Veillot), although incest avoidance seems most important (Daniels & Walters 2000). Female long-tailed tits *Aegithalos caudatus* (L.) also divorce if they have bred successfully in the previous year, perhaps also to minimize the risk of nuclear family incest (Hatchwell *et al.* 2000). Further, extra-pair mating in cooperative breeders spans the entire range of values known from birds (reviewed by Cockburn 1998).

Fairy-wrens *Malurus* spp. are cooperative breeders with the highest known rates of extra-pair mating (Brooker *et al.* 1990; Mulder *et al.* 1994). Long-term studies of *M. elegans* Gould and *M. splendens* (Quoy & Gaimard) reveal negligible rates of divorce, but high levels of female natal philopatry and extreme levels of socially incestuous pairings (Russell & Rowley 1996, 2000). This implicates exclusive dependence on extra-pair mating as a means of mate choice. However, although high rates of extra-pair mating are universal within the genus, restrictions on female dispersal are not. Natal dispersal by females is obligate in superb fairy-wrens *M. cyaneus* (Mulder 1995). Here we use data from a long-term study of this species to show that female divorce and breeding dispersal are also common. We analyse the causes of dispersal, and show that natal dispersal, divorce and extra-pair mating are all important components of female mating tactics. We also present an analytical framework that should improve comparison of divorce rates within and between species and populations.

Methods

SOCIAL ORGANIZATION

We commenced colour-banding *M. cyaneus* at the Australian National Botanic Gardens in 1986, and have

kept continuous censuses of social relationships of the population since 1988. We try to see each bird every week during the non-breeding season (March–August), and at least three times per week during the breeding season (September–February). Females may produce as many as eight clutches and fledge three broods in a breeding season. Hence, divorce is possible within as well as between seasons.

Male *M. cyaneus* live their lives on the territory on which they are born, or disperse to a neighbouring territory (Mulder 1995). By contrast, females disperse once or twice in the first year of their life, usually making one long-distance movement, before they also become highly philopatric in their new territory.

On each territory we could identify unambiguously a dominant male and female that associated closely, particularly during the fertile period of the female. These birds dominate feeding sites and social interactions and sing more than subordinate birds. Dominance correlated perfectly with age, although in some cases two or more male nest mates were the oldest birds on the territory. In these cases, dominance could be predicted by determining which male acquired breeding plumage first each year (Mulder & Magrath 1994; Dunn & Cockburn 1999; Peters *et al.* 2000). We defined the relationship between the dominant male and a female as a socially monogamous pair, and subordinate males as helpers. It was also possible to define a dominance hierarchy among helpers using age and moult. Helpers do not exhibit mate-guarding. Subordinate females rarely persisted on the territory once the owner became reproductively active, leaving either of their own volition or being driven out by aggression from the owner (Mulder 1995).

Dispersal distances were measured as the number of territories traversed. Following Mulder (1995), we recognized two types of natal dispersal. Females moved either directly to a breeding vacancy from their natal territory (usually shortly before they commenced breeding), or moved to a subordinate role on a foreign territory already occupied by a pair or group (usually at the end of the breeding season in which they were fledged). Females moving to a foreign territory appeared to leave of their own volition and be accepted passively by their new group. Females on foreign territories used them either as a staging post before moving to a vacancy, inherited the breeding vacancy if the dominant female died (inheritance) or attempted to pair with a male helper and split the territory into two (fission).

Pairs were deemed to be established once birds were observed together on a territory without aggression or chases. Vigorous counter-singing often occurred when one bird moved onto the territory to form the partnership. However, where relationships were established between birds already present on the territory (because of death or dispersal of one of the dominants), the new partner was accepted passively.

We defined divorce as the departure of one member of the pair to a new breeding opportunity without any

prior aggression, either leaving their former partner unpaired or paired with a subordinate male or female on the territory. The dispersing bird was assumed to be the initiator. We contrast divorce with the rare case of eviction, where aggression by one bird in a pair led the evicted bird to skulk in the interstices between territories or occupy unfavourable habitat temporarily (e.g. rain forest). Social relationships were broken up by invasion of a foreign bird or by fusion of two territories. We distinguished usurpation, where the victim is forced out of the territory, and relegation, where the victim (always a male) adopted a helper role. The social norm involved a single female paired to one male and sometimes assisted by male helpers. However, we also recorded rare cases of polygyny, where a dominant male paired simultaneously to more than one female; polygyny, where two females bred on a territory and interacted with all the males in a group; plural breeding, where two pairs shared the same territory; and sequential polyandry, where a female moved freely over the territories held by two males and built her nest sequentially on both territories. These complex relationships were rare and very unstable, and are not considered in detail here.

PATERNITY ANALYSIS AND GENDER DETERMINATION

We obtained blood samples of all birds by puncturing the brachial vein with a hypodermic needle. We extracted DNA using conventional methods. We determined the sex of juveniles by the genetic test described by Griffiths *et al.* (1998). We used six to seven hyper-variable microsatellite loci to determine paternity of all fledglings. Microsatellite analysis in *M. cyaneus* has been described previously, including accounts of isolation of microsatellite loci (Double *et al.* 1997a), their statistical power in distinguishing between close male relatives (Double *et al.* 1997b) and the exclusion methods we use in assignment (Double & Cockburn 2000). Here we report new results for the effect of different mating and dispersal patterns on the probability of incest.

EFFECTS OF PRIOR SUCCESS

We sampled every breeding bout in the lifetime of females. These data enabled us to examine the causes and consequences of prior success for movement decisions. Because some females disperse out of the study area in order to breed our data for the long-term fate of daughters are imperfect, but the extreme philopatry of males means that the fate of sons (in either dominant or helper positions) produced by females is known precisely. In this study, we assessed the number of adult sons alive on 1 November in each year. By this stage in the breeding season the costly annual moult is usually close to complete, and any territory rearrangements associated with the onset of breeding have occurred.

