Demography of an Afrotropical passerine in a highly fragmented landscape

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Abstract

Demographic attributes of discrete subpopulations of animals and plants that constitute a larger (meta)population network may affect the strength and direction of local population responses to habitat loss or degradation. To address this question in an Afrotropical context, we studied survival rates, population densities, sex ratios and age distributions in seven white-starred robin *Pogonochila stellata* populations inhabiting differently sized forest remnants in a highly fragmented Kenyan landscape. Sex ratios were strongly male biased, especially during the non-breeding season, but the level of bias did not differ between age groups nor fragment sizes. Juvenile to adult ratios were smallest in the medium-sized fragment, but did not differ between the largest and smallest fragments. Low population density combined with a skewed sex ratio in the medium-sized fragment pointed towards a local scarcity of females, which was supported by the presence of unmated territorial males. Based on capture–recapture analysis, all populations were considered stable on average. When combining demographic patterns with those emerging from a recent population genetic study and removal experiment, our results support the notion that small populations inhabiting tiny habitat remnants may play an important role in augmenting the long-term survival of spatially structured populations.

Introduction

Habitat destruction often causes subdivision of formerly continuous continuous habitat blocks into discrete habitat fragments of variable quality, each containing isolated subpopulations of plants and animals. Over time, these subpopulations may acquire dissimilar demographic attributes – such as population density, trends and structure. Although it has been argued that only large forests can ensure long-term species survival (Diamond, Bishop & Van Balen, 1987; Ghazoul, 1996; Beier, Van Drielen & Kankam, 2002), small fragments, too, may play an important role as local refuges or demographic sinks, especially when no larger tracts of suitable habitats remain (Pulliam, 1988; Dias, 1996; Turner & Corlett, 1996; Brokaw, 1998; Semlitsch & Bodie, 1998; Renjifo, 1999; Schwartz, 1999; Foppen, Chardon & Liefveld, 2000; Murphy, 2001).

The viability of each local subpopulation can be evaluated from its demographic attributes, which, together with the characteristics of the surrounding landscape, determine its role in the persistence of the spatially structured population. Albeit differences in population density may point to the presence of demographic sources or sinks, this needs to be supported by additional evidence, such as patterns of sex-ratio variation and productivity (Vickery, Hunter & Wells, 1992). Adult sex ratios could play an important additional role contingent on the mating system. For instance, in socially monogamous species, there may be a lack of breeding opportunity or reduced breeding success for females at low population densities, where they have little opportunity to select a mate (Legendre et al., 1999; Møller & Legendre, 2001). Conversely, male-biased sex ratios could lead to a scarcity of females, especially at very low population densities, resulting in fewer paired males (Bayne & Hobson, 2001).

Although it is the adult sex ratios that are often most relevant, knowing when in the life cycle sex biases first appear (and hence its likely causes) may be essential for conservation (e.g. Dhondt & Hochachka, 2001; Ewen et al., 2001). For example, assuming even sex ratios at hatching and fledging (Clutton-Brock, 1986), the usual female-biased natal dispersal in birds (Greenwood & Harvey, 1982) and mortality associated with dispersal (Waser, Creel & Lucas, 1994) could lead to male-biased sex ratios at the immature and adult stages. Still, the facultative nature of adult dispersal could ameliorate such biases (Clarke, Saether & Roskåhl, 1997). Generally, sex-ratio skews are particularly important if they have net negative ramifications on...
productivity, where lower bird densities coupled with skewed adult sex ratios result in overall reduced reproductive success. In capture-recapture studies, productivity can be estimated by the ratio of juveniles to adults trapped (Doménech & Senar, 1997).

