The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine

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Summary

1. Variation in survival, a major determinant of fitness, may be caused by individual or environmental characteristics. Furthermore, interactions between individuals may influence survival through the negative feedback effects of density dependence. Compared to species in temperate regions, we have little knowledge about population processes and variation in fitness in tropical bird species.

2. To investigate whether variation in survival could be explained by population size or climatic variables we used capture–recapture models in conjunction with a long-term data set from an island population of the territorial, cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*). The lack of migration out of the study population means that our results are not confounded by dispersal.

3. Annual survival was high, both for adults (84%) and juveniles (61%), and did not differ between the sexes. Although there was significant variation in survival between years, this variation could not be explained by overall population size or weather variables.

4. For territorial species, resource competition will work mainly on a local scale. The size of a territory and number of individuals living in it will therefore be a more appropriate measure of density than overall population density. Consequently, both an index of territory quality per individual (food availability) and local density, measured as group size, were included as individual covariates in our analyses.

5. Local density had a negative effect on survival; birds living in larger groups had lower survival probabilities than those living in small groups. Food availability did not affect survival.

6. Our study shows that, in a territorial species, although density-dependent effects might not be detectable at the population level they can be detected at the individual territory level – the scale at which individuals compete. These results will help to provide a better understanding of the small-scale processes involved in the dynamics of a population in general, but in particular in tropical species living in relatively stable environments.

Key-words: *Acrocephalus sechellensis*, individual covariates, local density, mark–recapture.

Introduction

Understanding the factors that influence population dynamics is of fundamental importance to many areas

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in biology. Survival is a key variable in population dynamics as it is often a major source of individual variation in lifetime reproductive success (Clutton-Brock 1988; Newton 1989). Indeed, in many populations a large proportion of individuals will die before having the chance to reproduce (Newton 1989). In long-lived species especially, small differences in survival may have large evolutionary effects and far-reaching consequences for the dynamics of the population.

Survival may vary due to individual differences in genotype or phenotype (e.g. sex or mass), but may also change over time for each individual due to ageing (Clobert *et al.* 1988; Lebreton *et al.* 1992). Survival may also vary due to density-dependent processes, a key process often used to explain why populations normally fluctuate between certain boundaries (Murdoch 1994; Sæther, Engen & Matthysen 2002). However, it has long been recognized that many natural populations will remain relatively constant when left undisturbed, and that density dependence will be impossible to detect, or be confounded, in these circumstances (Murdoch 1994; Sæther 1997). Consequently experiments involving deliberate perturbations of population size, e.g. through translocations, are needed to test the causality of density dependence in natural populations. Although many studies have investigated the role of density dependence on life history traits (for reviews see: Sinclair 1989; Newton 1998; Both 2000), the detection of such processes is also dependent on the spatial scale at which such effects are investigated (e.g. Ray & Hastings 1996; Wilkin *et al.* 2006). Intra-specific competition for resources, one of the main density-dependent processes (Newton 1992), will work mainly on a local scale in territorial species. The size of the territory and number of individuals living in it will therefore be the appropriate measure of density with which to investigate such effects (Both & Visser 2000). In contrast to non-cooperatively breeding species, where increased density may result in a negative effect on survival, in cooperatively breeding species a higher local density may be advantageous if individuals survive or reproduce better in larger cooperative groups (Woolfenden 1975; Brown 1987; Magrath 2001; Clutton-Brock 2002). Finally, the effects of density dependence may also be confounded if individuals of higher quality are able to obtain higher-quality territories (Garant *et al.* 2005). Consequently territory quality, as well as local density, should be taken into account when analysing density-dependent effects.

Environmental factors also play an important role in survival. In passerines, survival is often affected by food availability (Jansson, Ekman & Broemssen 1981; Newton 1998), which can be affected in turn by rainfall and temperature fluctuations. Moreover, such climatic factors can also influence survival directly. Variation in natal environment can influence the life-histories of complete cohorts (van der Jeugd & Larsson 1998; Lindström 1999; Reid *et al.* 2003). However, cohorts which are successful, because of factors such as food availability, may also be influenced by negative feedback effects through density dependence.

