Cooperative breeding and density regulation in small island populations of the Seychelles warbler
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Chapter 1

Introduction
Currently, one eighth of all bird species, one quarter of all mammals, and one third of all amphibians are threatened with extinction (Beissinger & McCullough 2002). Biodiversity threats are especially prominent in the tropics, where biodiversity is highest and habitat loss and fragmentation is proceeding at an ever increasing pace. As a result, conservation biology in the tropics often has to deal with small isolated populations. Understanding the factors that influence the number of individuals within such populations and determining how we can manipulate such factors is one of the main challenges ecologists now face.

**Population regulation**

Survival, reproduction and dispersal are the key-processes in regulating numbers and thereby population dynamics (Murdoch 1994; Sæther *et al.* 2002). An important discussion in population ecology focuses on the question of how, and to what extent, density-dependent and density-independent processes affect fluctuations in numbers (Sibly & Hone 2003). Density independent factors, e.g. climate, affect reproduction and survival at all population sizes in contrast to density dependent factors, which change in effect as populations grow. Understanding what determines changes in numbers, especially when population sizes are small, is crucial not only for our understanding of population regulation and persistence but also for the development of a predictive theory of how to manage and conserve threatened populations. 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 population viability analyses, which provide a quantitative assessment of the probability of a population to decline to extinction (Beissinger & Westphal 1998).

Studying what causes demographic rates (and therefore population numbers) to change requires long-term data sets with complete knowledge about individual life histories. Dispersal is an interesting phenomenon and important for the persistence of many populations, for example, by maintaining genetic variation (Keller *et al.* 2001), however incomplete knowledge of dispersal in most study systems causes local survival to be confounded by dispersal away from the study site. This problem is avoided by studying effects of density dependence in closed populations.

Although stable natural populations may be regulated in a strong density dependent manner, density dependence will often be impossible to detect, or confounded because density covaries with density independent factors like climate (Murdoch 1994; Sæther 1997). Therefore, experiments are essential to assess the causality of density dependence on demographic rates. 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). Intra-specific competition for resources, one of the main density dependent processes (Newton 1992), will work mainly on a local scale in territorial species. The size of the territory and number of
individuals living in it will, therefore, be the appropriate measure of density with which to investigate such effects (Both & Visser 2000).

With increasing densities competition will increase and the strength of selection will also increase. Furthermore, the traits selected under high densities might differ from those selected for under low densities, e.g. under high densities selection will favour cooperative breeding behaviour by increasing reproductive success of groups compared to pairs or individuals are selected to be relatively large at high density because at high competition it is more advantageous to be larger (Both et al. 1999).

Tropical environment

A characteristic of many tropical islands is that their faunas are particularly rich in endemic species and form a disproportional large part of global biodiversity (Collar & Stuart 1985; Stattersfield & Capper 2000). However, in the last few centuries these faunas have become the most restricted and threatened in the world, mainly because of anthropogenic factors such as habitat loss, disturbance and the introduction of predators or competitor species (Stattersfield & Capper 2000). Nonetheless, although many studies have investigated population regulation in temperate species there is little knowledge about how factors, such as environmental variation, affect survival and fecundity in tropical species (Martin 1996). In tropical areas, environmental factors are generally considered to vary relatively little between seasons (Karr 1976; Martin & Karr 1986; Loiselle & Blake 1991, 1992). Life histories are typically characterised by small clutches, long developmental periods and the extended parental care of juveniles associated with high survival probabilities for both juveniles and adults (Skutch 1949; Lack 1954; Martin 1996). Furthermore cooperatively breeding species are more prevalent in (sub)tropical areas than in temperate zones (Arnold & Owens 1999a). All these factors suggest that population regulation may differ considerably between tropical and temperate regions.

Small populations

Chance effects on birth and death rates become a particular risk in small populations (Diamond 1984; Pimm et al. 1988). Furthermore, at very low densities an increase in population size can have a positive effect on population growth, i.e. inverse density dependence, known as the Allee effect (Allee 1951; for review see: Courchamp et al. 1999). Another important feature of small population sizes is that with decreasing population sizes the chances of mating with relatives will increase and detrimental effects of inbreeding might threaten the persistence of small populations (Keller & Waller 2002).

The translocations of individuals to new suitable habitat is a powerful tool in the fight to save endangered species and could potentially become a major component
of conservation management worldwide (Fischer & Lindenmayer 2000; Bell & Merton 2002). Such (re)introductions provide a great opportunity to study density dependence as these populations usually start at very low densities, after which changes in vital rates can be studied as the population grows (Nicoll et al. 2003; Armstrong et al. 2005). Interestingly, increasing population densities can also have a large impact on behaviour: as density increases, breeding vacancies become rare and individuals have to delay reproduction, which is thought to facilitate the evolution of cooperative breeding (Koenig & Pitelka 1981; Emlen 1982).

