Age, sex and social influences on adult survival in the cooperatively breeding Karoo Scrub-robin

Penn LloydA,B,G, Thomas E. MartinC, Andrew TaylorA,D, Anne BraaeA,E and Res AltweggF

Abstract. Among cooperatively breeding species, helpers are hypothesised to increase the survival of breeders by reducing breeder workload in offspring care and increased group vigilance against predators. Furthermore, parental nepotism or other benefits of group living may provide a survival benefit to young that delay dispersal to help. We tested these hypotheses in the Karoo Scrub-robin (Cercomelochas arypeus), a long-lived, and facultative cooperatively breeding species in which male helpers make substantial contributions to the care of young. We found that annual breeder survival in the presence of helpers did not differ detectably from breeders without helpers or breeders that lost helpers. Furthermore, helpers did not gain a survival benefit from deferred breeding; apparent survival did not differ detectably between male helpers and male breeders followed from one year old. These results are consistent with other studies suggesting a lack of adult survival benefits among species where breeders do not substantially reduce workloads when helpers are present. They are also consistent with the hypothesis that males that delay dispersal make the ‘best of a bad job’ by helping on their natal territory to gain indirect fitness benefits when they are unable to obtain a territory vacancy nearby.

Additional keywords: cost of reproduction, delayed dispersal, juvenile survival, life history.

Received 24 July 2015, accepted 6 June 2016, published online 13 July 2016

Introduction

Extrinsic mortality is a critical factor influencing the evolution of life history traits (Law 1979; Michod 1979; Charlesworth 1994; Martin 2002, 2014). Knowledge of mortality schedules in relation to age, sex and social factors is therefore important for understanding the evolution of species-specific life history traits. For example, high mortality costs of natal dispersal (Du Plessis 1992; Ridley et al. 2008) may favour the evolution of delayed dispersal (Koenig et al. 1992; Russell et al. 2004; Tarwater and Brawn 2010) that, in turn, is thought to contribute to the evolution of cooperative breeding (Koenig et al. 1992; Hatchwell and Komdeur 2000). Among cooperatively breeding species, helpers that delay dispersal and defer breeding to assist with parental care on the natal territory may reduce the costs of reproduction to the breeding pair and reduce their mortality (Crick 1992). Furthermore, helpers may gain a survival benefit through parental nepotism (Ekman et al. 2000; Covas and Grier 2007). Reduced breeder mortality in the presence of helpers may be explained by decreased costs of parental care through reduced workload (Khan and Walters 2002; Cockburn et al. 2008; Kingma et al. 2010; Li et al. 2015; Paquet et al. 2015) or benefits of group living through decreased predation due to increased group vigilance (Pulliam 1973; Ridley and Reihani 2007a) and increased foraging efficiency (Hollén et al. 2008). However, the generality of the survival benefit to breeders from helpers is questioned by studies that have found no change in inbreeder mortality in the presence of helpers (Magrath and Yezerinac 1997; McGowan et al. 2003), or even an increase in mortality with group size (Brouwer et al. 2006; Paquet et al. 2015).

Confirming the benefits of helpers to breeder survival is complicated by correlations between the presence of helpers and the individual quality of breeders or territories on which helpers are produced, because breeders or territories of better quality
are more likely to have successful reproduction and therefore have helpers (Cockburn 1998; Dickinson and Hatchwell 2004). Certainly, individual quality and territory quality have a strong influence on individual survival (Smith 1981; Komdeur 1992). It is therefore important to control for both individual and territory quality in the assessment of helper benefits. This may be done by comparing the survival of adults occupying the same territories in the year following breeding seasons with and without the presence of helpers to control for the influence of both territory quality and individual quality (Cockburn 1998; Cockburn et al. 2008).

Here, we examine a variety of factors including age, sex, survey year, habitat type and breeding status, that might influence the survival of Karoo Scrub-robin (Cercotrichas coryphaeus) after they have reached one year of age. Our previous work on this species has shown it to be a long-lived and facultative cooperative breeder, in which females disperse within their first year whereas male offspring delay dispersal, either obtaining a breeding vacancy on a nearby territory or remaining on the natal territory to act as helpers to the breeding pair (Lloyd et al. 2009; Ribeiro et al. 2012; Lloyd et al. 2014). This behaviour results in 12–20% of pairs breeding with the assistance of one (typically) or more helpers in any year. Breeding females perform all nest building, incubation and nestling brooding duties, whereas males allofeed the females and assist the female with nestling feeding (Lloyd et al. 2009). Helpers contribute substantially to the care of young, resulting in increased nestling feeding rates, reduced nestling starvation and heavier nestling mass at fledging (Lloyd et al. 2009). In the presence of helpers, breeding females increased clutch size but reduced feeding rates to younger nestlings, whereas breeding males did not reduce nestling feeding rates in the presence of helpers (Lloyd et al. 2009). Thus, the variation in presence or absence of helpers and the associated change in offspring care make this species a good candidate for testing survival consequences of group living.

