Behav Ecol Sociobiol (2004) 55:278–285
DOI 10.1007/s00265-003-0679-z

ORIGINAL ARTICLE

David J. Green · Elizabeth A. Krebs ·
Andrew Cockburn

Mate choice in the brown thornbill (*Acanthiza pusilla*): are settlement decisions, divorce and extrapair mating complementary strategies?

Received: 2 June 2003 / Revised: 28 July 2003 / Accepted: 30 July 2003 / Published online: 5 November 2003

Abstract In socially monogamous birds, females may express mate preferences when they first select a breeding partner, through divorce and subsequent breeding dispersal to a new partner and through extrapair mating. We examined settlement patterns, divorce and breeding dispersal in a sedentary Australian passerine, the brown thornbill (*Acanthiza pusilla*), in relation to two traits known to influence extrapair paternity (male age and male size). Settlement decisions, divorce and territory switching behaviour were all female strategies that reduced their likelihood of breeding with 1-year-old males. Females preferred to settle in territories with 2+ -year-old males, were more likely to divorce 1-year-old males, and only switched territories if they had an opportunity to form a new pair bond with an old male. In contrast, female settlement and divorce decisions were not influenced by male size. Female thornbills obtain a direct benefit from preferring older males as social mates because breeding success improves with male age in brown thornbills. Nevertheless, divorce rates in this species were low (14% of pair bonds were terminated by divorce), and individuals rarely switched territories following the death of a mate. Both of these mating strategies appeared to be primarily constrained by the distance adults moved to initiate a new pair bond (1–2 territories) and by the limited availability of unpaired older males in the immediate neighbourhood.

Keywords Breeding dispersal · Divorce · Female choice · Monogamy · Natal dispersal

Communicated by M. Webster

D. J. Green (✉) · E. A. Krebs
Centre for Wildlife Ecology, Department of Biological Sciences,
Simon Fraser University,
Burnaby, B.C., V5A 1S6, Canada
e-mail: djgreen@sfu.ca

D. J. Green · E. A. Krebs
Department of Zoology and Entomology, School of Life Sciences,
The University of Queensland,
Brisbane, QLD 4072, Australia

A. Cockburn
Evolutionary Ecology Group, Division of Botany and Zoology,
Australian National University,
Canberra, ACT 0200, Australia

Introduction

Female birds may express mate preferences via initial choice of breeding partner, through divorce and subsequent breeding dispersal to a new partner and through extrapair mating. The relative importance of each form of mate choice is likely to vary in relation to the life history and demography of a species (Arnold and Owens 2002; Cezilly et al. 2000; Cockburn et al. 2003). For example, migratory species with part-time partnerships may have greater opportunity to select a new breeding partner or switch territories between breeding seasons than sedentary species with continuous partnerships (Ens et al. 1996). Settlement decisions and divorce consequently can have a marked effect on the reproductive success of migratory species (e.g. sedge warblers *Acrocephalus schoenbaenus,* Buchanan and Catchpole 1997, 2000; black kites *Milvus migrans,* Forero et al. 1999). In contrast, in sedentary species competition for breeding vacancies may force individuals to disperse to the first available vacancy and restrict their ability to use divorce as a strategy to obtain a better mate (Rowley 1983). For these species, extrapair mating may be the principal means of expressing mate choice (Møller 1992). However, the extent to which settlement decisions, divorce and extrapair mating are alternative reproductive strategies is poorly understood since most studies consider each form of mate choice independently (but see Ramsay et al. 2000).

Comparative studies, however, have shown that high rates of divorce are positively associated with high rates of extrapair paternity in socially monogamous birds (Cezilly and Nager 1995). This pattern suggests that divorce and extrapair mating are complementary strategies that allow females to express mate preferences rather than alternatives whose relative frequencies are dependent on ecological conditions (Cezilly and Nager 1995). Empirical data from black-capped chickadees (*Poecile atricapillus*) also suggest that divorce and extrapair mating are female strategies that function to improve the quality of mates (Ramsay et al. 2000). Nevertheless comparative studies have found that different factors influence divorce and extrapair rates in birds. Divorce rates are consistently higher in breeding pairs that fail to fledge any young than in pairs that breed successfully (Dubois and Cezilly 2002). This pattern would be predicted if pairs are more likely to divorce if they are incompatible (Coulson and Thomas 1983; Rowley 1983) or if individuals use divorce to obtain a mate of higher quality (Ens et al. 1993). In contrast, rates of extra-pair paternity are higher in those species with reduced paternal care and higher rates of adult mortality (Arnold and Owens 2002). These patterns are consistent with the argument that extrapair mating is more likely in species where female behaviour is not constrained by their dependence on male care (Mulder et al. 1994; Gowaty 1996; Bennett and Owens 2002).

