S25-5　Population predictions for Seychelles warblers in novel environments

Jo RIDLEY[1*], Jan KOMDEUR[2], David RICHARDSON[3], William J. SUTHERLAND[1]

1. Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK; j.ridley@uea.ac.uk
2. Zoological Laboratory, Animal Ecology, University of Groningen, P.O. Box 14, 975 AA Haren, The Netherlands; j. komdeur@biol.rug.nl
3. Dept. of Animal Ecology, University of Lund, SE-223 62 Lund, Sweden; david.richardson@zooekol.lu.se

Abstract　A major challenge for population ecology is to be able to predict population sizes in novel conditions, as in those following habitat loss or translocation. To do this successfully, we show here that it is necessary to understand the behavioral basis of dispersal decisions as they affect fitness. The Seychelles warbler, like many socially complex species, lives in family groups. This leads to the stable usage of sink habitats through kin competition. Sink usage means that bird density is not representative of habitat quality, and consequently that simple extrapolations from current habitat occupancy mis-estimate the effects of habitat loss. Similarly, per territory reproductive success for Seychelles warblers declines with density within a habitat class, in common with many territorial species. This too undermines the use of simple extrapolations to predict the consequences of habitat loss. Retrospective predictions for two actual translocations show some success, while the extent to which they fail emphasizes the need for full understanding of the links between the environment occupied and reproductive success.

Key words　Population size prediction, Sink usage, Reproductive success, Seychelles warbler; Habitat quality, Habitat loss

1　Introduction

Many species of birds breed in social groups within which reproduction is unequally shared: 3.2% breed cooperatively (Sibley and Monroe, 1990), and many more breed in groups including either non-breeders or with high levels of reproductive skew (Cockburn, 1996; Heg et al., 2000; Ekman et al., 2001). Species threatened by habitat loss or change include many with socially complex systems (Fitzpatrick et al., 1991; Virkkala, 1991; Walters et al., 2002), producing a demand for population models that can predict the consequences of such threats, and guide conservation management to mitigate them. Existing models of group-living species (e.g., Breininger et al., 1998; Root, 1998; Walters et al., 2002), are based on patterns of dispersal or correlated habitat use. Because dispersal rates are measured in contemporary environments, it is unsafe to assume that they will be the same in modified habitats. This view is reinforced by recent evidence that, for socially complex species, models based on fixed probabilities of dispersal produce far less sensible predictions than those based on optimal dispersal decisions (Stephens et al., 2002).

By 1959, the global population of the Seychelles warbler (*Acrocephalus sechellensis*) had become restricted to Cousin Island where, because the native vegetation had been replaced largely with coconut plantations, only 26–29 birds survived (Komdeur et al., 1998). Since then, the population has rebounded from habitat restoration, reaching a plateau of around 320 birds in 1982 (Komdeur, 1992; Komdeur et al., 1998). Translocations of birds to other islands have further improved the prospects of the species. Here we compare the success of different modelling approaches for predicting population sizes for island populations of the Seychelles warbler. First we illustrate why family-based groups and territoriality compromise simple extrapolations for predicting consequences of habitat loss. Secondly, we attempt to predict retrospectively the success of the translocations to Aride and Cousine Islands, and in so doing, demonstrate the significance of interspecific interactions in population predictions.

2　The model

2.1　Seychelles warbler life history

The life history, study site and methodology for the Seychelles warbler study have been covered in detail elsewhere (Komdeur et al., 1995). In brief, the Seychelles warbler is a cooperatively breeding insectivore that is endemic to the Seychelles archipelago and which maintains year-round territories. Territory quality is estimated by the number of leaf insects present, enabling territories to be divided into three categories of quality: low, medium or high (Komdeur, 1992). On Cousin Island, high quality territories are situated in the center of the island, surrounded concen-

