Experimental evidence for density-dependent reproduction in a cooperatively breeding passerine

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Abstract. Temporal variation in survival, fecundity, and dispersal rates is associated with density-dependent and density-independent processes. Stable natural populations are expected to be regulated by density-dependent factors. However, detecting this by investigating natural variation in density is difficult because density-dependent and independent factors affecting population dynamics may covary. Therefore, experiments are needed to assess the density dependence of demographic rates. In this study, we investigate the effect of density on demographic rates of the Seychelles Warbler (*Acrocephalus sechellensis*). This species, endemic to a few islands in the Indian Ocean, went through a severe population bottleneck in the middle of the last century, with only ~30 individuals left on one small island, but has since recovered. Our monitoring shows that since reaching the island's carrying capacity, population density has remained stable. However, we detected neither density-dependent reproduction nor survival on the basis of natural density variation during this stable period. For conservation reasons, new populations have been established by transferring birds to nearby suitable islands. Using the change of numbers during the process of saturation as a natural experiment, we investigated whether we can detect regulation of numbers via density-dependent survival and reproduction within these new populations. We found that populations were mainly regulated by density-dependent reproduction, and not survival. Variation in density between islands can be explained by food abundance, measured as insect density. Islands with the highest insect densities also had the highest bird densities and the largest breeding groups. Consequently, we suggest that the density-dependent effect on reproduction is caused by competition for food.

Key words: Acrocephalus sechellensis; cooperative breeding; density-dependent reproduction; density-dependent survival; endangered birds; food availability; insect density; population dynamics; Seychelles Islands, Indian Ocean; Seychelles Warbler; translocation.

INTRODUCTION

Density dependence is a process that explains why populations normally fluctuate between certain numbers (Murdoch 1994, Sæther et al. 2002). Although many studies find negative relationships between density and reproduction (Kluyver 1951, Perrins 1965, Alatalo and Lundberg 1984, Arcese et al. 1992) or survival (Tinbergen et al. 1985, Francis et al. 1992, Lieske et al. 2000), this is not the case in all studies (van Balen and Potting 1990, Nur and Sydeman 1999, Loison et al. 2002, Festa-Bianchet et al. 2003). Furthermore, even within species

there can be considerable variation in the occurrence of density dependence (Both 2000). In contrast to the negative effects of increasing densities, at very low densities an increase in population size can have a positive effect on population growth, a phenomenon known as the Allee effect (Allee 1951; for a review see Courchamp et al. [1999]).

The mechanism by which density dependence occurs is not only important for our general understanding of population regulation, but also determines to a large extent the outcome of evolutionary life history models (Mylius and Diekmann 1995), quantitative models of cooperative breeding (Pen and Weissing 2000), and population viability analyses, which provide a quantitative assessment of the probability that a population will decline to extinction (Beissinger and Westphal 1998). Density-independent factors, such as climate, also affect the fluctuation of populations. Detecting density dependence depends to a large extent on the relative scale and

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the covariation of density-dependent and independent factors (Murdoch 1994, Sæther 1997). Consequently, the most fruitful way to assess the mechanisms that lead to density dependence in demographic rates has been to manipulate population density and study its effects. Many studies have done this indirectly by manipulating resources, e.g., by adding or removing nest boxes (Tompa 1967, Alatalo and Lundberg 1984, Török and Tóth 1988, Dhondt et al. 1992, Both 1998), or by supplementary feeding (Ewald and Rowher 1982, Davies and Lundberg 1984, Arcese and Smith 1988, Hoodless et al. 1999). However, manipulating density directly has the advantage that problems with possible confounding factors, such as individual quality, are avoided. Unfortunately such experiments are rare, especially on wild living vertebrates (but see Both and Visser 2000). Translocations of populations to uninhabited islands (e.g., as part of conservation programs) can provide experimental manipulations of density, as such populations start at low densities but undergo rapid changes in vital rates as the population grows (Armstrong and Ewen 2002, Nicoll et al. 2003, Armstrong et al. 2005).

Studies on density dependence in avian populations have been restricted to temperate regions. The question is then whether tropical species exhibit the same patterns of population regulation. Tropical species generally have higher survival rates and lower reproduction; consequently, density-dependent effects on these demographic rates may be different. Here we investigate whether we can detect regulation of numbers via density-dependent survival and reproduction using data from translocations of the tropical Seychelles Warbler (*Acrocephalus sechellensis*) to three different islands, done as part of the ongoing conservation of this species. The Seychelles Warbler went through a severe bottleneck with the ~30 last remaining individuals left on Cousin Island (29 ha) between 1920 and 1968 (Crook 1960, Loustau-Lalanne 1968). This population, which has since recovered and stabilized at ~320 adult individuals, has been studied since December 1985 (Komdeur 1992, Richardson et al. 2003). In order to save the species from extinction, new populations were established by transferring birds to the islands of Aride (1988), Cousine (1990), and Denis (2004). The Seychelles Warbler is a facultative cooperatively breeding species; although warblers can breed independently in their first year, a lack of suitable habitat in the saturated populations drives some individuals into becoming subordinates within their natal territory (Komdeur 1992). A previous study showed that neither the natural variation in density, nor the experimental reduction in density caused by the removal of warblers for translocation, was associated with a change in either juvenile or adult survival probabilities on Cousin Island (Brouwer et al. 2006). We now investigate whether this is also true for reproduction. Furthermore, we will use the change in numbers in the newly established populations during the

process of saturation as a natural experiment to examine how survival and reproduction are influenced by density. In addition to studying the regulatory mechanisms within islands, we will also investigate differences between islands. We seek to explain what limits population size by including island-specific bird and food density measures and, subsequently, we investigate the consequences for body mass and size. We predict that islands with higher food density will also have higher bird density, but that there will be no difference in body mass or size because higher food abundance will be averaged out by higher bird densities. By studying both the limiting factors and density-dependent patterns, we hope to shed light on what important density-dependent processes are occurring in these populations. Finally, we include a simple population model to address the consistency of the estimates and the relative importance of model components.

METHODS

Study species

The Seychelles Warbler is an insectivorous species that has long-term pair bonds. Both sexes of subordinates sometimes help with territory defense and the rearing of young (Komdeur 1994a, Richardson et al. 2002). Parentage analysis has shown that joint-nesting occurs frequently, with 44% of subordinate females producing offspring and 40% of offspring resulting from extra-group paternity (Richardson et al. 2001). Group size is defined as the number of independent birds resident in the territory, irrespective of whether they reproduce themselves. The main breeding peak is between July–September, with some breeding activity between January and March, although year-round breeding was observed after translocation (Komdeur 1996).

