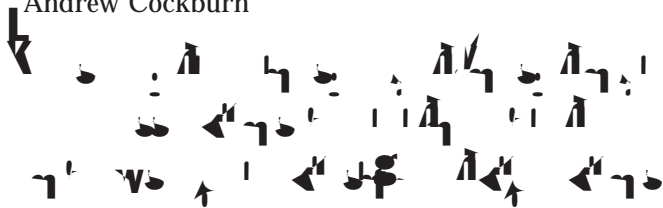


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territories) and by the limited availability of unpaired older males in the immediate neighbourhood.

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

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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 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



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

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).

Females appeared to initiate most divorces, switching

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

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

- 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 origins 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