Cooperative breeding and density regulation in small island populations of the Seychelles warbler
Brouwer, Lyanne

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Experimental evidence for density dependent reproduction in a cooperatively breeding passerine

Lyanne Brouwer, Joost M. Tinbergen, Christiaan Both, Rachel Bristol, David S. Richardson, and Jan Komdeur
Abstract

Temporal variation in survival, fecundity and dispersal rates are 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 Seychelles warblers (*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 ca. 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 did neither detect 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 investigate whether we can detect regulation of numbers via density dependent survival and reproduction within these new populations. We found that reproduction, but not survival, decreased with increasing population density. Variation in mean reproduction 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. This study provides an example of how conservation management can be used to explore population regulation processes.
Introduction

Populations fluctuate between years as a result of temporal variation in survival, fecundity and dispersal rates. Such variation in demographic rates is often caused by interplay between density dependent and density independent processes. Analysis of these processes is crucial to population dynamics as density dependence is a key factor often used to explain why populations normally fluctuate between specific boundaries (Murdoch 1994, Sæther et al. 2002). In contrast, density independent factors, like climate, affect reproduction or survival irrespective of population size. The influence of both types of processes varies by environment and according to species’ life history and they interact to affect population size and stability. Research on population regulation has focused on density dependent processes, and while many studies find negative relationships between density and reproduction (Kluyver 1951, Perrins 1965, Alatalo & Lundberg 1984, Arcese et al. 1992) or survival (Tinbergen et al. 1985, Francis et al. 1992, Lieske et al. 2000), not all studies do (van Balen & Potting 1990, Nur & 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 negative effects of increasing densities, at very low densities an increase in population size can have a positive effect on population growth, known as the Allee effect (Allee 1951, for review see: Courchamp et al. 1999).

The existence of density dependent processes regulating populations is undisputed but whether they can be detected depends to a large extent on the relative scale and the co-variation of density dependent and independent factors that affect the fluctuation of populations. Factors which can confound the study of density dependence are, for example, incomplete knowledge of dispersal patterns or inter- and intra-annual variation in quality of territories or population composition. Although very stable natural populations are expected to be regulated strongly by density dependence, detecting this may be difficult because of the lack of variation in population density (Murdoch 1994, Sæther 1997). Consequently, the most fruitful way to assess the causality of density dependence on 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 & Lundberg 1984, Török & Tóth 1988, Dhondt et al. 1992, Both 1998), or by supplementary feeding (Ewald & Rowher 1982, Davies and Lundberg 1984, Arcese & Smith 1988, Hoodless et al. 1999). Manipulating density directly is a better solution as changes in density are then less confounded by factors such as individual quality. However such experiments are rare especially on wild living vertebrates (but see: Both & Visser 2000). In the present study we both investigate density dependent patterns within a very stable population and utilize experimental populations to investigate the causality of density dependent processes.

Despite all the attention, the underlying mechanisms regulating populations remain largely unknown. Many studies assume that a crowding mechanism regu-
lates abundance (Sinclair 1989, Murdoch 1994). Crowding might result in a density dependent increase in agonistic interactions among conspecifics for limiting resources such as food (Newton 1998), territory space (McCleery & Perrins 1985), nest sites (Brawn & Balda 1988) or mating opportunities (Karvonen et al. 2000) and, consequently, to a decrease in demographic rates. All individuals within a population may be affected by density to the same extent, or alternatively this may differ between individuals. For example, at low population densities all individuals reside in high quality habitat, but with increasing density new individuals are forced to settle in lower quality habitat, resulting in a decline in average demographic rates (Kluyver & Tinbergen 1953, Brown 1969). In the present study we aim to investigate the underlying mechanisms regulating populations by analyzing whether the variance in reproduction increased as a result of lower quality habitat being occupied.

Translocations of individuals to suitable uninhabited islands are employed as successful tools to save species and have been a major component of conservation management (Bell & Merton 2002). We aim to utilize translocation populations as an experimental study of density dependence, as such populations start at low densities but undergo rapid changes in vital rates as the population grows (Armstrong & Ewen 2002, Nicoll et al. 2003, Armstrong et al. 2005). Although analyzing trends can have the disadvantage that there are natural changes through time, we can control for this by using data from a stable population.

