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Fidelity at the frontier: divorce and dispersal in a newly colonized raptor population

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Divorce and breeding dispersal are key life history parameters that can be influenced by, and in turn have an influence on, the structure of populations. Variation in these parameters in small populations can potentially play an important role in the colonization of new areas, yet to date there has been little empirical investigation of this process. We studied the circumstances surrounding divorce in a newly established population of black sparrowhawks, *Accipiter melanoleucus,* on the Cape Peninsula, South Africa over an 11-year period between 2001 and 2012. Divorce was more likely following breeding failure and individuals that divorced and dispersed improved their subsequent breeding success. Territory quality had no influence on the frequency of divorce, and dispersing individuals did not move to territories of higher quality. During the study period the population size increased approximately three-fold, but because the range expanded, nest density did not increase significantly. In the first half of the study (2001–2006), divorce rates were low (4%) compared with rates previously reported for raptors and other birds. In the latter half (2007–2012) divorce rates were 14%. Although there was weak support for a difference in divorce rates between these two periods there was no evidence that divorce rates varied with population size or nesting density. Our results suggest that adaptive hypotheses ('better option' or 'incompatibility') best explain patterns of divorce in this expanding population and that potential feedbacks between divorce and population processes were unlikely to have played an important role during the growth of this recently established population.

Mating systems can be considered as dynamic arrangements in which individuals make decisions over whom they partner with depending on the prevailing circumstances (Emlen & Oring, 1977; Reynolds, 1996). Changes in the population size and density can determine the availability of potential partners or territories and strongly influence mating decisions (Kokko & Rankin, 2006). In turn, these decisions may have implications for demographic processes such as population growth. Such dynamic two-way interactions can be important in small populations, potentially driving extinctions through Allee effects, or facilitating the colonization of new areas (Bessa-Gomes et al., 2003; Stephens & Sutherland, 1999). For example, the population growth of reintroduced Critically Endangered Seychelles magpie robins, *Copsychus seychellarum*, was initially rapid, but as populations increased, higher rates of competition for territories suppressed offspring production (Lopez-Sepulcre, Norris, & Kokko, 2009). Similarly, if divorce leads to lost breeding opportunities for divorce victims (Moody, Wilhelm, Cameron-MacMillan, Walsh, & Storey, 2005), lowering of divorce rates at low population density could mean improved population growth, counteracting potential Allee effects (Kokko & Rankin, 2006).

In range-expanding populations colonizing new areas, individuals are frequently exposed to novel environmental conditions and changing demographic pressures. In monogamous territorial species, an individual's decision of whether to stay with the same partner, divorce, disperse or attempt to force its way into a breeding partnership depends on the relative costs and benefits of the available options (Coulson, 1972; Ens, Safriel, Harris, 1993). Among other factors these costs and benefits will depend on the availability and quality of alternative partners, the availability and quality of alternative territories and the availability of information with which to assess these alternatives (Choudhury, 1995). Varying population size, breeding density, territory quality and familiarity of individuals with their environment can therefore have a strong influence on the breeding decisions of a population colonizing a new area.

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A number of hypotheses have been proposed to explain why individuals should divorce rather than stay with the same partner in subsequent breeding attempts. Adaptive hypotheses suggest that divorce should be viewed as a reproductive strategy enabling individuals to maximize their own fitness (Coulson, 1972). In this scenario, divorce would be expected to occur if the net fitness benefits of switching to a more compatible or higher quality partner or territory outweigh the benefits of staying with the old partner. The incompatibility hypothesis posits that divorce occurs when the combined qualities of a pair result in reduced fitness, independently of their respective intrinsic qualities (Coulson, 1966). The better option hypothesis suggests that divorce is the consequence of a decision made by one member of a pair to improve its own future breeding performance (Baeyens, 1981; Ens et al., 1993). While both hypotheses predict that divorce is more likely after reproductive failure, they differ in their predictions of how breeding success will change in subsequent breeding attempts: the incompatibility hypothesis predicts that both partners improve their breeding success whereas the better option hypothesis predicts that only one partner improves. In both scenarios, one, or both, members of a pair deserts or chases away its partner (Ens, Choudhury, Black, 1996). Alternatively, the forced divorce hypothesis proposes divorce to be a nonadaptive process, resulting from the intrusion of a third individual who outcompetes one member of the pair (Taborsky & Taborsky, 1999). Mate switching should therefore be independent of previous breeding success, and neither individual should necessarily benefit from partner change, although the new mate may be of better quality or greater compatibility than the previous one and the nondispersing partner may therefore benefit as a result (Choudhury, 1995).

