

Evolutionary conservation advice for despotic populations: habitat heterogeneity favours conflict and reduces productivity in Seychelles magpie robins

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Individual preferences for good habitat are often thought to have a beneficial stabilizing effect for populations. However, if individuals preferentially compete for better-quality territories, these may become hotspots of conflict. We show that, in an endangered species, this process decreases the productivity of favoured territories to the extent that differences in productivity between territories disappear. Unlike predictions from current demographic theory on site-dependent population regulation (ideal despotic distribution), we show that population productivity is reduced if resources are distributed unevenly in space. Competition for high-quality habitat can thus have detrimental consequences for populations even though it benefits individuals. Manipulating conflict (e.g. by reducing variation in habitat quality) can therefore prove an effective conservation measure in species with strong social or territorial conflict.

Keywords: evolutionary conservation; habitat selection; sociality; interference; territorial conflict

1. INTRODUCTION

It is essential for ecologists and conservation biologists to understand the effects of resource distribution on habitat selection and the growth of populations. Behavioural ecology teaches us that this is not a trivial exercise of calculating the amount of resources available per individual (Sutherland 1996). Rather, models of demography and animal distributions should incorporate an understanding of individual interactions in the competition for resources because this often predicts individual differences in reproductive success (Sutherland 1996; Sutherland & Norris 2002).

Individual preference for good-quality sites, particularly in territorial species, is often argued to have a stabilizing effect that increases the probability of population persistence (Brown 1969; Rodenhouse *et al.* 1997; Gill *et al.* 2001). This occurs because any population decline will induce individuals that have bred in poor habitats, or not bred at all, to fill the vacancies left in the better habitats, keeping the densities in important core areas constant (Brown 1969; Hunt 1998). However, selected to maximize their own fitness relative to others, individuals may compete for resources in ways that are suboptimal for the population (Rankin *et al.* 2007). Individuals are unlikely to remain passively assigned to poor habitat or status as long as there are no vacancies,

as assumed by models of territorial species demography, or ideal despotic distribution (IDD; Fretwell & Lucas 1970). Instead, they may attempt to improve their breeding career actively; such attempts to take over high-quality habitat have been shown in several territorial species (Arcese *et al.* 1992; Iguchi & Hino 1996). In social species, subordinate individuals can seriously harm breeder and group performance (Bourke & Franks 1995; Young & Clutton-Brock 2006).

The effect of such takeovers on population persistence has been little investigated. If higher interference from potential competitors disproportionately targets high-quality territories, reducing their productivity, this will even out differences in reproductive output across territories. Moreover, preference for the highest-quality territories may preclude the colonization of suboptimal but viable habitat. Together, these factors could mask the correlation between habitat quality and individual performance. We explore this possibility and its demographic consequences in a socially territorial species of bird: the Seychelles magpie robin, *Copsychus sechellarum*.

The Seychelles magpie robin is a good example of a species where non-breeding individuals can negatively affect the performance of breeders. The species live in groups that defend a common territory, and consist of a dominant breeding pair and a number of non-breeding subordinates (from none to eight), which can be either undispersed offspring or unrelated immigrants (Watson *et al.* 1992; Komdeur 1996). Subordinates

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often engage in aggressive disputes with dominant individuals, which come at a demographic cost to the population and are associated with the takeover of the territory by either the local subordinates or members of a neighbouring group (López-Sepulcre *et al.* 2009). Territories vary in quality, and data from a translocation to the island Cousin show that founder individuals defended exclusive territories on the highest-quality areas while newer recruits subsequently defended lower-quality territories (Njoroge 2002).

We ask three specific questions. (i) Do individuals preferentially compete for better territories? (ii) Are the negative consequences of competition for breeding positions stronger in better territories? (iii) How does this affect productivity at the population level?