We test the causality of density dependence by using data from translocations of the Seychelles warbler (Acrocephalus sechellensis) to three different islands done as part of ongoing conservation of this species. The Seychelles warbler is a facultative cooperative breeding species endemic to a few islands in the Indian Ocean. The species went through a severe bottleneck with only ca. 30 individuals left on Cousin Island (29 ha) between 1940 and 1968 (Crook 1960, Loustau-Lalanne 1968). This population, which has since recovered and stabilized at around 320 adult individuals, has been studied since 1986 (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) and Cousine (1990), which were subsequently monitored (Komdeur 1994a). As these three islands are located within an area of only a few km², a fourth population was established in 2004 on Denis Island, 60 km north of Cousin, to reduce the chance of extinction through natural disasters such as tropical storms or tsunami.

Here we investigate whether we can detect regulation of numbers via density dependent survival and reproduction. A previous study showed that both the natural variation in density and the experimental reduction in density caused by the removal of warblers for translocation was not 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, the change in numbers during population growth to saturation in the newly established populations will be used as a natural experiment in which to examine how survival and reproduction are influenced by density. In addition to studying the regulating mechanisms, we
will also investigate inter island differences in what limits population size by including food density measures. By studying both the limiting factors and density dependent patterns we hope to shed light on what the important density dependent processes are in these populations.

**Methods**

**Study species**  
The Seychelles warbler is an insectivorous species that has long term pair bonds. Dominant pairs maintain territories all year round and although warblers can breed independently in their first year, a lack of suitable habitat in a saturated population drives them to become subordinate within their natal territory (Komdeur 1992). Both sexes of subordinates occasionally help with territory defense and the rearing of young (Komdeur 1994b, 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–March, although after translocation year-round breeding was observed (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); at 04°19’ S, 55°39’ E), Aride (68ha; at 04°13’ S, 55°44’ E) and Denis (144 ha of which 140 ha are natural habitat; at 03°48’ S, 55°40’ E). On Cousin, data were collected as part of the long term study of the Seychelles warbler population. Except for in 1992, this population has been monitored every year since 1986. From 1991 to 1994 only a part of the population was monitored (68% of territories). As the number of territories is relatively constant across years (average ± S.E. 1986–1990, 1995–2006: 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. During the main breeding season, each territory was checked for breeding activity at least once every two weeks by following the resident female for 30 minutes (Komdeur 1992). Territory borders were mapped based on observations of individual warblers and the outcome of disputes between groups. For conservation reasons, 29 warblers were translocated each to Aride in 1988 and Cousine in 1990 (Komdeur 1994a). 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 1993–2000 capture-recapture data was collected by mist netting, allowing us to estimate survival and resighting probabilities separately. From 1995-2000, except for 1997, each
territory was checked for the number of birds. In addition, during the main breeding season in 1995 and 1996, and all year round in 1999, the study area was completely 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 whole area which was covered by territories was estimated and in 1999 all territories sizes were measured separately. 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 was 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 of 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. 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. In addition insects were counted on Cousin throughout the study period. Insects were counted on the under side of 50 leaves of each of the three main tree species on at least 15 different locations per island, for more details see Komdeur (1992).

In 2004 a population of Seychelles warblers was established on Denis Island. 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 will probably be underestimated, as some juveniles may have died before being recorded.

During each monitoring period as many birds as possible were caught, either as a nestling or after fledging using mist nets, and ringed with a unique combination of three ultra-violet-resistant colour rings and a British Trust for Ornithology metal ring. Body mass to the nearest 0.1 g and tarsus size 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 of the years where both the main breeding season and the minor breeding season were completely monitored: 1986–1989, 1998–1999 and 2004–2005. For this analysis reproduction was defined as the total number of fledglings produced per territory in a year, with the total number of territories remaining relatively constant. Estimates of the available insect prey and foliage cover were used to calculate territory quality according to Komdeur (1992),
but without including territory size as a component of the calculation. Territory size and group size are correlated, therefore we investigated the effect of territory size separately by including the relative territory size per bird by dividing territory size by 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 1994b). 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 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. on average 144.5 ± 22.9 (N=18) mm rain in June and July) which resulted in very few territories with nesting activity.

To investigate whether the change in numbers and, consequently, the increase in density of the newly established populations resulted in a change in reproduction we analyzed the per capita (per breeding season) reproduction on Aride, Cousine and Cousin in one model. For Aride and Cousine all breeding seasons in which reproduction data was collected were used, 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 investigate 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 ringed as juveniles and were of known age. As 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 ringed as juveniles and were of known age. On Denis 93 birds were monitored between 2004 and 2006. Of these, 25 individuals were ringed 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 & Burnham 1999).
Data analyses
In the analyses of natural variation in reproduction on Cousin there are many repeats of the same territories between years which might be inter-correlated. 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 in MLwiN 2.02 (Rasbash et al. 2004). Reproduction was fitted using a Poisson response model with logit-link function and the 2nd order PQL estimation procedure. To investigate the effect of density on reproduction between populations, the average per territory reproduction was log transformed and then fitted as 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 density also lead to differences in structural size measurements we analyzed body mass and tarsus size 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 day time, we do not think this could cause a bias in the data as similar catching strategies were performed in all populations. Body mass and tarsus size were fitted using a normal response model. As measurements from the same bird or of the same observer might be inter-correlated, 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 mentioned above were performed in MLwiN 2.02 (Rasbash et al. 2004). Model selection was based on stepwise backwards elimination of the non-significant terms in the order of their significance assessed by the Wald statistic. The final model contained all significant explanatory terms. All eliminated terms were reintroduced to the final model to confirm their lack of contribution. Means are expressed with standard errors.