In this paper, we examine settlement patterns, divorce and breeding dispersal of a sedentary Australian passerine, the brown thornbill. Brown thornbills, despite their small size (ca. 7 g), have relatively low adult mortality rates (37%; Green and Cockburn 1999) and long lifespans (up to 17 years; Baker et al. 1999). Competition for breeding vacancies is therefore likely to be intense and individuals are predicted to settle in the first breeding vacancy available and have limited opportunities to use divorce to obtain a better partner (Rowley 1983). However, Morton et al. (2000) argue that the apparently low rates of divorce and breeding dispersal in tropical species with year-round territoriality is an artifact of the lack of detailed studies on these species.

If the initiation and termination of a pair bond are strategic decisions made by an individual to maximise their fitness then individuals need to be able to assess the relative quality of potential mates or territories. Previous work has demonstrated that female brown thornbills obtain direct benefits from selecting old males as mates since reproductive success improves with male age in this species (Green 2001). Paternity analysis suggests that female brown thornbills could also gain genetic benefits from having old and/or large mates since females paired to small and/or young males are more likely to cuckold their partners (Green et al. 2002). If females' mate choice is expressed when initiating or terminating a pair bond, we can make the following predictions. First, females dispersing from their natal territory should settle in territories defended by older and larger males in preference to territories defended by younger and smaller males. Young and/or small males would therefore be expected to take longer to attract a dispersing female. Second, females should be more likely to divorce small and/or young males. New mates should also be older and/or larger than previous partners. Here we use data collected over five breeding seasons to test these predictions. We also evaluate the relative importance of direct and indirect benefits for settlement and divorce decisions in brown thornbills.

Methods

Study species and population

Brown thornbills are members of the old Australian passerine family Acanthizidae (Blakers et al. 1984). We studied a population of brown thornbills in and adjacent to the Australian National Botanic Garden in Canberra, Australia, between June 1995 and May 2000. The vast majority of birds (>95% in each year) were banded with an Australian Bird and Bat Banding Scheme aluminium band and a unique combination of three colour bands. Pairs defended small (ca. 2 ha) territories year round (Green and Cockburn 1999). We monitored 15–30 pairs per year, following the fate of 89 different pairs over the course of the 5-year study. Females laid up to three clutches and occasionally fledged more than one brood during a breeding season that extended from July to December. Hence, divorce could occur both between breeding attempts and between breeding seasons.

Population sex ratios became increasingly male biased as the season progressed [July 1: mean adult sex ratio (male/female) =1.09, range 1.00–1.21; Nov. 1: mean =1.28, range 1.20–1.43] due to the higher mortality of breeding females. Juvenile females born in the study area began to disperse at the end of October and vacancies left by adult females that had died during the breeding season were typically filled by unbanded immigrants between November and February (Green and Cockburn 2001).

Molecular sexing

Adult brown thornbills cannot be reliably sexed on the basis of morphological measurements or plumage. We therefore determined the sex of all birds using a DNA-based test that relies on PCR amplification of a section of the CHD1 genes (CHD1-W and CHD1-Z) located on the avian sex chromosomes (see Griffiths et al. 1998 for details of the method). The DNA used to sex individuals was isolated from blood samples (10–70 μl) from the brachial vein collected at the time of banding. Molecular sexing always confirmed the gender of adults sexed using behavioural cues (*n*=58 pairs).

Field methods

We monitored the study population continuously over the year, attempting to see each bird at least 3 times per week during the breeding season and once a month during the non-breeding season. Regular censuses allowed us to record adult mortality, document territory switching of adults and determine when banded juveniles or unbanded immigrants gained a breeding vacancy. If a bird was missing or a new bird was observed on the territory we revisited that territory within 7 days to confirm any changes. Pair bonds were considered to have formed if two birds were observed foraging together on a single territory that contained no other adult birds during all visits to the territory over a 1-month period (minimum =3 censuses). We defined the first day the birds were observed together as the date the pair bond was initiated. Where new pair bonds included an unbanded bird, the pair initiation date was based on the date that the new pair were first observed together and not the date that the unbanded bird was first caught and banded. We attempted to catch unbanded birds that entered the study population after they had been observed on a territory for two consecutive censuses.

Pair bonds could be broken as a result of the death of one member of the pair, divorce, or usurpation of the territory by another individual of the same sex. We defined divorce as the departure of one member of the pair for a new mate on a different territory leaving the remaining partner unpaired. This contrasts with usurpation where a foreign bird replaced one member of the pair, but the individual that departed did not move directly to a new territory or mate although they were observed outside their former territory on at least one occasion. Neither divorce nor usurpation appeared to be prompted by within-pair aggression; we never observed any aggressive interactions between pair members that later split up. Birds that moved outside the study area were located during systematic searches of suitable habitat conducted during the autumn and winter following each of the breeding seasons (see Green and Cockburn 2001 for details). The distance moved following social change is expressed as the number of territories traversed. Individuals that remained on their territory after a pair bond was terminated were assigned a dispersal distance of 0.