Study area and data collection

Data were collected on four different islands belonging to the Seychelles: Cousin (29 ha; 04°20' S, 55°40' E), Cousine (26 ha, of which 19 ha are natural habitat; Komdeur [1996]; 04°19' S, 55°39' E), Aride (68 ha; 04°13' S, 55°44' E), and Denis (144 ha, of which 140 ha are natural habitat; 03°48' S, 55°40' E). For an overview on details of each population and timing of data collection, see Table 1. On Cousin, data were collected as part of the long-term study of the Seychelles Warbler population. Except for 1992, this population has been monitored every year since December 1985. From 1991 to 1994, only a part of the population was monitored (68% of territories). Because the number of territories is relatively constant across years ($N = 112.3 \pm 1.2$ territories, mean $\pm$ SE, for 1986–1990, 1995–2006), population size for these years was estimated by multiplying the number of birds observed by the proportion of territories monitored. During the main breeding season, each territory was checked for breeding activity at least once every two weeks by following the

TABLE 1. Summary showing years of data collection and results for each of the populations of Seychelles Warblers (*Acrocephalus sechellensis*).

Data collected	Cousin	Aride plateau	Cousine	Denis
Establishment year	. . .	1988 ($N = 12$ birds)	1990 ($N = 29$ birds)	2004 ($N = 58$ birds)
Annual reproduction	1986–1989, 1998, 1999, 2004, 2005	1989–1991, 1999	1991	2004, 2005
Seasonal reproduction (main season)	1986–1991, 1993–2005	1989–1991, 1995, 1996, 1999	1991, 1995–1997	. . .
Mark–recapture/resighting	1986–1991, 1993–2005	1988–1991, 1993–2000	1990, 1991, 1994–1999	2004–2006
Density at establishment (no. birds/ha)	. . .	2.3	1.5	0.41
Asymptotic density (no. birds/ha)	10.8	25.0	6.8	. . .
Territory size (ha), mean ± SE	0.23 ± 0.01 ($N = 107$ territories)	0.16 ± 0.01 ($N = 34$ territories)	. . .	. . .
Group size, mean ± SE	2.8 ± 0.1 ($N = 107$ groups)	3.3 ± 0.2 ($N = 36$ groups)	2.7 ± 0.2 ($N = 41$ groups)	. . .
Insect density/count (1990), mean ± SE	74.7 ± 10.4 ($N = 3$ monthly counts)	233.7 ± 44.7 ($N = 3$ monthly counts)	124.0 ± 35.2 ($N = 3$ monthly counts)	. . .
Insect density/count (1996), mean ± SE	127.0 ± 26.7 ($N = 3$ monthly counts)	231.7 ± 54.7 ($N = 3$ monthly counts)	86.0 ± 14.7 ($N = 3$ monthly counts)	. . .

Notes: Ellipses indicate that no data are available. Insect density/count is the mean number of insects per 150 leaves (50 leaves of each of the three main tree species) counted on at least 15 locations per island.

resident female for 30 minutes (Komdeur 1992). Territory borders were mapped based on observations of individual warblers and the outcome of disputes between groups (Komdeur 1991).

For conservation reasons, 29 warblers each were translocated to Aride in 1988 and Cousine in 1990 (Komdeur 1994*b*). The total Aride population was studied from establishment in September 1988 until November 1991. After 1991, research focused only on the most accessible plateau area (5.2 ha) of the island. Each year between 1993 and 2000, capture–recapture data were collected by mist-netting, allowing us to estimate survival and resighting probabilities separately. From 1995 to 2000, except for 1997, each territory was checked for the number of birds. In addition, during the main breeding season in 1995 and 1996, and year-round in 1999, the study area was monitored for reproduction. Furthermore, point sampling and line transect sampling were carried out across the whole island in 1997 and on the plateau in 2003 to estimate population size (Betts 1998). In 1988, the total size of the area that was covered by territories was estimated; in 1999 each territory was mapped, allowing individual territory sizes to be estimated.

The population on Cousine Island was studied for two months after the founding of the population in July 1990 and then during the main breeding seasons in 1991 and 1995–1997. In 1994 and 1998, each territory was checked for the number of birds. Furthermore, during the main breeding seasons of 1994–1999, mark–recapture data were collected by mist-netting, and in 1994, 2002, and 2006 several visits during the main breeding season resulted in estimates of the number of territories and birds. In the years in which the populations were completely monitored, population sizes were estimated as the number of independent birds (i.e., excluding juveniles fed by adults), after correcting for the

resighting rate for that period (number of counted individuals/resighting rate). As resighting rates were very high for these periods ($P > 0.9$), the estimates are very accurate.

In 2004 a population of Seychelles Warblers was established on Denis Island by Nature Seychelles. This population was studied for two months after the translocation in June 2004, and then in January 2005 and in July–August 2005 and 2006. As birds within this population are attempting to breed year-round, the estimated yearly reproduction probably will be underestimated, as some juveniles may have died before being recorded.

During each monitoring period, as many birds as possible were caught, either as nestlings or after fledging (using mist nets), and were banded with a unique combination of three ultraviolet-resistant color bands and a British Trust for Ornithology metal band. Body mass to the nearest 0.1 g and tarsus length to the nearest 0.1 mm were recorded.

Reproduction

To investigate whether reproduction on Cousin is related to natural variation in density and whether group size, territory size, and territory quality are associated with reproduction, we analyzed reproduction in the years when both the main breeding season and the minor breeding season were monitored: 1986–1989, 1998–1999, and 2004–2005. For this analysis, reproduction was defined as the total number of fledglings observed per territory in a year, with the total number of territories remaining relatively constant. Because territory size and group size are correlated, we investigated the effect of territory size separately by including the relative territory size per bird (territory size/group size). 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 negatively affects reproductive success (Komdeur 1994a). Therefore, group size was also included as a squared effect. Although the removal of birds from Cousin in 1988, 1990, and 2004 gave us the opportunity to investigate the effects of reduced density on reproduction, this analysis suffered from some difficulties. First, the transfer of birds in 1988 occurred after the breeding season; consequently, effects of reduced density on reproduction could only be tested in 1989, at which time the population had already returned to its original level. Second, after the transfer of 1990, the population was not intensively monitored for reproduction. Third, the transfer in 2004 was followed by an extreme drought (26.2 mm rain vs. the average 144.5 ± 22.9 mm rain (mean $\pm$ SE; $N = 18$ years) in June and July) which resulted in very few territories with nesting activity.

