CHAPTER 1

General introduction
Natal dispersal

Should I stay or should I go? Beside being a famous song of The Clash (1982), this question forms the heart of this thesis. The subtitle reminds the reader that this thesis is not on whether or not to leave a lover, but on whether or not to leave the natal site. Actually, in this thesis we describe different aspects of natal dispersal, which is the movement of an individual from its site of birth to its site of first (attempted) reproduction (Greenwood 1980). Natal dispersal is one of the most important and least understood life-history traits (Clobert et al. 2001; Handley and Perrin 2007) and influences the dynamics, distribution and genetics of natural populations (Stenseth and Lidicker 1992). Consequently it has received considerable research attention. Natal dispersal may be assessed indirectly by examining the genetic structure within and between populations (Koenig et al. 1996; Sugg et al. 1996) or directly by marking and following individuals from birth to breeding. The latter method may be preferable, because it allows researchers to study variation in natal dispersal at the level of the individual. However, study areas are usually finite and the resulting dispersal data subsequently biased (i.e. long-distance dispersers may erroneously be assumed dead). Therefore, what is known about dispersal may be less accurate than the literature suggests (Baker et al. 1995; Koenig et al. 1996; 2000; Lahaye et al. 2001). For example, a lack of data on long-distance dispersers will bias dispersal distributions towards philopatry. To circumvent this problem we collected data on natal dispersal in the Seychelles warbler, a species that lives in populations with almost no emigration or immigration (Komdeur et al. 2004a). We studied the population on the tiny Cousin Island (29 ha, figure 1.1) that is part of the Seychelles archipelago in the Indian Ocean.

Outline of the thesis

Natal dispersal consists of a spatial and a temporal component: where do individuals disperse to and when in life do they disperse? The first part of this thesis deals with the spatial component. In most resident species, the natal dispersal distance is the farthest distance an individual will travel during its life. Therefore, knowing how far individuals disperse contributes to understanding the dynamics and genetic structure of a population (Greenwood and Harvey 1982; Horn 1984; Rockwell and Barrowclough 1987; Hanski 2001). In chapter 2 we describe how far individuals disperse from their natal territory and what factors affect natal dispersal distance, e.g. disperser sex, local density and age when dispersing. A recurring observation in many other studies is that natal dispersal is sex-biased, either in distance and/or in the timing of dispersal. As a result the evolution of sex-biased dispersal has received as much attention as the evolution of dispersal itself (Johnson and Gaines 1990). The main explanations for sex-biased dispersal involve inbreeding avoidance, local resource competition and local mate competition (Clark 1978; Greenwood 1980; Dobson 1982; Moore and Ali...
In chapter 2 we discuss if these processes are linked to the pattern of natal dispersal distances that we observed in our study population. In chapter 3 we investigate the possible relation between sex-biased dispersal and inbreeding avoidance in more detail. By calculating relatedness values between potential dispersers and all opposite-sex breeders in the population, we determined the spatial distribution of related individuals around the natal territories of dispersers. Furthermore, using natural and experimental data, we assess whether the occurrence of territory inheritance depends on the relatedness of the potential inheritor to the surviving opposite sex breeder. Finally, we assessed whether dispersers pair with individuals to which they are less related than may be expected on the basis of random mate choice.

Many studies present distributions of natal dispersal distance and argue that natal dispersal is biased towards short distances. However, to support this statement, observed natal dispersal distances should be compared to expected natal dispersal distances.
distances, based on opportunities to disperse (explained in Box A). Few studies have done so, most likely because determining when and where opportunities for successful natal dispersal occur is difficult. We were able to compare observed natal dispersal distance with expected natal dispersal distance, because a) in the Seychelles warbler, opportunities for successful dispersal arise when a breeder dies and b) we knew when and where such opportunities arose (chapter 2). This comparison gave us a first hint about the effect that living near a vacancy may have on the chances of occupying that vacancy. This so called proximity advantage re-appears in chapter 4, in which we portray the process of territory acquisition. Beside the effect of proximity we assess the effects of age and size of the competitor on territory acquisition. Furthermore, we describe and assess how often young follow the various routes to territory ownership and present data on foraying behaviour of young warblers.

The second part of this thesis deals with the temporal component of natal dispersal. For species in which independent offspring delay dispersal, understanding the causes of this delay may shed light on the evolution of group living (Ekman 2006; Covas and Griesser 2007). We describe the causes of (delayed) dispersal in chapter 5 with a focus on the presence of parents in the natal territory. In this chapter we also determine the fates of young that dispersed when both parents were still in the natal territory or when a parent had been replaced with a stepparent.

In chapter 6 we focus on the change in dispersal behaviour that seems to have occurred over the years of study. The sex-bias in delayed dispersal that was previously observed (Komdeur 1996) seems to have disappeared in later years of study, suggesting that natal dispersal is not a stable trait, but a plastic response to local social and environmental conditions (Baglione et al. 2002). We discuss the possible link between this change and the shift in the distribution of territory quality that has occurred since the start of the Seychelles warbler study on Cousin.