Most of what is known about survival comes from studies of temperate species. There is little knowledge about how factors such as environmental variation affect survival and population regulation in tropical species (Martin 1996). In tropical areas, environmental factors are generally considered to vary relatively little between seasons (Karr 1976; Martin & Karr 1986; Loiselle &

Blake 1991, 1992). Life histories of species in these regions are characterized typically by small clutches, long developmental periods and extended parental care of juveniles associated with high juvenile and adult survival probabilities (Skutch 1949; Lack 1954; Martin 1996). Another important feature is that cooperatively breeding species are more prevalent in (sub)tropical areas than in temperate zones (Arnold & Owens 1999).

Studies investigating the effect on survival of both density dependence and territory quality at an individual level are lacking, despite the fact that they would give a better understanding of the small-scale processes of population regulation. Furthermore, we know of no study which has investigated the long-term effect of local density on survival in a cooperatively breeding species. Here we analyse the long-term data set from a population of the Seychelles warbler (*Acrocephalus sechellensis*), a long-lived tropical endemic confined to a few small islands in the Seychelles. In the 1960s, the entire world population of Seychelles warblers was restricted to just 26–29 individuals on Cousin Island. This population, which has since recovered and stabilized at around 320 adult individuals, has been studied since 1985 (Komdeur 1992; Richardson, Burke & Komdeur 2003). The transfers of Seychelles warblers to the islands of Aride and Cousine allowed us to test the causality of density dependence. The Seychelles warbler is also a cooperatively breeding species, with group sizes varying from one to six birds per territory. As the population is a closed system, with no migration on or off the island (Komdeur *et al.* 2004), accurate, unbiased survival probabilities can be calculated without the problems encountered by most other studies, where local survival estimates are confounded by dispersal away from the study site. By using capture–recapture models we investigate whether juvenile and adult survival is regulated by density dependence, both on a local and on a population level. This analysis should, for the first time, provide insight into the long-term effect of group living on survival. To determine if group size effects are caused by territory quality, we also investigate the effect of an index of territory quality per individual on survival. Finally, we test whether temporal variation in survival can be explained by environmental factors such as rainfall and temperature.

Methods

STUDY AREA AND DATA COLLECTION

The data were collected as part of the long-term study of the Seychelles warbler population on Cousin Island (04°20′ S, 55°40′ E). Except for 1992, this population has been monitored every year since 1985. During the main breeding season, each territory was checked for breeding activity at least once every 2 weeks by following the resident female for 30 min (Komdeur 1992). Nests were observed throughout the breeding cycle. Birds were either ringed as nestlings or as fledglings while still

resident in the natal territory and dependent on their parents (birds of known age and origin), or later when independent (birds of unknown age and origin). Birds were ringed with a unique combination of three UV-resistant colour rings and a British Trust for Ornithology ring. Blood samples (c. 15 μL) were collected by brachial venipuncture and diluted in 800 μL of 100% ethanol in a 2·0-mL screw-cap microfuge tube and stored at room temperature. Molecular sexing using the polymerase chain reaction (PCR) method was used to determine the sex of each sampled individual since 1994 (Griffiths *et al.* 1998). As part of a conservation project, 29 warblers were translocated to each of the islands of Aride (1988) and Cousine (1990) (Komdeur 1994a). These translocations created an experimental reduction in density on Cousin Island.

To investigate whether environmental conditions play a role in survival, weather data were obtained from the Meteorological Services of Praslin Island, an island 2 km south of Cousin Island. Each year was divided into four periods of 3 months. Mean temperature (°C) and total rainfall (mm) were calculated for the main breeding season period. Furthermore, total rainfall was calculated for the prebreeding season, for the period when fledglings were still dependent on their parents and for the period when the young were able to forage independently. As variation in temperature between years is largest in the breeding season, only the effect of breeding season temperature on survival was tested. As both very dry and very wet years might have strong effects on survival probabilities, the squared effects were also tested.