To investigate whether increasing density in the newly established populations resulted in reduced reproduction, we analyzed the relationship between density and per capita (per breeding season) reproduction on Aride, Cousine, and Cousin simultaneously. For Aride and Cousine, we used all breeding seasons in which reproduction data were collected, and the same seasons were selected for Cousin. In a cooperative breeding system, reproduction can be defined in several ways and the method of analysis may illuminate different biological processes. We first investigated the per capita reproduction in relation to population density. However, with increasing density, group sizes will also increase and therefore any reduction in per capita reproduction might be a result of increasing group sizes. Consequently, we also investigated the fledgling production per territory in relation to population density.

Survival

To estimate survival, we constructed the capture–resighting histories of all marked individuals that were monitored on Aride, Cousine, and Denis. On Aride, 539 birds were monitored between 1988 and 2000; of these, 188 individuals were banded as juveniles and were of known age. Because only the plateau area was completely monitored, dispersal may have caused survival to be underestimated. Consequently, the survival probabilities for Aride represent local, rather than true, survival. On Cousine, 183 birds were monitored between 1990 and 1998. Of these, 51 individuals were banded as juveniles and were of known age. On Denis, 93 birds were monitored between 2004 and 2006. Of these, 25 individuals were banded as juveniles on Denis Island. The resighting period was defined as the main breeding season. The resighting history files were used as input files in the program MARK (White and Burnham 1999).

Food abundance

Seychelles Warblers take 98% of their food from the underside of leaves of the three main tree species: *Pisonia grandis*, *Morinda citrifolia*, and *Ficus* sp. (Komdeur 1991, Komdeur 1994b). Consequently, to get an estimate of food abundance for each territory on Cousin, estimates of insect density per square decimeter leaf area and vegetation abundance scores were used to calculate territory quality following Komdeur (1992), with the difference being that territory size was now excluded from the calculation and investigated separately. This allows us to investigate effects of quality independently from territory size. Insect density was estimated by counting total insect numbers on the underside of 50 different leaves of each of the three main tree species at 15 different locations. The division into the 15 regions was based on the amount of wind-driven salt spray, which causes defoliation (Komdeur 1991). Insects were counted in the most central territory in each region and these were extrapolated to all territories within that region (Komdeur 1991). Leaf area was assessed by measuring the area of 250 leaves at 50 random sites on the island (five leaves per species per site). Vegetation abundance was scored by determining the presence or absence of all plant species at 20 random points in the territory in the following height bands: 0–0.75 m, 0.75–2 m, 2–4 m, and at 2-m intervals thereafter. One estimate of territory quality was available for each territory for the period 1986–1989 (Komdeur 1992). To calculate the quality for each territory in 1998 and 1999, vegetation abundance scores measured during the main and minor breeding season of 1999 were used in combination with insect counts from 1998 and 1999, respectively. To get an estimate of territory quality for 2004 and 2005, the average vegetation abundance scores of the main breeding season in 2004 and minor breeding season in 2005 were used with insect counts from 2004 and 2005, respectively.

During the breeding seasons of 1990 and 1996, three insect counts (each a month apart) were performed to estimate food abundance on the three islands simultaneously. Insects were counted on the underside of 50 leaves of each of the three main tree species on at least 15 different locations per island.

Data analyses

For the Cousin population, the natural variation in reproduction on individual territories was analyzed as function of density and a number of covariates. There are many repeats of the same territories between years that might be intercorrelated. Similarly, different territories might be correlated within year due to between-year differences. Consequently, we modeled year identity and territory identity as cross-classified random effects, with reproduction (number of fledglings) of each territory nested within these random effects. Reproduction was fitted using a Poisson response model with log-link function.

To investigate the effect of density on reproduction between populations, the average per territory reproduction ($\log_{10}$-transformed to normalize data) was analyzed using a normal response model with year

defined as a random effect to account for systematic differences between years. Similarly, in the analyses of the effect of density on group size, year was included as a random effect.

To investigate whether differences in population and insect density also lead to differences in structural size measurements, we analyzed body mass and tarsus length measurements from adult birds. As no data are available during the process of saturation, we only investigate whether the difference in population densities between the populations had any effect. Tarsus measurements of translocated birds were not taken into account when measured in the new population. Although body mass might fluctuate over the season and time of day, we do not think this could cause a bias in the data because similar catching strategies were performed in all populations. However, because body mass and tarsus length are correlated, we used the residuals of a regression on body mass and tarsus size. Residual body mass and tarsus size were fitted using a normal response model. Because measurements from the same bird or of the same observer might be intercorrelated, bird identity and observer identity were included as cross-classified random effects, with the measurements nested within these random effects.

To investigate whether insect densities differed between populations, monthly insect counts were fitted as a normal response model with month included as a random effect. All analyses previously mentioned were performed in program MLwiN 2.02 (Rasbash et al. 2004). Model selection was based on stepwise backward elimination of the nonsignificant terms in the order of their significance assessed by the Wald statistic. The final model contained all significant explanatory terms and their effect sizes were based on this model. All eliminated terms were reintroduced to the final model to estimate their effect size and confirm their lack of contribution. Means are expressed with standard errors.

To investigate the effect of population density on survival probabilities for Aride and Cousine, we employed an a priori approach in which a set of candidate models was created based on biological reasoning. Previous analyses showed that the survival of Seychelles Warblers on Cousin varied between years and was lower in their first year of life (juvenile survival) than for older birds (adult survival) (Brouwer et al. 2006). Furthermore, there was no variation in survival or in resighting probability between the sexes and no association with territory quality (Brouwer et al. 2006). Consequently, our global model allowed survival and resighting rate to vary between years. For Aride, birds banded as juvenile were included as a group in the analysis and their survival probabilities were allowed to vary between the age classes (first year and older). However, for Cousine, only a few juveniles were banded over a long time span and therefore these were only included in the analysis as an adult after their first year of life. Akaike's information criterion corrected for sample size (AIC_c) was used to select the most parsimonious model for the resighting probabilities, with better fitting models resulting in lower AIC_c values (Akaike 1973). As we are interested in the effect of density on survival probabilities, we do not use model selection to get the most parsimonious model for the survival probabilities, but use the global model for survival to investigate the effect of density (for Aride, full year × age model; for Cousine, full year model). We calculated the normalized Akaike weights to assess the relative likelihood of competing models. We checked the goodness of fit for the global model by using median $\hat{c}$ procedure, which showed some evidence for overdispersion (Aride, $\hat{c} = 1.16 \pm 0.03$; Cousine, $\hat{c} = 1.32 \pm 0.03$; Denis, $\hat{c} = 1.04 \pm 0.05$). Therefore, AIC_c values were adjusted to allow for the extent of overdispersion measured by $\hat{c}$, through quasi likelihood ($QAIC_c$). Population density was included in the most parsimonious model (regarding resighting) as a linear constraint on survival probabilities to test whether survival rates changed with increasing population density. Years in which no estimate of population density was available were extrapolated from nearest known numbers available. Additionally, a random-effects variance components model was used to assess true temporal variation in survival vs. sampling variation using Markov Chain Monte Carlo (MCMC) methods in program MARK (Burnham and White 2002, Franklin et al. 2002). Due to the limited number of years with data for Cousine, this was done for the Aride data set only (Burnham and White 2002). The means of the two hyperdistributions of annual survival parameters (one for each age class) were modeled with a design matrix including density as a temporal covariate. Flat priors were used for the sigma and beta parameters. Initial estimates for the other parameters were taken from the original maximum likelihood model including year as a fixed variable. A chain of 50 000 iterations was run, of which the first 10 000 were discarded (burn-in).