STATISTICAL ANALYSIS

Dispersal

We used logistic regression to estimate the probability that a dispersing supernumerary females would settle on a foreign territory. We tested the following explanatory variables: season, age of dominant female, age of dominant male (which is correlated with male quality; Dunn & Cockburn 1999), number of male helpers, number of male juveniles and number of female natal juveniles (those that had been born on the territory and overwintered there). The latter three variables were correlated positively with each other, so we also tested separately the total number of supernumerary individuals (number of male helpers + number of male juveniles + number of female natal juveniles). Initially models were fitted with all explanatory variables, and then variables were dropped progressively from the model until only significant terms remained ($P < 0.05$).

Dispersal directly to a breeding vacancy could not be analysed in the same way. At the start of each breeding season any vacancies were filled rapidly by females dispersing from natal or foreign territories, except in 1995, reflecting a shortfall of females resulting from poor productivity during a severe drought in 1994/1995. Dispersal direct to a vacancy therefore reflects availability of unpaired males holding territories.

Divorce

Divorce rates are expressed commonly as the proportion of pairs in which divorce occurs among those pairs where both partners survive to breed in two seasons. This is often all that can be measured sensibly for birds that are monitored only during the breeding season (Ens *et al.* 1996), as is commonly the case where birds return from migration or aggregate to breed in colonies. However, the definition excludes pairings where divorce occurs rapidly (as predicted by the errors of mate choice hypothesis; Black 1996) and then one partner dies, or where divorce affects one individual more than once in a year. The definition is also conceptually awkward when birds divorce during the breeding season. Recognizing these difficulties, some authors prefer to quantify the proportion of relationships that are terminated by divorce, or the number of individuals that experience divorce (Marzluff *et al.* 1996). However, there is a large difference between observing that a pair persisted without divorce for 20 years and concluding that divorce did not occur in the case where one partner dies a few days after the relationship is established. Comparisons should control for the different power of these observations, but no method has been proposed to achieve this goal.

We therefore propose the use of survival analysis to determine the fate of relationships. Bennetts *et al.* (2001) make a comparable proposal for the study of

dispersal. Survival analysis distinguishes between: (i) failure, where the individual cases are terminated by the event of primary interest, so we can conclude that divorce occurred after a given period; and (ii) censorship, where the individual cases are terminated by causes other than the fate of primary interest, or where the individual cases are ongoing at the time observations cease. Here we can say that divorce had not occurred after a given time (Collett 1994). We treated relationships that were terminated by death or causes other than divorce or which were extant on 1 December 2001, as censored, because we could not evaluate whether divorce would have occurred if the relationship had persisted. By contrast, we treated divorce as failure of the relationship. This allows us to express the probability that relationships lasting any given length will be terminated by divorce. We used Cox's (1972) proportional hazards approach to evaluate factors that could explain the risk of divorce. Models were fitted with JMP3.0 for Macintosh. In making these contrasts, we proceeded via exploratory analysis using Kaplan–Meier plots followed by a variety of hierarchical tests. For example, the fate of first and subsequent pairings were examined separately because the first relationship formed by a female generally was established via a completely different route than subsequent relationships. For both we analysed how the path by which a female acquired a mate influenced the probability of divorce. In later relationships we also examined the influence of relatedness and territory fidelity on divorce. We continued analysis until no further structure could be identified.

Effects of prior success

Reproduction data were used to examine density-dependent constraints on productivity by examining the effect of a female's prior reproductive success (number of living adult sons on her territory or in adjacent territories) on her reproductive success 1 year later, after a season of reproduction. We included only data where the female lived with her sons for the full year. Because some females were sampled more than once, we used restricted maximum likelihood (REML) models with female as a random variable, and assessed the effects of year and the number of sons already present. REML models were estimated using Genstat for Windows.

Other

We used log-linear models to analyse problems of contingency. We used two-tailed tests in all analyses. Our data are based on observations of the initiation of 874 pairings, 60 of which were continuing on 1 December 2001. Our sample sizes vary between analyses because of constraints on our knowledge of some variables. For example, genealogy cannot always be fully resolved because some birds are sired by males from outside the

study area, some assessments of territory productivity or changes in female circumstances were influenced by death of one or both of the pair, and early in the study the ages of some of the birds could not be compared because both were banded as adults. In all analyses, we controlled for year of sampling where appropriate. We do not discuss seasonal effects in detail here. They are virtually all associated with the low productivity and recruitment associated with a severe drought in the 1994/1995 breeding season and a less severe drought in the 1997/1998 breeding season.

Results

ACQUISITION OF FIRST BREEDING POSITIONS

Female fairy-wrens that were recruited into the breeding population generally bred for the first time in the season after they were fledged (362/374; 97%). However, eight birds did not lay eggs in their first season, and five bred in the season in which they were fledged. Breeding in the season of fledging occurred late in the breeding seasons of 1995 (three) and 1998 (two), immediately after severe droughts that occurred in 1994 and 1997, where many males had spent most of the breeding season without any females on their territory. Deferred breeding occurred sporadically throughout the study.

Females move from their natal territory to breed (373/374; 99.7%). The single exception moved into a vacant neighbouring territory, but that territory fused subsequently with her natal territory (Table 1). Some dispersal is driven by persistent aggression by the dominant female (Mulder 1995). However, young females were unwilling to breed on their natal territory, even if they were the only supernumerary on the territory and their mother died after the start of the breeding season in which the young female would commence reproduction ($n = 5$). In four of these cases the female was not a relative of the dominant male on the territory, as a consequence of extra-group paternity.

We could distinguish the dispersal history of 279 natal dispersers; the remainder moved directly to a breeding vacancy from an unknown location. Females moved either directly to a breeding vacancy from their natal territory (74; 27%) or spent time as a subordinate in a foreign group before pairing with a male (205; 74%) (Table 1). Moving to a foreign territory allowed access to options for breeding that were not available to birds moving from their natal territory into a breeding vacancy. The additional options included fission of the territory and inheritance of the territory on the death of the dominant hen (Table 1).