Seychelles warblers are insectivorous, taking 98% of their insect food from leaves (Komdeur 1991). Therefore, the number of insect prey available, the territory size and foliage cover were used to calculate an index of territory quality following Komdeur (1992). Territory quality was calculated for each territory in 1987, 1990, 1996–99 and 2003–04. For the remaining years, territory quality for each territory was calculated as the average from the preceding and following periods. Median territory quality did not increase during our study period ($r_6 = 0·04$, $n = 8$, $P = 0·93$). Repeating the analyses including only those years in which territory quality was measured gave similar results (not shown).

For each bird, local density was calculated as: (i) natal local density: group size during the individual's first year of life and (ii) lifetime local density: the average group size from the individual's second year onwards. Group size reflects local density, as territory size does not increase proportionally with group size (territory size = $0·16 + e^{0·09} \times$ group size, $F = 16·6$, d.f. = 429, $P < 0·001$). For 4 years for which accurate territory sizes were available, the average territory size (in ha ± SE) per group size was as follows: group size = 1: $0·16 ± 0·04$ ($n = 6$); group size 2: $0·22 ± 0·01$ ($n = 229$); group size = 3: $0·23 ± 0·01$ ($n = 142$); group size = 4: $0·25 ± 0·01$ ($n = 43$); group size = 5: $0·27 ± 0·05$ ($n = 8$); group size = 6: $0·27 ± 0·03$ ($n = 3$). Natal territory quality was the

territory quality during the individual's first year of life. Lifetime territory quality was calculated as the mean quality of all the territories inhabited by an individual from the second year onwards. To disentangle territory quality effects from group size effects, natal food availability was calculated by dividing natal territory quality by the number of birds in the territory. Lifetime food availability was calculated as the mean quality (per individual) of the territories inhabited from the second year onwards. After performing these calculations natal food availability was still correlated with natal group size ($r = −0·18$, $n = 438$, $P < 0·001$); and lifetime food availability was still correlated with average lifetime local density ($r = –0·13$, $n = 736$, $P = 0·001$), although the variation in territory quality explained by group size was only 3·2% and 1·7%, respectively.

Overall population size was estimated for each year, except for 1991–94, as the number of birds older than 3 months of age alive in the breeding season, after correcting for the resighting rate. In 1991–94 only a portion of the population was monitored (68% of territories). As the number of territories is relatively constant across years (average ± SE 1986–90, 1995–2004: $n = 112·3 ± 1·2$), population size for these years was estimated by multiplying the number of birds observed by the proportion of territories monitored.

SURVIVAL ANALYSES

To estimate survival, we constructed the capture–resighting histories of 991 marked individuals that were monitored between 1986 and 2004. Of these, 438 individuals were ringed as juveniles and were of known age. Another 553 individuals were ringed as adults, and therefore only a minimum age could be assigned to these individuals. Two resighting periods were defined; the first from 1 July to 1 September during the main breeding season, the second from 1 January to 1 March. However, most birds were re-sighted within the first 2 weeks of each study period. Individuals were recorded as present if observed or caught at least once within this period or absent if not. No capture–resighting data were available for 1992 and data for January–March were available only in 1998, 1999 and 2003. If not available, dummy variables were created by including zeros in the encounter histories, with the survival parameter (Φ) set equal to 1 and the resighting parameter (recapture, P) set equal to 0. The resighting history files were used as input files in the program MARK (White & Burnham 1999).

To investigate survival and resighting probability, we employed an a priori approach in which a set of candidate models was created based on biological reasoning. First, we investigated whether survival and resighting vary between age classes, cohorts or years using the data set of known-age birds. As Seychelles warblers are dependent on their parents for at least 3 months, and stay in their natal territory until they are at least 6 months of age (Komdeur 1996a), survival and resighting rates

may differ between 1-year-old and older birds. Consequently, we allowed survival and resighting rate to vary between years and between these age classes in the global model. Secondly, we included birds of unknown age to analyse the effects of sex and group (ringed as juvenile or adult). The most parsimonious model resulting from this analysis was then used to investigate the effects of density, territory quality and weather variables. The effect of sex on survival was analysed using individuals ringed between 1994 and 2004 for which blood samples were available for molecular sexing, thereby creating two groups of 417 males and 370 females. Population density and weather variables were tested by including the covariate as a linear constraint on survival probabilities. Local density, territory quality and food availability were included as individual covariates for each bird whereby lifetime local density and food availability were always tested as an interaction with age. The individual covariates were analysed by using the logit link function, with values of the individual covariates standardized to Z-scores (by subtracting the mean and dividing by the standard deviation). Model notation was followed according to Lebreton *et al.* (1992).

