Cooperative breeding and density regulation in small island populations of the Seychelles warbler
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Summary and general discussion
The faunas of tropical islands are particularly rich in endemic species, and constitute a disproportionately large proportion of global biodiversity (Collar & Stuart 1985; Stattersfield & Capper 2000). In the last few centuries island faunas have become among the most threatened in the world, mainly because of anthropogenic effects such as human disturbance and the introduction of predators or competitor species (Stattersfield & Capper 2000). In contrast to species from temperate regions, we have little knowledge of the processes that regulate populations of tropical bird species, despite that fact that this knowledge is crucial to their conservation. In this thesis I studied population regulation in small isolated populations of the cooperatively breeding Seychelles warbler (Acrocephalus sechellensis). As this is a vulnerable species, direct manipulation of density through permanent removal of birds was not possible. However, translocations carried out as a part of a conservation project gave me the possibility to study density dependence of reproduction and survival in newly established populations. In addition I investigated the proximate mechanisms involved in helping behaviour and the long-term fitness consequences of group living. In this final chapter I will summarize some of the major findings of my research, discuss these in a general framework and explore their relevance to conservation.

**Tropical environment**

The life history strategies of tropical species are typified by high survival rates and small clutch sizes. In chapter 2 we showed that in the Seychelles warbler annual adult survival was high (84%) compared to European passerines, which usually have probabilities of < 50% (Sæther 1989; Peach *et al.* 2001). One of the reasons for this may be that the absence (or infrequency) of periods of severe food shortage and/or climatic severity in the tropics allows for high rates of survival. Our findings support this hypothesis as although we found temporal variation in survival, we did not detect an effect of weather variables (chapter 2). In temperate regions, the weather is a very important factor that influences survival, either indirectly, via food availability (Newton 1998), or directly, e.g. via thermoregulation (Cuthill & Houston 1997). We found no evidence that temperature was associated with survival in Seychelles warblers, though this was not surprising as the variation in mean temperature between years is extremely limited (range mean temperature: 25.6–26.6 °C). That rainfall did not affect survival (chapter 2) or reproduction (chapter 3) is surprising, as rainfall is known to influence insect numbers in our study area (Komdeur 1996b). However, the two years with extreme levels of rainfall, i.e. drought (1986) or flood (1997) also coincided with the lowest survival probabilities (Figure 2.1). This might indicate that survival is influenced by extreme weather conditions, but that our data set does not span enough years, to detect any significant effect. Alternatively, we may not be able to detect effects on post-fledging survival as mortality might have occurred before the fledging stage. Although the initiation of the breeding season was related to increasing rainfall (Komdeur 1996b), average annual
reproduction was not affected by the amount of rainfall (chapter 3). The ability of the Seychelles warbler to time their reproduction to periods with high food availability and choose whether to lay one or two eggs (Komdeur 1996b) might allow it to avoid adverse conditions. Moreover, with a life expectancy (period after which 50% of population is still alive) of 4 years after surviving their first year, many birds will never face the kind of severe weather conditions, and consequently selection event, which occurred less than once a decade. However, such sporadic events can have major ramifications for the evolution of a species, like for example, in the inbred population of song sparrows (*Melospiza melodia*) on Mandarte island, where outbred individuals survived better than inbred individuals under environmental stress (Keller *et al.* 1994). Or in Darwin’s finches (*Geospizinae*) where oscillating selection acts on morphological characters depending on the food supply (Gibbs & Grant 1987). So if selection is normally weak in the Seychelles warbler, the strong selection events every decade might be have important consequences for the species’ evolution.

