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Population regulation in group-living birds: predictive models of the Seychelles warbler

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Summary

1. A major challenge for population ecology is to predict population responses to novel conditions, such as habitat loss. This frequently involves understanding dispersal decisions, in terms of their consequences for fitness. However, this approach requires detailed data, and is thus often inappropriate for urgent problems on poorly known species. This may be resolved by developing a predictive framework based on well-studied species, for applying to those that are less well understood.

2. Population size, group sizes and habitat occupancy of the Seychelles warbler (*Acrocephalus sechellensis*) can be predicted by determining the evolutionary stable dispersal strategy. For densities near to demographic equilibrium, regulation results from the combined effects of non-breeding and use of sink habitats.

3. In the Seychelles warbler, resident male non-breeders compete for breeding vacancies on neighbouring territories. The resulting kin competition is a key process for predicting the observed balance between regulation by non-breeding and regulation by sink use. Family groups, in which offspring delay dispersal, hoping to fill a vacancy on a local territory, are common among group-living species. This suggests that kin competition may frequently play a central role in the population regulation of socially complex species.

4. Although all the model variants considered are complex, predictions are shown to be insensitive to a range of simplifications, illustrating that, despite significant evolutionary import at the individual level, some behaviour can be unimportant when considering population level questions. Identifying which behavioural strategies have significant demographic consequences is key to the further development of population models based on fitness maximizing behaviour.

Key-words: cooperative breeding, density dependence, habitat selection, kin selection, offspring quality.

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Introduction

Many species of birds breed in social groups within which reproduction is shared unequally (Cockburn 1996; Heg *et al*. 2000; Ekman *et al*. 2001), with 3·2% breeding cooperatively (Sibley & Monroe 1990). Further, many of these socially complex species are threatened by habitat loss or change (Fitzpatrick, Woolfenden & Kopeny 1991; Virkkala 1991; Walters, Crowder & Priddy 2002). This produces a demand for

population models that can predict the consequences of such threats and guide conservation management aimed to mitigate them. Although previous modelling has yielded some theoretical expectations for which processes regulate these species' abundance (Sutherland 1996; Kokko & Sutherland 1998; Ridley & Sutherland 2002), there remains a need to establish which processes are important in real systems.

Predicting the size of a population following habitat change depends on predicting how individuals occupy the available habitat, and habitat occupancy in turn is largely determined by dispersal decisions. However, because dispersal events are relatively rare, measuring dispersal rates is not easy. An alternative approach is to use our understanding of the fitness consequences

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of dispersal in order to predict dispersal rates, and thus populations' responses to habitat change. Existing models of group living species (e.g. Breininger *et al.* 1998; Root 1998; Walters *et al.* 2002) are based on current dispersal patterns or their corollary, habitat use patterns. However, it is unsafe to assume that dispersal rates measured in contemporary environments will be accurate in modified habitats. This perspective 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 fitness-based dispersal decisions (Stephens *et al.* 2002).

In order to use fitness to predict dispersal, we first need an appropriate measure of fitness. However, although a rich theoretical literature exists for the selective pressures of social evolution (Frank 1998; Kokko & Sutherland 1998; Irwin & Taylor 2000; Kokko & Lundberg 2001), it indicates that socially complex species present numerous obstacles to estimating fitness from field data, including variable sex ratios, as well as spatial variation in both dominance and reproductive output. To reconcile theory and data we focus on the Seychelles warbler [*Acrocephalus sechellensis* (Oustalet) (Sylviidae)], for which we have a comprehensive characterization of individuals' birth and death rates in a range of habitats (Komdeur 1992, 1994b).

Our first aim is develop a model with which to predict habitat occupancy by the Seychelles warbler around demographic equilibrium. To do this we use survivorship and fecundity rates to derive a sufficient measure of fitness with which to predict dispersal. Secondly, through the serial simplification of the fitness measure used and behavioural strategies included, we show which processes are essential for predicting habitat occupancy, and which influence predictive ability more weakly.

Model

SEYCHELLES WARBLER LIFE HISTORY AND MODEL STRUCTURE

The life history, study site and methodology for the Seychelles warbler study have been covered in detail elsewhere (Komdeur *et al.* 1995). In brief, this is a cooperative breeding species, endemic to the Seychelles archipelago. The warbler is purely insectivorous and maintains year-round territories. Territory quality was measured as estimated number of leaf insects present in a territory, and territories were divided into three categories of quality: low, medium or high (Komdeur 1992). The high-quality territories are in the island's centre, with medium, then low-quality territories forming approximately concentric surrounding bands (Fig. 1). Under natural conditions the size and number of these territories on the island remain approximately constant over the years (Komdeur 1996). Therefore, in
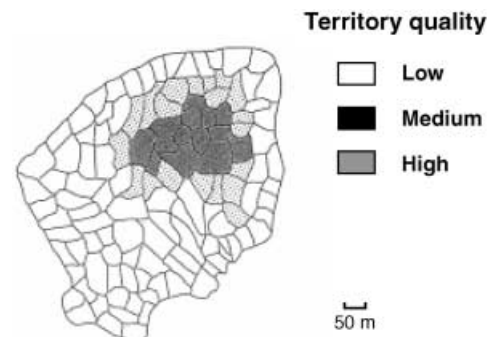
Fig. 1. Map of Cousin Island (29 ha) showing the distribution of high-, medium- and low-quality Seychelles warbler territories (Komdeur 1992).

this model we do not vary the numbers of these territories; a limitation that means the model can predict habitat occupancy close to demographic equilibrium, but cannot predict population dynamics in unsaturated environments. Although we do not incorporate changes explicitly in the sizes of territories, such changes are implicit in the model in that smaller groups have lower fecundities partly because they have smaller territories (Komdeur & Edelaar 2001b).