MODEL SELECTION AND GOODNESS-OF-FIT

Akaike's information criterion, corrected for the sample size (AIC_c), was used to select the most parsimonious model (Akaike 1973; Burnham & Anderson 2002). Additionally, we calculated the normalized Akaike weights to assess the relative likelihood of competing models. The goodness-of-fit of the global model was checked by using parametric bootstrap procedures. The variance inflation factor (c) was calculated by dividing the model deviance by the bootstrapped deviance. Both the known-age ($c = 1·16$) and the unknown-age ($c = 1·29$) data set fitted the data well with no strong evidence for overdispersion. Therefore, AIC_c values

were adjusted to allow for the extent of overdispersion measured by c, through quasi-likelihood ($QAIC_c$). For one model to be selected above another $\Delta QAIC_c$ should be > 2 (Burnham & Anderson 2002). To account for model selection uncertainty, we used model averaging techniques which weigh the impact of all models for a given parameter according to its AIC_c weight (Burnham & Anderson 2002).

## Results

EFFECTS OF YEAR, AGE AND SEX

The most parsimonious model for the known-age data set showed that survival was lower in an individual's first year of life than older birds and varied between the years (Table 1, model 1). The resighting probability was lower for individuals in their first 2 years of life than for older birds (Table 1, model 1). After including the unknown-age birds, the most parsimonious model showed that the resighting probability, but not the survival probability, of birds ringed as adults was higher than that of adult birds ringed as juveniles (Table 2, model 5 vs. 6 and model 1 vs. 2). Furthermore, the model best supported by the data showed that the resighting and survival probabilities varied between years and also differed between the age classes, with similar variation between years for both age classes (Table 2, model 1). This final accepted model was 3·7 times better supported by the data than the next most parsimonious model (Table 2, model 1 vs. model 2). Figure 1 shows the weighed survival estimates per year for both age classes. On average the annual survival probability for birds in their first year was $0·61 \pm 0·09$ (resighting probability = $0·87 \pm 0·05$) and $0·84 \pm 0·04$ (resighting probability = $0·92 \pm 0·03$) for adult birds. The final model was used to investigate whether survival probabilities varied between the sexes and/or were influenced by density and environmental factors.

Table 1. Summary of model selection statistics of year and age effects in survival and resighting probabilities of the subset of Seychelles warblers of known age ($n = 438$), (t) = year, (a) = age, (.) = constant, (c) = cohort

No.	Model	No. Par.	$\Delta QAIC_c$	Quasi deviance	QAIC weights
1	$\Phi_{(t+a1,2+)}P_{(a1-2,3+)}$	23	0	306·2	0·72
2	$\Phi_{(t+a1-2,3+)}P_{(a1-2,3+)}$	23	1·87	308·1	0·28
3	$\Phi_{(t\times a1-2,3+)}P_{(a1-2,3+)}$	40	13·4	284·1	0
4	$\Phi_{(t\times a1-2,3+)}P_{(a1-2,3,4+)}$	41	14·7	283·2	0
5	$\Phi_{(t\times a1-2,3+)}P_{(t+a1-2,3+)}$	58	15·4	247·3	0
6	$\Phi_{(t\times a1-2,3+)}P_{(a1,2+)}$	40	16·7	287·3	0
7	$\Phi_{(t\times a1-2,3+)}P_{(.)}$	37	21·4	298·4	0
8	$\Phi_{(t\times a1-2,3+)}P_{(t)}$	55	22·2	260·7	0
9	$\Phi_{(t\times a1-2,3+)}P_{(c)}$	54	26·4	267·0	0
10	$\Phi_{(t)}P_{(a1-2,3+)}$	22	29·5	337·8	0
11	$\Phi_{(t\times a1-2,3+)}P_{(t\times a1-2,3+)}$	70	30·9	236·5	0
12	$\Phi_{(c)}P_{(a1-2,3+)}$	20	63·6	376·0	0
13	$\Phi_{(a1,2+)}P_{(a1-2,3+)}$	4	68·5	413·5	0
14	$\Phi_{(a1-2,3+)}P_{(a1-2,3+)}$	4	71·1	416·1	0
15	$\Phi_{(a1-2,3,4+)}P_{(a1-2,3+)}$	5	71·7	414·7	0
16	$\Phi_{(.)}P_{(a1-2,3+)}$	3	103·5	450·6	0