Mulder (1995) has shown previously that females that disperse to a subordinate position on a foreign territory are those fledged early in the breeding season. About a quarter of territories attract foreign females (161/683; 24%). In a multiple logistic regression model the probability of settlement by a dispersing female was

Table 1. The paths by which female superb fairy-wrens acquired their first mate. Females could gain a vacancy directly from their natal territory or via a foreign staging post (this is unknown for some females)

Mode of acquisition	Subcategory	Gained vacancy from	<i>n</i>
Inheritance (<i>n</i> = 48; 12.8%)	Death of owner	Foreign	46
	Owner ousted	Foreign	2
Fission (<i>n</i> = 74; 19.8%)	Subordinate first	Foreign	65
	Immediately	Foreign	7
	Immediately	Natal	1
Moved to pair with male on a territory lacking a female (<i>n</i> = 244; 65.2%)	Subordinate first	Foreign	79
	Immediately	Natal	71
	Immediately	Unknown	94
Other (<i>n</i> = 8; 2.1%)	Bred on fused natal territory	Natal	1
	Established a new territory	Foreign	2
	Established a new territory	Natal	1
	Polygynandry	Foreign	1
	Polygyny	Foreign	1
	Plural breeding	Foreign	1
	Sequential polyandry	Unknown	1
Total directly from natal source			74
Total from foreign			205
Total from unknown			96

not affected by the age of the dominant female (contrasting females that are 1, 2, 3, 4, 5 and 6 years and older, $\chi^2 = 5.2$, d.f. = 5, $P = 0.39$), or age (and hence quality) of the dominant male ($\chi^2 = 4.4$, d.f. = 5, $P = 0.48$). Season was an important predictor in all models because there were more dispersers in productive years where many females fledged early ($\chi^2 = 33.4$, d.f. = 12, $P < 0.001$). The probability of settlement increased with any variable reflecting the size of the group in which the female settled (number of male helpers, number of juvenile males, number of juvenile natal females). These were correlated highly, so they are difficult to treat independently. Indeed, the best predictions were obtained by summing the supernumerary individuals. Controlling for season, dispersers settled in subordinate roles on foreign territories more often as the total numbers of helpers and natal juveniles increased ($\chi^2 = 61.7$, d.f. = 1, $P < 0.001$; Fig. 1). Twenty territories attracted two early dispersers (20/161; 12%). The Poisson distribution was used to estimate the number of territories that should attract various numbers of early dispersers given a mean of 0.27 per territory. There was no evidence of departure from the Poisson ($\chi^2 = 1.91$, d.f. = 2), with 18.4 and 1.7 cases predicted for settlement by two and ≥ 3 subordinates, respectively.

Females generally moved long distances before settling in a subordinate role on a foreign territory. Among the 39 females fledging and then settling as a subordinate within the study area, 36 (92%) moved three or more territories. This figure is extremely conservative, as the sample is biased towards short dispersal movements. For females moving to a foreign

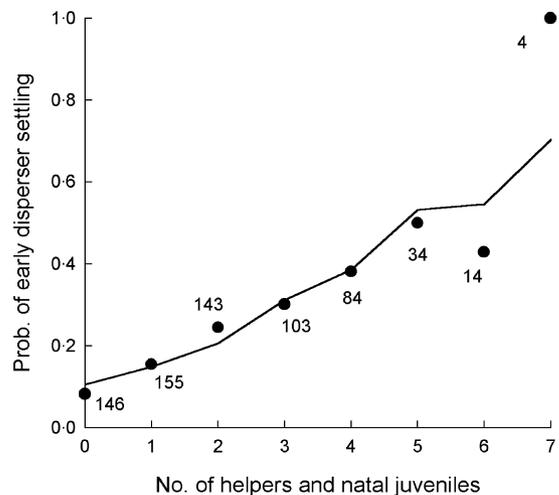


Fig. 1. The probability that a dispersing female will settle as a subordinate on a territory in relation to the supernumerary individuals (adult male helpers, juvenile males, juvenile natal females) already on the territory. The points (with sample sizes) represent the proportion of winters in which groups of a given size attracted an early disperser that remained present until the middle of winter (1 June). The line is the prediction from a logistic regression model, which is irregular because it is averaged for year effects; large groups are more likely in some years of the study.

territory from outside the study area, we could be sure that a further 47 had moved at least three territories. We were uncertain of the distance traversed by the remainder, as they settled near the edge of the study area.

When females that had spent the winter on a foreign territory dispersed for a second time in order to gain a vacancy, they usually settled in an immediately

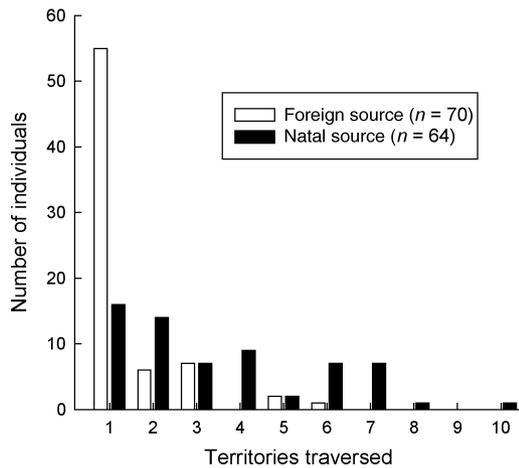


Fig. 2. The number of territories traversed by females dispersing to their first breeding vacancy either directly from their natal territory or having spent the winter as a subordinate on a foreign territory. Long dispersal distances are underestimated as many long dispersal attempts are not detected.

adjacent territory (Fig. 2). By contrast, females that had overwintered on their natal territory before taking up a vacancy moved much further ($\chi^2 = 40.0$, d.f. = 1, $P < 0.001$; Fig. 2).

REMATING

We observed 500 cases of a female changing her social mate ($n = 241$ females; mean = 2.07 ± 1.48 SD, range = 1–9). Changes usually took place when the partner of the female died (299/500, 60%). He was generally replaced by the senior helper in the group if one was present, or in the absence of helpers, with an immigrant male dispersing from a helper role on a neighbouring territory (Table 2). Apart from death of her social mate, there were numerous additional triggers for remating. The most common of these was divorce initiated by the female (104/201, 52%), on which we focus in this paper.