Territorial groups typically comprise a dominant pair (henceforth, simply: 'breeders'), together with some retained offspring, 88% of whom are female (Komdeur 1999). Retained females (henceforth 'helpers') alloparent and achieve a minor share of the reproduction (Richardson *et al.* 2001). Retained males (henceforth 'queuers') rarely alloparent, with 78% instead attempting to acquire a breeding position on either their natal territory or on a territory adjacent to their natal territory following the death of the occupying male breeder (Komdeur & Edelaar 2001a). These queuing and helping strategies, open to offspring, lead to different dispersal choices. Male offspring must frequently choose between queuing and becoming non-resident 'floaters' in the low-quality habitat (Komdeur 1992), whereas females choose between the direct fitness benefits of their share of reproduction, combined with the inclusive fitness benefits of alloparenting, and the direct fitness benefits of seeking a territory vacancy. Together these decisions determine how many offspring are retained, or equivalently habitat occupancy.

The approach we use to predict habitat occupancy is an individual-based simulation. Dispersal costs are not included because distance to the vacancy has no effect on dispersal. Individual warblers of the various categories are known to sample different territories all over the island at a regular basis, by observations (Komdeur 1991) and by radiotelemetry studies (Komdeur J., Daan S., Madsen V. & Tinbergen JM, unpublished observations). For Seychelles warbler populations near saturation, there is usually only one nesting attempt in the spring (Komdeur 1996). Mortality occurs throughout the year, with some indication of a peak in the autumn during lean years (JK, unpublished data). Accordingly, a discrete time model framework was
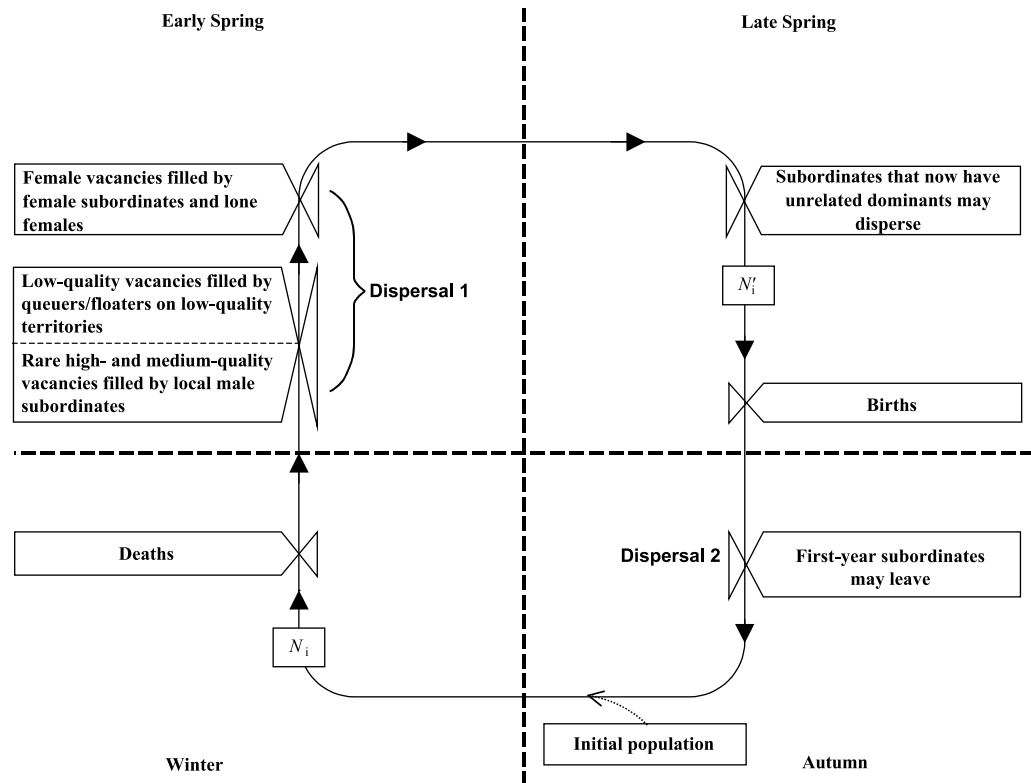
Fig. 2. A schematic of the model structure used. Within the model death is a discrete event, thus we can derive population sizes only at their peak (immediately after breeding) and at their trough (immediately before breeding). The Seychelles warbler population is censused in December, with all adult birds being counted. Under the assumption that mortality rates do not vary seasonally, the average of N_i and N_i' is closely comparative with the census data, and it is this measure that we use throughout the paper.

employed. Each year included the following sequence of events (to be read in conjunction with Fig. 2).