2. MATERIAL AND METHODS

(a) *Study species and population monitoring*

The Seychelles magpie robin is a social bird endemic to the Seychelles archipelago in the Indian Ocean. Until recently, it survived only on the 210 ha island of Fregate (Norris & McCulloch 2003), from where it has been successfully translocated to three new islands: Cousin, Cousine and Aride. The entire world population of the species has been individually monitored since July 1988, during which time the population has grown from 23 individuals on a single island to 149 on four islands by December 2004 (BirdLife International 2005).

For this study, we consider data from the islands of Cousin (28 ha) and Cousine (29 ha), for which we have gathered habitat quality data. Every individual magpie robin has been individually marked with colour rings and monitored on a monthly basis since their introduction to both islands (November 1995 for Cousin, November 1996 for Cousine). Monitoring patrols are carried out regularly to identify the location (i.e. territory) and social status of every individual (see Bristol *et al.* 2005 for details of the long-term monitoring protocol). When a breeding individual dies or loses its dominant position to another adult, a takeover event is recorded. Takeovers do not necessarily involve the death of the displaced breeder. We consider a new individual to be the dominant when it breeds successfully, guards the nest or excludes the previous dominant individual from populations with the dominant of the opposite sex. These criteria are applicable to both males and females. Breeding attempts are conspicuous; only the dominant pair breeds, and females lay a single egg per nesting attempt. We categorize individuals as adults 11 months after fledging, which is the time adult plumage is acquired and sexual maturity reached (Gretton 1993).

(b) *Measurement of territory quality and delimitation of territorial boundaries*

Seychelles magpie robins live on predator-free islands and nest-boxes are provided in excess through management. We therefore assessed territory quality in terms of the abundance of their primary food source: the burrowing cockroach *Pycnoscellus indicus*. This has earlier been shown to be a good measure of habitat quality and it determines the settling order in novel habitat (Le Maitre 2002; Njoroge 2002). Random 25 × 25 m plots were selected on each island within the boundaries of magpie robin territories (45 plots on Cousin, 30 on Cousine). Each month from October 2003 to January 2004, we generated random coordinates

within the plot to place a single soil trap (if the selected place was found to be rocky or physically impossible to place the trap, we selected the nearest possible location within the plot area). Traps were modified pitfalls made from a plastic cylinder (5 cm deep × 9 cm diameter) with four notches (1 cm deep × 2 cm long) cut in the top to allow free passage of invertebrates. The trap was dug into the soil with its top set flush to the surface, filled with loose soil and covered with a flat stone. We collected traps after four weeks and counted all invertebrates in them. Our surrogate measure for territory quality was the number of cockroaches larger than 5 mm in length, averaged across all four collection months and plots within the territory (see Bristol *et al.* 2005 for further details).

Territory boundaries are defined by observations of territorial displays during routine monitoring. Such group displays, which confront the members of each of the neighbouring territories, are very conspicuous and occur repeatedly at very precise locations throughout the edge of the territory. This allows the delineation of territory boundaries. Most changes in territory boundaries represent the fission or fusion of territories (i.e. the appearance of a new boundary within a previously existing territory, or the disappearance of a previous boundary and consolidation of the social group to a single breeding pair).

(c) *Statistical analyses*

We checked for variation on cockroach abundance among territories by fitting a generalized linear model (GLM) including territory and collection month as factors. Since the data for the number of cockroaches in each trap were over-dispersed ($\mu = 8.02$, $\sigma^2 = 187.64$), we used a negative binomial error distribution and a log-link function.

Reflecting aseasonal breeding and single-egg clutches, a basic measure of breeding success is the time interval between two fledging events. These events fall in two categories: takeover intervals, during which a change of pair occurred, and all others. We correlated territory quality and productivity for territories that existed during the collection of invertebrate data. Territory productivity was calculated as the number of fledglings per month (i.e. the inverse of the average interval between two successfully fledged chicks). We used two different measures of productivity. The average territory reproductive success includes all types of intervals between fledging events (I and II in figure 1a). The potential reproductive success is calculated excluding all takeover intervals (II in figure 1a). The difference between the potential and the average can be used to evaluate the effect of territory takeovers, as the former excludes the effect of this type of interference. We compared the relationship between territory qualities measured in 2003–2004 and contemporary levels of productivity via a paired linear mixed model where territory quality and the type measure of territory reproductive success (realized and potential) were included as explanatory variables.