To investigate survival and resighting probabilities 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, with similar variation between the years for both age classes (Brouwer et al. 2006). Furthermore, there was no variation in survival nor 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 ringed 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 just few juveniles were ringed over a long time-span and therefore these were only included in the analysis as an adult after their first year of life. Due to the small dataset for Denis, juvenile survival probabilities were not allowed to vary over time and their resighting probabilities were kept similar to those of adults. For the populations of Aride and Cousine we then used the most parsimonious model to test whether survival rates changed with increasing population density, whereby population density was included as a linear constraint on survival probabilities. Years in which no estimate of population density was available were extrapolated from nearest known numbers available. Akaike’s information criterion corrected for sample size ($\text{AIC}_c$) was used to select the most parsimonious model, with better fitting models resulting in lower $\text{AIC}_c$ values (Akaike 1973). 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 little 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, $\text{AIC}_c$ values were adjusted to allow for the extent of overdispersion measured by $\hat{c}$, through quasi likelihood ($\text{QAIC}_c$). 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 $\text{QAIC}_c$ weight (Burnham & Anderson 2002). The weighed averages were then used to investigate the relation between population density and survival between populations in a linear regression.

**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 (average: $10.8 \pm 0.2$ birds/ha, C.V. = 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. 3.1). 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: 12 out of the 29 translocated birds established themselves on the plateau area (2.3 birds/ha). The population on the plateau increased tenfold to an asymptote of around 120 birds (25 birds/ha) in 1998, and was relatively stable thereafter (Fig. 3.1). A survey in 1997 indicated that the total population size was 1600 birds (23.5 birds/ha) (Betts 1998), a more than fifty-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). Denis Island is the largest island and therefore had the lowest density of 0.41 birds/ha (58 birds)
when first established in 2004 and 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 however the size of the territories simultaneously decreased fivefold, from an average of 0.81 ha ($N = 6$) in 1988 to $0.16 \pm 0.01$ ha ($N = 34$) in 1999. Average territory size at saturation (1999) on Aride was significantly smaller than the average territory size on Cousin ($0.23 \pm 0.01$ ha, $N = 107$; $U = 701.0$, $P < 0.001$).

As density increased so did group sizes: on Aride group size increased from $2.0 \pm 0.3$ ($N = 6$) in 1988 to $3.3 \pm 0.2$ ($N = 36$) 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 $1.6 \pm 0.2$ ($N = 11$) in 1991 to $2.7 \pm 0.2$ ($N = 41$) birds per territory in 1998, though 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 ($3.3 \pm 0.2$), which were significantly larger than on Cousin ($2.8 \pm 0.1$, $N = 107$; $U = 1552$, $P = 0.04$) and Cousine ($U = 541.0$, $P = 0.02$). Group sizes on Cousine were not significantly smaller than on Cousin ($U = 2063.0$, $P = 0.41$). 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 ($r$) are shown as the slopes of the relation between log population densities and year (Fig. 3.1). Population growth rates clearly decrease with increasing population densities during the process of saturation. Population density alone did not account for all the observed variation between islands; at very low densities during the year after translocation the population growth rates on Cousine and Denis Island were similar ($r = 0.015$) but were lower.
than on Aride ($r = 0.12$) (Fig. 3.1). However, over a number of years (1991–1995) the population growth rates were similar for Aride and Cousine, but the final population density on Aride was twice as high as that on Cousine, and was also higher than on Cousin, suggesting that the limiting factors differed in magnitude between islands.

**Reproduction**

On Cousin the average per capita reproduction was $0.27 \pm 0.03$ 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 3.1). Furthermore, no correlation was found between territory quality and annual fledging production (Table 3.1). The available territory space per individual (= territory size/divided by groups size) was however, positively associated with reproduction, independent of group size (Table 3.1). In addition, reproduction was positively related to group size, but did not increase further after group size five (Table 3.1, Fig. 3.2).