Male age and body size

Sixty-eight new pair bonds formed during this study. We classified males as being either 1 year old, 2 or more (2+) years old, or of unknown age at the time pair bonds were initiated. Males classified as being 1 year old at pairing had all been banded as either nestlings (*n*=21) or fledglings (*n*=1). Males could be classified as being 2+ years old at the time a pair bond was initiated if their exact age was known (*n*=12) or if they had been banded as an adult over a year before pairing occurred (*n*=27). Male age at the time of pairing was unknown if the new pair was formed when an unbanded male moved into the study area (*n*=5) or a new female joined a territory held by an unbanded male (*n* =2). The site fidelity of breeding males (see Results) makes it likely that unbanded males that moved into the study area were dispersing juveniles, rather than adult males. However, the conclusions from this study do not change qualitatively, and in fact are strengthened, if we assume that the five unbanded males that moved into the study area were 1-year-old birds.

We used scores from the first component of a principal component analysis of three linear size measurements (tarsus, head-bill, and wing) as an index of male body size. Mean values for each trait were used when individuals were captured multiple times. PC1 explained 41% of the variation in male size and the respective character loadings for tarsus, head-bill, and wing were 0.71, 0.71, and −0.06.

Statistical analysis

Settlement decisions of juvenile females were evaluated by examining the effect of male age and size on the time taken for unpaired males defending a territory on 1 November to attract an unbanded immigrant female. We used the number of days from 1 November rather than the number of days after a male was widowed or divorced as breeding vacancies were not filled by female floaters, and juvenile females only start to leave their natal territories at the end of October. Unpaired males that attracted resident females or that dispersed to take up a new breeding opportunity were excluded from this analysis.

We used survival analysis to examine factors influencing the fate of brown thornbill pair bonds. Survival analysis methods have recently been used in a wide variety of ecological studies that measure the time to discrete events (see Fox (2001) for a review and Cockburn et al. (2003) for an example of this approach for the study of divorce). Survival analysis distinguishes between *failure* (where the event of interest has occurred and we can say that divorce took place at a specific time) and *censorship* (where the event has not occurred by the time observations cease or had not occurred before the individual was lost to the study for other reasons) (Collett 1994). Censored data points still provide valuable information because for each case we can say that divorce had not occurred by a specific time. This analytical approach is therefore able to control for differences between pair bonds that persist for years without divorce and pair bonds that end soon after being initiated when one partner dies (Cockburn et al. 2003). We evaluated whether male size or male age (at the time the pair bond was initiated) influenced the risk of divorce using Cox's (1972) proportional hazards models. Cox's proportional hazards models are regression models for censored data that estimate the baseline hazard function non-parametrically before estimating how continuous or categorical predictors affect the hazard function (Fox 2001). We treated relationships that were terminated by death or usurpation or which were ongoing at the end of the study (24 May 2000) as censored, because we could not evaluate whether divorce would have occurred if the pair bond had persisted. By contrast we treated divorce as the failure of the pair bond. Models were fitted with SPSS 11.0. Kaplan-Meier plots are used to show the estimated probability that a pair will not divorce if the pair bond persists for a given length of time.

Results

Settlement decisions

Territories that were vacant on 1 November (when juvenile females begin to disperse) were not filled randomly. One-year-old males took 3 times longer to attract a dispersing female than older males ($F_{1,15}$=21.8, P<0.0001; Fig. 1). After controlling for male age, size did not influence a male's ability to attract a female ($F_{1,15}$=0.27, P=0.61).

Pair bonds

Brown thornbills formed pair bonds that could persist for up to 159 weeks. However, over 50% of pair bonds were terminated during their first year and only 14% of pair bonds persisted for more than 2 years (Fig. 2). Pair bonds were usually terminated as a result of the death of one member of the pair (68 of 79 cases), but were also occasionally broken as a result of divorce (8 cases) or the

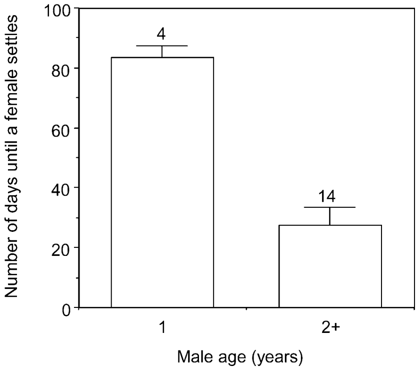

Fig. 1 Relation between the age of solitary male brown thornbills (*Acanthiza pusilla*) defending territories at the end of the breeding season and the time they take to attract a dispersing female. Sample sizes are presented above the *bars*