Table 2. Summary of model selection statistics of year and group (ringed as adult) effects in survival and resighting probabilities of the Seychelles warbler ($n = 991$), (t) = year, (a) = age, and (g) = group (ringed as adult)

No.	Model	No. Par.	$\Delta QAIC_c$	Quasi deviance	$QAIC_c$ weights
1	$\Phi_{(t+a1,2+)}P_{(t+g+a1-2,3+)}$	42	0	831·0	0·77
2	$\Phi_{(t+g+a1,2+)}P_{(t+g+a1-2,3+)}$	44	2·6	829·4	0·21
3	$\Phi_{(g+t\times a1,2+)}P_{(t+g+a1-2,3+)}$	60	7·3	801·3	0·02
4	$\Phi_{(t\times g+a1,2+)}P_{(t+g+a1-2,3+)}$	60	26·4	820·4	0
5	$\Phi_{(t\times g+t\times a1,2+)}P_{(t+g+a1-2,3+)}$	76	31·0	792·0	0
6	$\Phi_{(t\times g+t\times a1,2+)}P_{(t+a1-2,3+)}$	75	37·3	800·4	0
7	$\Phi_{(t\times g+t\times a1,2+)}P_{(g+t\times a1-2,3+)}$	94	39·6	763·0	0
8	$\Phi_{(t\times g+t\times a1,2+)}P_{(t\times g+a1-2,3+)}$	92	55·6	783·2	0
9	$\Phi_{(t\times g+t\times a1,2+)}P_{(t\times g+t\times a1-2,3+)}$	111	67·0	754·7	0
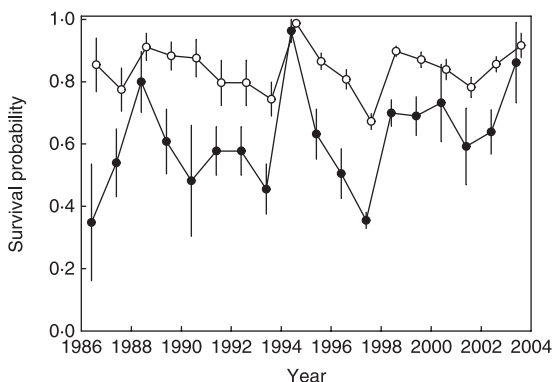
Fig. 1. Maximum likelihood probabilities (± SE) of juvenile (●) and adult (○) survival for Seychelles warblers between 1986 and 2004. Estimates are derived by model averaging.

Survival and resighting probabilities did not differ between the sexes. A model with equal survival and resighting probabilities for both sexes was 2·2 times better supported by the data than the next most parsi-monious model with different survival probabilities ($\Delta QAIC_c = 1·63$; $\beta \pm SE = 0·07 \pm 0·12$).

EFFECTS OF DENSITY

The translocations of 29 birds caused experimental reductions in density of 10% and 9% in 1988 and 1990, respectively. Although the population has been fairly stable since 1982 (Komdeur 1994a), the number of birds within the population does fluctuate a little between years (average: 308, range: 265–358, coefficient of variation = 10%). However, population size did not explain between yearly variation in survival for either juveniles or adults (Table 3a, models 4 and 5 vs. model 2). As the total number of birds in the population does not necessarily reflect local competition, we also inves-tigated density on an individual scale. Individuals that lived in high-density territories throughout their life had lower adult survival than individuals that lived in low-density territories (Table 3a, model 1 vs. model 2;