**Population regulation**

In a closed population, the population size is determined by both density dependent and density independent processes affecting reproduction and survival. We investigated whether survival was density dependent in a saturated population of Seychelles warblers, but did not detect any evidence for this (chapter 2). Furthermore, we were unable to detect density dependent survival or reproduction after the removal of birds from the saturated population. However, the fact that within a year of the removal the population had increased back to the carrying capacity observed before the removal is, in itself, direct evidence for density dependence (Figure 3.1). Although many studies have shown associations between vital rates and density, the causal effect of density can only be shown by the use of experiments. As part of a conservation program, Seychelles warblers were translocated to a number of new islands. After translocation the newly established populations quickly expanded in size as a result of rapid rates of reproduction, but after a few years population growth rates started to decline (Figure 3.1). In chapter 3, we show that this decline in growth rate was a consequence of a decrease in reproduction, but not in survival, indicating that these populations are regulated by density dependent reproduction. Such density dependent reproduction has been observed in many other studies, but only few of these are experimental (Kluyver 1951; Kluyver 1971; Dhondt *et al.* 1992; Both 1998). Furthermore, these few experimental studies were normally performed by manipulating resources and very rarely by experimentally manipulated density itself (e.g. Armstrong *et al.* 2005) as done in the Seychelles warbler. Density dependent survival is hard to prove because of the difficulty in distinguishing between survival and dispersal in most study systems. Some experimental studies, which could control for dispersal, did find that survival decreased with
increasing densities (Armstrong & Ewen 2002; Nicoll et al. 2003; Armstrong et al. 2005). However, in the Seychelles warbler system, where dispersal was virtually impossible, we have no indication that density dependent survival occurred at the population level, either within or between populations (chapter 2 and Figure 3.4).

The detection of density dependence may also depend on the spatial scale at which such effects are investigated (e.g. Ray & Hastings 1996; Wilkin et al. 2006). In territorial species, especially year-round territorial species such as the Seychelles warbler, competition for resources will work mainly on a local scale, i.e. the territory (Both & Visser 2000). Consequently, we investigated the effect of local density, measured as group size during an individual’s life, on survival in the saturated Cousin population. Individuals living in larger groups had lower survival probabilities than birds living in smaller groups (Figure 2.2). Therefore, although density-dependent survival was not detectable at the population level it was detected at the territory level - the scale at which individuals compete.

We showed that monitoring populations before and after translocation events can provide useful experiments and uncover interesting results which cannot be detected in saturated populations. Monitoring reproduction and well as survival can also add important information about which mechanisms regulate populations during the process of saturation. As such mechanisms can have consequences for the success of translocations, investigating and understanding them may also be important for conservation.

**Food availability as a density dependent mechanism?**

The newly established populations on Aride and Cousine grew rapidly to asymptotic levels, but these levels differed among all the islands, with higher population densities, larger groups and larger birds on islands with higher insect densities (chapter 3). Hence, we suggest that the density dependent reproduction was caused by competition for food (chapter 3).

At the territory level, increasing density (larger group sizes) was associated with lower survival (chapter 2). Studies on non-cooperative, group living animals have shown that the negative effects of increasing group size can be caused by larger groups attracting more predators (Begon et al. 1990), or because of increased competition for food (Krause 1994; Bednekoff & Lima 2004). As adult Seychelles warblers do not suffer from any predation pressure, competition for food is the most likely cause of the reduction in survival with increasing group size observed in the Seychelles warbler. Although the effects of both population and local density on survival are consistent with the idea that competition for food is causes the density dependent effects, manipulation of food itself, e.g. by supplementary feeding, is required to confirm this. In practice such an experiment might be hard to perform as removing food is too risky as this might have severe effects on the warbler and other (endangered) species. The disadvantage of adding food in a territory is that this will
also attract more competitors or potential egg predators (Wright’s skinks (*Mabuya wright*), Seychelles fodie (*Foudia sechellarum*) and Seychelles Magpie Robin (*Copsychus seychellarum*), therefore this should be done in such a way that only warblers can profit from it.

**Rearing conditions**

It is obvious that variation in rearing conditions will have immediate effects on offspring fitness, however they may also have important long-term fitness consequences (Lindström 1999). Rearing conditions can only be distinguished from parental/territory effects by the cross-fostering of nestlings. In the Seychelles warbler variation in rearing conditions is besides parental quality, also caused by variation in the number of nest mates, group size and territory quality of the rearing territory. However, none of these factors were associated with either juvenile or adult survival or recruitment (chapter 4). Furthermore, although there was variation in juvenile survival between seasons, this did not affect a cohorts’ adult survival probability (chapter 2). The long period over which Seychelles warbler offspring are dependent on their parents might counterbalance any negative effects experienced during early life. Alternatively, selective disappearance (mortality) of low quality individuals may result in cohorts which experienced adverse conditions having similar adult survival probabilities as other cohorts.