Death: when a randomly drawn number from the interval [0,1] was higher than the territory specific survivorships (Table A1), the individual died.

Dispersal (1): vacancies were filled by randomly selecting helpers, queuers or floaters from a pool of all those whose fitness would be increased by the move.

Eviction: helpers and queuers may leave their territories following the establishment of a new breeder (NB: the capacity of breeders to evict differs among model variants, see Table 1). Territories were considered in a random sequence, with helpers and queuers moving to either the best available breeding vacancy, or if there were none, to become floaters.

Breeding: for expected fecundities less than 1, if a randomly drawn number from a [0,1] interval was less than the expected fecundity, an offspring was born. Otherwise, births were drawn from a normal distribution using observed standard deviation data (Table A2). Births were then divided into males and females following Table A3, and added to the group as the next lowest helper or queuer. Following Richardson *et al.* (2001), a male breeder from a randomly chosen territory was given paternity 40% of the time, or else the dominant male took paternity. Following Richardson, Burke & Komdeur (2002), a helper randomly selected

from the same territory was given maternity 26% of the time, or else the dominant female took maternity.

Dispersal (2): the year's offspring may disperse either to the best breeding vacancy or, failing this, to be floaters. They were considered in a sequence determined first by age (youngest first), and secondly by their territory (chosen randomly).

ESTIMATING FITNESS AND MODEL PARAMETERIZATION

This is an individual-based model in which individuals are born, have one or more opportunities to disperse, may become breeders, and finally die. With the exception of dispersal, all of these are determined directly by the empirical measures of survivorship and fecundity detailed in Tables A1–A3. Dispersal, by contrast, occurs when so doing increases an individual's fitness (which individual is an assumption we vary within the model; see Table 1), meaning that dispersal is determined only indirectly by survivorship and fecundity rates. Accordingly, we first derive estimates for the lifetime reproductive success of breeders and non-breeders in this system. Then, as lifetime reproductive success is founded on the simplification that all offspring are of equal value, we incorporate two weightings to generate a more accurate measure of fitness (also summarized in Table 1).

Table 1. Key to model codes and terminology. Model codes comprise two parts: the first ($D_?$) indicates whether the breeder's, or potential disperser's fitness is maximized by dispersals, and the second ($\omega_?$) the fitness measure used

Code	Description
D_{IFD}	All dispersal decisions maximize the disperser's fitness
D_{ij}	Offspring related to breeders:
	· Yearlings – all dispersal decisions maximize breeder's fitness
	Helpers/queuers – all dispersal decisions maximize the disperser's fitness
	Offspring not related to breeders:
	Dispersal decisions may maximize either the breeder's or the disperser's fitness, with breeders able to control the dispersal of offspring of both sexes, or only the same sex, or neither. The following notation describes these scenarios; where 'o' denotes the fitness of the offspring, and 'b' that of the breeder, is maximized by the dispersal decision

	1st subscript (i)			2nd subscript (j)		
Scenario abbreviation	D_{0j}	D_{1j}	D_{2j}	D_{i0}	D_{i1}	D_{i2}
Dispersal by queuers	o	o	b	o	b	b
Dispersal by helpers	o	b	b	o	o	b

	The subscript's values follow from the annual probabilities of facing an incoming breeder, whose fitness interests would win out, are $(1 - L^{0,1, \text{ or } 2})$. Higher subscript values mean dispersal is more despotic
ω_I	Lifetime reproductive success
ω_{II}	ω_I weighted by the depreciative effect, of a longer queue, on future offspring
ω_{III}	ω_{II} weighted to account for male germlines typically staying in the same habitat for multiple generations
Breeder	The dominant pair, who gain majority shares of the reproduction on each territory
Helper	Female residents, over 1 year old, who both help the breeders, and obtain minority shares of the reproduction
Queuer	Male non-breeding residents, over 1 year old, who have the prerogative to breeding vacancies on neighbouring territories
Floater	Non-breeders, over 1 year old, who float over the low-quality territories

For a breeder with h helpers, in habitat k, with constant annual survival L_k and fecundity $M_{k,h}$ lifetime reproductive success ω_I is, by serial expansion:

$$\omega_I(\alpha_k) = \sum_{i=j}^{\infty} L_k^i M_{k,h} = \frac{M_{k,h}}{1 - L_k} \qquad \text{(eqn 1)}$$

where $j = 0$ before the breeding season and 1 after it. k is a habitat quality index. It varies from 1 to 4, not the 1–3 that might be expected given three habitat types (Fig. 1), because the prerogative to local vacancies that males enjoy means the quality of a territory depends not just on its intrinsic quality, but also on the quality of the adjoining territories. To this end, we assume all territories have six neighbouring territories with qualities as detailed in Table A4. Because some low-quality territories border medium-quality territories and some do not, we split this territory class into two: near-low (those adjoining medium quality territories) and far-low (those not doing so).