trically with medium, then low quality territories on the outer rim (Fig. 1). Territorial groups typically comprise a dominant pair (henceforth "breeders"), together with some retained offspring, 88% of which are female (Komdeur, 1999). Retained females (henceforth 'helpers') alloparent and achieve a minor share of reproductive success (Richardson et al., 2001). Retained males rarely alloparent, 78% of them queueing to acquire a breeding position on either natal or adja-
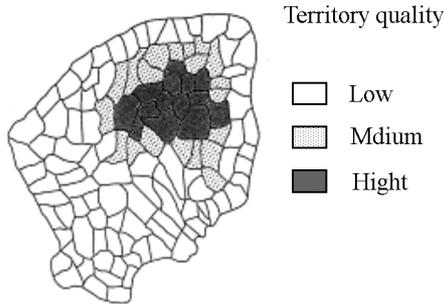
cent territories upon the death of the male breeder (Komdeur and Edelaar, 2001a).

2.2 Model structure

The structure of the model employed is detailed elsewhere (Ridley and Sutherland, 2002; Ridley et al., 2003). Because our aim here is to analyze the potential of the model to guide conservation management, rather than validate its methodology, we include only a summary of key features useful for understanding its output. The model is individual- and fitness- based: individuals hatch, have one or more opportunities to disperse, possibly to become breeders, and finally die (Fig. 2). Survivorship and fecundity are determined directly by empirical measures (Ridley et al., 2003). Survivorship varies with habitat quality only (Komdeur, 1992), whereas fecundity varies with both habitat quality and group size, being highest at intermediate group sizes (Komdeur, 1994). Dispersal, by contrast, is determined only indirectly by empirical data: it occurs when so doing increases individual fitness.

Fitness is estimated as lifetime reproductive success, weighted firstly to account for kin competition among
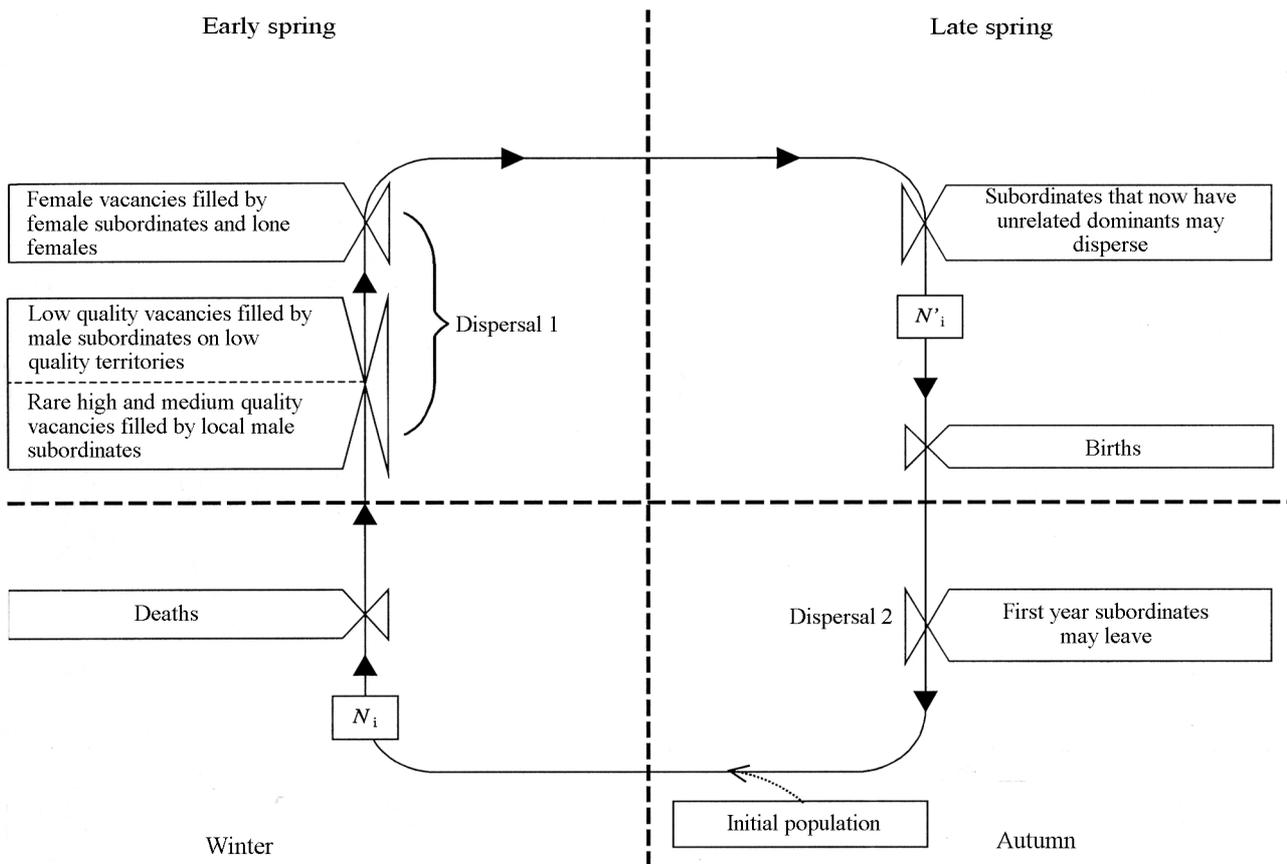
Fig. 1   Map of Cousin Island (29 ha) showing the distribution of high, medium and low quality territories of the Seychelles warbler
From Komdeur (1992).