To investigate the relation between population density and survival between populations, weighed averages of annual survival estimates were used in a linear regression with population density. Due to data limitations, juvenile survival probabilities for the Denis population were not allowed to vary over time and their resighting probabilities were kept similar to those of adults. To estimate annual survival probabilities we used model-averaging techniques whereby the impact of all time-dependent survival models were weighed for a given parameter according to its $QAIC_c$ weight (Burnham and Anderson 2002).

Population model

To address the consistency of the estimates and the relative importance of density-dependent reproduction and survival, the population trajectories were projected using a deterministic population model based on our estimates of survival and reproduction. The following
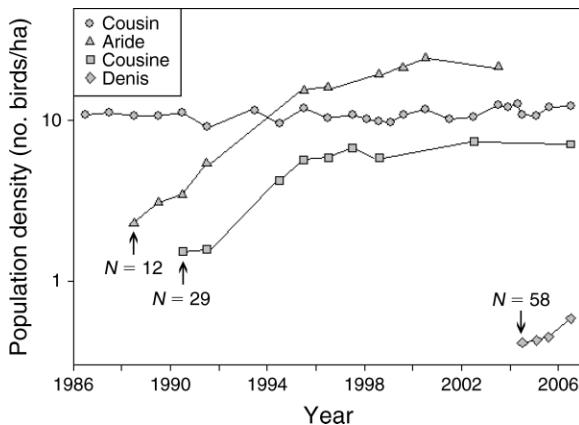
Fig. 1. Temporal fluctuations of population density (on $\log_e$ scale) of Seychelles Warblers (*Acrocephalus sechellensis*) on the islands of Cousin, Aride (plateau), Cousine, and Denis. Arrows with sample sizes (number of birds) indicate the introduction of birds to each island.

model was used to calculate population size (N) at $t + 1$:

$$N_{t+1} = N_t F_{(N_t)} P_{j(N_t)} + N_t P_{a(N_t)}$$

with

$$\log F_{(N_t)} = \text{constant} + \beta_{(F)} N_t$$

$$\text{logit} \, P_{j(N_t)} = \text{constant} + \beta_{(P_j)} N_t$$

$$\text{logit} \, P_{a(N_t)} = \text{constant} + \beta_{(P_a)} N_t$$

where F is annual reproduction, P_j is juvenile survival, and P_a is adult survival. The relationship between annual reproduction and density ($\beta_{(F)}$) was fitted using the model from Table 3 whereby the relationship between seasonal and annual reproduction was calculated from the years where both estimates were available. The relationship between survival and density ($\beta_{(P)}$) was derived from including population density as a linear constraint on the survival probabilities. As these data were not available for juveniles on Cousine, the effect was assumed to be similar as for adults. In the population model including density-dependent reproduction only, survival was kept constant at the mean of the population. Similarly, when including density-dependent survival only, reproduction was kept constant at the mean of the population.

RESULTS

Population dynamics

The population of Seychelles Warblers on Cousin Island has been fairly stable since 1986 with only little natural fluctuation in the number of birds between years (10.8 ± 0.2 birds/ha, mean ± SE; CV = 0.10). The translocations of 29 birds in 1988 and 1990 caused experimental reductions in density of 10% and 9%, respectively, within the 10% natural variation (Fig. 1).

The translocation of 58 warblers in 2004, however, reduced the population density by 16%. In all cases the population recovered within one or two years to its original size, suggesting strong density dependence.

After the transfer in 1988, the birds on Aride experienced extremely low densities. Twelve out of the 29 translocated birds established themselves on the plateau area (2.3 birds/ha; Table 1). The population on the plateau increased 10-fold to an asymptote of around 120 birds (25 birds/ha) in 1998, and was relatively stable thereafter (Fig. 1). A survey in 1997 indicated that the total population size was 1600 birds (23.5 birds/ha) (Betts 1998), a more than 50-fold increase in density since the introduction. The population on Cousine Island showed a similar pattern of population growth. After the release of 29 birds (1.5 birds/ha) in 1990, the population grew to an asymptotic size of around 130 individuals by 1996 (6.8 birds/ha). In 1999 a project was started to regenerate the habitat in the formerly unsuitable (garden) area on Cousine, resulting in an increase of total population size to 175 birds in 2007; however, density remained constant at 6.7 birds/ha. Denis Island is the largest island and therefore had the lowest density of 0.41 birds/ha (58 birds) when first established in 2004; numbers had only increased to 82 birds (0.59 birds/ha) by 2006.

During the process of population growth on Aride, the number of territories increased as a result of birds expanding their range over the island, but the size of the territories simultaneously decreased fivefold, from an average of 0.81 ha ($N = 6$) in 1988 to 0.16 ± 0.01 ha ($N = 34$) in 1999. Average territory size at saturation (1999) on Aride was significantly smaller than the average territory size on Cousin (Table 1; $N = 107$; $U = 701.0$, $P < 0.001$).

As density increased so did group sizes: on Aride group size increased from 2.0 ± 0.3 ($N = 6$) in 1988 to 3.3 ± 0.2 ($N = 36$) birds per territory in 1999 and was significantly density dependent ($\chi_1^2 = 13.0$, $P < 0.001$). Similarly, group sizes on Cousine increased from 1.6 ± 0.2 ($N = 11$) in 1991 to 2.7 ± 0.2 ($N = 41$) birds per territory in 1998, although this density-dependent trend was not quite significant ($\chi_1^2 = 3.22$, $P = 0.07$). After saturation, territories on Aride contained the largest groups, which were significantly larger than on Cousin (Table 1; $U = 1552$, $P = 0.04$) and Cousine (Table 1; $U = 541.0$, $P = 0.02$). Group sizes on Cousine were not significantly smaller than on Cousin (Table 1; $U = 2063.0$, $P = 0.41$). On Denis, cooperative breeding has not been observed in the two years since the translocation and all territories still consist of single birds or pairs.