There is a simplification implicit in eqn 1 to the effect that current conditions are indicative of future conditions, in that an individual decides its dispersal preferences by choosing between the lifetime reproductive success with a group that is always of size x and a group that is always of size $x - 1$. Although this is not true for groups that are substantially too large, from the perspective of fitness maximization, it is approximately true for groups near to their optimal size. To predict habitat occupancy accurately, the key dispersal decisions are those where the costs and benefits are finely balanced, and this is the case only for those groups approaching their optimal size. Hence, although the constant-group-size assumption is in some cases flawed, these are not the cases that matter to predicting habitat occupancy.

Besides breeders, there are three other classes of individuals: helpers, queuers and floaters (described in Table 1). The choices they face are illustrated in Fig. 3. The fitness of helpers comprises their inclusive fitness benefits through alloparenting and their direct fitness benefits through cobreeding. Both these benefits can be derived directly from eqn 1, by incorporating relatedness discounts and share-of-reproduction discounts, respectively. Relatedness discounts reflect the average relatedness of a breeder to their offspring, i.e. 0·5 in models where there was no cuckoldry, appropriately less where there was. For both queuers and floaters, residual lifetime reproductive success is given by eqn 1 discounted by the probability of surviving long enough to obtain a vacancy. For queuers these probabilities were recalculated for each potential dispersal, depending on the number of local competitors (Fig. 3). While for floaters, the probabilities were estimated from the fraction of floaters that died while still floaters, averaged over the previous 10 years the model had run. Though highly robust (Houston *et al.* 1988), these dynamic-state-variable methods can be flawed. Specifically, these parameters might either converge on a stable value, but this value might be sensitive to initial conditions, or no stable value might be reached. However, we did not encounter either of these problems.

For individuals that chose to delay dispersal, there was a possibility that following the death of a parent, incoming breeders could evict them. When either a
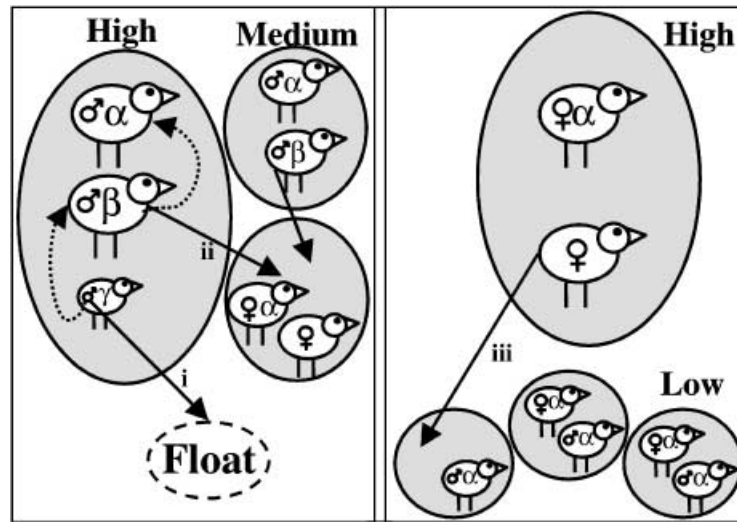
Fig. 3. A representative sample of the dispersal decisions made within the model, illustrated with a subset of the territories modelled. In the left panel there is a high-quality territory, its two medium-quality neighbours, and the option of floating, and not being associated with a territory. Dispersal decision **i** relates to the newly fledged gamma male on the high-quality territory, who is deciding between staying and possibly ascending the queue, and leaving to float. Dispersal decision **ii** relates to the male beta on the high-quality territory, choosing between taking a vacancy on a neighbouring medium-quality territory, for which it must compete with all other male betas neighbouring the territory with the vacancy, and waiting for a vacancy on a high-quality territory. In the right panel there is a high-quality territory with three distant low-quality territories. Dispersal decision **iii** relates to the helper on the high-quality territory. The best female vacancy available is on a lower-quality territory, and thus she is choosing between this available vacancy and helping her parents. As the potential disperser in case **i** is newly fledged this is a Dispersal 2 decision (Fig. 2), while because the potential dispersers in cases **ii** and **iii** are adult helpers and queuers, respectively, these are Dispersal 1 decisions (Fig. 2).

queuer or a helper wished to leave following the death of a parent, we assumed they could always do so. In cases where a helper or queuer wished to stay, but the incoming breeder's fitness was maximized by the helper or queuer leaving, we considered all possible model variants with respect to who's fitness was maximized by their leaving. These variants are summarized in Table 1.

Thus far we have described the simplest possible fitness estimates, because all offspring are treated as being of equal value. We now introduce two weightings which account for the variation in the prospects of offspring, and thus give more accurate measures of fitness. The first weighting depends on the number of queuers on a territory, because the number of queuing males increases and future male offspring will have to queue for longer before (possibly) obtaining a local breeding vacancy. This means the residual reproductive value of a breeder declines with the number of queuers, i.e. retained offspring depreciate future offspring. The calculation of offspring depreciation discounts (OD_Q) to account for this effect are described in Ridley & Sutherland (2002).