While the previous analysis was performed with productivity measures contemporary to the measurements of territory quality, the subsequent analyses are performed on the entire dataset from the time of introduction of the species on the island. Territorial boundaries have changed during the study period (see above). We therefore calculated the quality of territories that existed prior to invertebrate data collection by averaging cockroach densities of 2003–2004 across all plots lying within the focal territory boundaries. This

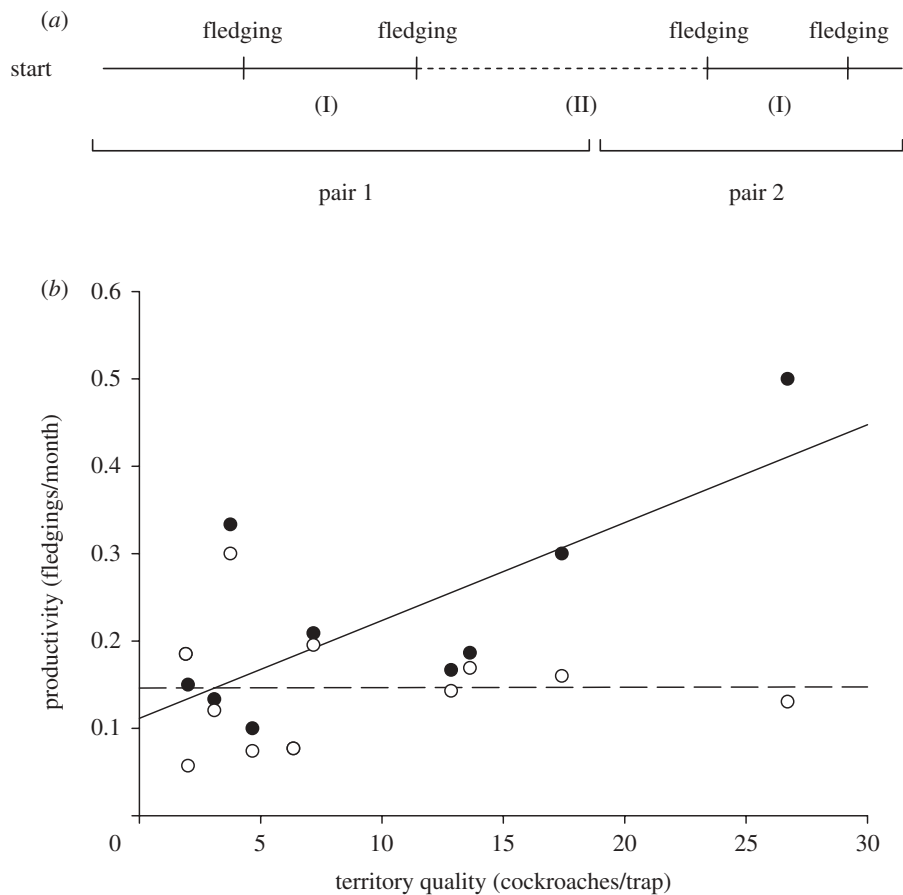


Figure 1. (a) Schematic of a territory's timeline illustrating the two types of interval distinguished to calculate territory productivity. The first type of interval (I) represents the time elapsed between two fledging events of a given pair. The second type of interval (II) accounts for periods of territory takeover, when there is a change of breeding pair between two consecutive fledging events. (b) Relationship between territory quality and monthly productivity. Regardless of territory quality, all territories perform equally well (dashed line). However, when takeover intervals (II in figure 1a) are excluded from the calculation of productivity, there is a positive relationship between quality and productivity (solid line). This indicates a stronger effect of territory takeovers on productivity for the high-quality territories.

procedure assumes that cockroach densities have not changed over the studied years. This assumption remains robust even if total abundances vary, as long as relative differences between territory qualities persist, as these should influence competition and settlement decisions at any given time. A comparison with measures of territory quality in previous studies on Cousin supports the assumption: the ranking of territories in terms of invertebrate abundance has remained the same (Njoroge 2002).