The population growth rates (r) can be derived by estimating the slopes of the relationship between $\log_e$ population densities and year (Fig. 1). Population growth rates clearly decrease with increasing population densities during the process of saturation. Population density alone did not account for all of the observed variation between islands; at very low densities during the year after translocation, the population growth rates

TABLE 2. Results from analyses examining annual reproductive output per territory (no. fledglings) of Seychelles Warblers on Cousin Island for 8 years between 1986 and 2006 ($N = 902$ territories).

Parameter	$B \pm SE$	χ^2	df	P
Final model				
Intercept	-2.91 ± 0.38		1	
Territory size/bird	3.24 ± 0.81	14.0	1	<0.001
Group size	1.12 ± 0.20	27.4	1	<0.001
Group size^2	-0.09 ± 0.03	11.7	1	<0.001
Random effects				
σ^2_{year}	0.16 ± 0.15			
$\sigma^2_{territory}$	0.01 ± 0.01			
Rejected				
Population density	0.14 ± 0.20	0.50	1	0.48
Territory quality	0.002 ± 0.01	0.02	1	0.89
Total rainfall	0.001 ± 0.001	0.46	1	0.50
Breeding season rainfall	0.001 ± 0.001	0.10	1	0.75

Notes: Results are derived from a hierarchical cross-classified model whereby reproduction was fitted using a Poisson response model with log-link function. Density, total rainfall, and breeding season rainfall are year variables and, consequently, are modeled on the year variation, whereas the other variables are modeled at the level of the individual territories. B is the estimate of the effect size (β); values of B are on the scale of the link function used (log scale).

on Cousine and Denis Island were similar ($r = 0.03$), but were lower than on Aride ($r = 0.29$) (Fig. 1).

Reproduction

On Cousin the average per capita reproduction was 0.27 ± 0.03 fledglings per year (range 0.17–0.42). Reproduction varied between years, but the variation was unrelated to population density, the amount of rainfall during the breeding season, or the total amount of rainfall in that year (Table 2). Furthermore, no association was found between the index of territory quality and annual fledgling production (Table 2). The available territory space per individual, however, was positively associated with reproduction, independent of group size (Table 2). In addition, reproduction was positively related to group size, but did not increase further after group size five (Table 2, Fig. 2).

The per capita reproduction was strongly negatively related to the population density on both Aride and Cousine: after translocation, reproduction was initially high but declined as the population grew (Fig. 3a, b). The seasonality of reproduction was also affected by the translocation: on Aride, year-round breeding occurred when the population was at a low density and this became seasonal with increasing density. This was not caused by differences between years, as reproduction on Cousin was always seasonal. The per capita reproduction on Aride was, on average, 5.6 times higher in the first three years after translocation than on Cousin, and twice as high as in the first year on Cousine (Fig. 3a). At low density, reproduction on Cousine was also higher than at saturation on Cousin (Fig. 3a). Analysis of the per capita reproduction per breeding season showed

that, with increasing density, reproduction decreased significantly on Aride and Cousine (Table 3a, Fig. 3b). The strength of the decrease in reproduction with increasing density was stronger on Cousine than on Aride (Table 3a, Fig. 3b). Furthermore, the natural variation in density on Cousin was also negatively associated with reproduction (Fig. 3b). After the populations reached their stable size, per capita reproduction was very similar among the islands.

Although group size also increased with increasing density, and could therefore have caused the decrease in per capita reproduction, this was not the case. Analysis of reproduction at the territory level gives similar results; with increasing density, reproduction significantly decreased both on Aride and Cousine (Table 3b).

To investigate whether the variance in reproduction per territory increased as a result of lower quality habitat being occupied, the variance in reproduction at low density was compared with that at high density. However, with increasing density the variance in reproduction on Aride and Cousine did not change (Levene's test: for Aride, $F_{5,32} = 0.86$, $P = 0.36$; for Cousine, $F_{8,42} = 0.62$, $P = 0.44$).

Survival

Resighting probabilities on Aride varied between years in a similar way for both age classes. This model was better supported by the data than when allowing resighting to vary between age classes only ($\Delta QAIC_c = 83.6$), between the age classes and years ($\Delta QAIC_c = 2.1$), or between years only ($\Delta QAIC_c = 4.5$). On average the annual survival probability was 0.68 ± 0.05 (resighting probability $= 0.56 \pm 0.14$) for juveniles and 0.77 ± 0.02 (resighting probability $= 0.79 \pm 0.07$) for adults (all values mean $\pm$ SE). Resighting probabilities on Cousine did not vary between years; a model including constant resighting was better supported by the data than year-
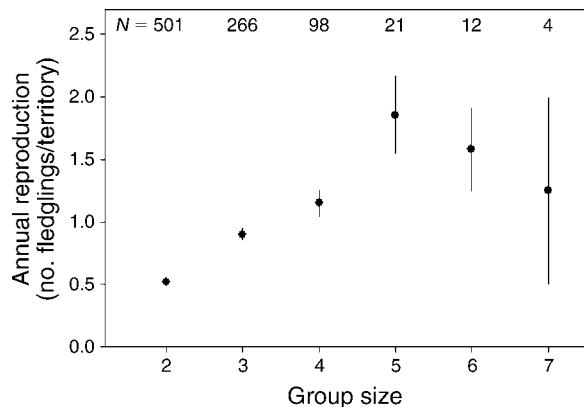

FIG. 2. Annual reproduction (mean $\pm$ SE) of Seychelles Warblers in relation to group size on Cousin Island. Values are corrected for territory size and between-year and territory variation according to the final model in Table 2. Numbers at the top of the panel indicate the total number of individuals sampled.
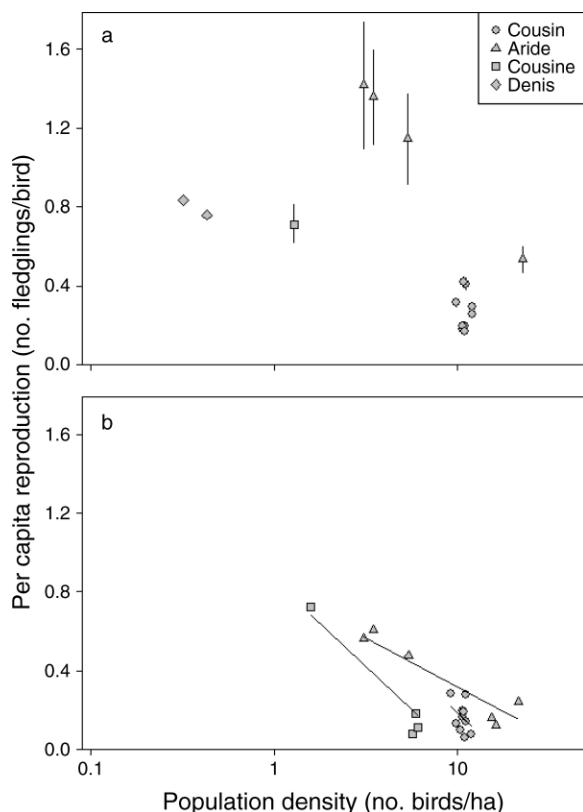
FIG. 3. Per capita reproduction in relation to population density (on $\log_{10}$ scale) for Seychelles Warblers of the islands of Cousin, Aride, Cousine, and Denis (a) per year and (b) during the main breeding season (July–September). Lines are regression lines according to the model shown in Table 3a. Data in panel (a) are given as mean ± SE.