The second weighting, P_k, also follows from the prerogative of queuers to local breeding vacancies. This localized dominance means that not only do breeders on the higher-quality habitat have relatively high lifetime reproductive success, but so too do their male descendants. Whenever there is variation in habitat quality, and offspring do not, in effect, join a pool from which they settle randomly across all habitat types, the fitness differentials among habitat types are underestimated by

lifetime reproductive success (Rousset 1999). We use a dynamic state variable approach to calculate P_k. P_k were initially set to 1 in all four habitat types. A male born into each habitat was given an 'allele' detailing its natal habitat. These alleles were inherited by all the males' offspring, and the model run until all individuals carried genes with the same value, i.e. the gene had gone to fixation. This cycle was iterated during a 100 000-year run of the model to yield the habitat-specific probabilities of new mutations going to fixation. These probabilities were then weighted by the habitat-specific proportion of offspring that were male and used as the starting point for the next iteration, and the whole process was iterated until fixation probabilities stabilized. Thus we have our most sophisticated measure of fitness:

$$\omega_{III} = \omega_{II} \times P_k = \omega_I \times OD_Q \times P_k \qquad \text{(eqn 2)}$$

STATISTICAL ANALYSIS

The observed group sizes (Table A1) were collected over a 6-year period. Accordingly, these were compared with model predictions by finding the probability that a randomly selected 6-year sequence of model output ($n = 395$) was different from the observed group sizes, using unpaired t-tests.

Results

All models where run from a starting population of 14 pairs in the high-quality habitat. Unless stated

otherwise, all results presented are based on 500-year runs of the model. Output for the first 100 years was ignored. The average of the remaining 400-year output yielded data that were consistent, between different model runs, to 2 decimal places.

WHICH MODEL BEST FITS THE OBSERVED HABITAT OCCUPANCY

Our most complex formulation of fitness (ω_{III}) predicts patterns of habitat occupancy similar to observed patterns (Fig. 4), although with some sensitivity to the dominance assumptions made. We find better fits to observed data where dispersal by first-year offspring is determined by what maximizes their parents' fitness, but where dispersal by older offspring maximizes the disperser's fitness ($D_{IFD}\omega_{III}$ yields worse predictions than all the other model variants illustrated in Fig. 4). Further, where the departure of a helper or queuer harmed its own fitness, but improved the fitness of a newly settled, unrelated breeder, those models assuming such dispersals maximized the unrelated breeder's fitness produced marginally more accurate predictions (better predictions by model variants illustrated to the right of Fig. 4). Given this perspective, and our knowledge that a male who has started budding off their own territory is less likely to leave if its parents die (Komdeur & Edelaar 2001b), we assume henceforth that queuers can be evicted by unrelated male breeders, but not by unrelated female breeders, but that helpers can be evicted by both (i.e. model variants of the form $D_{21}\omega_?$, where '?' could be any of the possible values in Table 1).

Having established a robust model, based on ω_{III}, we consider briefly its implications for predicting the consequences of habitat loss. Because the model is based on data from a population close to its demographic equilibrium there are logically only two mechanisms by which population growth rate can decrease as density increases. First, more non-breeders (this decreases per capita fecundity with the exception of a first helper on a medium-quality territory, see Table A2) and secondly, more breeders on the low-quality territories (i.e. a buffer effect). These low quality territories are sinks (e.g. for a lone pair: $\omega_I = 0.2/0.24 = 0.83$; NB in sexual species, each individual must produce two offspring for demographic stability). Where sinks are used, the densities of individuals are not representative of habitat quality, which undermines the use 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. We illustrate this by comparing the predictions for our best-fit model ($D_{21}\omega_{III}$), with an approach that simply extrapolates from current habitat occupancy. The latter approach is especially compromised when either low- or high-quality habitat is removed (Table 2).