Divorce

Female-initiated divorce may occur at any time during the first 500 days of a relationship, accounting for about 20% of new pairings over that time (Fig. 3). Relationships lasting beyond this interval were stable, until a further acceleration of divorce that occurred in relationships that had persisted for 700 days. This increased the divorce rate to one third of all relationships after 1000 days (Fig. 3). Because survival models used are most robust when the log-transformed survival data are linear (Collett 1994), we distinguished between early divorce (affecting relationships persisting

Table 2. The paths by which female superb fairy-wrens formed subsequent pairings

Mode of acquisition	Subcategory	Relatedness to new mate	<i>n</i>
Mate died ($n = 299$; 59.8%)	Paired with helper	Unrelated	92
	Paired with helper	Son	71
	Moved to vacant territory	Unrelated	18
	Neighbouring helper moved in	Unrelated	110
	Neighbouring dominant subsumed territory	Unrelated	8
Female-initiated divorce ($n = 104$; 20.8%)	None	Unrelated	104
Male-initiated divorce ($n = 9$; 1.8%)	Paired with helper	Unrelated	5
	Paired with helper	Son	2
	Moved to vacant territory	Unrelated	2
Mate replaced by another male as dominant on same territory ($n = 19$; 3.8%)	Mate first evicted after aggression by the female	Unrelated	3
	Partner usurped	Unrelated	12
	Partner usurped	Son	1
	Partner relegated to a helper role	Unrelated	3
	Partner usurped	Unrelated	3
Two territories fused ($n = 23$; 4.6%)	Partner usurped	Unrelated	3
	Partner relegated to a helper role	Unrelated	15
	Neighbour died and female subsumed the territory and paired to mate	Unrelated	5
	Eviction	Unrelated	4
	Polygyny	Unrelated	14
Female replaced owner ($n = 4$; 0.8%)	Sequential polyandry	Unrelated	1
	Other female died	Unrelated	1
Complex mating associations ($n = 15$; 3.0%)	Other female left	Unrelated	6
	Female abandoned	Unrelated	3
	Territory fissioned	Unrelated	1
	Male died, territories fused	Unrelated	1
	Paired with helper	Unrelated	6
Complex associations end ($n = 12$; 2.4%)	Paired with helper	Son	1
	Paired with immigrant	Unrelated	3
	Not applicable	Unrelated	5
Loses mate when territory fissions ($n = 10$; 2.0%)	Paired with helper	Unrelated	6
	Paired with helper	Son	1
	Paired with immigrant	Unrelated	3
Mate switch where initiating sex could not be determined ($n = 5$; 1.0%)	Not applicable	Unrelated	5

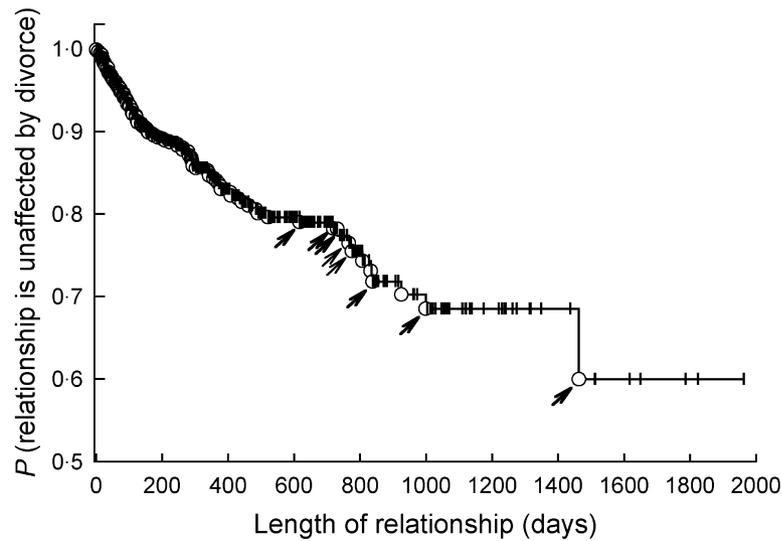


Fig. 3. Kaplan–Meier plot estimating the probability that a relationship will persist without female-initiated divorce occurring. Divorces are indicated by circles, and failure of the relationship through other causes (usually death of one of the pair) by vertical lines. Arrows depict divorces in long-standing relationships (> 600 days) where a son of the female initiating the divorce has achieved the senior helper position on the territory.

for less than 600 days) and late divorce (> 600 days). We analysed early divorce by treating relationships persisting more than 600 days as censored at 600 days.

We analysed the fates of first and subsequent pairings separately. Females paired for the first time did not divorce if they inherited the foreign territory on which they had settled to spend the winter. However, about one in five relationships were terminated by divorce if the female obtained only part of the territory through fission or moved directly to a vacancy ($\chi^2 = 12.2$, d.f. = 2, $P = 0.002$; Fig. 4a). Among females moving directly to a vacancy we were able to contrast: (i) whether they gained the vacancy via a foreign territory or directly from their natal territory; and (ii) whether their final movement to a vacancy entailed movement to an neighbouring territory or a longer-distance movement involving crossing one or more territories. These variables are correlated highly (Fig. 2) so the small sample sizes for the rare cases of long distance movement from a foreign territory of short movements from a natal territory ($n = 16$ in each case) mean that interaction terms between the two variables could not be analysed. Divorce was less likely when the distance was short ($\chi^2 = 4.8$, d.f. = 1, $P = 0.03$, Fig. 4b) and as a corollary, when the female moved from a foreign territory ($\chi^2 = 5.8$, d.f. = 1, $P = 0.02$; Fig. 4c).

Most cases of divorce in subsequent pairings occurred when mothers divorced their sons. Females usually paired to their sons when the original partner died and was replaced by the senior helper (her son). In these cases females associated closely with their sons and continued to build nests and rear young. However, two-thirds of all mother-son pairings were terminated by divorce within 500 days (Fig. 4d). The most appropriate statistical contrast is with pairings where the territory

was inherited by an unrelated helper after the dominant died. Divorce was much less likely when the helper was unrelated ($\chi^2 = 28.9$, d.f. = 1, $P << 0.001$; Fig. 4d).

In order to dissect the probability of divorce in other cases further, we analysed separately relationships with unrelated males. We could distinguish several contexts: (i) where the territory occupied by the female remained at least the same size, but her partner changed (possible partners included a promoted unrelated helper, a solitary immigrant male, or an immigrant male usurping the female's original partner or relegating him to helper status); and (ii) where the territory of the female decreased because of fission or she changed her territory (because she was left unpaired and moved to a new vacancy, or she divorced away from her partner). Females generally accepted a change of partner, but were likely to divorce again if their territory changed ($\chi^2 = 6.8$, d.f. = 1, $P = 0.009$; Fig. 4e). The common subcategories of these two classes did not differ in the likelihood of divorce.