We performed randomization tests to detect associations between relative territory quality and subordinate presence, as well as the total amount of time spent in takeover intervals (II in figure 1a). We calculated this association (denoted Q) as

$$Q = \frac{\sum_{i,m} s_{i,m} q_i}{\sum_{i,m} s_i}$$

Here, q_i is the quality of territory i and s is the measure of interest for territory i in month m . We first calculated Q for s representing the number of subordinates. Second, we calculated Q for the occurrence of a takeover interval (noted as 1 if month m of territory i was in a type II interval, and 0 otherwise; figure 1a). We created a null distribution for each type of association Q by keeping territory histories (location of boundaries) fixed and reassigning qualities to territories,

using a random permutation of territory qualities that were present in each month on the focal island. The observed statistic was compared with a null distribution based on 10 000 randomizations.

In order to assess the effect of spatial heterogeneity on the levels of conflict and productivity across the island, we divided the history of each island into periods within which territorial boundaries remained unchanged. For each period, we measured the number of territories, their mean quality (measured as cockroach density) and their coefficient of variation. The degree of conflict was measured as the proportion of territories in a given month that were in a takeover interval (type II, figure 1a) and modelled as a binomial process with as many draws as territories, using a generalized linear mixed model (GLMM; Pinheiro & Bates 2000). The data for each month within a period were entered separately and grouped by period as a random effect. This was done to (i) maintain the binomial nature of the data, and (ii) account for the fact that different periods lasted for a different number of months, and hence their weight on the model should differ. Island productivity was measured as the total number of chicks fledged in the island in a given month and modelled as a Poisson process within a GLMM where, again, months were grouped within periods of unchanged territory composition. Both island-wide conflict and productivity were initially modelled as functions of the number

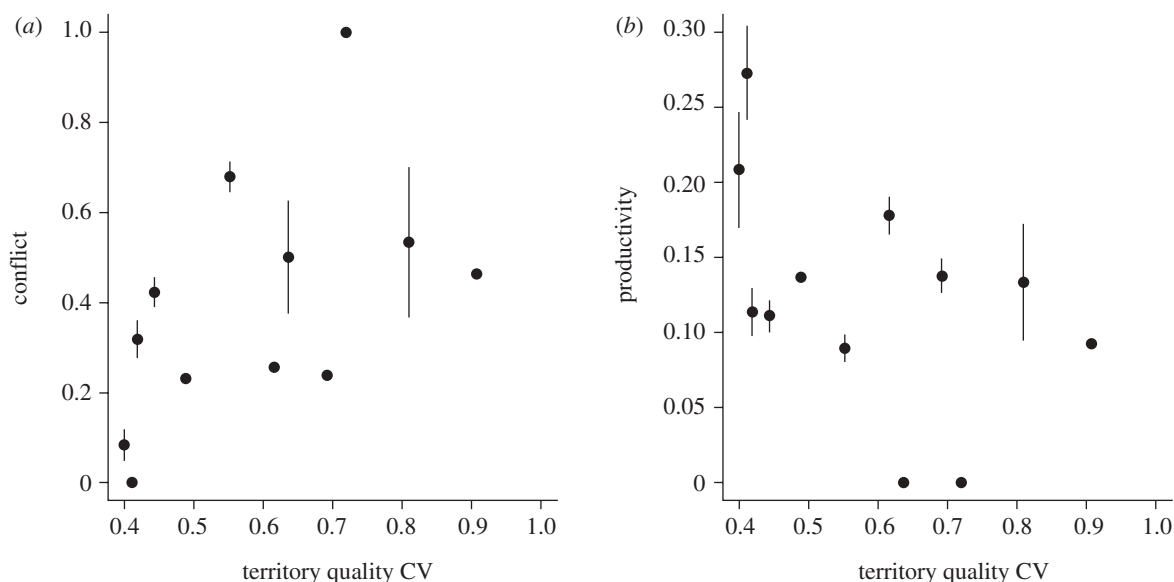


Figure 2. Relationship between island variation in territory quality and the island levels of (a) conflict, measured as the proportion of territories under takeover per month, and (b) productivity, determined as island monthly fledging production, here divided by the number of territories. Each data point represents values for different periods in a given island with different territory compositions.

of territories, their mean quality and the coefficient of variation of their qualities. Terms that had a T statistic lower than 1, and therefore were highly non-significant, were removed from the final model.