The long period of offspring dependence, the stable environment and the ability of parents to synchronize reproduction with high food availability may all mean that parental effects are more important than environmental variation in rearing conditions in the Seychelles warbler. An indication that maternal effects play a role in determining offspring fitness comes from chapter 6; here we showed that maternal, but not paternal heterozygosity was positively associated with offspring survival, but only in seasons with low survival (Figure 6.1).

**Territory quality**

Although Komdeur (1992) found that territory quality was associated with reproduction and survival, we did not find this in our analysis. There was no association between territory quality and survival (chapter 2) or reproduction within the saturated populations (chapter 3). Furthermore, the quality of the rearing territory did not affect offspring recruitment (chapter 4). The former association between territory quality and reproduction (Komdeur 1992) is due to the inclusion of territory size in his calculation of territory quality. We now showed that territory size, and not the quality measure, was positively associated with reproduction, independent of group size (chapter 3). That previous studies found that survival was associated with territory quality (Komdeur 1992) while this study did not, can probably be explained by
the fact that the earlier studies were less thorough; mark-recapture analyses were not used, sample sizes were much smaller and no between-year variation was taken into account.

Although the comparisons in densities between islands shows that insect availability is very important and, therefore, that a relation between reproduction and territory quality within the saturated Cousin population is expected, our measure of territory quality might not be accurate enough to detect this. Insect availability was only 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. This indicates that an index, rather than the true territory quality, was measured.

Cooperative breeding

In cooperatively breeding species, positive effects of group size on reproduction or survival are widespread (Rood 1990; Allainé et al. 2000; Clutton-Brock et al. 2001; Magrath 2001; Conner et al. 2004; Khan & Walters 2004; Hatchwell et al. 2004), but negative effects are rarely reported. Removal of Seychelles warbler helpers has shown that the presence of one or two helpers improved the reproductive success of a group, but that the presence of three or more helpers had a negative effect (Komdeur 1994b). We showed that birds that had lived in larger groups during their life had lower survival probabilities than birds in smaller groups (Figure 2.2). These results indicate that living in a group of five or more birds in total will not be profitable for Seychelles warblers in the Cousin population, as both reproductive success and survival decreased for such groups. In smaller groups, however, the presence of subordinates which help does increase both the juvenile and adult survival of the helped offspring (Figure 4.3). This effect is caused by the presence of active helpers per se and not by the presence of non-helping subordinates, indicating that helpers do really help. Finally, we ruled out the possibility that this effect was due to a non-causal relationship between the presence of helpers and parental/territory quality, as cross-fostering showed that only the number of helpers in the rearing, but not in the original territory, affected offspring survival.

A fundamental drawback of most studies on cooperatively breeding species relates to the poverty of accurate cost-benefit analyses of group living. Although costs in cooperative breeding seems obvious as individuals refrain from reproduction and risk mortality while waiting for breeding opportunities, helping itself can also be costly (e.g. Taborsky 1984; Heinsohn & Cockburn 1994). Furthermore, cooperative breeding can occur in many forms and helping behaviour varies both within and between species and is therefore not a discrete strategy with two levels (disperse or stay and help), but rather a continuous variable (Heinsohn 2004). The shape of the costs and benefits curves will differ between species as a result of variation in life
histories and social system, but might also differ within species as a result of environmental variation, for example, for Seychelles warblers on Aride (with higher insect densities) the optimal group size is probably larger than for the Cousin population. Benefits gained by increased reproduction will depend on the relatedness between group members and offspring, but will also differ between group members (i.e. primary and subordinate). Cost-benefit analyses of cooperative breeding will only get more complex with our findings that helping can also have long-term fitness effects for the offspring helped, and that also living in groups itself can have costs. However, hopefully this can contribute to our understanding of the large variation in helping behaviour both within and between species.