**Cooperative breeding**

In cooperatively breeding species individuals refrain from reproduction and instead help to rear kin instead of reproducing themselves. This intriguing behaviour occurs in at least 3% of bird and mammal species (Brown 1987) and in some fishes (Taborsky 1994). Increasing density may not only promote cooperative breeding, but interestingly, cooperative breeding might in turn affect the way that density dependence shapes demographic rates; higher density may be advantageous if individuals survive or reproduce better in larger cooperative groups (Woolfenden 1975; Brown 1987; Balshine et al. 2001; Magrath 2001; Clutton-Brock 2002; Hatchwell et al. 2004; Heg et al. 2005). Although an increase in reproductive success with large group sizes could be the consequence of helping itself (Brown et al. 1982; Mumme 1992; Shreeves & Field 2002; Brouwer et al. 2005), long-term effects on fitness caused by the presence of helpers has rarely been shown (but see: Hatchwell et al. 2004).

Numerous adaptive hypotheses have been suggested to explain the evolution of cooperative breeding, e.g. kin-selection (Komdeur & Hatchwell 1999; Griffin & West 2003), pay to stay (Balshine-Earn et al. 1998b), group augmentation (Clutton-Brock 2002) and the role of ecological (Arnold & Owens 1999b; Hatchwell & Komdeur 2000) and life history factors (Arnold & Owens 1998). However, the proximate mechanisms underlying this behaviour have received considerably less attention. To gain insight into the mechanisms that contribute to delayed breeding and helping, hormones levels of breeders and non-breeders within cooperatively breeding species can be investigated (e.g. Schoech et al. 1996). Differences in blood hormone levels, e.g. testosterone, would indicate that there are fundamental differences between breeders and non-breeders in their reproductive physiology. Consideration of both functional and mechanistic explanations can improve our knowledge of what determines which individuals show cooperative breeding behaviour and it might contribute to our understanding of the large variation in helping behaviour both within and between species.
A long-term study on the Seychelles warbler

Here we studied cooperative breeding and population regulation in the Seychelles warbler (*Acrocephalus sechellensis*), a species endemic to just a few small islands in the Indian Ocean. This species went through a severe bottleneck, and the total world population consisted of only 30 individuals remaining on the island of Cousin between 1920 and 1968 (Crook 1960; Loustau-Lalanne 1968). Although the species must have formerly inhabited at least three, but probably more, islands in the Praslin group of the Seychelles archipelago (Diamond 1980; Collar & Stuart 1985), habitat loss caused by planting of coconuts (*Cocos nucifera*) and the introduction of predators such as rats and cats was responsible for the near extinction of this species. With the purchase of Cousin Island in 1968 by the International Council for Bird Protection (ICBP, now BirdLife International) a recovery programme was started. Restoration of the original native habitat allowed the warbler population to recover. Studies on warbler habitat use on Cousin suggested that continuous dense scrubby vegetation would allow the highest numbers of warblers (Bathe & Bathe 1982), which can explain why the species was also known as the Seychelles brush warbler (Penny 1974). However, at that time scrubby vegetation was the only suitable habitat available and further regeneration of the habitat showed that mature *Pisonia* woodland did not form a closed canopy as had been thought. The Cousin Island population recovered and stabilized at around 320 adult individuals by 1982. The vulnerability of a single small population to catastrophic events raised the idea of establishing new populations. Three translocation were performed by transferring birds form the founding island of Cousin to the islands of Arde (68ha; 1988), Cousine (26ha; 1990) (Komdeur 1994a), and Denis (2004) (Figure 1.1). In 2000 the world population of Seychelles warblers was estimated at 2060 (BirdLife International 2000) and the IUCN Threat Status changed from “endangered” into “vulnerable” (BirdLife International 2000). The Seychelles warbler has been the focus of intense study since 1985, first by Jan Komdeur and since 1997 also by David Richardson in collaboration with Terry Burke (Komdeur 1992; Richardson et al. 2003).

Seychelles warblers are facultative cooperative breeders; instead of breeding independently many individuals become subordinate within their natal territory (Komdeur 1992). Some of these subordinates help with incubating or feeding of the nestling. Group size varies from two to seven birds per territory. The development of microsatellite markers for this species (Richardson et al. 2000) has enabled accurate genetic parentage analyses and shown that the breeding system is even more complex than previously thought. Richardson et al. (2001) showed that in 44% of cases female subordinates were co-breeding and that 40% of all offspring were fathered by a male from outside the territory. As the population is a closed system, with virtually no dispersal on or off the island (Komdeur et al. 2004), almost all parentage can be assigned and importantly, accurate, unbiased survival probabilities can be calculated.

Here we study population dynamics in four populations of Seychelles warblers. Translocations to previously uninhabited islands allow us to test the causality of den-
sity dependence, using the change of numbers in the populations from early establishment through to saturation as a natural experiment. Furthermore, we investigate the proximate mechanisms involved in helping behaviour and the long-term fitness consequences of group living.