SIMPLIFYING THE FITNESS MEASURE USED

First we consider model sensitivity to removing the effect of unbalanced dispersal rates on reproductive values (i.e. we compare model predictions using ω_{II} with those using ω_{III}, Table 1). Surprisingly, the effect of this simplification is weak (approximately 0.2 birds per territory), although slightly stronger where dispersal is more 'free' ($D_{00}\omega_{III}$ cf. $D_{21}\omega_{III}$ in Fig. 5). The weakness of this effect is surprising, because a genetic mutation occurring in the poorest territories is much less likely (e.g. 10 times less for $D_{21}\omega_{III}$) to go to fixation than mutations occurring in the better territories. This means that for ω_{II} the difference in fitness between the
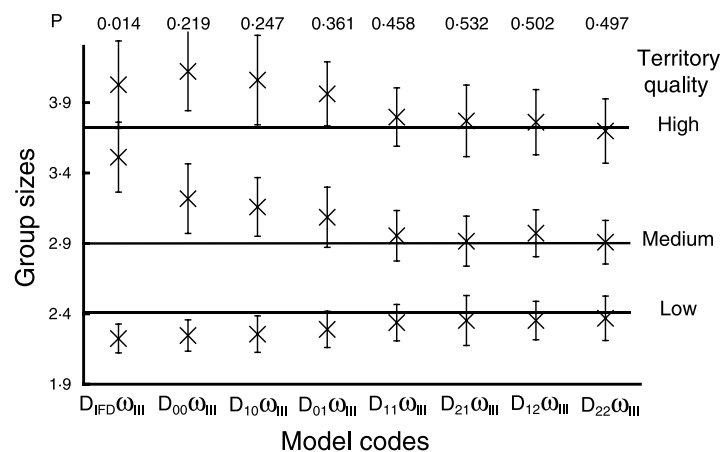
Fig. 4. Predicted mean group sizes (± 1 SD) for high-, medium- and low-quality territories, under a range of model assumptions, compared with observed group sizes (solid lines with shading indicating ± SE). The model codes describe model variants as outlined in Table 1. The *x*-axis can be thought of as moving from 'free' dispersal (model $D_{IFD}\omega_{III}$) to highly 'despotic' dispersal (model $D_{22}\omega_{III}$), indicating that the more despotic assumptions produce the best fits to observed data. We do not incorporate a full sensitivity analysis, however, for overall changes of less than 5%, to the fecundity and survivorship parameters used, average group sizes change by 0.0026% and 0.0114%, respectively, for each 1% the inputs are changed. NB: the 'group' sizes indicated for the low-quality territories include floaters and thus are strictly density figures (birds/territory) rather than group size figures.

Table 2. Population size predictions using different models. Simple extrapolations, e.g. subtracting 3·7 birds (the current group size) for each high quality territory removed, produces population estimates where births do not equal deaths, and thus considerably misestimate the consequences of habitat loss

	Estimated population size from $D_{21}\omega_{III}$	Estimated population size by extrapolating from current habitat occupancy	Percentage error
50% of high-quality habitat removed	234	294	25·8
50% of medium-quality habitat removed	276	291	5·5
50% of low-quality habitat removed	275	213	−22·4
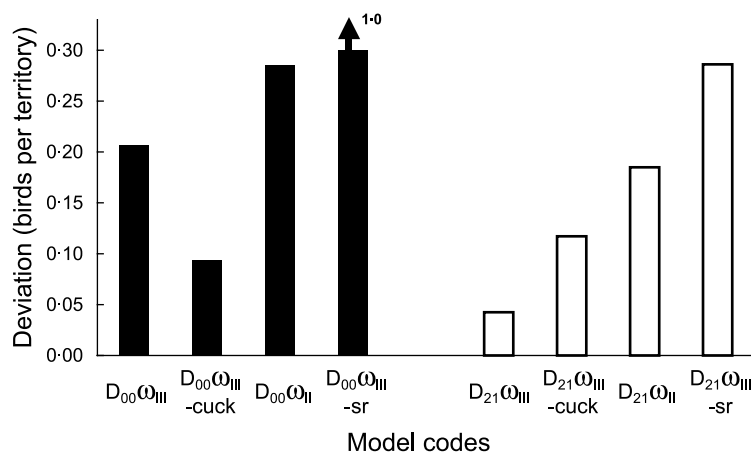
Fig. 5. An analysis of the loss in predictive ability for various model simplifications. The *y*-axis shows the deviation from observed habitat occupancy; -cuck means without extra pair paternity and egg dumping by helpers, -sr means with offspring sex ratios set to 50 : 50. For the difference between ω_{II} instead of ω_{III} see Table 1. $D_{00}\omega_{III}$ and $D_{21}\omega_{III}$ are included to allow comparisons between Figs 4 and 5.

poorest and better territories is 10 times smaller than for ω_{III}. So, although the difference between these fitness measures is huge for individual decisions, and thus also for evolutionary dynamics, their importance to population dynamics is minor.

Next we reduce our model to one based on lifetime reproductive success (ω_I). For the Seychelles warbler, such an approach predicts habitat occupancy hugely different from that observed. Using the assumptions that each additional alloparent reduces per territory fecundity by 70% (Table A2), while the number of male queuers has no similar effect produces equilibrium group sizes of 13 birds on high-quality territories, eight on medium-quality territories and zero birds on low-quality territories, compared with the observed figures of 3·7, 2·9 and 2·4, respectively. However, this comparison is only qualitatively informative. For smaller groups our 70% rate-of-fecundity-decline assumptions is a close approximation, and its detail has almost no effect on model predictions: for each 1% incremental change to the rate at which excess helpers cause fecundity to decline (Table A2), there is a 0·0016% change in average group sizes predicted (calculated as an average for changes of less than 5%). However, this insensitivity does not extend to model predictions for group sizes greatly in excess of those observed. That models based on ω_I perform so poorly, while those based on ω_{II} are relatively successful, does not mean that offspring

depreciation is the complete explanation for why large groups are not seen. However, it does suggest that negative density dependence at the group level is necessary to explain this system, and the function describing this negative density dependence must be similar to the offspring depreciation function.