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. 3.3A and 3.3B). The seasonality of reproduction was also affected by the translocation, on Aride year round breeding occurred when the population was at a low density. 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. 3.3A). At low density reproduction on Cousine was also higher than at saturation on Cousin (Fig. 3.3A). Analyzing the per capita reproduction per breeding season showed that with

<table>
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<tr>
<th>Parameter</th>
<th>B ± S.E.</th>
<th>$\chi^2$</th>
<th>d.f.</th>
<th>$P$</th>
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<td><strong>Final model:</strong></td>
<td></td>
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<tr>
<td>Intercept</td>
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<td>Group size$^2$</td>
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<td>11.7</td>
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<td>&lt; 0.001</td>
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<td><strong>Random effects:</strong></td>
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<tr>
<td>$\sigma_{year}^2 = 0.16 ± 0.15$</td>
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<tr>
<td>$\sigma_{territory}^2 = 0.01 ± 0.01$</td>
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<tr>
<td><strong>Rejected:</strong></td>
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</tr>
<tr>
<td>Density</td>
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<tr>
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<tr>
<td>Total rainfall</td>
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<tr>
<td>Breeding season rainfall</td>
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<td>0.10</td>
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<td>0.75</td>
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</table>

Table 3.1 Results of hierarchical cross-classified model examining the annual reproductive output per territory (measured as no. fledglings/bird) of Seychelles warblers on Cousin Island between 1986-2006, ($N = 902$ territories). Density, total rainfall and breeding season rainfall are year variables and consequently modeled on the year variation, whereas the other variables are modeled at the level of the individual territories.
increasing density reproduction decreased significantly on Aride and Cousine (Table 3.2A). The strength of the decrease in reproduction with increasing density was stronger on Cousine than on Aride (Table 3.2A). 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. Analyzing the reproduction at the territory level gives similar results; with increasing density reproduction significantly decreases both on Aride and Cousine (Table 3.2B).
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, Aride: $F_{5,32} = 0.86$, $P = 0.36$; Cousine: $F_{8,42} = 0.62$, $P = 0.44$).

### Survival

The most parsimonious model for the Aride data set showed that survival and resighting probabilities were lower in an individual's first year than later in life (Table 3.3A, model 1). Furthermore resighting, but not survival, varied between years in a similar way for both age classes (Table 3.3A, model 1). On average the annual survival probability was $0.68 \pm 0.05$ (resighting probability = $0.56 \pm 0.14$) for juveniles and $0.77 \pm 0.02$ (resighting probability = $0.79 \pm 0.07$) for adults. The most parsimonious model for the Cousine data set showed that survival, but not resighting probabilities, varied between years (Table 3.3B, model 1). The average annual adult survival probability was $0.83 \pm 0.07$ (resighting: $0.95 \pm 0.02$).

### Table 3.2

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. Estimates of effect sizes are x10 on log scale.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>A) Final model:</th>
<th>B) Final model:</th>
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</thead>
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<td>Density</td>
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<tr>
<td>Population*</td>
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<tr>
<td></td>
<td></td>
<td>$(\beta_{\text{Cousine}} 1.69 \pm 1.73)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$(\beta_{\text{Cousine}} -0.84 \pm 0.33)$</td>
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<tr>
<td></td>
<td>$(\beta_{\text{Cousine}} -0.62 \pm 0.58)$</td>
<td>0.29</td>
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<tr>
<td>Random effect:</td>
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<tr>
<td>$\sigma_{\text{year}}^2 = 2.68 \pm 1.44$</td>
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</tbody>
</table>

* reference category is Aride population and is given by the intercept
† reference category is Aride population and is given by the density main effect
Increasing density during the process of saturation did not result in decreasing survival rates for adults on Aride and Cousine or for juveniles on Aride (Table 3.3A, models 2 and 3; Table 3.3B, model 3). Furthermore, when comparing between island variation there is no indication that higher density results in lower survival probabilities ($r = 0.14$, $P = 0.27$; Fig. 3.4).