The study population inhabits two different habitat types: dune thicket (a taller, dense shrubland with less open ground, potentially less suitable for a ground-feeding insectivore such as the Karoo scrub-robin) and sand-plain fynbos (shorter, more open shrubland) (Low and Rebelo 1996). Nest mortality from predation was substantially greater in sand-plain fynbos than dune thickets, but nestling feeding rates and nestling pre-fledging mass were also greater in sand-plain fynbos, suggesting sand-plain fynbos provided higher habitat quality (Lloyd et al. 2009). Thus, comparisons of habitat quality on survival are also included in this system.

We examined variation in survival among individuals to test two main predictions: 1) helpers have higher survival than breeders, controlled for age, due to reduced costs of reproduction and territory defence or benefits of group living and 2) breeders, particularly females, have higher survival in the presence of helpers because of reduced parental effort. We included sex, age and habitat type as covariates in our analyses to test for predicted higher mortality among breeding females due to higher costs of parental care, and control for the potential confounding effects of an initial increase in annual survival with age because of increasing experience (Clobert et al. 1988; Komdeur 1992; Martin 1995; Holmes et al. 1996) and greater survival among adults occupying territories in higher quality, sand-plain fynbos habitat.

**Methods**

We studied a colour-banded population of Karoo Scrub-robin occupying up to 104 territories per year within a 260 ha area of the 2900 ha Koeberg Nature Reserve (33°41’ S, 18°26’ E), on the west coast of South Africa. It has a mediterranean climate with hot, dry summers and cool, wet winters and a mean annual rainfall of 375 ± 77 mm (±1 standard deviation; Lloyd et al. 2009). The vegetation is coastal shrubland, comprising a mosaic of two distinct vegetation types: dune thicket and sand-plain fynbos (Low and Rebelo 1996), covering 30% and 70% of the study area.

Banding of adults with a unique combination of three colour bands and a numbered metal band commenced in 2001 and continued annually to 2008. Birds were either caught opportunistically, using mist-nets at any time of the year within a 90 ha core area of the 260 ha study area, or targeted in the vicinity of their nests during the breeding season (August–October) using a mist-net or spring traps baited with a mealworm. All nestlings were weighed and banded with a numbered metal band and either: (1) a single coloured plastic band (2001–2004) or (2) a unique combination of three colour bands (2005–2007) approximately five days before fledging. Resighting effort was confined to the 3-month breeding season, August–October 2001–2008, when continuous resighting of birds and intensive monitoring of nests took place throughout the study area. A concerted effort was made to resight the band combinations of all individuals attending each nest attempt on all known territories within the study area, with the locations of all territories mapped each year. Birds were sexed and assigned breeding status on behaviour: only females built nests and incubated, whereas only the breeding male mate-guarded the female during nest-building (Lloyd et al. 2009).

Although banding occurred opportunistically during the non-breeding season, capture histories were restricted to resighting and recapture information obtained during the breeding season of each year, such that individuals only entered the survival analysis dataset in the year they were first resighted during the breeding season or trapped as an adult attending a nest. Furthermore, any opportunistic recaptures or resightings during the non-breeding season were ignored in the creation of the capture histories to avoid inflating resighting probability and the apparent survival estimate. Nonetheless, due to the intensive resighting effort in the breeding season, there were no instances of individuals banded in the non-breeding season of any year being resighted or recaptured for the first time beyond the first subsequent breeding season after banding.