SIMPLIFYING THE BEHAVIOURAL INFORMATION USED

First we remove the manipulation of sex ratios, using a 50 : 50 ratio in all instances instead of the observed ratios (Table A3). This has a marked effect on model predictions (see $D_?\omega_{III}$-sr in Fig. 5). Models incorporating sex ratio manipulation predict a slight excess of adult females (52 : 42), whereas removing sex ratio simplification produces the opposite result (42 : 58 for $D_{00}\omega_{III}$, 49 : 51 for $D_{21}\omega_{III}$). As it is females that alloparent, fewer females produces a smaller carrying capacity, and thus smaller group sizes. Model sensitivity to this manipulation is magnified where helpers can stay following the death of a parent ($D_{00}\omega_{III}$-sr is more different from reality than $D_{21}\omega_{III}$-sr, Fig. 5).

We also consider the effect of assuming breeders completely monopolize breeding on their territories, as opposed to the observed levels of cobreeding (Richardson *et al*. 2002) and cuckoldry (Richardson & Burke 2001). Model variants are highly insensitive to this

simplification (see $D_9\omega_{III}$-cuck in Fig. 5). This simplification has little effect on dispersal decisions by helpers because, at least while their parents persist, they are related approximately equally to siblings and their own offspring. For males, cuckoldry reduces the fitness differentials among different habitats, because males on sink habitats gain more through the chance to produce offspring on good quality habitat than vice versa. This means that where dispersal is relatively free males are more likely to disperse, and consequently removing cuckoldry from the model has a greater effect than is the case where dispersal is more despotic (compare $D_{00}\omega_{III}$-*cuck* with $D_{21}\omega_{III}$-*cuck* in Fig. 5).

Discussion

POPULATION REGULATION

In the specific case of group-living species, some territories must offer lifetime reproductive success of more than one, because these are the only territories that can sustain groups (Kokko & Sutherland 1998). If some individuals produce more than one replacement, for a population to be in equilibrium some individuals must produce less. This can either arise through some individuals not breeding, either as residents or floaters, or by some individuals breeding in sinks. As such, if individuals in group-living species refuse to breed on any territory offering a lifetime reproductive success of less than one, then the number of non-breeders is maximized (Kokko & Sutherland 1998) or, alternatively, all density dependence arises through non-breeding. By contrast, if a given species does use sink territories (e.g. Pen & Weissing 2000) this decreases the number of non-breeders needed to regulate the population.

We show that for this population there is sink usage, and suggest that kin competition is the only available hypothesis to explain this. Theoretical perspectives suggest temporal environmental heterogeneity (Kokko, Sutherland & Johnstone 2001), of a scale not seen on Cousin, is the only viable alternative hypothesis. Given that many, although not all, group living systems are founded on the family (Cockburn 1998), and that kin competition appears to be an almost inevitable consequence of this (Ridley & Sutherland 2002), we believe that sink usage will be a widespread form of regulation in group-living species. Where this is the case, the accurate prediction of individual behaviour in the source habitats is of paramount importance to predicting population dynamics. They produce more offspring, and these offspring also have priority access to the better habitat.

GROUP DYNAMICS

Our model suggests that for helpers on low-quality territories, any breeding vacancy is better than helping. Whereas, for the better territories, helpers should take all breeding vacancies, with the exception of lone helpers on high- and medium-quality territories, who should ignore low quality vacancies: a pattern that fits well with observed patterns (Komdeur 1994a). For queuers within the model, only the highest queuers on the better territories refuse vacancies on low-quality territories. Again, this prediction is close to observed patterns (Komdeur & Edelaar 2001a). Our model also indicates that parents and offspring usually agree over dispersal decisions. However, this was not always the case, with disagreement most often being between parents and mid-ranking queuers. As a consequence, habitat occupancy varies according to whether dispersal strategies were decided by the dispersers themselves or by their parents (cf. D_{IFD} with all other model variants in Fig. 4).

We would also note that in a system with queuers, who enjoy local dominance, a queuer's fitness depends not just on the quality of the individual's home territory but also on the quality of those neighbouring it. This means that queue lengths will increase as the quality of the habitat surrounding the home territory increases. This effect has consequences for predicting the consequences of environmental change and how we manage it. Specifically, habitat fragmentation reduces the likelihood of a good territory being surrounded by other good territories and so will lead to delayed breeding being less common. This means that aggregations of high-quality habitat, surrounded by completely unsuitable habitat, will have high levels of non-breeding and thus lower per capita birth rates than might naively be predicted. We predict that surrounding reserves with buffer zones of intermediate-quality habitat will mitigate this effect.

BIOLOGICAL INTERPRETATION OF DOMINANCE INDICES

Within the model our dominance indices have clear meanings, i.e. who can evict whom (see Table 1). However, we would emphasize that our solutions indicate only which parties have 'won' the evolutionary contest over helper or queuer residency. Overt aggression between dominants and either helper or queuers is rarely seen on Cousin (Komdeur 1999). That said, these dominance indices are open to more general interpretation. In reality, not all males queue for vacancies on neighbouring territories; instead some choose to bud off a territory of their own from their birth territory, and progressively seize land from adjacent territories (Komdeur & Edelaar 2001b). Where budding forms new territories, the initial group size will be two. This is an identical starting group size to where breeders evict any non-related helper or queuer following their settling into a breeding vacancy. This, in turn, means that high-dominance indices better describe a budding system and low indices a system whereby territories come with their occupants included. As such, rather than viewing our ignorance of these indices as a weakness of the approach, it can be seen as a strength in

that it allows us to model a system with both budding and seizing of neighbouring breeding vacancies.