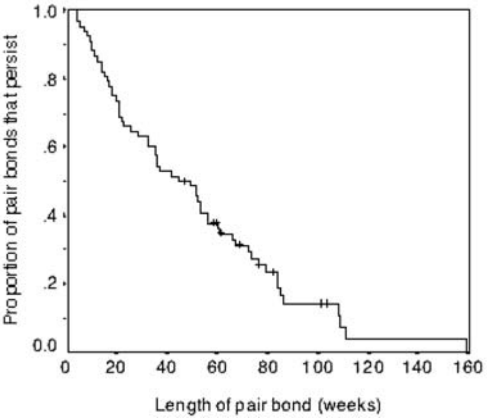

Fig. 2 Kaplan-Meier plot estimating the probability that a pair bond will persist for a given length of time. Estimates are based on 68 pair bonds. *Steps* indicate the time pair bonds are terminated by death, divorce or usurpation while the *vertical lines* indicate pair bonds that were ongoing at the end of the study

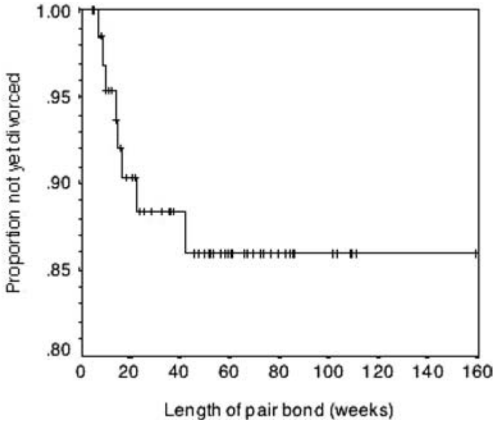

Fig. 3 Kaplan-Meier plot estimating the probability that a pair will not divorce if the pair bond persists for a given length time. Estimates are based on 68 pair bonds. *Steps* indicate the time pair bonds were broken by divorce. *Vertical lines* depict pair bonds that were terminated by other causes (death or usurpation) or that were ongoing at the end of the study

usurpation of the territory by an unpaired neighbour (3 cases).

Divorce

Divorce occurred only during the first year of a pair bond (Fig. 3). However, divorce was infrequent and accounted for the termination of only 14% of pairings over that period (Fig. 3). In a majority of cases (5 of 8) divorce occurred before pairs had attempted to breed, and most occurred within 20 weeks of pair initiation. Divorce occurred following both breeding attempts that failed (*n*=1) and breeding attempts that successfully fledged young (*n*=2). The divorce rate is frequently defined as the proportion of breeding pairs that do not breed together in the following season even though they have the opportunity to do so (Choudhury 1995). Using this definition, the divorce rate was calculated to be 7% (*n*=42 pair-years).

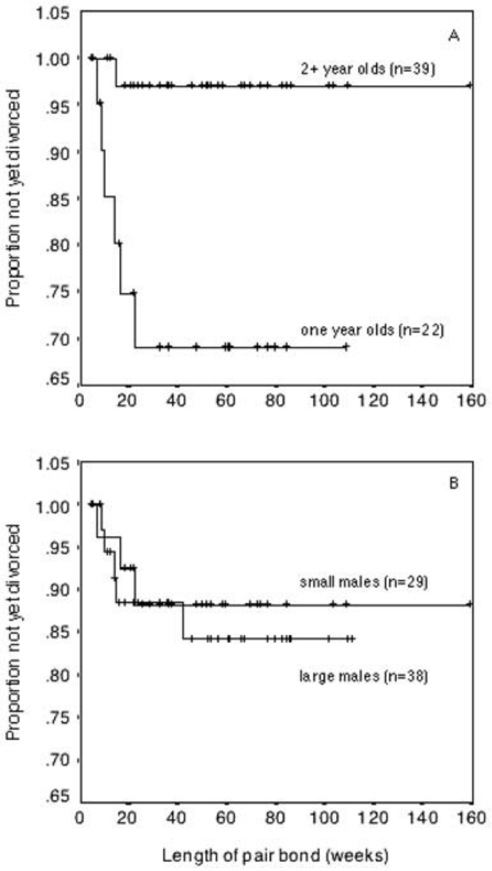

Fig. 4 Kaplan-Meier plot estimating the probability that a pair will not divorce in relation to **a** male age at the time a pair bond is initiated (1 year old or older) and **b** male size. Male size is calculated as the first principal component of a principal component analysis (see Methods; large males have a positive PC1 score, small males a negative PC1 score). *Steps* indicate the time pair bonds were broken by divorce. *Vertical lines* depict pair bonds that were terminated by other causes (death or usurpation) or that were ongoing at the end of the study

Females appeared to initiate most divorces, switching territories and partners while leaving their mates unpaired in seven of eight cases observed. Males left by their mates took, on average, 18 weeks to re-pair (range 4–25 weeks, *n*=6, one male died before initiating a new pair bond). In contrast, the one female left by her mate established a new pair bond within 2 weeks. Consequently, females never forfeited a breeding opportunity as a result of divorce, but three of eight male divorcees forfeited an entire breeding season.