We estimated apparent survival (the probability of surviving until the next year and staying in the study area) and resighting (the probability of resighting an individual at time t given that it was alive and in the study area at that time) probabilities using multi-state capture-mark-recapture models (Lebreton and Pradel 2002). These models extend the classical Cormack-Jolly-Seber class of open population capture-mark-recapture models (Lebreton et al. 1992) to allow for individuals to be encountered in different states. In this study, the states consisted of different
types of breeding status (see below). In addition to estimating survival and resighting probabilities, multi-state models estimate the transition probabilities between states, for example the probabilities of switching between different types of breeding status. We fitted all models in program MARK version 7.1 using standard maximum likelihood methods (Lebreton et al. 1992; White and Burnham 1999; Lebreton and Pradel 2002). We tested goodness-of-fit using the median c procedure in program MARK for the most complex model fitted for each of the three analyses. We based our analyses on model selection using the sample-size adjusted Akaike’s Information Criterion (AICc), and present the results for all models that were fitted.

Our capture-mark-resighting dataset was sparse, particularly with respect to known-age females; consequently, including all factors of interest in a global model would have led to small group sample sizes and over-fitting. We therefore conducted three separate analyses. The first analysis examined the influences of habitat (dune thicket vs sandplain fynbos), sex, and breeding state (helper vs breeder) on apparent survival \((n = 364\) individuals). As only males help, this analysis defined two breeding states among males, namely helper and breeder. Once males became breeders they never returned to the helper state; therefore the corresponding transition probability was set to zero. We also included the two-way interactions between habitat and sex, and between habitat and state because we had prior expectations that these interactions might be important. Based on field knowledge, we included the main effects of sex and state on the recapture probability, and the main effect of habitat on the transition probability. The starting model therefore included the main effects of habitat, sex and breeding state on survival, sex and breeding state effects on resighting probability and habitat effects on the transition probability.

To test whether helpers have higher survival than breeders, controlling for age, the second analysis included only males known to be 1 year old at first encounter \((n = 72\) individuals, of which 27 were breeders and 45 were helpers at 1 year old; 51 of these birds were encountered again 1 year later, 45 as breeders and 6 as helpers). This analysis therefore used a subset of the data used in the first analysis. We used a two-age-class model to compare survival through the first year to annual survival through subsequent years, and also allowed the transition probabilities to differ between age classes. Given the lack of evidence of an effect of habitat on survival in the first analysis (see results), habitat was not included as a variable in this second analysis.

The third analysis examined the potential influences of sex, habitat and social state on apparent survival of breeding birds \((n = 341\) individuals). Three categories of social state were recognised: (1) breeding as a pair and not previously known to have bred with helpers present; (2) breeding with one or more helpers present and (3) breeding as a pair when previously known to have bred with helpers present. The transition probabilities between states were allowed to differ. By definition, transitions from state (2) or (3) back to state (1) were not possible and we set them to zero. The comparison of the second and third social states aims to control for the influence of territory or individual quality in the examination of the influence of helpers on apparent survival of breeding adults. Since we were mostly interested in the effect of having helpers per se, and only 16\% of cooperative groups had more than one helper (Lloyd et al. 2009), all pairs with helpers were treated as a single category, regardless of how many helpers were present. We treated vegetation type as a grouping factor; as only 5 out of the 364 individuals moved between territories with different vegetation types, we assigned these individuals to the vegetation type where they had been recorded more often. We also retained sex as a grouping factor for this analysis.

The survival of young from independence (3 weeks post-fledging) to the start of the next breeding season was determined for a limited sample of 23 male fledglings from 2005 that had been sexed through molecular sexing from a blood sample taken before fledging, using a method outlined in Griffiths et al. (1998). The estimation of juvenile survival was restricted to male offspring due to their limited natal dispersal.

**Results**

Data on 364 individuals were included in the survival analysis, comprising 206 males (67 of which acted as helpers in one or more years) and 158 females. A total of 88 individuals (72 male, 16 female) banded as nestlings were monitored from a known-age of 1 year old. The first analysis used all data to examine the influences of habitat type (dune thicket vs sandplain fynbos), sex and breeding state (helper vs breeder) on apparent survival. There was no evidence for lack of fit of the most complex model (Model 7, Table 1: \(\hat{c} = 1.03\), s.e. = 0.02). The best supported model (Model 1, Table 1) had constant survival \((0.78, 95\%\) confidence interval: 0.75–0.80), resighting probability varying with sex (females: 0.96 [0.92–0.98]; males: 0.99 [0.97–1.00]), and a constant transition probability between helper and breeder states \((0.75 [0.62–0.84])\). There was little support for an effect of habitat type on either survival or the transition probability between breeding states. Models including habitat (Models 3, and 5–10, Table 1) were \(\Delta AIC_c >2\) above the best model, with relatively small Akaike weights. Apparent survival also did not differ strongly between helpers and breeders, with the best model that allowed survival to vary with breeding state (Model 2, Table 1) differing by \(\Delta AIC_c = 1.77\) from the best supported model that assumed constant survival between breeding states. Models 2, 3 and 5–9 had similar deviances to the simpler Model 1, indicating that the addition of these extra parameters did not improve model fit.