dependent resighting probabilities ($\Delta QAIC_c = 6.1$). The average annual adult survival probability was 0.83 ± 0.07 (resighting: 0.95 ± 0.02).

Including density as a linear constraint on survival showed that increasing density did result in decreasing survival rates for adults on Aride ($\beta = -0.0084 \pm 0.0038$; Fig. 4a) and Cousine ($\beta = -0.0089 \pm 0.0045$; Fig. 4a), but not for juveniles on Aride ($\beta = 0.0123 \pm 0.0065$; Fig. 4b). Removing the sampling variance for the Aride estimates in a random-effects model resulted in similar, but not significant, effects of density on adult ($\beta = -0.0107 \pm 0.0069$) and juvenile ($\beta = 0.0056 \pm 0.0062$) survival. Furthermore, when all annual survival estimates for the different populations are combined, there is no indication that higher density resulted in lower survival probabilities (for juveniles, $r = 0.14$, $P = 0.45$; for adults, $r = 0.01$, $P = 0.97$; Fig. 4).

Food as cause of density dependence?

We showed that populations on the three islands differed in their asymptotic population size, the territory size, group size, and the reproductive output for the same density. To understand these differences between

populations, we analyzed insect densities on the three islands. In 1990, insect density on Cousin was lower than on Aride (Table 1; $\chi_1^2 = 17.7$, $P < 0.001$) and on Cousine (Table 1), although this last difference was nonsignificant ($\chi_1^2 = 1.7$, $P = 0.19$). By 1996, after both islands had reached saturation, insect availability was only 1.8 times higher on Aride than Cousin, and 0.7 times lower on Cousine in comparison to Cousin (Table 1; Aride, $\chi_1^2 = 16.4$, $P < 0.001$; Cousine, $\chi_1^2 = 2.5$, $P = 0.11$). Over the years (1987, 1990, 1996–1999, 2003–2005) insect densities on Cousin did not change systematically ($F_{1,9} = 0.62$, $P = 0.45$). Although based only on the small data set of three islands, it is striking that the island with least food (Cousine) has the lowest asymptotic density with the strongest density dependence of reproduction, whereas the island with the highest food availability (Aride) has the highest asymptotic density, the highest annual reproduction at low density, and the weakest density dependence.

Insect density could explain the main patterns in reproduction and asymptotic population density between populations, but does it also affect growth of birds? For this we investigated whether there are differences in residual body mass and tarsus length of the birds on the different islands. Both residual body mass and tarsus length differed significantly among islands, with Aride having the largest (but similar to Cousin) and relatively heaviest birds, and Cousine having the smallest birds (Fig. 5). That these differences

TABLE 3. Relation between population density and the average: (a) per capita and (b) per territory reproduction per breeding season for Seychelles Warblers on the islands of Cousin, Aride, and Cousine.

Parameter	$B \pm SE$	χ^2	df	P
a) Final model				
Intercept	-2.47 ± 1.04		1	
Density	-0.26 ± 0.07	12.3	1	<0.001
Population†		1.02	2	0.31
β_{Cousin}	3.37 ± 6.23			
$\beta_{Cousine}$	1.69 ± 1.73			
Density × population‡		6.67	2	0.04
β_{Cousin}	-0.62 ± 0.58			
$\beta_{Cousine}$	-0.84 ± 0.33			
Random effect, σ^2_{year}	2.68 ± 1.44			
b) Final model				
Intercept	2.24 ± 1.18		1	
Density	-0.25 ± 0.09	8.07	1	0.004
Population†		0.29	2	0.87
β_{Cousin}	2.77 ± 7.48			
$\beta_{Cousine}$	1.04 ± 2.21			
Density × population‡		5.60	2	0.06
β_{Cousin}	-0.62 ± 0.70			
$\beta_{Cousine}$	-0.10 ± 0.04			
Random effect, σ^2_{year}	0.14 ± 0.11			

Note: Estimates of effects sizes (B) have been multiplied by 10 and are on the scale of the link function used (log scale).

† Reference category is Aride population and is given by the intercept.

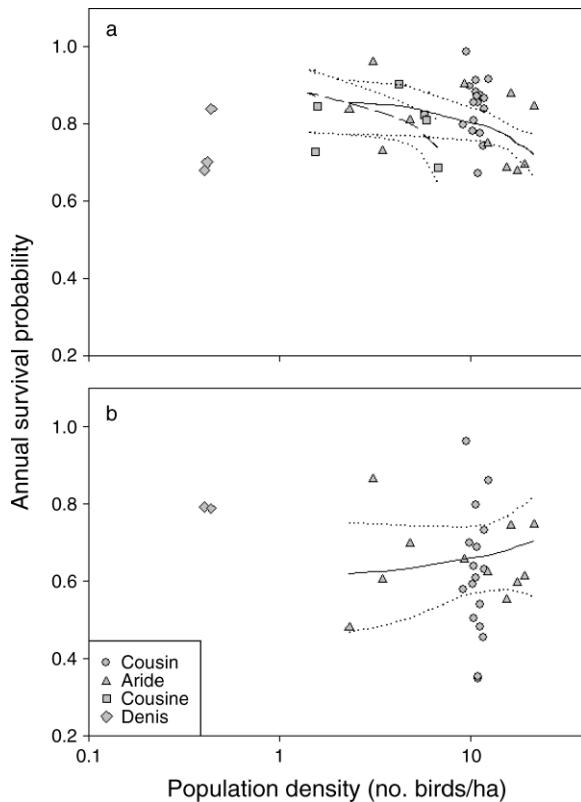‡ Reference category is Aride population and is given by the density main effect.