We here examine if and how adult densities, sex ratios and productivity vary among discrete populations of the white-starred robin *Pogonochelia stellata* (Bennun, Dranzoa & Pomeroy, 1996) in the fragmented Taita Hills forest of south-east Kenya. Despite there being no significant differences in mean home-range size among the seven populations under study (Githiru, 2003), we predict that populations living in higher quality (i.e. larger) forest fragments will show a higher density due to the greater availability of territories of adequate quality (e.g. Porneluzi & Faaborg, 1999) and more even sex ratios (e.g. Lens et al., 1998). Given the higher densities and parity in sex ratio in populations of high-quality patches, we further predict higher levels of productivity in these populations as well. Although conservation biology is mainly concerned with the conservation of rare and endangered species, it is often difficult to study such species and to obtain good insights into processes underlying the problems they face. Therefore, study of related but more common species which still persist in the majority of the habitat remnants, such as the white-starred robin in the Taita biodiversity hotspot (Lens, Adriaensen & Matthysen, 1999; Lens et al., 2002), offers a unique chance to obtain insights into landscape-wide patterns and processes applicable in the management of the rarer species (Perrins, 1991; Walters, 1998).

**Methods**

**Study species and study area**

The white-starred robin is a forest-dependent species inhabiting montane forests of eastern to southern Africa (Keith, Urban & Fry, 1992). It forages at all levels in the forest, most frequently in the undergrowth and at ant trails (Oatley, 1982b; Willis, 1985). It is territorial, socially monogamous and does not show much antagonism towards conspecifics (Oatley, 1982a; Keith et al., 1992). Mean home-range sizes in this study area were found to be 0.67 ± 0.28 ha (n = 20) (Githiru, 2003). Age was determined using body plumage following Jackson (2001): juvenile – bird in full juvenile plumage or with no more than c. 20% immature body plumage; immature – bird in distinct body plumage intermediate between juvenile and adult, with more than c. 20% new immature body feathers and a maximum of c. 90% new adult body feathers; and adult – bird in full adult body plumage, with more than c. 90% new adult body feathers. Individuals retain their juvenile plumage for about 3 months post-fledging, and the immature plumage until their second year; only individuals in the full adult plumage are known to breed (Oatley, 1982c). Between 1996 and 2002, a total of 303 individuals was sexed by analysis of the highly conserved W-chromosome linked gene, CHD-W (Ellegren, 1996); methodological details in Lens et al. (1998, 1999). Molecularly sexed males and females differed significantly in wing length for each age group (ANOVA: age: $F_{2,297} = 98.7$; sex: $F_{1,297} = 355.2$; age × sex $F_{2,297} = 6.7$; all P < 0.001).

The Taita Hills forests, located in south-east Kenya (03°20’S, 38°15’E, maximum altitude 2228 m), are an Endemic and Important Bird Area (Stattersfield et al., 1998; Bennun & Njoroge, 1999). Extensive forest loss over the last four decades has seen the forest reduced to a network of 11 remnant patches scattered across hilltops and ridges (Brooks et al., 1998). Data for this study were collected from the following forest fragments: Ngangao (135 ha; ‘largest fragment’); Chawia (95 ha; ‘medium-sized fragment’); Fururu 8 ha, Ndiwenyi 4 ha, Macha 3 ha, Mwachora 3 ha and Yale 3 ha (hereafter referred to as ‘smallest fragments’) (Fig. 1). Based on the structural quality of the vegetation (basal area per unit area, stem density, canopy cover, shrub density, stratification and extent of herbaceous ground cover; Wilder, Brooks & Lens, 2000), and levels of plant species richness and diversity (Githiru, 2000), smaller fragments also showed higher levels of habitat disturbance. At the time of our study, the medium-sized fragment (Chawia) was undergoing the strongest level of forest degradation from the neighbouring human population (M. Githiru & L. Lens, pers. obs.).