All models were fitted by penalized quasi-likelihood using R v. 2.9.2 (R Development Core Team 2005).

3. RESULTS

Territory quality (i.e. cockroach abundance) varied significantly among territories (negative binomial GLM, $\chi^2_{15,249} = 7.53$, $p < 0.0001$) but not among collection months ($\chi^2_{3,246} = 1.11$, $p = 0.33$). Non-descendent subordinate individuals preferentially settled in territories of higher quality (randomization test, $p = 0.027$).

Territory quality did not predict overall reproductive success ($R^2 = 10^{-5}$; figure 1b), even though it strongly correlated with reproductive success outside periods of dominance takeover ($R^2 = 0.51$). The difference between the two slopes was significant (GLMM, interaction territory quality \times type of success measure = 0.011 ± 0.003 , $T = 3.97$, $p = 0.003$, territory as grouping factor $\sigma^2 = 0.003$). This implies that takeover intervals (type II) are longer and/or more abundant in higher-quality territories. This result was confirmed by the randomization tests, where the total time taken by takeover intervals (type II) was significantly longer in better territories ($p < 0.0001$).

Island variation in territory quality had an effect on the island-wide levels of conflict, as measured by the proportion of territories per month that are involved in a pair takeover (i.e. the month is classified as type II, figure 1a). Neither the mean territory quality of the occupied territories nor the number of territories affected the levels of conflict (both $T_{10,206} < 1$ and $p > 0.4$). The final model thus just included the coefficient of variation in territory quality, which positively affected the island-wide levels of conflict (effect = -2.24 ± 0.70 , $T_{12,206} = 2.46$, $p = 0.03$; figure 2a).

Island-level productivity was not significantly affected by mean island territory quality ($T_{10,206} = 0.105$, $p = 0.92$), and it was therefore excluded from the final model. The final model showed a significant positive effect of the number of territories on island productivity (effect = 0.37 ± 0.12 , $T_{11,206} = 3.22$, $p = 0.008$) and a marginally significant negative effect of territory quality variation (measured as the coefficient of variation) on island productivity (effect = $0-1.85 \pm 0.84$, $T_{11,206} = -2.19$, $p = 0.05$; figure 2b).

4. DISCUSSION

Our study shows important links between individual behaviour and population performance that have significant implications for conservation. These can be summarized in three points that address the three questions posed in the introduction. First, when available habitat differs in quality, competition for territories disproportionately targets the best territories. Second, while the true potential of high-quality territories is revealed in time periods without takeover disputes, intense competition, as a whole, depresses their reproductive output. Takeovers take long enough and are frequent enough that the net productivity of good territories no longer exceeds that of poor ones. Third, for a given set of resources, conflict increases and population productivity is reduced if these are distributed unevenly in space. Inequality sets the stage for competition that has harmful population-wide consequences.

While population modelling normally assumes that differences in habitat quality directly drive productivity differences in territorial systems, our results illustrate how these fitness differences can be substantially modified by behavioural decisions that respond to habitat differences. Territorial systems are assumed to follow an IDD (Fretwell & Lucas 1970), whereby individuals monopolize resources and have a fitness that is proportional to their amount. On the contrary, the ideal-free distribution

(IFD; Fretwell & Lucas 1970) assumes that individuals distribute in such a way that their fitness is equalized and it is the distribution of individuals, not the fitness, that is proportional to the amount of resources. The Seychelles magpie robin dataset shows how despotic systems can produce an equal-returns situation (as in the IFD) when the assumption that territory owners can completely avoid interference from others is relaxed. The pressure of individuals competing for high-quality territories disturbs offspring production to the extent that the correlation between territory quality and reproductive output vanishes. However, the underlying quality of the territory has not changed: when the delays caused by territory takeovers are excluded, the correlation between territory quality and reproductive success reappears (figure 2*b*).