FIG. 4. Annual survival probabilities of Seychelles Warbler (a) adults and (b) juveniles in relation to population density for each of the four island populations. Estimates of survival are derived by model averaging. Lines show the estimated effect (and 95% confidence interval) of density according to the global model with density included as a covariate for Aride (solid line) and Cousine (long-dashed line [in panel (a) only]). For Cousine, only a few juveniles were banded over a long time span, and therefore these were only included in the analysis as adults after their first year of life.

are due to effects of population density seems unlikely because on the island of highest density (Aride), the birds are biggest and relatively heaviest. Sample sizes for the Denis population were too small to reach conclusions. As no size measurements are available during the process of population saturation on Aride and Cousine, we cannot test whether an increase in density within islands leads to lower body mass or structural size.

Population model

The predictions of the population models for Aride including density-dependent reproduction and survival, or density-dependent reproduction alone, closely matched the observed asymptotic density (Fig. 6a). In contrast, a model including density-dependent survival alone did not reach the asymptotic density within the observed time period (Fig. 6a). The observed asymptotic density for the Cousine population was higher than any of the predictions of the models, although models including density-dependent reproduction and survival, or density-dependent reproduction only, were better

predictors than density-dependent survival only (Fig. 6b). For both populations the observed growth trajectory was lower than those according to the models including density-dependent reproduction and survival, or reproduction only. The population model shows that, for both populations, density-dependent survival is not needed to create density dependence, but density-dependent reproduction is.

DISCUSSION

Density dependence

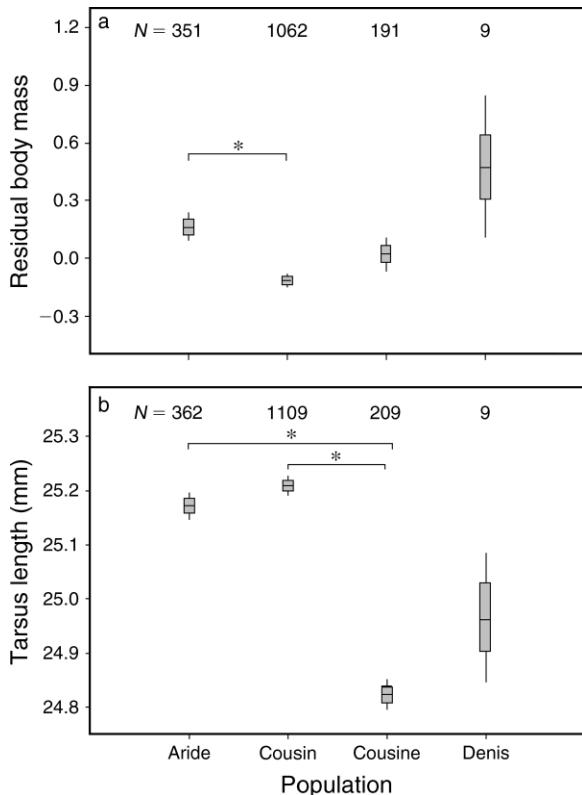After translocation to new islands, the Seychelles Warbler populations were initially far below carrying

FIG. 5. Box and whisker plots showing mean ± SE (in gray) and 95% CI for (a) residual body mass and (b) tarsus length measurements of adult Seychelles Warblers for the populations of Aride (density during measurements = 18.1 ± 1.4 birds/ha; all values reported as mean ± SE), Cousin (density during measurements = 10.8 ± 0.2 birds/ha), Cousine (density during measurements = 6.0 ± 0.6 birds/ha), and Denis (density during measurements = 0.57 birds/ha). The estimate of variation that could be attributed to systematic differences between individuals (for residual body mass, $\sigma^2 = 0.52 \times 10^{-3} \pm 0.07 \times 10^{-3}$; for tarsus, $\sigma^2 = 1.06 \pm 0.06$; all values reported as mean ± SE) and observers (for residual body mass, $\sigma^2 = 0.38 \times 10^{-3} \pm 0.13 \times 10^{-3}$; for tarsus, $\sigma^2 = 0.07 \pm 0.03$) has been used to correct the values in this figure by calculating the residuals of the predicted values according to observer and individual variation and the actual values. Numbers at the top of each panel indicate the total number of birds sampled. An asterisk between bracketed populations indicates significance at $\alpha = 0.05$.
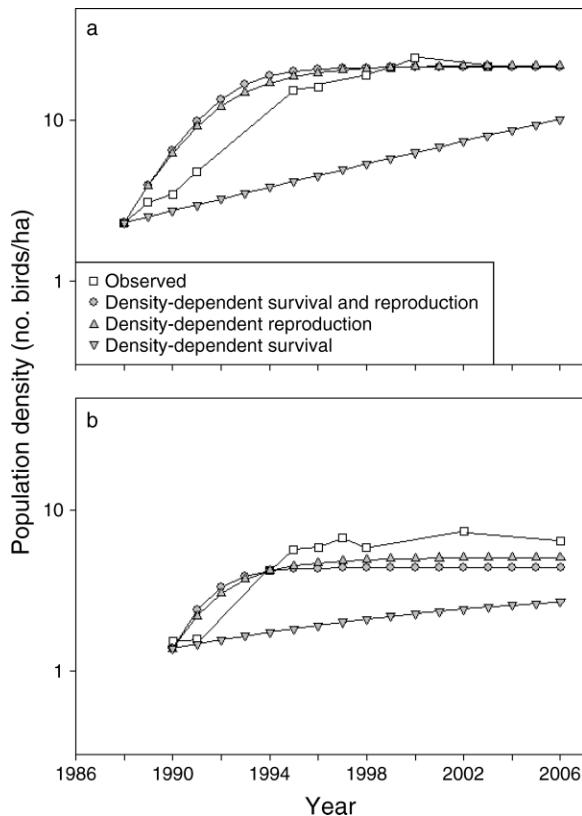
FIG. 6. The observed and predicted trajectories of population density according to a population model including density-dependent reproduction, density-dependent survival, or both for the populations of Seychelles Warblers on (a) Aride and (b) Cousine.

capacity but grew rapidly to reach an asymptotic level, which differed among islands. This experiment provided good evidence that reproduction was strongly negatively related to population density. Asymptotic population density was higher on the island with higher food abundance, and birds were larger there. Furthermore, the strength of the decline with population density was weaker for the island with high food abundance, and initial annual reproduction was higher there, although this could be a result of between-year variation. The reduced productivity is probably caused by a combination of fewer birds breeding, fewer nesting attempts per territory, and reduced egg production per nesting attempt, but unfortunately we do not have sufficient data to investigate this further. We found some evidence for density-dependent survival; however, the results were ambiguous; although increasing density was negatively associated with adult survival, it was positively associated with juvenile survival. Furthermore, density-dependent survival was not necessary to explain density dependence in the population models for Cousine and Aride. This indicates that our survival estimates are not accurate enough to exclude the possibility that density-dependent survival occurs, mainly caused by small

sample sizes and thus large confidence intervals of the survival estimates at low density. A previous study of the effect of reduced density, caused by removal of birds, on survival probabilities also showed that survival was not important in regulating population density (Brouwer et al. 2006). Altogether, these results indicate that regulation of numbers takes mainly place via density-dependent reproduction, probably caused primarily by competition for food. Although the predicted asymptotic density for Aride reflected the observed level well, this was not the case for Cousine. Most likely, reproduction was underestimated, as an increase of at least 6% in the mean survival for both adults (>0.89) and juveniles (>0.67) was needed to reach the observed asymptotic density.