The second analysis was restricted to males known to be 1 year old at first encounter to test whether males breeding for the first time at 1 year old had reduced survival compared with males that helped in their first year. There was no evidence for lack of fit of the most complex model (Model 2; Table 2: \(\hat{c} = 1.07\), s.e. = 0.03). Four models received similar support from the data \((\Delta AIC_c <1\), similar Akaike weights, Table 2). The best-supported model (Model 1; Table 2) assumed constant survival across state and age. The other three models included interactive effects of age and breeding state (Model 2), only age (Model 3) and only breeding state (Model 4). The data were insufficient to distinguish between these models and model-averaged estimates indicated survival was similar in all groups of males (Fig. 1). The transition probability from helper to breeder was 0.82 (0.65–0.92) for males between their first and second year and 0.25 (0.03–0.76) for older males.
Table 1. Summary of model selection results for models examining the potential influence of habitat type (‘hab’: dune thicket vs sandplain fynbos), sex and breeding state (‘state’: helper vs breeder) on apparent survival

The factors included in each model part are given in parentheses, and empty parentheses mean the respective probability is assumed to be constant. Two-way interactions are indicated by ‘•’ and ‘+’ indicates additive effects. Each model summary includes Akaike’s Information Criterion adjusted for small sample size (AICc), change in AICc (ΔAICc), Akaike weight (ωi) representing the relative support for a particular model compared with the other models, number of parameters estimated (K), and deviance. Φ = apparent survival, P = resighting probability, Ψ = transition probability between ‘helper’ and ‘breeder’ states.

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔAICc</th>
<th>ωi</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.00</td>
<td>0.44</td>
<td>4</td>
<td>265.89</td>
</tr>
<tr>
<td>2</td>
<td>1.77</td>
<td>0.18</td>
<td>5</td>
<td>265.64</td>
</tr>
<tr>
<td>3</td>
<td>2.73</td>
<td>0.11</td>
<td>6</td>
<td>264.57</td>
</tr>
<tr>
<td>4</td>
<td>2.84</td>
<td>0.11</td>
<td>3</td>
<td>270.75</td>
</tr>
<tr>
<td>5</td>
<td>2.95</td>
<td>0.10</td>
<td>6</td>
<td>264.79</td>
</tr>
<tr>
<td>6</td>
<td>4.98</td>
<td>0.04</td>
<td>7</td>
<td>264.78</td>
</tr>
<tr>
<td>7</td>
<td>6.56</td>
<td>0.02</td>
<td>8</td>
<td>263.33</td>
</tr>
<tr>
<td>8</td>
<td>9.87</td>
<td>0.00</td>
<td>10</td>
<td>263.54</td>
</tr>
<tr>
<td>9</td>
<td>11.79</td>
<td>0.00</td>
<td>11</td>
<td>263.42</td>
</tr>
<tr>
<td>10</td>
<td>14.46</td>
<td>0.00</td>
<td>10</td>
<td>268.14</td>
</tr>
</tbody>
</table>

The analysis is based on 364 individuals.

Table 2. Summary of model selection results for models examining the potential influence of age class (‘age’: 1 year old vs 2 years and older) and breeding state (‘state’: breeder vs helper) on apparent survival among males followed from 1 year old

The factors included in each model part are given in parentheses, and empty parentheses mean the respective probability is assumed to be constant. Each model summary includes Akaike’s Information Criterion adjusted for small sample size (AICc), change in AICc (ΔAICc), Akaike weight (ωi) representing the relative support for a particular model compared with the other models, number of parameters estimated (K), and deviance. Φ = apparent survival, P = resighting probability, Ψ = transition probability between ‘helper’ and ‘breeder’ states. The analysis is based on 72 individuals.

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔAICc</th>
<th>ωi</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>203.21</td>
<td>0.53</td>
<td>5</td>
<td>56.74</td>
</tr>
<tr>
<td>2</td>
<td>203.45</td>
<td>0.77</td>
<td>5</td>
<td>56.74</td>
</tr>
<tr>
<td>3</td>
<td>205.04</td>
<td>2.36</td>
<td>6</td>
<td>56.15</td>
</tr>
<tr>
<td>4</td>
<td>206.83</td>
<td>3.14</td>
<td>3</td>
<td>63.38</td>
</tr>
</tbody>
</table>

The analysis is based on 72 individuals.