**Food as cause of density dependence?**

To assess whether food plays an important role in both the island differences in reproduction and the density dependence within islands, we investigate whether there are differences in body mass and tarsus length of the birds on the different islands. Both body mass and tarsus length differed significantly among islands, with Aride having the largest (but similar to Cousin) and heaviest birds, and Cousine having the smallest birds (Fig. 3.5). That these differences are due to effects of population density seems unlikely because on the island of highest density (Aride) the birds are biggest and heaviest. As no size measurements are available during the process of population saturation on Aride and Cousine we cannot test whether an increase of density within islands leads to lower body mass or structural size.
Food abundance, measured as insect density, might explain variation in body mass between populations better than density. In 1990, food abundance on Aride (233.7 ± 44.7 insects, $N = 3$) was on average 3.1 times higher than on Cousin (74.7 ± 10.4 insects, $N = 3$) ($\chi_{1}^{2} = 17.7$, $P < 0.001$). On Cousine (124.0 ± 35.2 insects, $N = 3$) food abundance was on average 1.7 times higher, but this was not significantly different ($\chi_{1}^{2} = 1.7$, $P = 0.19$). By 1996, after both islands had reached saturation, insect availability was only 1.8 times higher on Aride (231.7 ± 54.7 insects) than Cousin (127.0 ± 26.7 insects), and 0.7 times lower on Cousine (86.0 ± 14.7 insects).

**Figure 3.4** Annual adult and juvenile survival probabilities of Seychelles warblers in relation to population density for each of the four populations. Estimates of survival are derived by model averaging (see Table 3.3).

**Figure 3.5** A) Body mass and B) tarsus length measurements of adult Seychelles warblers for the populations of Cousin, Aride, Cousine and Denis, corrected for observer (bodymass: $\sigma^2 = 0.08 \pm 0.04$; tarsus: $\sigma^2 = 0.07 \pm 0.03$) and between individual (bodymass: $\sigma^2 = 0.71 \pm 0.06$; tarsus: $\sigma^2 = 1.06 \pm 0.06$) variation. Numbers on top indicate total sample sizes.
insects) in comparison to Cousin (Aride: $\chi_1^2 = 16.4, P < 0.001$; Cousine: $\chi_1^2 = 2.5, P = 0.11$). Over the years insect densities on Cousin remained constant ($F_{1,9} = 0.62, P = 0.45$). Therefore the island with least food (Cousine) has the lowest asymptotic density and the smallest birds, while the island with the highest food availability (Aride) has the highest density, the highest reproduction at low density, the largest groups per territory and the biggest birds.

Discussion

Density dependence

After translocation to new islands, the Seychelles warbler populations were initially far below carrying 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 individual birds were structurally bigger there. Furthermore, the strength of the decline with population density was weaker for the island with high food abundance and initial reproduction was higher there, although this could be a result of between year variation. These results indicate that regulation of numbers takes place via density dependent reproduction, probably caused primarily by competition for food.

We found no evidence that survival was important in regulating population density, which concurs with the results of a previous study of the effect of reduced density, caused by removal of birds, on survival probabilities (Brouwer et al. 2006). As our results are based on the establishment of multiple new populations, and not on fluctuations caused by changing environmental conditions or the manipulation of resources, 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 suggests that juvenile survival was higher (average 82%) during the first three years after translocation, however even at high densities high (even underestimated) estimates are not uncommon (e.g. 1996: 0.75 ± 0.08). In the comparison with other bird species in which density dependence was observed, it should be noted that these were all on 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, and juveniles may thus be less affected by competition.
We did not detect an association between the relatively low levels of natural and experimental fluctuations in a saturated population and mean reproduction. However, 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.

**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 isolated populations we showed that insect availability was associated with both 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. Although insect densities on Cousin remained constant since 1986, it is unclear whether insect densities on Cousine decreased as a result of the introduction of warblers on the island. Although birds in the population with lowest food abundance (Cousine) were smallest, they had similar body weight to birds in the original Cousin population and must therefore have been relatively heavier. As 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 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 at 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 & 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 micro-climate, or even different levels of depletion by the predators. Unfortunately, we do not yet have the data to investigate this further, nor to investigate whether the introduction of the birds on islands had any significant effect on the food availability.

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 territory size 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 relation 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, and eventually group sizes on the island with highest food availability (Aride) becoming significantly larger than in all other populations. Instead of establishing new territories, more subordinates stayed in the natal territory, because the costs of defending a territory are possibly too high at such high densities. Alternatively, as territory size is also associated with reproduction, such territories might be too small for successful reproduction and 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 as 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 reproduction, but not survival, decreased with increasing population density. Variation in mean reproduction 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 behaviour and reproduction can add important information about the mechanism regulating populations during the process of saturation. The mechanism by which density dependence occurs determines to a large extent the outcome of evolutionary life history models (Mylius & Diekmann 1995), quantitative models of cooperative breeding (Pen & Weissing 2000), but also popula-
tion viability analyses, which provide a quantitative assessment of the probability of a population to decline to extinction (Beissinger & Westphal 1998). Consequently, our results can contribute to this field, especially because our results are based on a tropical species, the area where biodiversity threats are especially prominent nowadays.

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