Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2009, **78**, 219–225 doi: 10.1111/j.1365-2656.2008.01475.x

Reproductive conflict delays the recovery of an endangered social species

Andrés López-Sepulcre[1,2,3]*, Ken Norris[4] and Hanna Kokko[1]

[1]Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Sciences, University of Helsinki, FI-00014 Helsinki, Finland; [2]Evolutionary Ecology Unit, Department of Biological and Environmental Sciences, University of Jyväskylä, FI-40014 Jyväskylä, Finland; [3]Department of Biology, University of California, Riverside, CA 92521, USA; and [4]Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, Earley Gate, Reading RG6 6AR, UK

Summary

1. Evolutionary theory predicts that individuals, in order to increase their relative fitness, can evolve behaviours that are detrimental for the group or population. This mismatch is particularly visible in social organisms. Despite its potential to affect the population dynamics of social animals, this principle has not yet been applied to real-life conservation.

2. Social group structure has been argued to stabilize population dynamics due to the buffering effects of nonreproducing subordinates. However, competition for breeding positions in such species can also interfere with the reproduction of breeding pairs.

3. Seychelles magpie robins, *Copsychus sechellarum*, live in social groups where subordinate individuals do not breed. Analysis of long-term individual-based data and short-term behavioural observations show that subordinates increase the territorial takeover frequency of established breeders. Such takeovers delay offspring production and decrease territory productivity.

4. Individual-based simulations of the Seychelles magpie robin population parameterized with the long-term data show that this process has significantly postponed the recovery of the species from the Critically Endangered status.

5. Social conflict thus can extend the period of high extinction risk, which we show to have population consequences that should be taken into account in management programmes. This is the first quantitative assessment of the effects of social conflict on conservation.

Key-words: interference behaviour, IUCN Red List, population regulation, population viability, territorial conflict

Introduction

Conflicts between individuals over reproduction can promote behaviours that have negative consequences at the level of a group or a population (Haldane 1932; Williams 1966; Frank 1998) because natural selection maximizes relative rather than absolute fitness (Wright 1969). Consequently, investigations of the behavioural and individual-level determinants of demography have highlighted a theoretical possibility that individual conflict can impact demographic processes of conservation concern, extinction included (Dieckmann & Ferrière 2004; Parvinen 2005; Rankin & López-Sepulcre 2005). In social species, where reproduction is limited to a few individuals in the group, reproductive conflict and its consequences have been a common subject of study for decades (Frank 2007). Despite this, and the conservation interest of social species, the consequences of reproductive conflict in a real-life conservation context remain unexplored.

Social species are assumed to fare better when sufficient numbers of nonreproductives are present, due to helping activities or other forms of group benefit (Courchamp, Grenfell & Clutton-Brock 1999). However, sociality necessarily implies conflict between individuals over reproductive dominance (Frank 1998). Arguments for a positive effect of a nonbreeder fraction on population dynamics (Hunt 1998; Grimm *et al.* 2005) ignore the fact that conflict for breeding positions can incur costs to the population (Kokko & Sutherland 1998; López-Sepulcre & Kokko 2005). Indeed, in several species of social animals, nonbreeding individuals have been shown to decrease breeder performance with aggressive and interference behaviours (Arcese *et al.* 1992; Bourke & Franks 1995; Iguchi & Hino 1996; Komdeur 1996; Young & Clutton-Brock

---

*Correspondence author. E-mail: andresls@ucr.edu

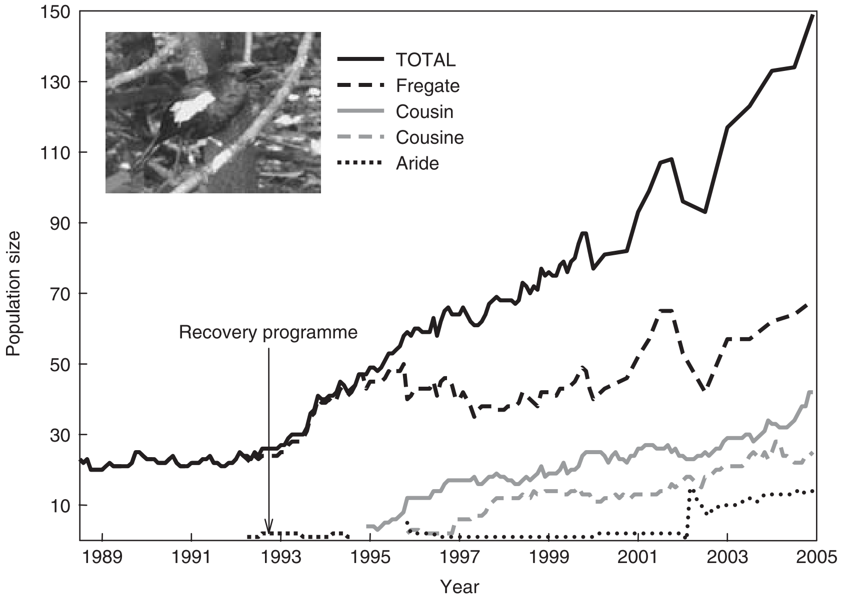

Fig. 1. Time series of Seychelles magpie robins' monthly abundances on the four islands it inhabits. Since January 2000, data for Frégate – and hence total population – was gathered biannually only. The arrow indicates the date when the species' recovery programme was fully implemented. (Inset) A Seychelles magpie robin (photo: A. López-Sepulcre)

2006). Similarly, competition for breeding, in the form of territory takeovers, has well known detrimental effects in infanticidal species (Häcklander & Arnold 1999; Veiga 2004; Whitman *et al.* 2004; Andreassen & Gundersen 2006). One would thus expect that territorial and social conflicts, which feature prominently in struggles for reproductive dominance, would impact population performance negatively.