Divorce was more likely to occur in pair bonds where males were 1 year old rather than 2+ years old when pair bonds were established (χ^2=7.47, *df*=1, *P*=0.006; Fig. 4a). Female divorcees also usually formed new pair bonds with males that were older than their original partners (five of seven cases where both male ages were known), only initiating a pair bond with a younger male once (Wilcoxon sign rank test $Z=-1.63$, $P=0.10$). This pattern did not arise because there were more unpaired 2+ -year-old males than unpaired 1-year-old males available at the time divorce occurred (study population: mean number of 2+ year olds=1.63, 1 year olds=2.38; within a two territory radius of the female: mean number of 2+ year olds=0.63, 1 year olds=1.0). Small males were, in contrast, no more likely to be divorced by females than large males ($\chi^2=0.62$, $df=1$, $P=0.43$; Fig. 4b). Female divorcees also did not consistently form new pair bonds with males that were larger than their original partners (three of eight cases; Wilcoxon $Z=-0.63$, $P=0.53$). Male divorcees rarely initiated a new pair bond with a female that was older (one of seven cases) or larger (three of seven cases) than their original partners.

Territory switching behaviour

Adult brown thornbills were extremely philopatric and rarely switched territories following divorce or the death of a mate (Fig. 5). Females were more likely to switch territories than males as a result of divorce (Fisher's exact test $P=0.04$; Fig. 4), but did not switch territories significantly more than males following the death of a mate ($\chi^2=1.66$, $df=1$, $P=0.20$). Neither females nor males moved more than two territories in order to re-pair following either divorce or the death of a mate (Fig. 5).

Males that switched territories always moved to neighbouring territories containing females that were 2+ years old, but these events were rare. These females were usually, but not always, unpaired (Table 1). In contrast, males that remained on their original territory after divorce or the death of their mate were more likely to form new pair bonds with immigrant females that were probably dispersing juveniles (22 of 30 cases, Table 1, Fisher's exact test $P=0.00$).

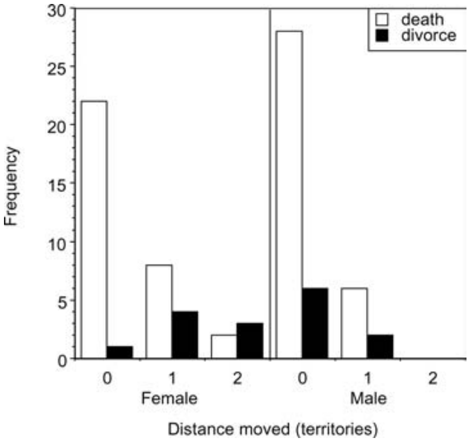

Fig. 5 Frequency histogram showing the dispersal distances of female and male brown thornbills following the death of their mate or divorce

Females that switched territories usually formed new pair bonds with 2+ -year-old males or with unbanded males on territories outside the study area rather than with 1-year-old males (Table 1). Females that remained on their original territory were more likely to re-pair with 1-year-old males (Table 1, Fisher's exact test $P=0.05$).

Adult thornbills were occasionally forced to move when an unpaired neighbour usurped their territory (females $n=2$; males $n=1$). The evicted females eventually formed new pair bonds with new males two and three territories away. The evicted male attempted to establish a territory immediately adjacent to his old one, but disappeared before attracting a new mate and is assumed to have died.

Discussion

Brown thornbills that obtained a breeding position in our population rarely switched territories following either

Table 1 Effects of philopatry and form of mate loss on subsequent pair bonds formed by male and female brown thornbills (*Acanthiza pusilla*). New partners may be of known age (1 or 2+ years old) and breeding status (unpaired or paired) or be immigrants of unknown age and breeding status

Philopatry	Loss of mate	*n*	No new partner	New partner			
				1year old unpaired	2+ years old unpaired	2+ years old paired	Unknown
Male							
Remained	Widowed	28	3		4	3	18
	Divorced	6	1			1	4
Switched	Widowed	6			5	1	
	Divorced	2			2		
	Usurped	1	1				
Female							
Remained	Widowed	22	1	10	8		3
	Divorced	1		1			
Switched	Widowed	10		1	7	2	
	Divorced	7		1	5		1
	Usurped	2			1		1

divorce or the death of a mate. Breeding dispersal, when it did occur, was restricted to movements within the immediate neighbourhood. These results are unsurprising given that competition for breeding vacancies among brown thornbills appears to be intense. Brown thornbills are sedentary, have low adult mortality rates and their habitat is fully occupied by territories that pairs defend throughout the year (Green and Cockburn 1999). Despite these constraints we found that female settlement decisions and breeding dispersal movements were non-random and were likely to improve reproductive success.