Fig. 2   Summary of key features incorporated in the model for population size prediction in the Seychelles warbler
Death: appropriate to territory specific survivorships (Komdeur, 1992). Dispersal 1: vacancies filled by randomly selected helpers, queuers or floaters from a pool of all those whose fitness would be increased by the move. Eviction: helpers and queuers leave territories following the establishment of a new male breeder, moving to either the best available breeding vacancy, or if none, to become floaters. Breeding: according to territory quality (Komdeur, 1992) and number of helpers (Komdeur, 1994; Ridley et al., in review), sex ratios (Komdeur et al., 1997), rates of cuckoldry (Richardson et al., 2001) and co-breeding (Richardson et al., 2002). Dispersal 2: yearlings dispersed, either to the best breeding vacancy, or failing this, as floaters.

queues (Ridley and Sutherland, 2002) and secondly to account for density dependent changes in per territory reproductive success. It is assumed that kin competition arises among those male subordinates that queue on better quality territories because longer queues depreciate the reproductive value of future offspring. Density dependence in territory quality occurs because territories are larger, and the cost of their defence lower, when there are fewer birds in a habitat.

3 Results

3.1 Predicting effects of habitat loss on population size

Our model is contrasted first with two simpler approaches for predicting the consequences of habitat loss on population size. The first approach assumes that current group sizes would remain unchanged by habitat loss. High quality territories on Cousin Island at present hold 3.7 birds, medium 2.9 birds, and low 2.4 birds (Komdeur, 1992). Where dispersal is based on fitness maximization, a progressive removal of high and medium quality habitat should lead to falling group sizes in low quality habitat until hatchings and deaths are in balance. In contrast, the assumption that group sizes stay constant leads to markedly high population predictions, with hatching and death rates out of balance (Fig. 3).

A second, more sophisticated approach predicts the consequences of habitat loss on the basis of current rates
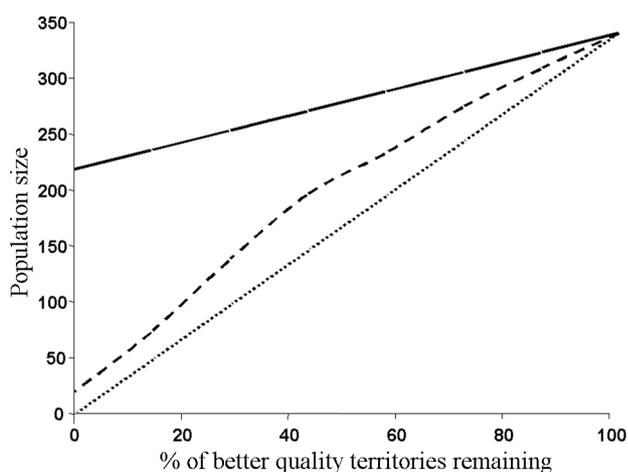