Hormones and behaviour

A lack of unoccupied habitat seems to provide a clear explanation as to why Seychelles warblers delay dispersal and become subordinate within a territory (Komdeur 1992). However, this cannot explain why, despite the high levels of extra-pair paternity seen in this species, male subordinates never gain paternity outside their own territory and only seldom within (Richardson et al. 2001). However, birds are able to breed independently in their first year of life, as this occurs in the new translocated population (pers. obs.; Komdeur 1992; Komdeur 1996a). To gain insight into the proximate mechanisms that contribute to delayed breeding and, subsequently, to helping, we investigated circulating hormone levels in male breeders and non-breeders. We investigated blood testosterone levels as this is a key hormone in the stimulation of male reproductive behaviour (for review see: Nelson 2000). Primary males had significantly higher testosterone levels during the nest building stage, and significantly larger cloacal protuberances (an indication of sperm storage) throughout the entire breeding season, than did subordinate males (chapter 5). Experimental promotion of subordinates to primary status (through the permanent removal of primary males), showed that promoted males increased their cloacal protuberance, but not their testosterone, to levels equal to those seen in normal primary males (Figure 5.2a). Lower body mass and measure of immunocompetence for subordinate males suggest that they are in poor body condition, possibly caused by physiological suppression by the primary male (physiological suppression, Wingfield et al. 1991; Wingfield & Farner 1993; Schoech et al. 1997). It appears that more time is needed after promotion for previously subordinate males to be able to increase their testosterone to the levels usually seen in primary males. Repeating the experiment and subsequently sampling promoted subordinates at different time intervals might show what time frame is needed for the males to produce the typical primary male testosterone levels.
Small populations

Due to anthropogenic influences which have resulted in fragmentation and loss of habitat, many populations have decreased in size and become more scattered. As a result many species worldwide are now threatened with extinction (Gaston et al. 2003). The population dynamics of island populations are highly relevant to the conservation of bird species, as a large proportion of endangered birds occur on islands (Bell & Merton 2002) and most bird species extinctions have occurred on islands (Caughley & Gunn 1996). Small and/or isolated populations are inherently more vulnerable to external environmental perturbations, but also to chance fluctuations in local survival and fecundity, for example caused by insufficient numbers of one sex to sustain productivity. Although we do know that severe weather can affect survival in the Seychelles warblers, the limited fluctuations in numbers in the saturated Cousin population (Figure 3.1) show that the population has a strong ability to quickly respond to perturbations. The warblers are long-lived, territorial year round and time their reproduction to coincide with high food availability (Komdeur 1996b), and therefore appear to be very flexible to response to severe events. Furthermore, their cooperative breeding system might act as a buffer for periods of high mortality; subordinates quickly occupy breeding vacancies when these become available (Eikenaar et al. unpublished data) and by doing so prevent the overall breeding population being affected. In general, cooperative breeding might be a very successful strategy to buffer effects of environmental or demographic stochasticity. This was also shown in individual-based simulation models of the Red-cockaded woodpecker (Picoides borealis) (Walters et al. 2002), and by the presence of a non-breeding class in wolves (Canus lupus) (Vucetich & Creel 1999).