Changing environmental conditions or manipulation of resources could directly affect both reproduction and the fluctuation in numbers. However, because our results are based on the establishment of multiple new populations, the decline in reproduction must have been caused by increasing density itself. Although density-dependent reproduction is a commonly reported phenomenon, density-dependent survival is more difficult to detect because of the difficulties in distinguishing between survival and dispersal in most systems. However, studies that have investigated survival often show that juvenile, but not adult, survival probabilities might be regulated in a density-dependent way (Clutton-Brock et al. 1987, Dhondt et al. 1990, Arcese et al. 1992, Armstrong and Ewen 2002, Nicoll et al. 2003, Armstrong et al. 2005). In our study, juvenile survival may have been biased by dispersal, as our estimates were based on the plateau area of Aride only. Estimates based on the whole Aride population suggest that juvenile survival was higher (average 0.82) during the first three years after translocation. However, even at high densities, high (even underestimated) estimates are not uncommon (e.g., 1996 survival: 0.75 ± 0.08). In comparison with other bird species in which density dependence has been observed, it should be noted that these were all temperate species with lower annual survival rates and often larger broods. In contrast, our species has a typical tropical life history, with small brood sizes, long-lasting parental care, and high juvenile survival rates; juveniles may thus be less affected by competition.

We did not detect an association between the relatively low levels of natural fluctuations in a saturated population and mean reproduction. Nevertheless, the rapid recovery of the population back to saturation after each translocation of significant proportions of the population is, in itself, direct evidence for density dependence. Although larger group sizes were associated with higher reproduction on a territory, this did not result in a higher per capita reproduction and thus can explain the paradoxical result of decreased per capita reproduction with increasing density.

Food as cause of density dependence?

Food availability has been shown to affect reproduction and survival in many species (for reviews see Martin 1987, Boutin 1990, Newton 1998). However, in most studies relationships between population size and food availability can always be confounded by selection on specific high-quality individuals settling in areas with high food availability, rather than a direct effect of food availability. In closed populations, we showed that insect availability was associated with asymptotic population density, reproduction at low density, and the structural size of individuals. Another indirect line of argument to suggest that food played a major role in competition is found in the reduction of reproduction with a large number of subordinates in the territory, and negative effect of territory space per individual on reproduction (which is an effect of density on the local level). Although insect densities on Cousin have remained constant since 1986, it is unclear whether insect densities on Cousine and Aride decreased as a result of the introduction of warblers on the island. Although birds in the population with lowest food abundance (Cousine) were smallest, relatively to their size they did not have the lowest body mass. Because structural size is determined during the early growth period, it seems plausible to suggest that the availability of food during the nestling period may be responsible for limiting their growth. Structural size also has been shown to be strongly heritable in different bird populations (Merilä et al. 2001), and therefore the possibility that natural selection or founder effects may have played a role cannot yet be excluded. An alternative explanation is that birds are selected to be relatively large at high density because with high competition it is more advantageous to be larger (Both et al. 1999). We do not have the data to show that selection for large size is indeed stronger when density increases, but it may be the case that, under high densities, a larger proportion of resources is allocated to chick quality rather than quantity (Mesterton-Gibbons and Hardy 2004). The reason why insect availability differs between the islands in our study remains unknown. It could be a consequence of different vegetation composition, renewal rates as a consequence of differences in the food webs, or differences in microclimate, or even different levels of depletion by the predators. Unfortunately, we do not yet have the data to investigate this further.

Komdeur (1992) found that territory quality was associated with reproduction, but our analysis on reproduction within the saturated population failed to find the same effect. However, this difference can be explained by the inclusion of territory size in the earlier studies' calculation of territory quality. We now show that the available territory space per individual was positively associated with reproduction, independent of group size. Although the between-island comparison shows that insect availability is very important and

therefore that a relationship between reproduction and territory quality within the saturated population is expected, our measure of territory quality might not be accurate enough to detect this. Insect availability was counted at 15 sampling points across the island (Komdeur 1992) and not in each territory separately. Furthermore, our measurement of territory quality includes estimates of foliage cover, which might not directly or proportionally translate into increased insect availability. Consequently, our results show that an index, rather than true territory quality, was measured.

Cooperative breeding

Offspring hatched in the newly established populations did not delay dispersal to stay as a subordinate in the territory until one and two years after translocation on Cousine and Aride, respectively. As the population densities on these islands further increased, so did group sizes. Eventually, group sizes on the island with the highest food availability (Aride) became significantly larger than in all other populations. Instead of establishing new territories, more subordinates stayed in the natal territory, possibly because the costs of defending a territory are too high at such high densities. Alternatively, because territory size is also associated with reproduction, such territories might be too small for successful reproduction and might not outweigh the benefits of staying and gaining indirect fitness benefits, especially as territory sizes were already significantly smaller than in the Cousin population.

Increased population density and, consequently, group size resulted in a decrease in per capita reproduction. However, not only did fewer individuals start to reproduce independently but also reproduction decreased at the territory level. This was not a consequence of lower quality habitat being occupied, resulting in lower average reproduction, because the variance in reproduction per territory at high and low density did not change. We suggest that, with increased density, crowding results in increased competition for food, which in turn leads to a decrease in both the number of individuals able to reproduce and the number of offspring produced per bird.

Conclusion

We found that populations of Seychelles Warblers are mainly regulated by density-dependent reproduction. Variation in density between islands could be explained by food abundance, measured as insect availability. Islands with the highest insect availability also had the highest bird densities. Hence, we suggest that the density-dependent reproduction observed is caused primarily by competition for food. However, experiments (e.g., supplementary feeding) are needed to confirm this. We show that next to monitoring numbers, data on behavior and reproduction can add important information about the mechanism regulating populations during the process of saturation. Because the

mechanism by which density dependence occurs determines to a large extent the outcome of predictive theories, i.e., population viability analyses, our results can contribute to this field, especially because they are based on a tropical species, the area where biodiversity threats are especially prominent nowadays.

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