Fig. 3 Three predictions for the progressive removal of high and medium quality habitat for populations of the Seychelles warbler on Cousin Island

If habitat occupancy, or equivalently, habitat specific group-sizes are assumed to be constant and independent of habitat loss (solid line), a markedly larger population size is predicted than if dispersal, and thus habitat occupancy, is determined by attempts to maximize individual fitness (dashed line). If hatching and death rates are assumed to vary with density, consistent with observed data (Komdeur, 1996) and the rate of increase, the low quality habitat on Cousin Island is a pseudosink (Watkinson and Sutherland, 1995). Accordingly, the assumption that habitat specific hatching and death rates are density independent overestimates the consequences of removing the better quality habitat (dotted line).

of hatching and death. According to it, no population will survive once all high and medium quality habitat is lost because on Cousin Island, at present, hatching rates are lower than death rates in low quality habitat. As density falls, however, territory sizes increase and so does the per territory reproductive output (Komdeur and Edelaar, 2001b), in common with many territorial species. If this increase is incorporated, as it is in our fitness maximizing model, the effect is sufficient to lift hatching rates above death rates such that lifetime reproductive success is above one in low quality habitat. In these circumstances, the population would persist at a lower density than at present (Fig. 3), but above the zero level that a simple extrapolation from current hatching and death rates suggests (Fig. 3).

3.2 Predicting effects of translocation on population size

In 1988 and 1989, birds were translocated from Cousin Island to Aride and Cousine Islands respectively. Beforehand, habitat quality on Aride and Cousine had been measured by insect density, a procedure found successful for identifying habitat on Cousin Island (Komdeur, 1992). Territory sizes average 250 m² on Cousin Island, and this, together with the insect density data, was used to estimate the potential number of high, medium and low quality territories on Aride and Cousine Islands (Table 1). We then ran the Cousin model for Aride and Cousine by altering the number of territories appropriately. For Cousine, the model prediction was reasonably good, whereas for Aride it underestimated true population size (Fig. 4).

4 Discussion

4.1 Sink usage and despotism compromise simple predictions

In territorial systems, density dependence may arise in two ways: intraspecific competition can effect falls in total reproductive success across territories or move individuals into poorer habitats and delay breeding. Seychelles warblers show evidence of both (Komdeur, 1992; Komdeur and Edelaar, 2001b; Ridley et al., 2003). In the case of the first, some territories will offer lifetime reproductive success of more than one because they are the only territories that can sustain groups (Kokko and Sutherland, 1998). For a population to be in equilibrium, individuals that produce more than one replacement must be counterbalanced by others that produce less: either they do not breed or they

Table 1 Territory numbers by habitat quality on the Seychelles islands of Cousin, Cousine and Aride, as used in the model

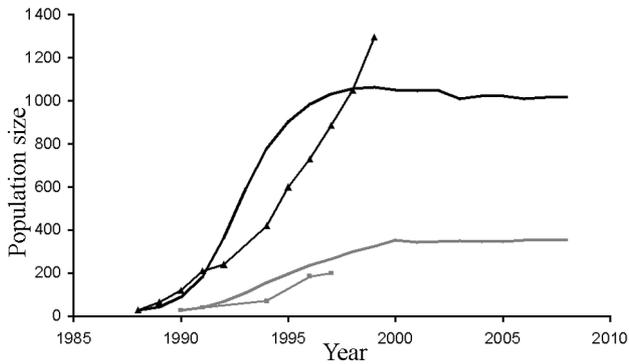|	Territory quality		
	High	Medium	Low
Aride	128	72	72
Cousin	14	20	89
Cousine	15	44	45

Fig. 4 Observed (lines with triangles) and model-predicted population sizes for Aride Island (black lines) and Cousine Island (grey lines)
While the prediction for Cousine is close, that for Aride is an underestimate.

breed in sinks.