Inbreeding may also become an important factor in the survival of small populations as the chances of mating with relatives increases as numbers decrease. Inbreeding between closely related individuals will result in decreased heterozygosity in offspring and might lead to the expression of recessive deleterious alleles or the loss of the heterozygote advantage. This could result in decreased fitness, known as inbreeding depression (Hartl & Clark 1997). Many studies have shown direct relationships between heterozygosity measured across multiple microsatellite loci and components of fitness (Coltman et al. 1998; Slate et al. 2000; Hansson et al. 2001; Amos et al. 2001; Bean et al. 2004). However it is unclear whether these correlations indicate inbreeding effects as heterozygosity at microsatellite markers may not reflect genome-wide heterozygosity, except in partially inbred populations and/or when very large numbers of markers are analyzed (Slate & Pemberton 2002). Heterozygosity-fitness correlations can also be explained by the ‘local effect’ hypothesis, in which the heterozygote advantage is a result of a genetic association between a neutral marker and a locus under selection (Lynch & Walsh 1998; David 1998). In the Cousin population, close inbreeding - resulting in decreased offspring multilocus heterozygosity - has been shown to occur for over 5% of Seychelles warbler offspring (Richardson et al. 2004). However, in chapter 6 we showed that
inbreeding depression was very weak; multilocus heterozygosity of an individual was not associated with its own survival, but multilocus heterozygosity of the mother was associated with offspring survival, however only in low quality seasons (Figure 6.1). Furthermore, heterozygosity at the individual loci was not correlated and therefore does not seem to reflect genome-wide heterozygosity.

Our results support the idea that even in small inbred populations, heterozygosity measured at microsatellites might not reflect genome-wide heterozygosity or, therefore, individual inbreeding. The absence of a heterozygosity-survival association could be caused by the fact that any recessive deleterious alleles that had an effect directly upon individual survival have been purged. As purging is likely to be most effective on alleles subject to strong selection (Hedrick 1994), the bottleneck in our population might have lead to purging of the deleterious alleles affecting individual survival directly, but not those alleles affecting offspring survival. Although inbreeding depression effects are weak at the individual level, at the population level this might be different. As the Cousine and Aride population originated from only 29 individuals, alleles that are rare in one population might be very common in another and also the variation in the number of alleles could differ. Investigating heterozygosity-fitness correlations between populations might show that there are differences between populations and that inbreeding depression could be stronger at the population level.

Effective population size

In this study we used the total population size \(N\), the number of adult individuals in the population, to investigate the dynamics and regulation of populations. However, the genetically effective population size \(N_e\) - the number of individuals that actually breed and contribute to future generations - is a more meaningful measure of population size for threatened and small populations. Effective population size is defined as the size of an ideal population (i.e. one that experiences no mutation, selection and migration and in which mating is random) that would undergo genetic drift at the same rate as \(N\) (Wright 1931). If only a few individuals are responsible for the majority of offspring, for example through gaining extra-pair fertilizations, the effective population size will be smaller than expected under social monogamy (Waite & Parker 1997). \(N_e/N\) can be calculated as follows (Nunney & Elam 1994; Parker & Waite 1997).

\[
N_e / N = \frac{4r(1-r)T}{r[A_f(1+I_{Af})+I_{bf}]+(1-r)[A_m(1+I_{Am})+I_{bm}]}
\]

Where \(r\) is the proportion of adult males in the population; \(A_i\) is the mean adult lifespan of sex \(i\); \(T = \) generation time (age of first reproduction + \(A - 1\)); \(I_{ai}\) stan-
standardized variance (variance/mean$^2$) in adult lifespan of sex i (= annual survival probability in case of age independent survival); and $I_{bi}$ standardized variance in reproductive success of sex i. As precise estimation of $N_e$ is rather complex (e.g. Araki et al. 2007), I calculate rough estimates for a Seychelles warbler population at low and high population density here. At low density where no cooperative breeding occurs almost all individuals participated in reproduction. Thus $r = 0.5$, $T = 6.25$, $A_i = 6.25$ for both sexes (chapter 2), $I_{ni} = 0.84$, $I_{bf} = 0.26$ (based on Aride) and assuming that $I_{bf} = I_{bm}$, $N_e / N = 0.53$. However, with increasing density, group size increased and cooperative breeding occurred (chapter 3), thus the proportion of birds participating in reproduction decreased and the variance in reproduction increased, $I_{bf} = 2.47$ (based on data Aride). Consequently $N_e / N$ would decrease to 0.44. However, the mean age of first reproduction increased from 1 to 3.5 (based on 60% annual recruitment rate, chapter 4) and therefore the generation time increased, $T = 8.75$. This results in $N_e / N = 0.62$ (Figure 7.1)

![Figure 7.1](image)

**Figure 7.1** Population density in relation population size ($N$) and effective population size ($N_e$).

These are only rough estimates, in which I assumed that $I_{bf} = I_{bm}$, however extra-pair paternity will increase $I_{bm}$ and co-breeding will decrease $I_{bf}$. Furthermore, measured over multiple years $I_{bi}$ will even increase more. Although I expected $N_e$ to decrease with increasing population density, the increase in generation time counter-balances the effect of the increased variance in reproduction. This again shows that dynamics of cooperatively breeding species can be very different from monogamous species.