Settlement decisions of juvenile females and natural patterns of divorce observed in this study suggest female brown thornbills attempt to avoid breeding with young males. Young males both take longer to attract a dispersing female than older males and are more likely to be divorced in favour of an older mate. These mating tactics will have a direct effect on female reproductive success as both fledging success and post-fledging survival improve with male age in brown thornbills (Green 2001). Paternity analyses also suggest that females may improve the genetic quality of their young by preferring to pair with older males since female brown thornbills paired to young males are more likely to cuckold their mates (Green et al. 2002).

Female preferences for older males as social mates appear likely to be based primarily on the direct benefits obtained from older males. Two lines of evidence suggest that indirect benefits do not have a large effect on settlement or divorce decisions in brown thornbills. First, if females select social mates on the basis of their genetic quality we would predict that females would divorce at any time if they could obtain a mate of higher quality. However, we found that divorce was restricted to the first year of a pair bond. Second, although male size also influences extrapair paternity in brown thornbills (Green et al 2002) we found no evidence to suggest that male size has an effect on settlement or divorce decisions.

Studies of dispersal have frequently attempted to distinguish between the relative importance of mate and territory quality in settlement and divorce decisions (e.g. Arvidsson and Neergard 1991; Dhondt and Andriaensen 1994; Desrochers and Magrath 1996; Cockburn et al. 2003). We did not measure territory quality, but nevertheless believe that male quality is the driving force behind settlement and divorce decisions for three reasons. First, although male age has a dramatic influence on annual reproductive success the location of a territory does not. Territories that were artificially watered were no more productive than territories in adjacent natural woodlands (Green and Cockburn 1999). Second, females do not divorce young males after pair bonds have been established for over a year even though territory boundaries do not change significantly between years. Third, territories defended by young males were distributed throughout the study area and were often defended by older males in previous years of the study. Other studies demonstrate that settlement and divorce decisions may be based either on male traits (e.g. large cactus finch *Geospiza conirostris,* Grant and Grant 1987; black-capped chickadees, Otter and Ratcliffe 1996) or on aspects of territory quality (e.g. blackbird *Turdus merula,* Desrochers and Magrath 1996; blue tits *Parus caeruleus,* Blondel et al. 2000).

Brown thornbill females appear able to distinguish between males that are 1 year old or older, but the cue used by females is unclear. Age-dependent cues that have been demonstrated to play an important role in female mate choice in birds include plumage coloration or ornamentation (e.g. Grant and Grant 1987; Manning 1989), song rate or song repertoire size (e.g. Alatalo et al. 1990; Hasselquist et al. 1996), and energy demanding behavioural displays (e.g. Dunn and Cockburn 1999). Song rate in brown thornbills during the breeding season does not vary with male age (Green et al. 2002). Solitary males also do not appear to use behavioural displays to attract dispersing females. Age-specific plumage variability in brown thornbills has not been described, but features such as the streakiness of their breast feathers or the size/colour of their rufous-brown rump patch may deserve further examination.

Male brown thornbills, in contrast to females, appear to obtain no fitness advantage as a result of divorce. Male divorcees took far longer to form a new pair bond than females and as a result occasionally forfeited an entire breeding season. When they did re-pair there was also no evidence to suggest that they obtained a better mate; male divorcees rarely formed new pair bonds with females that were older or larger than their original mate. Other studies on birds suggest that divorce is usually initiated by females with males being more likely to be the victim of their mates decision to terminate the pair bond (for a review see Cezilly et al. 2000).

Brown thornbill pair bonds were most likely to be terminated by divorce when males were young and females could improve their breeding success by obtaining an older partner. Where females were paired to a 1-year-old male, 27% of pair bonds ended in divorce (*n*=22). The remaining 16 females had little opportunity to divorce and pair with an older male in an adjacent territory; in 14 cases no neighbouring 2+ -year-old male was widowed before the female had completed a breeding season with her mate, and in two cases the local vacancy was rapidly filled by another female. In brown thornbills, the high cost of obtaining information on breeding vacancies in non-neighbouring territories therefore appear to limit opportunities for females to use divorce to improve breeding success. Search costs have also been argued to be a major factor explaining variation in divorce rates among populations in the blue tit. Dhondt and Adriaensen (1994) found that divorce rates were low in populations with year-round territoriality and high in populations where birds flocked outside the breeding season. This, they argue, likely reflects the relatively low search costs of finding a new mate for flocking versus territorial birds.