**Study design**

Five 3-ha plots were randomly selected in the largest and medium-sized fragments, while the five smallest fragments were treated as a single plot each. Within each plot, three permanent mist-net lines each measuring between 54 and 57 m were simultaneously operated between 06:00-12:00 and 15:00–18:00 h on 2 consecutive days. Hence, the length of each ringing session per type of fragment (largest, 2006). 21–27 © 2005 The Zoological Society of London

**Figure 1** Relative position and size of eleven indigenous forest remnants in the Taita Hills (south-east Kenya). Fragments hosting the seven study populations (this paper) are indicated in black: NG, Ngangao; YA, Yale; FU, Fururu; ND, Ndiwenyi; MA, Macha; MW, Mwachora; CH, Chawia.
medium-sized and smallest) was 10 days. Between May 2000 and December 2001, six separate ringing sessions were conducted in each fragment, corresponding to six encounter occasions. Session 1 ran from 12 May to 30 June 2000, session 2 from 15 July to 28 August 2000, session 3 from 17 October to 3 December 2000, session 4 from 20 March to 3 May 2001, session 5 from 25 June to 8 August 2001 and session 6 from 3 November to 9 December 2001. Mean inter-session intervals were as follows: between session 1 and 2, 59 ± 2 days; between session 2 and 3, 94 ± 2 days; between session 3 and 4, 134 ± 23 days; between session 4 and 5, 93 ± 2 days; and between session 5 and 6, 120 ± 10 days. Sessions were temporally spaced out so as to encompass the breeding, warm–wet (October–March) and non-breeding, cold–dry (June–September) seasons while maximizing both breeding, warm–wet (October–March) and non-breeding, cold–dry (June–September) seasons while maximizing both the number of encounters and time between successive encounters. All captured robins were colour-ringed using a distinctive combination of a single aluminium ring and three plastic colour rings.

Statistical analyses

Estimation of densities

Encounter histories were composed of live recaptures only (see White & Burnham, 1999). Adult population densities, rates of change and recapture probabilities were calculated using the Burnham’s Jolly–Seber model in program MARK (White & Burnham, 1999). We used a Log link function to estimate the rate of population change (λ) and population density (N) and a Sin link function to estimate probabilities of survival (Φ) and recapture (p). Variation in time intervals between successive ringing sessions was integrated as a multiple of the shortest interval (59 days). Because recapture data were too sparse to include interactive and additive models, we tested the group (factor g; i.e. smallest–medium–largest) and time (factor t) effects separately for all possible models. The most parameterized model was—Φ(t) p(t) λ(t) N(t) where Φ is the 2-monthly apparent survival probability, p the recapture probability, λ the 2-monthly rate of population growth and N is the estimate of the population size at the start of the study; subscripts t and g refer to time- and group-dependent probabilities, respectively. The rate of population change, λ, was calculated as N(t+1)/N(t) (Leslie, 1966; Lande, 1988; Zanette, 2000).

The program RELEASE (within MARK) was applied to test if the global model adequately fitted the capture–recapture data (White & Burnham, 1999). We corrected for over-dispersion by incorporating a variance inflation factor (ι) in all model runs in MARK (Burnham et al., 1987; White & Burnham, 1999). Starting with the global model, Akaike’s information criterion (AIC) was applied for model selection from the set of candidate models incorporating group and time dependence (Anderson, Burnham & White, 1994; Burnham, Anderson & White, 1995). Due to the adjustment of the ω-value, AIC values for the models were adjusted to quasi-AIC values (QAIC). Only when the difference in QAIC values (ΔQAIC) between two models was greater than seven did we consider it compelling evidence for real difference between the models (White & Burnham, 1999). When less than seven, likelihood ratio tests (LRTs) were applied to test the significance of individual effects between nested models (Lebreton et al., 1992). Finally, we used the model averaging approach to estimate model parameters, based on the models with ΔQAIC values equal to or less than seven. Model averaging allows computation of the average of a parameter from all plausible candidate models, and thereby allows for the inclusion of model selection uncertainty in estimating precision of the parameter and producing unconditional estimates of variance and standard errors (ses) (White & Burnham, 1999).