Table 3. Summary of model selection statistics of (a) density dependence, (b) territory quality and (c) weather variables on survival probabilities of the Seychelles warbler. The resighting probability was similar for all models: $P_{(t+g+a1-2,3+)}$. (t) = year, (a) = age and (g) = group (ringed as adult), (lds) = lifetime local density, (natalld) = natal local density, (popsize) = population size, (fa) = lifetime food availability, (nfa) = natal food availability, (tq) = lifetime territory quality, (ntq) = natal territory quality and (bs) = rainfall in breeding season

| No.	Model	No. Par.	$\Delta QAIC_c$	Quasi deviance	$QAIC_c$ weights
(a)					
1	$\Phi_{(t+lds\times a1,2+)}$	45	0	3689·2	0·96
2	$\Phi_{(t+a1,2+)}$	42	6·7	3702·1	0·03
3	$\Phi_{(t+natalld\times a1,2+)}$	43	10·7	3702·0	0
4	$\Phi_{(popsize\times a1,2+)}$	25	137·3	3868·9	0
5	$\Phi_{(popsize+a1,2+)}$	24	137·6	3871·2	0
(b)					
6	$\Phi_{((t+a1,2+)tq)}$	61	0	3646·6	0·88
7	$\Phi_{((t+a1,2+)fa)}$	61	4·7	3657·4	0·09
8	$\Phi_{(t+tq\times a1,2+)}$	44	6·8	3694·5	0·03
9	$\Phi_{(t+a1,2+)}$	42	10·4	3702·1	0
10	$\Phi_{(t+fa\times a1,2+)}$	44	13·1	3700·8	0
11	$\Phi_{(t+ntq\times a1,2+)}$	44	14·3	3702·0	0
12	$\Phi_{(t+nfa\times a1,2+)}$	44	15·9	3701·5	0
(c)					
13	$\Phi_{(t+a1,2+)}$	42	0	3702·1	1
14	$\Phi_{((a1,2+)+bs+bs(2))}$	25	128·0	3859·6	0
15	$\Phi_{((a1,2+)+bs)}$	24	129·2	3863·0	0
16	$\Phi_{((a1,2+)\times bs)}$	27	129·4	3856·9	0
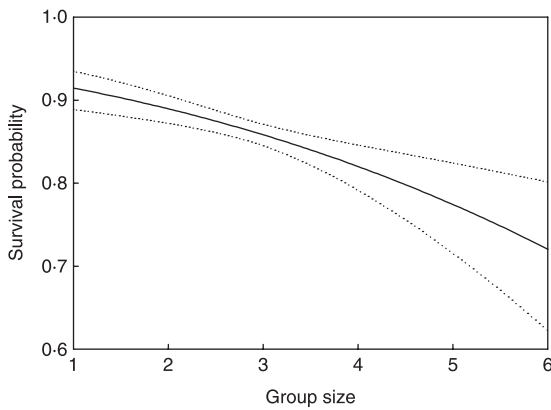
Fig. 2. Adult survival probabilities (–) of Seychelles warblers for an average year in relation to group size with 95% confidence interval (…).
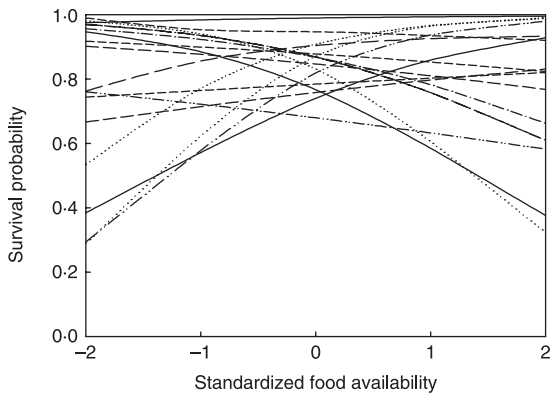

Fig. 3. Adult survival probabilities of Seychelles warblers for an average group size, in relation to lifetime food availability, shown in standard deviations from the mean for each year between 1986 and 2004.

Fig. 2). This model was 32 times better supported by the data than the starting model. However, natal local density did not influence juvenile or adult survival (Table 3a, model 3 vs. model 2).