Cezilly and Nager (1995) demonstrated that there was a positive association between divorce and extrapair paternity in birds. They interpreted this to mean that divorce and extrapair mating were synergistic tactics resulting from intrasexual competition for limited breeding opportunities and argued that both should increase with increased variation in mate quality. However, in species where females obtain primarily direct benefits from divorce and indirect benefits from extrapair mating it is difficult to predict the relationship between divorce and extrapair paternity rates. Brown thornbills conform to the general pattern observed by Cezilly and Nager (1995) since both divorce rates (this study) and extrapair paternity rates are relatively low (12% of broods; Green et al. 2002). However, the low divorce and extrapair paternity rates arise as a result of two separate constraints on female behaviour. Divorce in brown thornbills appears to be constrained by the costs of searching for a new mate and the limited opportunities to use divorce as a strategy to improve mate quality (see above). Extrapair mating on the other hand appears to be constrained by male mate guarding behaviour (Green et al. 2002).

Brown thornbills not only had low divorce rates, but also rarely switched territories following the death of a mate (24% of individuals whose mate died; *n*=66). Individuals that switched territories following the death of a mate did not move far, but were likely to improve their breeding success as they tended to form new pair bonds with older mates than individuals that remained on their natal territory. The philopatry exhibited by most adult brown thornbills in our unmanipulated population contrasts with the high rates of territory switching in the dusky antbird (*Cercomacra tyrannica*) following experimental removal of individuals from their territories (Morton et al. 2000). Several studies demonstrate that sedentary southern hemisphere passerines will switch territories and/or mates given the opportunity (Willis 1974; Greenberg and Gradwohl 1997; Morton et al. 2000; this study). However, our study suggests that the territory switching behaviour of sedentary passerines may be constrained by the relatively low mortality rates of these species under natural conditions.

In summary, our study demonstrates that settlement decisions, divorce and breeding dispersal of brown thornbill females are complementary strategies that reduce the likelihood of breeding with a 1-year-old male. Females settle in territories with old males in preference to territories with young males, divorce young males rapidly if a better option is available and switch territories following the death of their mate if this enables them to pair with an old male. Females obtain a direct benefit from these mating strategies as breeding success improves with male age in brown thornbills. Extrapair mating, in contrast, is a strategy that may enable females to improve the genetic quality of their young. Brown thornbill females are more likely to cuckold their mate when paired to small young males than large old males (Green et al. 2002). Since female brown thornbills obtain different benefits from extrapair mating and dispersal behaviours we believe that factors that influence rates of divorce and breeding dispersal are likely to differ from factors that influence rates of extrapair paternity.

Acknowledgements We are grateful to the staff of the Australian National Botanic Garden for allowing us to work in the Garden. We would like to thank Mike Double for assistance in the laboratory, Anne Peters and Matt Beitzel for help in the field and Mike Webster and two anonymous referees for useful comments on the paper. This research was supported by an Australian Research Council grant to A.C. and an ANU/OPRS postgraduate scholarship to D.G. The work complies with all regulations in Australia and was conducted under permits from the ANU Animal Experimentation and Ethics Committee, ACT Parks and Wildlife, Canberra Nature Park and the Australian Bird and Bat Banding Scheme.

References

Alatalo RV, Glynn C, Lundberg A (1990) Singing rate and female attraction in the pied flycatcher: an experiment. Anim Behav 36:601–603

Arnold KE, Owens IPF (2002) Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. Proc R Soc Lond B 269:1263–1269

Arvidsson BL, Neergard R (1991) Mate choice in the willow warbler – a field experiment. Behav Ecol Sociobiol 29:225–229

Baker GB, Dettmann EB, Scotney BT, Hardy LJ, Drynan DAD (1999) Report on the Australian Bird and Bat Banding Scheme, 1996–1997. Australian Bird and Bat Banding Scheme, Environment Australia, Canberra

Bennett PM, Owens IPF (2002) Evolutionary ecology of birds: life histories, mating systems and extinction. Oxford University Press, Oxford

Blakers M, Davies SJJF, Reilly PN (1984) The atlas of Australian birds. Melbourne University Press, Melbourne

Blondel J, Perret P, Galan M-J (2000) High divorce rates in Corsican blue tits: how to choose a better option in a harsh environment. Oikos 89:451–460

Buchanan KL, Catchpole CK (1997) Female choice in the sedge warbler *Acrocephalus schoenbaenus*: multiple cues form song and territory quality. Proc R Soc Lond B 264:521–526

Buchanan KL, Catchpole CK (2000) Song as an indicator of male parental effort in the sedge warbler. Proc R Soc Lond B 267:321–326