Fig. 1. Model averaged apparent annual survival estimates (with 95% confidence intervals) of male Karoo Scrub-robin followed from 1 year old, comparing the survival of helpers vs breeders in two age classes: survival from 1–2 years old (1) and annual survival after reaching 2 years old (2+).

The third analysis examined the potential influences of sex, habitat and social state on the apparent survival of breeding birds only. There was no evidence for lack of fit of the most complex model (Model 9, Table 3; δ = 1.01, s.e. = 0.02). Three models received support (ΔAICc <0.6, similar Akaike weights; Table 3). Although two of these models included an effect of social state on apparent survival (Models 1 and 3; Table 3), a model assuming constant survival (Model 2; Table 3) had similar support. The model averaged survival estimates were similar across all three breeding states (Fig. 2). Females did not benefit more from the presence of helpers, as the model including an interaction between sex and state (Model 7; Table 3) received very little support. Apparent survival again did not differ between males and females, as all models including a sex effect on survival (Models 6–9; Table 3) received less support than those that assumed no effect of sex (Models 1–5; Table 3). Finally, survival also did not differ between the two habitat types; models including an effect of habitat (Models 5, 8 and 9; Table 3) received less support than models that assumed no effect of habitat on survival. The transition probabilities were: 0.15 (0.12–0.19) for transitioning from breeding as a pair not previously known to have bred with helpers present to breeding with one or more helpers present; 0.68 (0.59–0.76) for transitioning from breeding with one or more helpers present to breeding as a pair after losing helpers and 0.18 (0.11–0.28) for...
 Helpers are often thought to receive survival benefits themselves (Ekman et al. 2000; Covas and Griesser 2007) and provide survival benefits to the breeders they help (Khan and Walters 2002; Cockburn et al. 2008; Kingma et al. 2010; Li et al. 2015; Paquet et al. 2015). Benefits may accrue from reduced parental effort or from group benefits in reducing predation risk (c.f. Pulliam 1973; Ridley and Raihani 2007b). Yet, results from this study provide further evidence that helpers do not always receive or provide benefits to survival, as found in a few other studies (Magrath and Yezerina 1997; McGowan et al. 2003; Brouwer et al. 2006; Paquet et al. 2015). The prediction that breeders may gain a survival benefit from breeding with helpers present was not supported. Survival of breeders in the year after breeding with one or more helpers present did not differ detectably from breeders in the year after losing helpers or from breeders not known to have bred with helpers present (Fig. 2).

The apparent lack of an effect of helpers on either male or female breeder survival may reflect the limited reductions in breeder parental investment despite helper contributions. Helpers increased the total feeding rates of offspring (Lloyd et al. 2009). Yet, in the presence of helpers, female Karoo Scrub-robins increased clutch size by 6% and did not reduce their feeding rates for older nestlings (Lloyd et al. 2009). Males neither reduced their rate of allofeeding females nor their nestling feeding rates where there were helpers (Lloyd et al. 2009). A positive effect of helpers on breeder survival has been found in species in which the breeders reduce their workload substantially in the presence of helpers (e.g. Khan and Walters 2002; Covas et al. 2008; Kingma et al. 2010; Li et al. 2015; Paquet et al. 2015). The significant contributions of Karoo Scrub-robin helpers to the care of young increase offspring fitness through reduced incidence of nestling starvation and increased mass at fledging (Lloyd et al. 2009). Thus, breeders with helpers may maintain their effort to enhance offspring survival rather than reducing parental effort to enhance their own survival.

Deferred breeding in long-lived, cooperatively breeding species could be an adaptive strategy if costs of reproduction are substantial, especially among young breeders, and deferring reproduction yields survival benefits (Covas and Griesser 2007).
For example, Siberian Jay (*Perisoreus infaustus*) offspring gained a survival benefit through parental nepotism if they delayed dispersal to remain on their natal territory through the winter of their first year (Ekman *et al*. 2000). We found little evidence to support this hypothesis in Karoo Scrub-robin, a relatively long-lived cooperatively breeding species. Males that deferred breeding in their first year had similar apparent survival to birds that bred in their first year at both of the age classes examined, namely survival from one to two years old, and annual survival after reaching two years old (Fig. 1). Due to the strong philopatry of males, the apparent survival estimates of males are unlikely to underestimate survival as a consequence of dispersal out of the study area. In our study population of 104 territories, the median natal dispersal distance (i.e. distance between natal territory and territory in which it first becomes a breeder) for males was one territory distance (range 0–7, with only 6 of 82 individuals dispersing beyond two territories) from the natal territory (Ribeiro *et al*. 2012) and we searched for banded birds up to two territory distances from the boundary of the study area.