EFFECTS OF ENVIRONMENTAL FACTORS

Lifetime territory quality did affect adult survival (Table 3b, model 8 vs. model 9); however, the effect was negative. After correcting for group size, lifetime food availability did not affect survival (Table 3b, model 10 vs. model 9), indicating that the negative effect of lifetime territory quality was caused by group size effects. Natal territory quality and natal food availability did not influence juvenile or adult survival (Table 3b, model 11 and model 12 vs. model 9). However, the effect of lifetime territory quality and food availability did vary between years (Table 3b, model 6 and 7 vs. model 9; Fig. 3). In none of the years did territory quality or lifetime food availability have a significant effect on survival.

Weather variables did not covary with population size, nor did they change systematically across the study period (all: $-0.37 < r < 0.37$, $P > 0.15$, $n = 17$). Variation

in temperature or rainfall during the breeding season did not explain variation in survival between years (Table 3c, shown for rainfall only: models 14 and 15 vs. model 13). Furthermore, the effect of rainfall in the breeding season did not affect age classes differently (Table 3c, model 16 vs. model 13). Similarly, the prebreeding season rainfall, the fledging period rainfall and the independence period rainfall did not affect either adult or juvenile survival ($\Delta QAIC_c > 119$, not shown). However, the two most extreme years, in relation to rainfall (breeding season rainfall: 1986: 60·3 mm and 1997: 1031·9 mm), also showed the lowest juvenile survival estimates (Fig. 1), indicating that extreme levels of rainfall did influence survival.

Discussion

DENSITY DEPENDENT SURVIVAL

Overall population density did not affect survival in our study. The experimental reduction of density caused by the translocations of warblers lies within the population's natural variation in density, which at only 10% corresponds with the low levels of between-year variation observed in other tropical species (Greenberg & Gradwohl 1986). In addition, long-lived species tend to have smaller annual population variability than short-lived species (Holyoak & Baillie 1996). Therefore, it is not surprising that we do not find an effect of population density on survival. Local density, measured as territory group size, did affect survival; birds living at higher local density had lower survival than those at low local density. In cooperatively breeding species, positive effects of group size on reproduction or survival are widespread (Rood 1990; Allainé *et al*. 2000; Clutton-Brock *et al*. 2001; Magrath 2001; Conner *et al*. 2004; Khan & Walters 2004), but negative effects are rarely reported. Studies on non-cooperative, group-living animals showed that the negative effects of increasing group size could be caused by larger groups attracting more predators (Begon, Harper & Townsend 1990) or increasing competition for food (Krause 1994; Bednekoff & Lima 2004). However, the species investigated all suffer from considerable predation pressure, which is not the case in the Seychelles warbler. Although eggs and small nestlings are predated upon by the endemic Wright's skinks (*Mabuya wright*), the Seychelles fodie (*Foudia sechellarum*) and Seychelles magpie robin (*Copsychus seychellarum*), there is no predation on adult warblers (Komdeur 1994a). Competition for resources is therefore the most probable cause of the decreasing survival with increasing group size observed in the Seychelles warbler.

In the Seychelles warbler, the negative effect on survival of living at high local density appears to be compensated for by a gain in reproductive success (Richardson, Burke & Komdeur 2002). Subordinates often gain direct fitness by co-breeding but, importantly, the dominants also gain from this through indirect kin

benefits as the subordinates are normally closely related to them (Richardson *et al.* 2001). Removal experiments have shown that the presence of one or two helpers improves the reproductive success of a group, but that the presence of three or more helpers has a negative effect on reproductive success (Komdeur 1994b). This means that living in groups that are too large will not be profitable for Seychelles warblers, as both reproductive success and survival decreases for groups containing more than five birds. Future research taking effects of the complicated breeding system of the Seychelles warbler (Richardson *et al.* 2001) into account could provide more insight in the effects of local and population density on reproduction.