Three of the 12 divorces that occurred after 600 days were temporary, as the female associated briefly with a new male but then returned to her original partner. In eight of the remaining cases, the divorce was initiated shortly after a son of the female achieved senior helper status (Fig. 3; mean = 18.7 ± 5.7 SD days, $n = 6$ where time of acquisition of senior helper status was known precisely). Reinspection of the divorces that occurred in shorter relationships revealed six other cases where a son had recently become a senior helper. Three of these occurred in cases where females changed their partner but not their territory, contributing to the sudden increase in divorces after a period of stability (Fig. 4e, mean = 29.3 ± 9.5 SD days, $n = 4$ where time was known).

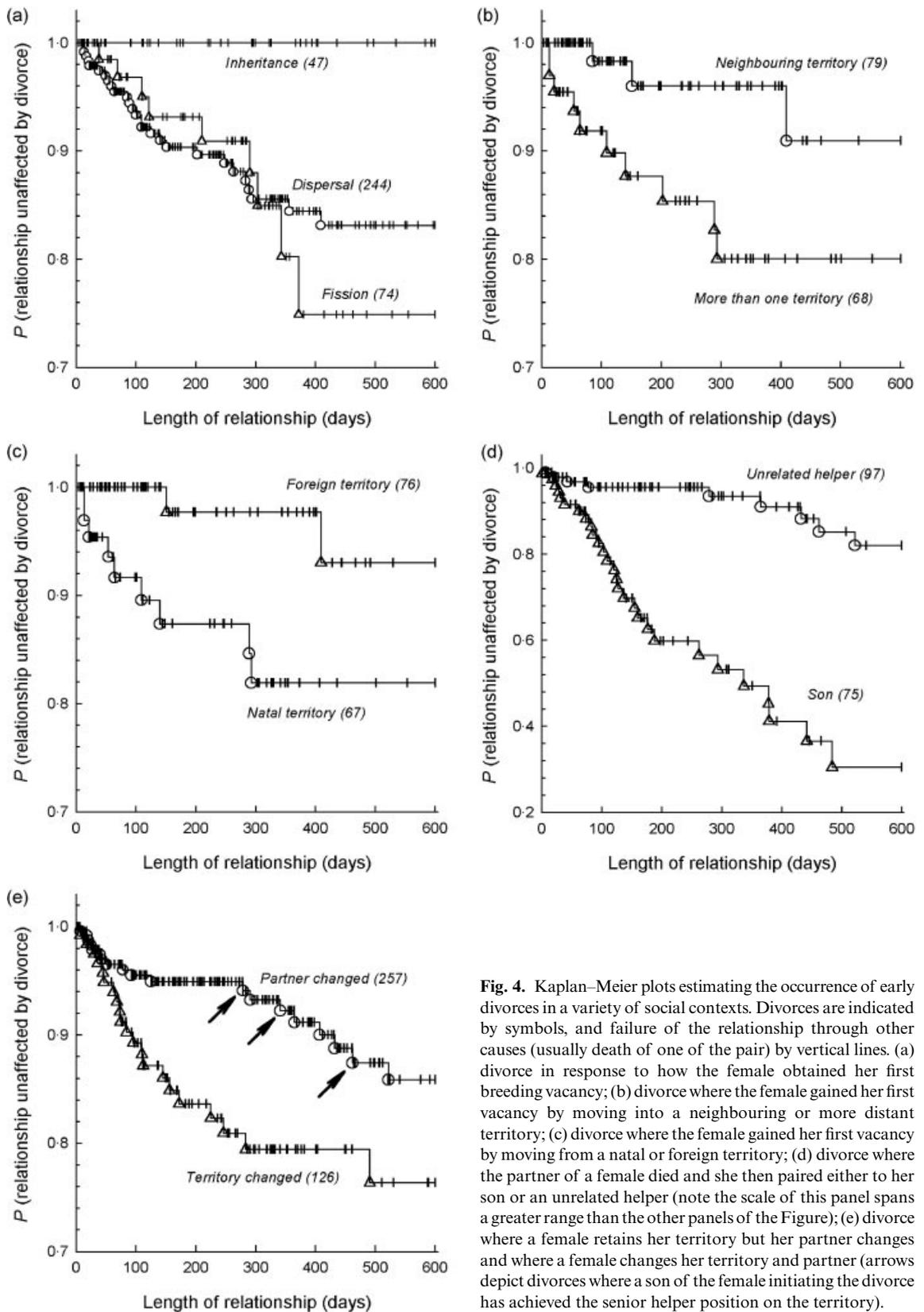


Fig. 4. Kaplan–Meier plots estimating the occurrence of early divorces in a variety of social contexts. Divorces are indicated by symbols, and failure of the relationship through other causes (usually death of one of the pair) by vertical lines. (a) divorce in response to how the female obtained her first breeding vacancy; (b) divorce where the female gained her first vacancy by moving into a neighbouring or more distant territory; (c) divorce where the female gained her first vacancy by moving from a natal or foreign territory; (d) divorce where the partner of a female died and she then paired either to her son or an unrelated helper (note the scale of this panel spans a greater range than the other panels of the Figure); (e) divorce where a female retains her territory but her partner changes and where a female changes her territory and partner (arrows depict divorces where a son of the female initiating the divorce has achieved the senior helper position on the territory).

Impact of divorce

In order to measure how divorce changed the conditions experienced by the females initiating the divorce

we distinguished three contexts: (i) females who were paired to their son; (ii) females with a son as senior helper; and (iii) females without relatives in senior positions. We excluded five cases where females divorced

Table 3. Effect of female-initiated divorce on the number of helpers that assist her and the age of the male to which she is paired

Relationship between female and senior males before divorce	Increased no. of helpers	Zero helpers on both	Same no. of helpers	Decreased no. of helpers	Ratio of increase to decrease
Unrelated	32	19	0	3	10·7
Paired to son	4	11	2	12	0·3
Son as senior helper	0	1	2	10	0·1
Relatives	4	12	4	22	0·2
	New partner older	New partner same age	New partner younger		Ratio of older to younger
Unrelated	24	11	17		1·4
Paired to son	18	6	2		9·0
Son as senior helper	3	0	8		0·4
Relatives	21	6	10		2·1

for short periods but then divorced again to return to their partner, as any benefits/losses were cancelled out on return to their original position.