**Future prospective**

The mechanism by which density dependence occurs determines to a large extent the outcome of evolutionary life history models (Mylius & Diekmann 1995), quanti-
tative models of cooperative breeding (Pen & Weissing 2000), but also population viability analyses, which provide a quantitative assessment of the probability of a population to decline to extinction (Beissinger & Westphal 1998). These analyses have become an important tool in the management of threatened species and our results can contribute to this field, especially as they are from a tropical species, a group for which there is, as yet, little information despite the fact that the majority of endangered species occur in the tropics.

Our results show that ecology cannot be considered independently from behaviour. During the process of population saturation not only did density start to affect reproduction, but also other factors, such as the breeding system and thus the behaviour of individuals, which changed as cooperative breeding developed. Although we now have a clearer idea of the regulation processes at the population level, to describe the processes at the individual level is more complicated. The Seychelles warblers’ complex breeding system, including extra-pair paternity, co-breeders and helpers, means that an estimate of the average reproduction per bird is not a good indicator of individual fitness. A pedigree currently being developed based on molecular parentage analyses should help us to get a better understanding of the processes and decisions which occur at the individual level, i.e. investment strategies, mate choice and dispersal. It is likely that individuals follow different strategies to maximize fitness, e.g. disperse and try to breed independently, stay and try to gain direct fitness benefits by co-breeding, or specialize in gaining EPP. Although some analysis of this has been done on a small data set (Richardson et al. 2002), long-term data might give insights into the strategies followed by individuals and their actual life time reproductive success and will allow accurate cost-benefit calculations of group living. Furthermore, genetic analyses for the newly established Denis population might give new insights into the processes occurring at low population densities, and will allow a more accurate calculation of effective population size. In addition, inbreeding can be measured directly and thus its effect on fitness.

Although knowledge about natural patterns and variation in populations is very useful, experiments are needed to assess the causality of correlations. The disadvantage of working with a ‘vulnerable’ species is that performing experiments always brings a certain risk for the population. Our study, however, provides an example of how conservation management can be used to experimentally explore population regulation and behavioural processes. With the expected increase of the warbler population the potential for experiments will also increase.

If the establishment of a fifth population and a total population size of > 5,000 birds can be reached, the Seychelles warbler will be considered for downgrading from ‘vulnerable’ to ‘near –threatened’ (Richardson 2001). The suitability of any island for a new Seychelles warbler population depends on a number of factors. However as we show that reproduction depends on insect availability, which in turn, depends on the occurrence of native broad leaved species, including *Terminalia*, *Pisonia*, and *Morinda*, these habitat requirements must be seen as a key factor. The threat of rising sea levels and the increased occurrence of severe weather also mean
that any new populations should, preferably, be established on islands with higher altitudes. However, the most important factor for a successful establishment is, undoubtedly, the absence of introduced predators (rats and cats) which limits the numbers of suitable islands drastically. As the Seychelles warbler is a long-lived species with low reproductive rate, the population growth rate will largely be affected by adult survival. Changes in adult survival caused, for example by predation, will therefore have large consequences for the viability of the population. Although the previous translocations to Aride and Cousine were successful, this does not guarantee that all newly established populations will be successful (see Box A) and the continued monitoring of not only numbers, but also individual behaviour is required on the new islands. However, the rapid increase of numbers after translocations and the flexibility of the species to respond to perturbations suggest that the risk of extinction is low and that there is a bright future for this remarkable species.