Because data for juvenile and immature birds were too sparse to allow modelling in MARK, we used a simpler index to estimate their densities, Ni = n/i and se(Ni) = [(n/i)p]^2 (var(p)/p^2) (Loery, Nichols & Hines, 1997), where Ni is the number of individuals at time i, ni is the total number of birds caught in interval i, and p and var(p) are the estimated capture probability at interval i and its variance. Because recapture probabilities of white-starred robins are independent of age (Githiru, 2003), adult recapture probabilities (derived from Jolly–Seber models) were used in this analysis.

Density estimates were based on the cruising-range concept (MacArthur & MacArthur, 1974). By dividing each plot into six 0.5 ha subplots, the three netlines (each at least 50 m from the closest one) were distributed as follows: one in the centre of the top-right subplot, a second between the two central subplots and a third in the centre of the bottom-left subplot. While this design was deemed optimal for sampling the entire plot, at least two of the three netlines were c. 25 m from the plot edge and could therefore catch individuals ranging outside the plots in the medium-sized and largest fragments. As white-starred robins have an average home-range size of 0.67 ha (Githiru, 2003), we appended 50 m on each plot side to calculate densities, hence resulting in 200 × 400 m (8 ha) plots. For the smallest fragments, the total patch area (21 ha).

Variation in sex ratios

Variation in sex ratios was statistically tested using general log-linear models with fragment size, season, age and sex as independent variables. Partial two- and three-way interactions were computed by comparing the relative fits of full and reduced models (Sokal & Rohlf, 1995). We applied a stepwise backward testing procedure and assumed a Poisson distribution because total sample size was not fixed before the start of the study (SPSS, 2001).

Variation in age ratios

Variation in juvenile:adult ratios (Domènech & Senar, 1997) was calculated using density estimates obtained following Loery et al. (1997). Immatures were excluded from this analysis as they are not known to breed and may have dispersed. We analysed a contingency table with factors fragment size and age using crosstabulations (SPSS, 2001).
Further pairwise testing was done using Fisher’s exact tests (StatSoft™, 1994).

Results

Survival and population density

The global model adhered to the underlying assumptions of the Jolly–Seber model (test 2: \( \chi^2 = 3.8, \) d.f. = 5, \( P = 0.59; \) test 3: \( \chi^2 = 8.8, \) d.f. = 7, \( P = 0.27; \) White & Burnham, 1999); the \( \hat{c} \)-value approximated 2, indicating that the data and model structure were appropriate. Of the candidate set of models, the model with the lowest QAIC was \( \Phi_p l_N^g \), indicating a constant probability of survival both among groups and over time, temporal variation in recapture probabilities, and differences in population growth rates and sizes among fragments of different sizes. Eleven other models had a \( \Delta \text{QAIC} \) value less than seven, but only three of these were hierarchically nested with the lowest QAIC model (shown in bold in Table 1). The first model had no group effect on lambda (i.e. \( \Phi_p l_N^g \)), while the second model had no time effect on recapture (i.e. \( \Phi_p l_N^g \)). As the corresponding LRTs were significant (\( \chi^2 = 14.2, \) d.f. = 2, \( P = 0.0008; \chi^2 = 30.3, \) d.f. = 5, \( P = 0.0001 \) respectively), both effects were retained. The third model with a group effect on survival \( \Phi_p l_N^g \) was omitted (LRT \( \chi^2 = 0.2, \) d.f. = 2, \( P = 0.90 \)). Thus, the lowest QAIC model was retained as the most parsimonious one. Based on this analysis, the largest fragment contained the highest population density (Table 2). While population growth rates significantly differed between fragments of different sizes, populations in all fragments appeared largely stable (Table 2).