Females did not appear to initiate divorce because they had experienced reproductive failure on a territory or with a particular partner. The majority of divorces took place quickly, before the pair had attempted to reproduce (Fig. 3). Divorces that terminated long-established relationships were dominated by females who had sons on the territory (Figs 3 and 4c). These females obviously had prior success on the territory.

We used the number of helpers as an index of change in social organization (Table 3). Unlike our analysis of natal dispersal, we could not consider easily the effect of the juveniles on the territory. Divorce occurs throughout the year, whereas the number of juveniles needs to be assessed at a given time, as it declines after the end of the breeding season because of death and dispersal. We used the age of the dominant male as an index of changes in mate quality (Table 3).

Females whose partner and senior helper were unrelated to them typically moved to territories with more helpers or moved from territories without helpers to other territories without helpers (Table 3). By contrast, females paired to sons or with sons as senior helpers were likely to reduce the number of helpers as a consequence of divorce (Table 3; contingency table analysis contrasting if the number of helpers increases, stay the same or decreases, $\chi^2 = 35·5$, d.f. = 4, $P < 0·001$). This effect holds for females with sons as senior helpers even when the senior helper is excluded from the helper count, as females with relatives generally move to territories without helpers (23/29 females divorcing sons; 6/9 females divorcing senior helpers).

We expected the number of helpers to be correlated with the age of the male, as young males often lack helpers. While such a correlation could make it difficult to distinguish between the two variables, effects of age were much weaker (Table 3). The strongest tendency was for females divorcing their sons to increase the age of their partner. However, the converse was true for females divorcing once their son attained the senior position. Females paired to sons or with sons as senior helpers did not differ from females without male relatives in the propensity to change the age of their

partners (Table 3; contingency table analysis where the classes were for the number of helpers to increase, stay the same or decrease, $\chi^2 = 1·0$, d.f. = 4).

PATERNITY ANALYSIS

Within-group paternity

Sons paired to mothers never gain paternity (0/74 young produced by 19 pairs). Helper males also never mate with their mother (0/335 young in 115 broods where paternity is fully resolved using microsatellite analysis). By contrast, unrelated helpers gain 8% (65/785 in 277 broods) of paternity when they are present, and this represents 22% (65/225) of within-group paternity.

Incestuous pairing after dispersal

We knew the genealogical situation of 11/16 females that gained a neighbouring vacancy from a natal territory. Three of these (27%) became socially or genetically incestuous. One female paired to her older full brother (who dispersed before she was born), although the one brood of four young they reared was entirely sired by an extra-group male. A second female paired to the half-brother of her sire, and allowed him four fertilizations of the 23 young they reared together. The third female chose the half-brother of her sire as an extra-group mate for one of the 27 young she produced. By contrast, in the 358 females that dispersed over greater distances, only one (0·3%) mated incestuously. A female dispersed seven territories from her natal territory and produced a daughter who dispersed back into the neighbourhood occupied originally by her mother. Her new neighbours were all close male relatives of her mother. Of nine young she produced eight were extra-group, of which three were sired by her mother's half-brother. The last offspring was sired by a helper who was a full nephew of the female's mother.

EFFECTS OF PRIOR SUCCESS

In a restricted maximum-likelihood model with the identity of the female as a random variable, the ability of females to increase the number of sons living in and

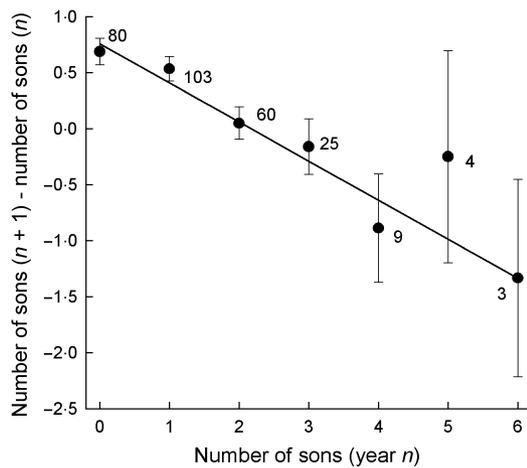


Fig. 5. Density-dependent constraints on recruitment of male sons, illustrated by depicting the change in number of living sons on 1 November from one year to the next, in relation to the number of sons present on 1 November in the first year. Data points are shown with standard errors and sample sizes. The line represents the restricted maximum likelihood estimates of the regression equation for an average year (1988) in a model with identity of the female as a random factor.

adjacent to her territory from 1 November one year until 1 November the next was unsurprisingly affected by season ($\chi^2 = 25.8$, d.f. = 12, $P = 0.01$), but also declined strongly as the number of sons already present increased ($\chi^2 = 38.0$, d.f. = 1, $P < 0.001$). Females with three or more sons in their neighbourhood in one year usually had fewer sons the following year, while females with zero or one son often increased their number of living sons (Fig. 5). The number of sons alive at any time never exceeded six, although females can breed for many years and are capable of recruiting five sons to adulthood in a single season.

Discussion

Virtually all *M. cyaneus* clutches contain extra-pair young (Mulder *et al.* 1994; Dunn & Cockburn 1999), and females control opportunity for extra-pair mating (Double & Cockburn 2000). Here we demonstrate two additional female reproductive tactics. First, females used foreign territories as staging posts to increase the likelihood of obtaining a territory in productive locations. Secondly, they increased their reproductive success by means of strategic divorce.

CONSPECIFIC CUEING AND NATAL DISPERSAL

Natal dispersal was obligatory for female *M. cyaneus*. Although maternal aggression can be involved in the decision to leave, females left their territory regardless of maternal aggression. However, clustering of close male relatives (Double *et al.* 1997b) may expose these females to a high risk of incest when she mates extra-pair, and she may have limited knowledge of her

relatedness to the dominant male (Dunn, Cockburn & Mulder 1995).