**Thesis outline**

In chapter 2 we investigate whether survival was density dependent in a saturated population of Seychelles warblers. Furthermore, we investigate whether the reductions in the population density on Cousin, caused by translocating birds to other islands results in an increase in juvenile and adult survival. As resource competition will mainly work on a local scale, i.e. the territory, we also investigate whether survival probabilities are associated with local density, measured as the average group size an individual lived in during its life. In addition, we investigate the effect environmental factors like rainfall and temperature have upon survival. We show that in a territorial species, although density dependent effects might not be detectable at the population level they can be detected at the individual territory level - the scale at which individuals directly compete.

As only experiments can test the causality of density dependence, we use the change in numbers during the process of saturation in the newly established populations on Aride, Cousine and Denis as a natural experiment to investigate this in chapter 3. We determine how reproduction and survival changed over the course of the populations' development and, in addition, study the effect of territory quality and food abundance on reproduction and survival. We show that the regulation of numbers takes place in a density dependent way and that the mechanism causing this is probably competition for food. Although the translocations to Aride and Cousine can be considered as being very successful, this does not guarantee success for future translocations. In Box A we investigate whether the recent translocation to Denis Island has, so far, been successful, by analysing the survival of warblers during the first two years after the establishment of the population.

Although environmental factors faced at some point can obviously affect an individual's fitness immediately, awareness is growing that conditions during the rearing period also strongly affect important fitness components later in life. (e.g. Magrath 1991; Sedinger et al. 1995; Lindström 1999; Green & Cockburn 2001; Cam et al. 2003; van de Pol et al. 2006). In cooperative breeding species, the presence of helpers adds an important component to these rearing conditions. For example, the presence of helpers has been shown to positively affect offspring survival and/or weight (Brown 1987; Emlen 1991). However, the long-term fitness consequences of helping on offspring have rarely been investigated (but see: Hatchwell et al. 2004). In chapter 4 we investigate, using multi-state capture-recapture models, how conditions during the rearing period of Seychelles warblers affect future survival and recruitment to a breeding position. Furthermore, we use data from a cross-fostering
experiment to determine whether effects were caused by the rearing factors per se rather than genetic or parental quality. Our results show that helping by subordinates within a territory can have long-term fitness consequences for the offspring helped.

The translocation of Seychelles warblers to new islands has shown that individuals of this species are able to reproduce in their first year of life, but that a lack of suitable habitat in a saturated population drives them to become subordinate in their natal territory (Komdeur 1992). Although habitat saturation seems the ultimate explanation for this behaviour, the proximate mechanisms involved are

**Figure 1.1** A map showing the four islands on which the Seychelles warbler occurs nowadays. In the 1960's the ca. 30 last remaining Seychelles warblers were confined to Cousin. New populations were established by translocations to Aride, Cousine and Denis.
unknown. In chapter 5 we determine the natural variation in plasma testosterone level and cloacal protuberance size - an indicator of sperm storage - in successfully reproducing primary males, and in apparently sexually inactive subordinate male Seychelles warblers. Testosteron has been known to play a role in male reproductive behaviour (for review see: Nelson 2000). Differences in testosterone levels between primaries and subordinates might indicate that subordinates are suppressed, however experiments are needed to test whether any relation between testosterone levels and status is really due to status per se rather than age, sexual immaturity or a lack of breeding opportunities for subordinate males. We experimentally promote subordinate males to primary status by permanently removing primary males from their territories. We then investigate testosterone levels and cloacal protuberance sizes of the promoted males. We show that primary and subordinate males do differ in their testosterone levels and size of cloacal protuberances, and that subordinate males are able to elevate their testosterone levels once social suppression is removed, although they do not appear to reach levels as high as primary males in the initial season after promotion.

In chapter 6 we investigate heterozygosity-survival correlations. In small isolated populations the probability that closely related individuals will mate will increase. Such inbreeding will result in decreased heterozygosity in offspring and may lead to the expression of recessive deleterious alleles, or to the loss of the benefits associated with heterozygosity at loci influencing fitness (Hartl & Clark 1997). Consequently, inbred individuals are expected to be less fit than outbred individuals, a phenomenon known as inbreeding depression (Hartl & Clark 1997). Inbreeding depression can have important consequences in wild populations and can contribute toward driving populations to extinction (Saccheri et al. 1998). Heterozygosity measured at microsatellite markers is generally assumed to reflect genome-wide inbreeding effects (e.g. Lynch & Walsh 1998). Although this might be true in partially inbred populations and when very large numbers of microsatellites are used, this is often not the case (Slate et al. 2004). Such correlations may also arise as a result of local effects with specific markers being closely linked to genes which determine fitness (Lynch & Walsh 1998; David 1998). We show that heterozygosity-fitness correlations can occur in bottlenecked populations but highlight the difficulty in distinguishing between the different hypotheses.

Finally, in chapter 7 we integrate some of the conclusions of the separate chapters and discuss these in a more general framework. Specifically, we discuss what the consequences of the establishment of new populations means for our understanding of population dynamics and conservation.
Top left: A ladder and some acrobatics are needed to check nests, which can be up to 25 m high in the trees. Top right: Warbler nests can be hard to find hidden between large Pisonia leaves. Bottom: Juvenile warbler with mosquito on his back; mosquitoes can infect warblers with avian malaria.