An alternative set of hypotheses proposes that patterns of divorce result from decisions over territories rather than mates. The musical chairs hypothesis (Dhondt & Adriaensen, 1994) postulates that, for species that do not maintain a year-round territory, individuals settle on the best available territory upon arrival, and different arrival times can cause partnerships to break up. The habitat-mediated hypothesis (Desrochers & Magrath, 1996) suggests that at least one member of a pair leaves to breed in a better territory, and divorce is a side-effect of territory choice. While the musical chairs hypothesis does not predict an association between breeding failure and divorce, such a pattern might be expected under the habitat-mediated hypothesis if individuals follow a 'win-stay, lose-switch' model (Hoover, 2003). As partner fidelity is frequently correlated with site fidelity (Cézilly, Dubois, & Pagel, 2000; Desrochers & Magrath, 1996; Naves, Monnat, & Cam, 2006) disentangling the relative importance of the two processes can be challenging (Bai & Severinghaus, 2012). However, some insight can be gained into the extent to which divorce decisions are habitat-mediated by exploring breeding dispersal decisions in relation to territory quality.

The costs and benefits proposed to underpin divorce and dispersal decisions might be expected to differ in colonizing populations, compared with those that are well established. For example, if divorce decisions are explained by the better option or incompatibility hypotheses then divorce might be less frequent in smaller or less dense populations owing to the relatively higher cost or constraints on finding alternative mates (Freed, 1987; Kokko & Rankin, 2006). Alternatively, if individuals in recently established populations tend to be younger, they may have a longer period over which to benefit from divorce (Ens et al., 1993; Wooller & Bradley, 1996) and consequently be more likely to divorce. If divorce rates are driven by habitat-mediated decisions and social information plays an important role in the assessment of habitat quality (Citta & Lindberg, 2007; Danchin, Boulinier, & Massot, 1998; Sergio & Penteriani, 2005; Stamps, 1988), then low numbers of conspecifics may impede the ability of individuals to assess territory quality and hence the benefits of dispersal (Mateo-Tomás & Olea, 2011). Additionally, in small populations, where habitat saturation is low, there may be little variation in territory quality (Komdeur et al., 1995) and hence few benefits of dispersal. However, when habitat saturation is low, the costs associated with establishing a territory in a previously unoccupied area may also be correspondingly low (Brown, 1969; Jones, Waser, Elliott, Link, & Bush, 1988; Matthysen, 2005) and high-quality territories may still be available (Komdeur et al., 1995), which could in theory promote higher divorce rates. Predicting precisely how population size may influence divorce rates thus requires an understanding of the processes that drive divorce and how these then might be related to population size.

There have been few empirical studies of the causes and consequence of divorce and breeding dispersal in newly established populations (Sarrazin, Bagnolinp, Pinna, & Danchin, 1996) and, to our knowledge, none have explored these processes during an unassisted colonization, which may have a number of advantages over studies of reintroduced populations (Sarrazin & Barbault, 1996). Here we investigated these processes in a population of black sparrowhawks, *Accipiter melanoleucus*, that has recently become established on the Cape Peninsula (Oettlé, 1994) in Western Cape Province, South Africa. The colonization of the Cape Peninsula represents the most recent range extension of a gradual southwesterly expansion of this species over the past few decades (Hockey & Midgley, 2009). Over the 12 years the population has been monitored (2001–2012) the number of known breeding pairs has increased from 13 to 49. During this period of rapid expansion, the breeding partnerships, outcomes of breeding attempts and subsequent movements of individually identifiable birds have been closely monitored, providing a highly unusual opportunity to explore the processes of divorce and dispersal in a recently established and expanding raptor population. In this paper we aimed to: (1) describe patterns of divorce and dispersal in this population; (2) assess support for the alternative hypotheses by investigating how variation in breeding performance and territory quality relate to patterns of divorce and dispersal; and (3) explore changes in divorce frequency as the population expands.

METHODS

Study Area and Species

The study area on the Cape Peninsula consists of a matrix of habitats including urban gardens, alien pine (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.) plantations, and small pockets of indigenous Afromontane forest and Fynbos. Altitude ranges from sea level to about 300 m, and the climate is temperate, with locally variable winter rainfall (Cowling, MacDonald, & Simmons, 1996). Mean annual rainfall is ca.1250 mm, with average monthly minimum and maximum temperatures of 12 and 21 °C, respectively (South African Weather Service). Black sparrowhawks have been expanding their range in South Africa in a southwesterly direction over recent decades (Hockey & Midgley, 2009). The first breeding record on the Cape Peninsula was in 1993 (Oettlé, 1994) and since then the population has rapidly expanded.

Field Procedures

Monitoring of the population began in 2001. Since that time we have fitted unique colour-ring combinations to as many breeding adult birds, and 3–4.5-week-old nestlings, as possible. Adults were trapped on territories using a bal-chatri trap baited with a live