Natal dispersal had two forms: direct dispersal to a breeding vacancy and dispersal via a staging post on a foreign territory. Dispersal via a staging post is available only to females fledged early in the breeding season (Mulder 1995). For these females, it offered considerable advantages. Not only did females have access to the territory via inheritance and fission, but they also had some choice of the foreign territory in which they settled, preferring territories with many supernumerary individuals (Figs 1 and 2). This pattern might occur for several reasons. First, females might be able to join large groups more easily because of confusion of identity. Secondly, large groups may provide more of the traditional benefits associated with group membership, such as reduced risk of predation or thermal benefits from huddling at the roost site. Thirdly, territories with helpers or juvenile males may be good candidates for fission of the territory, which is only possible if there is a helper or male juvenile. Finally, territories containing many supernumeraries have been productive in preceding years, providing a cue to the productivity of the local neighbourhood (conspecific cueing: Stamps 2001).

The use of productivity of conspecifics as a cue to settlement has a long history (reviewed by Stamps 1988) and has recently enjoyed renewed attention (Danchin, Heg & Doligez 2001; Stamps 2001). Several considerations suggest that it may be of importance in fairy-wrens in addition to the obvious advantages of obtaining a territory through fission. First, female *M. cyaneus* appear to have sophisticated individual recognition (e.g. Cooney & Cockburn 1995), suggesting that adults are unlikely to accept additional individuals just because they fail to detect them. Secondly, recruitment is density-dependent, so huddling and predator avoidance are unlikely to drive grouping. Thirdly, the presence of juvenile natal females does not facilitate fission, but does induce settlement by supernumerary females. Foreign females that inherit their territory or disperse to a vacancy next door appear to be satisfied with the territory and do not initiate divorce. However, they will initiate divorce if the territory fissions. Finally, females that divorce from established partnerships also appear to prefer territories with increased numbers of helpers.

In this context, although helper number and productivity are correlated, increased productivity seems not to be caused by the presence of helpers, but rather productive territories are more likely to have helpers (Dunn *et al.* 1995; Green *et al.* 1995). The situation is therefore quite unlike that prevailing in cooperatively breeding stripe-backed wrens *Campylorhynchus nuchalis* Cabanis, where subordinate females fight vigorously for territorial vacancies if the territory has several helpers, but are reluctant to accept vacancies lacking helpers (Zack & Rabenold 1989). In this species, there is a huge increase in productivity once helper number exceeds a certain size (Rabenold 1984). Danchin *et al.* (2001) emphasize the difficulty of concealing reproductive

success, and the advantage that conspecifics derive from using such public information as a cue to settlement. Such public information may be particularly useful and intrinsically honest in cooperatively breeding species with prolonged natal philopatry.

There are three caveats that need to be considered in comparing the relative success of direct dispersal and use of a foreign territory as a staging post. First, females are much more likely to gain a vacancy from a foreign territory (204/278; 73%). The relative frequency of birds overwintering on natal and foreign territories was evaluated by summing the number of each type on 1 June, in the middle of the non-breeding season. More females were living on their natal territory (249/430; 58%) than on foreign territories (181/430; 42%). This suggests that the greater recruitment of females from foreign territories is even more remarkable.

Secondly, because occupants of foreign territories usually disperse only a short distance, the majority of the dispersers from unknown locations may be moving from a natal territory. While this, in part, counters the disadvantage, even given the extreme assumption that all 96 individuals of unknown origin dispersed directly from their natal territory, birds settling from foreign staging posts retain a numerical advantage (204/374, 55%; compared to the frequency of overwintering females; $\chi^2 = 10.9$, d.f. = 1, $P = 0.004$).

Thirdly, we found little evidence of mortality associated with early dispersal to a foreign territory. Although early dispersers are sometimes the victims of aggression in transit, they ultimately appear to be accepted passively as group members. The sex ratio of the population is unaffected by early dispersal, suggesting that emigration and immigration are balanced. By contrast, the second phase of dispersal is accompanied by aggression on the part of the dominant female to both foreign and natal females, and leads to a sharp increase in the male bias in the population (Mulder 1995). There is hence a strong incentive for late dispersers to accept vacancies once they become available without the habitat choice that appears possible among early dispersers.

TERRITORY OR MATE?

Many discussions of dispersal and remating have attempted to distinguish the relative importance of the quality of the territory and the mate in settlement patterns and divorce decisions (Dhondt & Adriaensen 1994; Desrochers & Magrath 1996; Streif & Rasa 2001). Our data support the primacy of territory quality in settlement decisions by *M. cyaneus*. Birds overwintering on a foreign territory that gained their first vacancy by inheriting the entire territory or a neighbouring territory rarely initiated divorce, while females frequently initiated divorce if they were forced to move long distances to a vacancy or they lost part of their territory to fission (Fig. 4a–c). Similarly, females in second or later relationships were indifferent to a change

in mate, but were likely to initiate a change of mate if their territory changed (Fig. 4e). Birds appeared to use conspecific cueing in evaluating whether it was worth changing territory, and unless relatives were involved, were likely to gain more helpers as a consequence of divorce (Table 3). By contrast, although there was a tendency to increase the age of the mate via divorce, this effect is much weaker, and seems likely to be an artefact of a correlation imposed because very young males are unlikely to have helpers. Finally, most early divorces took place without testing the reproductive quality of the partner, and females had bred successfully (had sons) in divorces terminating long-term relationships.

The territory may be particularly important to female *M. cyaneus* because their social partner is not. The direct benefits contributed by the dominant male via provisioning nestlings and fledglings can be slight, particularly if helpers are present (Green *et al.* 1995; Dunn & Cockburn 1996). In addition, most fertilizations are extra-group, so females can gain any indirect benefits associated with male genotype by choosing the sire of their young (Mulder *et al.* 1994; Dunn & Cockburn 1999).

INCEST AVOIDANCE

Inbreeding avoidance is thought to be the primary cause of sex-biased natal dispersal in birds and mammals (Greenwood 1980; Cockburn, Scott & Scotts 1985; Pusey 1987; Wolff 1992, 1994; Wolff & Plissner 1998; Lambin, Aars & Pieltney 2001; Perrin & Goudet 2001). Among cooperative breeders, female red-cockaded woodpeckers with helpers divorce their sons after their partner dies, but accept unrelated helpers as mates (Daniels & Walters 2000). In long-tailed tits, females are more likely to divorce their partner if they have bred successfully, possibly to avoid pairing with philopatric sons in the future (Hatchwell *et al.* 2000).