Cezilly F, Nager RG (1995) Comparative evidence for a positive association between divorce and extra-pair paternity in birds. Proc R Soc Lond B 262:7–12

Cezilly F, Preault M, Dubois F, Faivre B, Patris B (2000) Pair-bonding in birds and the active role of females: a critical review of the empirical evidence. Behav Process 51:83–92

Choudhury S (1995) Divorce in birds: a review of the hypotheses. Anim Behav 50:413–429

Cockburn A, Osmond HL, Mulder RA, Green DJ, Double MC (2003) Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren. J Anim Ecol 72:189–202

Collett D (1994) Modelling survival data in medical research. Chapman and Hall, London

Coulson JC, Thomas CS (1983) Mate choice in the kittiwake. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 361–376

Cox DR (1972) Regression models and life-tables (with discussion). J R Stat Soc B 74:187–220

Desrochers A, Magrath RD (1996) Divorce in the European blackbird: seeking greener pastures? In: Black JM (ed) Partnerships in birds: a study of monogamy. Oxford University Press, Oxford, pp 177–191

Dhondt AA, Andriaensen F (1994) Causes and effects of divorce in the blue *tit Parus caeruleus*. J Anim Ecol 63:979–987

Dubois F, Cezilly F (2002) Breeding success and mate-retention in birds: a meta-analysis. Behav Ecol Sociobiol 52:357–364

Dunn PO, Cockburn A (1999) Extrapair mate choice and honest signaling in cooperatively breeding superb fairy-wrens. Evolution 53:938–946

Ens BJ, Safriel UN, Harris MP (1993) Divorce in the long-lived and monogamous Oystercatcher *Haematopus ostralegus*: incompatibility or choosing the better option. Anim Behav 45:1199–1217

Ens BJ, Choudhury S, Black JM (1996) Mate fidelity and divorce in monogamous birds. In: Black JM (ed) Partnerships in birds: a study of monogamy. Oxford University Press, Oxford, pp 344–395

Forero MG, Donazar JA, Blas J, Hiraldo F (1999) Causes and consequences of territory change and breeding dispersal distance in the black kite. Ecology 80:1298–1310

Fox GA (2001) Failure time analysis: studying times to events and rates at which events occur. In: Sceiner SM, Gurevitch J (eds) Design and analysis of ecological experiments, 2nd edn. Oxford University Press, New York, pp 235–266

Gowaty PA (1996) Battle of the sexes and orgins of monogamy. In: Black JM (ed) Partnerships in birds: a study of monogamy. Oxford University Press, Oxford, pp 21–52

Grant BR, Grant PR (1987) Mate choice in Darwin's finches. Biol J Linn Soc 32:247–270

Green DJ (2001) The influence of age on reproductive performance in the brown thornbill. J Avian Biol 32:6–14

Green DJ, Cockburn A (1999) Life history and demography of an uncooperative Australian passerine, the brown thornbill. Aust J Zool 47:633–649

Green DJ, Cockburn A (2001) Post-fledging care, philopatry, and recruitment in brown thornbills. J Anim Ecol 70:505–514

Green DJ, Peters A, Cockburn A (2002) Extra-pair paternity and mate guarding behaviour in the brown thornbill. Aust J Zool 50:565–580

Greenberg R, Gradwohl J (1997) Territoriality, adult survival, and dispersal in the checker-throated antwren in Panama. J Avian Biol 28:103–110

Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. Mol Ecol 7:1071–1075

Hasselquist D, Bensch S, von Schantz T (1996) Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. Nature 381:229–232

Manning JT (1989) Age-advertisement and the evolution of the peacock's train. J Evol Biol 2:379–384

Møller AP (1992) Frequency of female copulations with multiple males and sexual selection. Am Nat 139:1089–1101

Morton ES, Derrickson KC, Stutchbury BJM (2000) Territory switching behavior in a sedentary tropical passerine, the dusky antbird (*Cercomacra tyrannina*) Behav Ecol 11:648–653

Mulder RA, Dunn POD,Cockburn A, Lazenby-Cohen KA, Howell MJ (1994) Helpers liberate female fairy wrens from constraints on extra-pair choice. Proc R Soc Lond B 255:223–229

Otter K, Ratcliffe L (1996) Female initiated divorce in a monogamous songbird: abandoning mates for males of higher quality. Proc R Soc Lond B 263:351–354

Ramsay SM, Otter KA, Mennill DJ, Ratcliffe LM, Boag PT (2000) Divorce and extrapair mating in female black-capped chickadees (*Parus atricapillus*): separate strategies with a common target. Behav Ecol Sociobiol 49:18–23

Rowley I (1983) Re-mating in birds. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 331–360

Willis EO (1974) Populations and local extinctions of birds on Barros Colorado Island, Panama. Ecol Monogr 44:153–169