The low quality territories on Cousin Island are sinks; and given that many group-systems are founded on the family (Cockburn, 1998), and that kin competition appears to be an almost inevitable consequence (Ridley and Sutherland, 2002), sink usage will probably prove to be a widespread form of regulation in communal-living species. Where sinks are used, the densities of individuals are not representative of habitat quality. This undermines the use of both habitat quality indices (e.g., Burgman et al., 2001) and the matrix-type models based on field estimates of dispersal rates (e.g., Breininger et al., 1998; Root, 1998; Walters et al., 2002) for predicting habitat occupancy in novel environments. The only systems for which these approaches are valid are (1) those where there is no kin competition, and (2) those where dispersal is 'free' (*sensu* Fretwell and Lucas, 1970) and individuals cannot restrict one another's access to resources. It is only in the absence of both despotism and kin competition that population density is directly proportional to resource abundance alone. Because Seychelles warblers are subject to both despotism and kin competition, simple extrapolations fail to predict the consequences of habitat loss on population size.

4.2 Sinks can be pseudosinks

At low population densities, space is not limiting and the costs of territorial defence are lower. As a result, per territory reproductive success is higher at low densities, and on Cousin Island implies that the low quality territories are pseudosinks (*sensu* Watkinson and Sutherland, 1995). Using a restricted definition, Hunt and Law (2000) argue that territorial populations are 'not necessarily' subject to density dependence, while White (2001) argues that they are 'not' at all. In effect, they advocate the Ideal Despotic Distribution model (Fretwell and Lucas, 1970), whereby territorial systems comprise a fixed array of territories of fixed quality. White (2001) thus argues that any changes in density are correlates, and not causes of declines in mean fitness.

The Seychelles warbler bears all the hall marks of a

highly despotic species: there is high variance in fitness both within (Richardson et al., 2001) and among habitat types (Komdeur, 1992), and subordinates typically leave their natal territories following the establishment of a new breeder (Komdeur, 1999). That territory quality is density dependent in the Seychelles warbler, under any definition of the term, and also in other systems (Stamps, 1990; Calsbeek and Sinervo, 2002), suggests that this phenomenon is widespread. Thus Ideal Despotic Distribution models of territorial systems are not sufficient to model their population dynamics. Adopting the view that territorial populations are simply limited by resources will overestimate the dangers posed by habitat loss (Fig. 3). It will also overestimate the benefits of resource supplementation because a proportion of the additional resources will be spent on intra-specific fighting.

4.3 Predicting consequences of translocations

Our results show that predicting the size of populations following such substantial change as translocation remains a challenge. With hindsight, it is possible to identify at least two reasons why our modelling approach worked for Cousine but not Aride Island.

First, the model, though complex, is still a single species model and overlooks the roles of predation and parasitism. The Seychelles fody (*Foudia sechellarum*) is a significant egg stealer (Komdeur and Kats, 1999) on Cousin Island, and its presence on Cousine (29.4% eggs lost, $n = 17$) but not Aride (0% eggs lost, $n = 23$) is a likely cause of the differential success in predicting the population sizes for these two islands.

Secondly, the model for Cousin Island classes habitat into three types: high, medium and low quality. Territories in high quality habitat have more than 3 000 insects per m^2 of leaf area, with a maximum of ca. 4 500. However, while the maximum recorded on Cousine Island is similar to that on Cousin, it is ca. 12 000 on Aride. As a consequence, reproductive success is higher on Aride than on either of the other islands, such that on Aride there is nonstop breeding in super-quality territories (Komdeur, 1996). On Aride, moreover, 2-egg fully fertile clutches are the norm compared to mostly single-egg, partly fertile clutches on Cousin and Cousine. To predict population sizes accurately after major habitat change, the relationship between fecundity and resource availability will have to be understood and incorporated.

Thirdly, habitat on Aride Island is altogether different from that on Cousin or Cousine Islands, and has a much more complex vegetational structure. As a result, insect-density profiles are unlikely to yield a true representation of territory size and quality for the Seychelles warbler.

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