Variation in sex ratio

Overall, sex ratios were strongly male biased in the 492 individuals we sampled (Table 3). None of the three-way interactions with factor sex was significant (all \( P \) values > 0.21). Among the two-way interactions, season*sex was significant (\( \Delta G = 10.0, \) d.f. = 1, \( P = 0.0015 \), age*sex \( (AG = 5.6, \) d.f. = 2, \( P = 0.06 \) was marginally non-significant and fragment*sex \( (AG = 1.2, \) d.f. = 2, \( P = 0.56 \) was not significant. In general, the proportion of female captures was lower during the non-breeding season (non-breeding 24.7 ± 1.58%; breeding 45.5 ± 2.41%), whereas no significant relationships were detected with age or fragment size.

Variation in age ratio

The ratio of juvenile to adult birds varied among fragments of different sizes (\( G \)-test = 24.8, d.f. = 2, \( P = 0.0001 \)), with a lower rate in the medium-sized fragment (juvenile:adult, 27.5:1). None of the two-way interactions was significant (season*sex: \( G = 0.1, \) d.f. = 1, \( P = 0.74 \); age*sex: \( G = 1.2, \) d.f. = 2, \( P = 0.54 \); fragment*sex: \( G = 0.1, \) d.f. = 2, \( P = 0.70 \)). Among the three-way interactions, the sex*age*season interaction was significant (\( G = 7.8, \) d.f. = 2, \( P = 0.02 \)).

Table 1 Candidate models for capture-recapture analysis with \( \Delta \text{QAIC} \) values of seven or less (see text for rationale)

<table>
<thead>
<tr>
<th>Model</th>
<th>QAIC</th>
<th>( \Delta \text{QAIC} )</th>
<th>QAIC weight</th>
<th>Number of parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>269.0</td>
<td>0.00</td>
<td>0.446</td>
<td>13</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>271.4</td>
<td>2.42</td>
<td>0.133</td>
<td>10</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>271.6</td>
<td>2.63</td>
<td>0.119</td>
<td>11</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>273.1</td>
<td>4.19</td>
<td>0.055</td>
<td>8</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>273.3</td>
<td>4.32</td>
<td>0.051</td>
<td>15</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>273.5</td>
<td>4.53</td>
<td>0.046</td>
<td>6</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>274.2</td>
<td>5.23</td>
<td>0.033</td>
<td>13</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>275.1</td>
<td>6.18</td>
<td>0.020</td>
<td>12</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>275.4</td>
<td>6.49</td>
<td>0.017</td>
<td>10</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>275.6</td>
<td>6.67</td>
<td>0.016</td>
<td>12</td>
</tr>
<tr>
<td>( \Phi_p l_N^g )</td>
<td>276.2</td>
<td>7.25</td>
<td>0.012</td>
<td>6</td>
</tr>
</tbody>
</table>

These models were used for model averaging during parameter estimation (see Table 2). Models in bold are hierarchically nested within the model with the lowest QAIC and were examined with likelihood ratio tests. QAIC, quasi-Akaike’s information criterion.

Table 2 Demographic parameters estimated by the model averaging approach (for models see Table 1) using the least QAIC Jolly–Seber model for adult \( P \)ogonocichla \( s \)tellata, and density estimates (± sd) for adults, immatures and juveniles following Loery et al. (1997) (see text for details)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Standard error</th>
<th>Adults</th>
<th>Immatures</th>
<th>Juveniles</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Phi )</td>
<td>0.96</td>
<td>0.081</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_1 )</td>
<td>0.15</td>
<td>0.066</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_2 )</td>
<td>0.14</td>
<td>0.052</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_3 )</td>
<td>0.14</td>
<td>0.052</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_4 )</td>
<td>0.073</td>
<td>0.037</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_5 )</td>
<td>0.11</td>
<td>0.045</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_6 )</td>
<td>0.13</td>
<td>0.070</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \lambda_{\text{Large}} )</td>
<td>0.95</td>
<td>0.127</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \lambda_{\text{Medium}} )</td>
<td>1.01</td>
<td>0.150</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \lambda_{\text{Small}} )</td>
<td>1.01</td>
<td>0.148</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( N_{\text{Large}} )</td>
<td>213 (6)</td>
<td>88</td>
<td>215 ± 61</td>
<td>78 ± 24</td>
<td>126 ± 36</td>
</tr>
<tr>
<td>( N_{\text{Medium}} )</td>
<td>85 (2)</td>
<td>47</td>
<td>91 ± 27</td>
<td>24 ± 8</td>
<td>18 ± 5</td>
</tr>
<tr>
<td>( N_{\text{Small}} )</td>
<td>104 (5)</td>
<td>54</td>
<td>117 ± 35</td>
<td>40 ± 13</td>
<td>94 ± 28</td>
</tr>
</tbody>
</table>