The seventh chapter deviates from the ‘red line’ and deals with the timing of extrapair fertilizations. Mate guarding may cause a trade-off between the benefits of protecting paternity and the benefits of competing behaviours, such as pursuing extrapair fertilisations. Studies showing a temporal separation of mate guarding and extrapair copulations support this view. However, no studies have shown direct evidence for a trade-off between mate guarding and extra-pair fertilizations. In this chapter, we investigate the timing of extra-pair fertilizations in the Seychelles warbler, a species in which males intensively guard their mate during the fertile period.

In the final chapter, the synthesis, we briefly discuss what our study has contributed to the understanding of natal dispersal. We furthermore highlight the need for a reliable pedigree of the Cousin Island Seychelles warbler population, which amongst other purposes could be used to calculate fitness consequences of natal dispersal. Finally, we discuss the remarkable observation that subordinate females and breeding males in adjacent territories appeared to avoid mating with each other.
The two intermezzos describe first records for Seychelles of a Kermadec petrel (*Pterodroma neglecta*) and a little crake (*Porzana parva*), respectively. Amongst the research chapters, the two intermezzos may appear to be “strange fish in the tank”. However, both the chapters and intermezzos handle the same subject: dispersal. A difference is that the chapters deal with dispersal over short distances, whereas the intermezzos describe instances of extreme long-distance dispersal. Where the Seychelles warblers do not even disperse off their tiny islands, the petrel and crake that I discovered on Cousin had drifted many thousands of kilometres outside their usual ranges. This extreme variation in dispersal behaviour may help to appreciate more the view that natal dispersal is one of the most important, but least understood life-history traits.

**Box A  Implications of finite study areas for dispersal distances in year-round resident species**

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The insight that dispersal distance has important consequences for the dynamics and the genetic structure of a population has resulted in a vast number of studies presenting natal dispersal distance distributions. It is now widely recognized that the probability of detecting a disperser decreases with increasing distance from the natal territory. This results in biased distance distributions that are left skewed because short distances are over represented (e.g. Baker *et al.* 1995; Koenig *et al.* 2000). Here, we would like to point out that, for year-round resident species, the shape of a study area and the spatial arrangement of its territories also affect the distribution of dispersal distances. Because study areas are finite, only those individuals that disperse from the edges of a study area are able to disperse the maximum distance within a study area. Given a convex study area, individuals dispersing from the centre of a study area can not disperse further than half the maximum distance. This results in left skewed distance distribution plots that become more pronounced when the number of territories in a study area increases. How exactly the skew affects distance distributions will depend on where in the study area the dispersers originate from. When territories in the centre of a study area have higher reproductive success (e.g. Paton 1994; Doherty *et al.* 2002) and therefore produce more dispersers than territories in the edges, the skew in natal dispersal distributions will be stronger than when there are no spatial differences in disperser origin. A second type of skew that is caused
by a convex shaped study area only acts at the very left end of dispersal distributions. Because territories near the edge of a study area have fewer nearby territories than central territories, fewer birds disperse over very short distances than over intermediate distances. This skew is especially strong when there are relatively many edge territories, i.e. when the study population consists of few territories. This annihilates the first type of skew in the very left range of a dispersal distance distribution plot. It is important that such skews are acknowledged when explaining short distance dispersal with traits such as delayed dispersal in cooperatively breeding birds (Zack 1990; Walters et al. 2004), low competition, philopatry or optimal search strategies of the surrounding area (see Baker et al. 1995).

To demonstrate these skews, we here calculated and plotted the distribution of all inter-territory distances in a hypothetical circular shaped study area containing 75 territories (figure Box A 1A). A distribution of all inter-territory distances represents a situation in which dispersal is random with respect to distance and the same number of birds disperse from each territory. Such a distribution would be uniform when no skews were present. To show that also the spatial origin of dispersers affects dispersal distance distributions, we plotted the distributions of distances between the natal territory and all other territories of five individuals dispersing from the centre (figure Box A 1B) and five individuals dispersing from the edge (figure Box A 1C) of the hypothetical study area.

There are methods to circumvent the above described problem: in a few studies, observed dispersal distances were compared with expected dispersal distances that were based on random dispersal destinations. Random dispersal destinations may be expressed as the distribution of all inter-territory distances (Lahaye et al. 2001; Yáber and Rabenold 2002) or as the average distance of each disperser to territories in which a same-sex vacancy opened in the year of dispersal or preceding (Williams and Rabenold 2005). The former may be preferable when most offspring leave the natal territory after fledging to float through the population in search of a breeder vacancy. The latter may be more suitable for species in which most offspring delay dispersal and make forays from the natal territory to search for breeder vacancies. Because dispersal is probably the most important and least understood life history trait (Clobert et al. 2001), we urge all researchers that discuss dispersal distances in resident species to use similar simple methods to circumvent the skews caused by the structure of a study site.

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Figure Box A 1. Frequency distributions of dispersal distances in a circular study area containing 75 territories. Plotted are A) all inter-territory distances, B) distances of the natal territory to all other territories of five individuals dispersing from the five most central territories of the study area and C) distances of the natal territory to all other territories of five individuals dispersing from five territories in the outer edge of the study area. All territories were of equal size and were evenly spread over the study area. Minimal dispersal distance was 100 meters and distance category 1=100-200m, category 2= 200-300m etc..