Interference behaviour has been long recognized and incorporated into the IFD model (Sutherland 1983; Sutherland & Parker 1985, 1992) and applied empirically in the context of foraging (Tregenza *et al.* 1996). But interference, in the form of competition for territories, is also common in despotic systems; yet a version of the IDD with interference behaviour remains to be developed. While our case study describes this scenario in a social species, the principle of resource-driven conflict and its regulatory effect is likely to exist in a variety of systems.

The ideal despotic model, phrased in its original way or its various *alter egos* such as 'site-dependent population regulation' (Rodenhouse *et al.* 1997) or the 'habitat heterogeneity hypothesis' (Dhondt *et al.* 1992), has fuelled a rich body of empirical studies on the nature of density-dependent settlement in heterogeneous habitats, both in birds (Ferrer & Donazar 1996; Krüger & Lindström 2001; Kokko *et al.* 2004; Carrete *et al.* 2006; Burgess *et al.* 2008) and other animals (Levin *et al.* 2000; Calsbeek & Sinervo 2002; Morris *et al.* 2004; Bauer *et al.* 2005). Throughout the literature, a strong emphasis is put on distinguishing between despotic regulation and patterns expected from interference versions of the IFD (Ferrer *et al.* 2006). However, we argue that these should be viewed as two ends of a single continuum. Indeed, studies on saddlebacks *Philesturnus rufusater* in New Zealand (Armstrong *et al.* 2005) and bearded vultures *Gypaetus barbatus* in Spain (Carrete *et al.* 2006) show patterns associated with both processes. Our study adds to the evidence for such a continuum by providing a mechanistic understanding of the processes involved.

Because selection operates more strongly at the level of the individual than on populations or species, conflict between individuals can harm population-level performance up to levels of dramatic over-exploitation of resources and extinction (Parvinen 2005; Rankin & López-Sepulcre 2005; Rankin *et al.* 2007; Gandon & Day 2009). In the Seychelles magpie robin, an individual-based simulation showed that the levels of territorial conflict encountered in nature have delayed the recovery of the species from a state of extreme human-induced endangerment (López-Sepulcre *et al.* 2009). However, studies documenting such detrimental effects of conflict typically offer no practical solution, even though, from an applied perspective, it would often be beneficial to shift the focus from improving individual fitness to group fitness. While we know, for example, that natural selection favours cub infanticide during dominance takeovers in some mammals (e.g. Andreassen & Gundersen

2006), in detriment of population growth, the phenomenon is of little conservation relevance—or at best a cautionary note against exploitation—unless something can be done to dampen its negative effects. Our results suggest that there are ways to manipulate levels of conflict in the short term, speeding up recovery from acute endangerment and thus avoiding prolonged periods of high extinction risk. If conflict is a facultative response to available opportunities, it can be diminished by avoiding strongly heterogeneous distribution of habitats. Suggested manipulations include concentrating restoration efforts and supplementary feeding on the relatively poorer habitats, or choosing islands for reintroduction purposes partly based on the homogeneity of habitat qualities. This represents a novel approach to conservation whereby population growth is enhanced by manipulating selection pressures (in this case, habitat distribution) in order to minimize evolutionary conflicts and the consequential behaviours that are suboptimal for populations. Our study thus adds to the growing recognition that conservation programmes have more promise if they understand the evolutionary pressures that have shaped individual behaviours relevant to reproduction.

Evolutionary theory can prove an important and often overlooked tool to conservation (Ferrière *et al.* 2004). In this article, not only do we derive conservation advice drawing from well-established evolutionary principles, but we also illustrate how conservation data can prove extremely valuable for the refinement of evolutionary theories.

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