\( p \), recapture probability; subscripts 1–6, different ringing sessions; \( \lambda \), rate of population change; \( N \), population size at the start of the study (density estimates per hectare within parentheses). QAIC, quasi-Akaike’s information criterion.

Table 3 Number of \( P \)ogonocichla \( s \)tellata individuals captured during the breeding season (warm–wet season: October–April) and non-breeding season (cold–dry season: May–September) per fragment size, age and sex

<table>
<thead>
<tr>
<th>Fragment-size class</th>
<th>Age</th>
<th>Non-breeding</th>
<th>Breeding</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female</td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>Largest</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>10</td>
<td>66</td>
<td>21</td>
</tr>
<tr>
<td>Immature</td>
<td>7</td>
<td>28</td>
<td>10</td>
</tr>
<tr>
<td>Juvenile</td>
<td>4</td>
<td>14</td>
<td>9</td>
</tr>
<tr>
<td>Medium-sized</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>10</td>
<td>24</td>
<td>9</td>
</tr>
<tr>
<td>Immature</td>
<td>0</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Juvenile</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Smallest</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>11</td>
<td>31</td>
<td>17</td>
</tr>
<tr>
<td>Immature</td>
<td>1</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Juvenile</td>
<td>0</td>
<td>2</td>
<td>5</td>
</tr>
</tbody>
</table>
18:91) compared to the largest (126:215) and the smallest fragments (94:117) (a posteriori tests; all \( P < 0.001 \)). The largest and smallest fragments did not differ significantly in the ratio of juvenile to adult birds (\( P = 0.09 \)).

**Discussion**

Recapture probabilities varied with time but not among fragments, which validates the use of capture-recapture data for estimating population attributes in our study. Species (Remsen & Good, 1996). As predicted, the largest (and least disturbed) fragment showed the highest density of adult robbins. A recent removal experiment (Githiru, 2003) revealed a high density of (predominantly male) floaters in this fragment, and as some territories were visited by more than one floater, queuing strategies might be in operation. Given a mean territory size of 0.67 ha and one floater for every two adults on average, the estimated six adults ha\(^{-1}\) was within the expected range (Githiru, 2003). The cluster of small fragments showed an intermediate density (five adults ha\(^{-1}\)), while the very low density (two adults ha\(^{-1}\)) estimated in the medium-sized fragment suggests the presence of unoccupied habitat and the absence of floaters, probably as a result of ongoing habitat degradation and increasing levels of nest predation (Githiru, Lens & Cresswell, 2005). Comparable disturbance affecting the smallest fragments may be compensated by the higher levels of between-fragment dispersal (resulting in a fine-grained population system; Rolstad, 1991) as revealed by population genetic analyses (Galbusera et al., 2004). As a result, these patches support higher robin densities than would be expected from their size and quality (Quinn & Hastings, 1987; Burkey, 1988; Nunney & Campbell, 1993).