Ultimately, the survival benefits of deferred breeding *per se* are little studied. Among studies finding that individuals that defer breeding gain greater lifetime reproductive success than individuals that breed in their first year, the effect is largely a consequence of differences in territory quality, with birds that defer breeding gaining higher quality territories (Acorn Woodpeckers (*Melanerpes formicivorus*), Stacey and Ligon 1987; Seychelles Warblers (*Acrocephalus sechellensis*), Komdeur 1992 and Siberian Jays, Ekman *et al*. 1999). These habitat benefits do not indicate that deferring breeding, in itself, contributes to increased lifetime reproductive success. While we cannot discount the influence of variation in territory quality on deferment of breeding in Karoo Scrub-robin, there was no evidence that variation in habitat type, which was correlated with nestling feeding rates and nestling mass (Lloyd *et al*. 2009), had any effect on annual adult survival or probability of helping. Therefore, deferred breeding by male Karoo Scrub-robin is consistent with the hypothesis that males that are unable to obtain a breeding vacancy on a nearby territory make the ‘best of a bad job’ by helping on their natal territory and thereby gain indirect fitness benefits by increasing the production and fitness of young to which they are related (Lloyd *et al*. 2009; Ribeiro *et al*. 2012).

The observed minimum juvenile male survival rate was 0.65 through the first year after independence, or 0.50 from fledging if the observed survival of 0.77 between fledging and independence (Lloyd and Martin 2016) is incorporated. This estimate is unlikely to be biased low by dispersal out of the study area due to the strong philopatry of males (discussed earlier). This juvenile survival rate is relatively high for a passerine bird, but comparable with other southern hemisphere, cooperatively breeding species, for example 0.64 from fledging in Apostlebird (*Struthidea cinerea*; Woxvold 2004), 0.66 from independence in Sociable Weaver (*Philetairus socius*; Covas *et al*. 2004), 0.46 from fledging in Rufous Tree creeper (*Climacteris rufa*; Luck 2001) and 0.46 from independence in male Brown Thornbill (*Acanthiza pusilla*; Green and Cockburn 2001). High juvenile male survival in Karoo Scrub-robin is consistent with the hypothesis that delayed dispersal coupled with extended parental care, parental nepotism or benefits of group living promote juvenile survival, particularly among southern hemisphere species (Martin 1996; Ekman *et al*. 2000; Russell *et al*. 2004; Ridley and Raihani 2007b).

Benefits of cooperative breeding can be varied, ranging from survival benefits to helpers and breeders, as well as offspring, but not all benefits are observed in all species. Understanding the specific ecological contexts in which specific benefits accrue is needed to further advance understanding of the evolution of cooperative breeding. Detailed studies of individual species, as reported here, are crucial for providing this information. Ultimately, further study is required to better understand the true benefits of deferring breeding.

**Acknowledgements**

We thank volunteer banders from the Tygerberg Bird Club for extensive assistance with colour-banding birds, particularly Margaret McCall, Bob Ellis, Lee Silks, and Bridget de Kok. Many field assistants helped locate and monitor nests and resight the colour-band combinations of breeding adults each year, particularlySonya Auer, Ron Bassar, Simon Davies, David Nkosi, Davide Gagli, Pierre-Yves Perroi, Justin Shew, Anna Chalfoun, Riccardo Ton, Alexander Neu, Julia Taubman and Bettina Christ. We thank Gert Greef and Hilton Westman for permission to work at ESKOM’s Koeberg Nature Reserve. We thank Adrian Craig and two anonymous reviewers for comments that have improved the manuscript. This work was supported in part through National Research Foundation grants (to PL and RA) and National Science Foundation grants (INT-9906030, DEB-0841764, DEB-1241041 to TEM). Capture and banding activities were licenced by the Western Cape Nature Conservation Board and SAFRING, the South African bird-banding scheme, and approved by the Animal Ethics Committee, University of Cape Town and IACUC #059–10TMMWCWRU at the University of Montana. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the USA Government.

**References**