The importance of incest avoidance in *Malurus* is controversial. Brooker *et al.* (1990) argued that the high rate of extra-pair mating in *M. splendens* reflected inbreeding avoidance, as about 20% of social pairings are between nuclear family members. However, in *M. cyaneus* all females seek extra-pair copulations, yet incestuous pairings are rare and virtually confined to mothers and their sons. Dunn & Cockburn (1999) showed that females cuckolded younger males regardless of relatedness, suggesting that extra-group mating facilitated incestuous pairing, rather than *vice versa*.

None the less, incest avoidance appears to influence dispersal. Females that disperse to breed directly from a natal territory move much further than females dispersing from a foreign territory, who have already made a long-distance movement. Pairing with male relatives would be likely in the natal neighbourhood because philopatry and variance in male reproductive success mean that neighbourhoods can be dominated

by male relatives. Incest occurred in 27% of females that disperse to a neighbouring territory. Interestingly, the females that moved directly to a neighbouring territory also contributed two of the four females that found themselves evicted physically by an invading female. Eviction may have been possible because the evictees would have preferred to move further.

A role for incest avoidance is also compatible with the tendency of females to divorce their sons promptly when their son inherits the territory. However, as for its congeners, divorce of incestuously paired *M. cyaneus* was not inevitable. Some incestuous pairings persist for considerable periods (the longest relationship was 1138 days, and was ended by death of the male), despite vacancies emerging nearby, suggesting that some females will tolerate incestuous pairings. It may be unnecessary for fairy-wrens to divorce sons to avoid incest because females have access to extra-group paternity. Neither dominant nor helper males gained paternity with their mother, although mothers mated with unrelated dominants and helpers.

We suggest that divorcing sons has two additional explanations. First, incest taboos mean that the within-group success of sons is inhibited until their mother departs, curtailing the production of grandchildren of the mother. While fairy-wrens have access to extra-group success, this is most likely for older males (Dunn & Cockburn 1999), who are less likely to be living with their mother. Extreme variance in extra-group success among males also means that within-group success may be the only avenue for success of many males.

Secondly, the extreme philopatry of male fairy-wrens may constrain the productivity of long-lived females, because their only opportunities to place sons in breeding vacancies are on the natal territory or through dispersal by sons to neighbouring territories. The latter avenue will be restricted if helper males are already present, which is likely because of spatial contagion in reproductive success. There are strong density-dependent constraints on recruitment of male offspring, with the maximum number achieved only just exceeding the maximum number recruited in a single year (Fig. 5). Females could potentially evade these density-dependent constraints by vacating the territory in favour of their sons, so future sons join a queue for dominance on a new territory.

The idea that females move between territories to increase the number of territories occupied by their sons resembles conceptually the territorial bequeathal hypothesis, which has been used to explain breeding dispersal in female mammals (Stenseth 1978; Price & Boutin 1993). According to this view, abandonment of the territory is a form of parental investment in the offspring. Lambin (1997) showed that good evidence for territorial bequeathal is confined to where the female donates a physical resource that is difficult to replace, such as a burrow. However, we suggest that because female fairy-wrens disperse only when a vacancy is available, there are great fitness benefits

from establishing male offspring on many territories. The only five females to show breeding dispersal twice included the only three in the entire study to have sons living on four territories at the time of their death (of 27 females that had sons that might have prompted divorce in four or more years). This advantage has not been raised in earlier syntheses of hypotheses why females might divorce their partner (Choudhury 1995; Black 1996; Ens *et al.* 1996). We suggest calling this idea the imperialism hypothesis. This hypothesis may well apply to other cooperative breeders. We suspect the effect may also extend to any species with male philopatry. Anecdotal evidence supports this possibility (e.g. song wrens *Cyphorhinus phaeocephalus* Sclater; Brewer 2001).

Females divorcing their sons generally decrease the number of helpers but increase the age of their mate (Table 3). It is unlikely that they are deliberately selecting males of higher quality, given that most fertilizations are achieved through extra-pair mating. Remarkably, in one such divorce the female moved to pair with a male that did not acquire nuptial plumage, and was also sterile (Mulder & Cockburn 1993). Instead, we suspect that the tendency to increase the age of the mate is because sons are by definition younger than the female, so divorce disproportionately involves younger males. Indeed, females divorcing once their son has become the senior helper tend to pair with a younger male.

COMPARISON WITH OTHER FAIRY-WRENS

The other well-studied fairy-wrens do not exhibit the suite of dispersal behaviours described here, as divorce is rare, and females are also highly philopatric (Russell & Rowley 1996, 2000). *M. cyaneus* seems likely to be exceptional within the genus, including the sister species *M. splendens* (Rowley & Russell 1997). Sex-biased dispersal is probably derived rather than a maladaptive phylogenetic legacy. It may reflect adult female survivorship, which is lower in *M. cyaneus* than in other fairy-wrens (Rowley & Russell 1997). A consequent greater frequency of breeding vacancies could facilitate the evolution of different dispersal behaviours. However, it is difficult to test this hypothesis because dispersal and mortality rates are unlikely to be independent. Like most population studies, data are from favourable habitat where density is high. Studying population dynamics in marginal habitats with low survival may help untangle why social behaviour is so diverse in *Malurus*.

Conclusions

This study supports the view that dispersal and settlement decisions are complex behaviours subject to numerous influences (e.g. Gandon & Michalakis 2001; Lambin *et al.* 2001; Perrin & Goudet 2001; Ronce *et al.* 2001). The search for a unitary explanation or complete elimination of all but one of a suite of hypotheses

may be a futile task. Female superb fairy-wrens initially use conspecific cueing as the basis for settlement. They often divorce when their territory changes, yet generally accept new mates regardless of their source. However, females divorce their sons. While this is consistent with incest avoidance, we believe such divorce also enables sons to compete for within-group matings and liberates females from density-dependent constraints on local recruitment of sons in a society where males are highly philopatric.

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