Overall, sex ratios were strongly male biased. While this effect was more pronounced during the non-breeding season, the level of skew did not differ either between age classes or subpopulations. Comparable male-biased sex ratios were reported in South African populations of the white-starred robin (Oatley, 1982), and seasonal variation in this bias was associated with sex-dependent altitudinal migration during the non-breeding season (Dowsett, 1985; Burgess & Mlingwa, 2000). A critical lack of appropriate habitat in the Taita lowlands, however, makes a similar pattern of movements (and ditto explanation for the seasonal variation in sex ratios) unlikely in our study area. The absence of between-age variation in sex ratios suggests that the bias is already present in an early life stage, possibly indicating (1) facultative primary sex ratio variation (West, Reece & Sheldon, 2002), (2) non-adaptive effects of inbreeding (e.g. Sheffer, Hedrick & Velasco, 1999; Keller & Waller, 2002) and/or (3) enhanced female mortality at a young age (e.g. Oddie, 2000; Ewen et al., 2001). Of six successful nests (each with a clutch size of two) that were genotyped during the study period, five had a 1:1 sex ratio. While the small sample size prevents any conclusive argument, these results certainly do not point towards a male-biased sex ratio at hatching. The finding that all white-starred robin populations showed genetic migration-drift equilibrium and retained relatively high levels of genetic variability (Galbusera et al., 2004) does not suggest genetic inbreeding either. Hence, high female mortality during post-fledging seems the most likely cause for the observed male-biased sex ratio. Yet, knowledge of the mechanism(s) underlying this differential mortality requires long-term monitoring of large numbers of offspring through their entire dependency period.

Even though sex ratios were similarly skewed across populations, the net population impact can be expected to be larger at low densities when female numbers dwindle to levels at which territorial males start facing difficulties in mate location, especially in a monogamous species such as the white-starred robin (Legendre et al., 1999; Moller & Legendre, 2001). This argument is backed up by the presence of unmated territorial males in the medium-sized fragment (Githiru, 2003). At higher population densities, male-biased sex ratios may be reflected in smaller numbers of female floaters only. The absence of unmated territorial males and the presence of female floaters in the largest fragment (Githiru, 2003) suggest that mate location was not a limiting factor in that population. Likewise, unpaired territorial males were observed in eastern yellow robin *Eopsaltria australis* populations inhabiting low-quality forest fragments but not high-quality ones (Zanette, 2001), and a higher proportion of paired ovenbird *Seiurus aurocapillus* males occupied high-quality compared to low-quality forest fragments (Bayne & Hobson, 2001).

The low juvenile:adult ratio and higher density of immatures compared to juveniles (unlike in the other fragments; Table 3) in the medium-sized fragment suggests low productivity and a high rate of immigration. Reproductive output in this fragment was likely to be impaired by the deficiency of females and high level of nest predation alluded to earlier. The resulting low level of recruitment could, however, be partly redressed by first year birds and non-breeding adults immigrating from other populations. Population genetic analyses corroborate this assertion as individuals from the medium-sized and smallest fragments showed close genetic affinity (Galbusera et al., 2004).

In conclusion, the (1) stable rate of population change despite low productivity and high density of immatures (this study) and (2) low probability that any two genes share a common ancestor and relatively high estimate of number of immigrants per generation (Galbusera et al., 2004) in the medium-sized fragment suggest that this population may largely depend upon immigrants for its long-term survival. Populations inhabiting the smallest Taita Hills fragments, which are characterized by relatively high levels of productivity, probably supply most of these immigrants, as is supported by their close genetic affinity with the medium-sized population (Galbusera et al., 2004). However, owing to their extremely small sizes, these populations are likely to be vulnerable to environmental perturbations or human-induced events even at fairly small scales. Hence, at present, the large fragment (Ngangao) seems to host the only stable and viable source population for white-starred robins in the studied area. Yet, more data on per capita reproductive output from individuals in the different fragments are...
required to confirm (or disprove) source-sink dynamics in the Taita landscape. This notwithstanding, the available demographic and genetic data clearly back up the important role of the smallest forest fragments for augmenting the long-term survival of the Taita white-starred robin population as a whole, and more in particular, of the Taita endemics that occur sympatrically in this highly fragmented biodiversity hotspot.

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