SURVIVAL IN TROPICAL AND ISLAND SPECIES

The yearly adult survival calculated for the Seychelles warbler was high (84%) in comparison with other European passerines, which usually have probabilities of < 50% (Sæther 1989; Peach, Hanmer & Oatley 2001). This result concurs with the idea that the life history strategies of tropical species are typified by high survival rates and small clutch sizes. The absence (or infrequency) of periods of severe food shortage and climatic severity in the tropics allows high survival rates. However, even in comparison with related African passerines, survival is remarkably high in the Seychelles warbler; for example, the Cape reed warbler (*A. gracilirostris*) and African marsh warbler (*A. baeticatus*) have annual survival probabilities of $55 \cdot 7 \pm 8 \cdot 7\%$ and $76 \cdot 5 \pm 6 \cdot 9\%$, respectively (Peach *et al.* 2001). However, the survival probabilities reported in these studies may be underestimated through the inclusion of individuals that are presumed dead, when in reality they have migrated out of the study area. The inclusion of such migrants is not a problem in our study, as the population is confined totally to Cousin Island (Komdeur *et al.* 2004). Another important feature of island species is the absence of predators. The fact that nothing that preys upon adult Seychelles warblers will also contribute to the high survival rates observed. In addition, the island biogeography theory suggest that island species will have less parasites and pathogens than their mainland relatives (MacArthur & Wilson 1967), resulting in them experiencing less adverse effects on survival. Preliminary results of parasite studies in the Seychelles warbler confirm this theory (D. S. Richardson, personal communication).

Although lower than that of adults, the post-fledging survival of the Seychelles warbler was also relatively high (61%). This may be due to the prolonged parental care and delayed dispersal which juveniles undergo in this species as a response to habitat saturation and the birds' lack of willingness, or ability, to emigrate from the island (Komdeur 1992; Komdeur *et al.* 2004). Fledged Seychelles warblers are often fed until 3 months of age, which may enhance survival while developing foraging skills. Delayed dispersal has also been shown to promote juvenile survival in Siberian jays (*Perisoreus infautus*, Ekman, Bylin & Tegelstrom 2000) and brown thornbills (*Acanthiza pusilla*, Green & Cockburn 2001).

ENVIRONMENTAL EFFECTS ON SURVIVAL

In this study we found that, contrary to Komdeur (1992), higher food availability experienced during an individual's life did not result in higher survival. In his study there was a positive relationship between territory quality and survival; however, mark–recapture analyses were not used, sample sizes were much smaller and no between-year variation was taken into account. In the present study, we found a significant interaction between year and lifetime food availability/territory quality; however, this showed only that there was significant variation between years and that an index of territory quality, rather than the true territory quality, was measured. Although the repeatability of food availability during an individual's life was $0 \cdot 30 \pm 0 \cdot 02$ (calculated according to Lessells & Boag 1987), there might be too much variation, caused by changes in group size and food availability between years, to find an effect on survival. On the other hand, individuals may be mitigating (or avoiding) the negative effects on survival of living on a low quality territory by postponing or reducing reproduction. Indeed, in the Seychelles warbler reproductive success is influenced positively by territory quality (Komdeur 1992).

Although we found temporal variation in survival, we did not find an effect of weather variables. In temperate regions, the weather is a very important factor that influences survival either indirectly, via food availability (Newton 1998) or directly, e.g. via thermoregulation (Cuthill & Houston 1997). In our study, temperature did not affect survival, although this is not surprising as the variation in mean temperature between years is very limited (range mean temperature: $25 \cdot 6 – 26 \cdot 6$ °C). That rainfall did not affect survival estimates is surprising, as rainfall is known to influence insect numbers in our study area (Komdeur 1996b). However, the 2 years showing extreme levels of rainfall, i.e. drought (1986) or flood (1997), also show the lowest survival probabilities. This might indicate that survival is influenced by weather conditions, but our data set does not span enough years to detect any effects. Alternatively, we might not be able to detect effects on post-fledging survival as mortality might have occurred before this stage while the chick was still in the nest.

Our study shows that in a territorial species, although density-dependent effects might not be detectable at the population level they can be detected at the individual territory level – the scale at which individuals compete. These results will help to provide a better understanding of the small-scale processes involved in the dynamics of a population in general, but in particular in tropical species living in relatively stable environments.

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