Another part of the immense array of biology subsumed within our interadult dominance indices is the effect of relatedness on levels of helping. We have assumed that helpers continue to help at the same level as when their mother was alive, whereas in reality they help less following the death of a parent (Komdeur 1994a). As levels of helping will be one component in decisions over helper residency, and higher levels of dominance yield the best model predictions, this suggests that helpers usually produce insufficient benefits to unrelated dominants in this system, and thus are usually evicted.

Predicting accurately the population dynamics of social species' can require a complex model (Stephens *et al.* 2002). This is a worrying result, given the extensive body of theoretical work detailing the fitness consequences of group living, in particular, the dynamic and interdependent nature of reproductive skew, dominance and helping (Cant 1998; Kokko & Johnstone 1999; Johnstone 2000; Cant & Field 2001; Kokko, Johnstone & Wright 2002), but for most species, such data are unlikely to ever be available. Although our dominance indices draw a veil over this ignorance, we regard it as an immense blessing that habitat occupancy patterns show little sensitivity to these parameters, because it makes it markedly easier to predict the population dynamics for this species with less than perfect knowledge. This appears to be an instance where the costs and benefits of several behavioural processes are fundamental to their evolutionary dynamics, but in terms of population ecology they cancel out, and thus their detail can be ignored.

Conclusion

To fully realize the goal of extending this approach to other species will require quicker methods to measure survivorship and fecundity, as has been achieved recently for fish stocks (Denney, Jennings & Reynolds 2002). Further, this system is rare in that dispersal costs can be ignored, and although adding dispersal costs to the model would be trivial, measuring them is frequently not so easy. However, we have shown that an 'ideal' approach to population modelling can predict habitat occupancy at demographic equilibrium for a well-studied, group-living species. We also show that habitat use predictions are less sensitive to some of the mathematical and biological detail than might be expected. In particular, the extent to which breeders are despotic, in terms of reproduction and eviction, is far less important than the profound impact of kin competition on population dynamics.

Acknowledgements

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Appendix I

Table A1. The numbers of, group sizes on, and survivorship on, Cousin territories classified by their qualities. Data was collected during a continuous study from December 1985 to June 1991, during which period nearly the entire population was colour-ringed and censused

	High	Medium	Near-low	Far-low	Reference
Average yearly number of territories	14 ± 2·2	20 ± 1·3	30 ± 2·8	59 ± 1·4	–
Observed group sizes ± SD (territory years)	3·7 ± 0·9 (55)	2·9 ± 0·9 (60)	2·4 ± 0·2 (365)		(Komdeur 1992)
Annual survivorship (territory years)	0·91 (48)	0·88 (64)	0·76 (156)		(Komdeur 1992)

Table A2. The effect of helper number on annual production of yearlings (Komdeur 1994b). Large numbers of helpers decrease fecundity, resulting from increased risk of egg break caused by simultaneous incubation by more females, and greater depletion of food resources. (Komdeur 1994b). As we lack sufficient data for fecundities for large group sizes, these were assumed to decline by a constant parameter (70%), the fraction by which a second helper decreases fecundity on medium quality territories; 'helpers – 1 fec' denotes the per territory fecundity with one less helper. Data was collected during a continuous study from December 1985 to June 1991, during which period nearly the entire population was colour-ringed and censused

	Number of helpers			
Territory quality	0	1	2	> 2
High (sample size)	0·97 (28)	1·55 (13)	1·99 (11)	$0.7 \times$ (helpers – 1 fec)
Medium (sample size)	0·50 (38)	1·51 (12)	1·04 (6)	$0.7 \times$ (helpers – 1 fec)
Near-low/far-low(sample size)	0·20 (286)	0·32 (49)	0·12 (26)	$0.7 \times$ (helpers – 1 fec)

Table A3. Percentage of offspring that are male according to territory quality and number of existing helpers (Komdeur *et al.* 1997). There is an optimum number of alloparents (two on high quality territories, otherwise one), at which per territory offspring production is maximized (Komdeur 1994b). Breeders manipulate their offspring ratio to maximize their reproductive success (Komdeur *et al.* 1997), producing more females if they are short of helpers and vice versa. Data were collected in 1995

Territory quality	Number of helpers (sample sizes)		
	0	1	> 1
High (32)	0·13	0·13	0·85
Medium (27)	0·41	0·41	0·67
Near-low/far-low (57)	0·77	0·85	0·85

Table A4. The average yearly number and quality of territories neighbouring each territory in each of the four habitat classes during the study period 1985–91

Territory quality	Number of neighbouring territories that are			
	High	Medium	Near-low	Far-low
High	3	3	0	0
Medium	2	2	2	0
Near-low	0	2	2	2
Far-low	0	0	2	4