Here we examine competition for breeding territories and its demographic consequences in an endangered species of social bird: the Seychelles magpie robin, *Copsychus sechellarum*. In 1988, the species was considered one of the most endangered birds in the world (Collar & Andrew 1988), with only seven breeding pairs remaining on the island of Frégate (Komdeur 1996). Intensive conservation efforts, which included habitat restoration, supplementary feeding and nest-box provisioning, resulted in a rapid increase of the population (Norris & McCulloch 2003) enabling re-introductions to the islands of Cousin, Cousine, and Aride, and the subsequent downlistment from 'Critically Endangered' to 'Endangered' on the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List (2006). In 2004, the world population on all four islands combined totalled 149 individuals (Fig. 1).

Seychelles magpie robins live in territorial groups of 2–10 individuals with a single dominant pair. Only the dominant pair reproduces. (Watson *et al.* 1992; Komdeur 1996). A remarkably detailed data base comprises almost 16 years (June 1988 to December 2004) of monthly information for every individual of the entire world population. Taking advantage of these data and more fine-scaled behavioural observations, we first show significant costs of individual-level conflict, in the form of dominant pair takeovers, on the productivity of territories. Second, we assess the conservation relevance of these results, by using monitoring data to construct an individual-based model that recreates the recovery of the species and quantifies how conflict costs scale up to the population level. To our knowledge, ours is the first quantitative assessment of the population consequences of social conflict in a real-life conservation setting.

Materials and methods

POPULATION MONITORING

We created a data base using detailed individual-based data from June 1988 to December 2004. The data base contains a monthly register of every individual in the population, specifying its breeding and social status. All individuals in the population were routinely ringed with unique colour combinations and their location (i.e. territory) and dominance status noted on a monthly basis. New recruits were ringed as nestlings or, when the nest was inaccessible, soon after fledging. Through the period analysed in this study, monitoring frequency varied from daily to monthly. No adult has remained undetected for more than 2 months, and there are only six records of individuals moving between neighbouring islands. Missing individuals are therefore assumed dead after 3 months unsighted, and we assigned the week after the last sighting as the death date.

We noted the month of every single fledging event throughout the studied period. Individuals older than 10 months are recorded as adults in the data base (adult plumage is acquired 11 months after fledging, Gretton 1993). Both mature and juvenile nonbreeders are classified as subordinate offspring if they were produced by the current dominant pair, and as nondescendant subordinates otherwise. Nondescendant subordinates can be either immigrants from another territory or nondispersed individuals that were not produced by the current dominant pair.

We excluded data for Frégate after March 2000, when the whole population was temporarily brought into captivity as part of a rat eradication programme (Thorsen *et al.* 2000) and monitoring was thereafter carried out at longer intervals. For Cousin, Cousine and Aride, we used data from the start of the population up to the end of 2004.

Dominant individuals eventually die or lose their breeding position to other adults. In such a case, we recorded a takeover event. We considered a new individual to be the dominant when it either bred successfully, nest guarded, or excluded the previous dominant individual from copulating with the opposite sex dominant. These criteria were applicable to both males and females.

BEHAVIOURAL OBSERVATIONS

We carried out observations to detect differences in the levels of aggression of dominant individuals from territories with different group compositions (with and without subordinates). During each observation bout, we noted the number of 1-min intervals within which the focal individual was involved in an aggressive encounter. All observations were carried out on Cousin, Cousine and Aride between the months of October 2003 and March 2004. We divided observation days in three periods: 7–10 h, 11–14 h and 15–18 h. Before each observation period, an individual was randomly chosen from the pool of dominant individuals on the island, and searched for, for up to a maximum of an hour. If the search was unsuccessful (only twice in this study) a new individual was drawn. When an individual was found we allowed for 15 min of habituation before recording. We stopped observations after 1 hour or when the focal individual had been out of sight for longer than 7 min. We only included observations that lasted for more than 20 min in the analyses. This resulted in a total of 23 individuals (10 females and 13 males) from the three populations successfully observed during all three time periods.

STATISTICAL ANALYSES

We used generalized linear mixed models (GLMM, Pinheiro & Bates 2000) to identify the effects of nonbreeding individuals on the performance of breeders. The response variable throughout these analyses is the probability of an event occurring (e.g. takeover, aggressive encounter or fledging production) modelled as binomial distribution with a logit link. Grouping variables, such as territory or individual identity, were included as random factors to control for differences in the propensity of the event due to unaccounted factors (such as food availability or individual condition). For each analysis, we included all candidate explanatory variables as fixed factors. We fitted the models to the data using the penalized quasi-likelihood criterion (PQL; Breslow & Clayton 1993). In these analyses, we only considered the immediate effect of having subordinates in the territory on takeover rates. This does not account for any likely cumulative effect of having subordinates for longer than the month in question.

In order to test whether replacement pairs have a positive effect on territory productivity by replacing pairs that have lower productivity, we performed two randomization tests. The test statistics used were the mean difference between the last inter-fledgling interval of the old pair and either (i) the first interfledgling interval of the replacement pair, or (ii) a randomly picked interfledgling pair of the replacement pair. This was compared with a null distribution of mean differences where the order of the pair (old or new) was randomized. Randomized data sets were created 10 000 times. For the second comparison, the sample test statistic is not a fixed value, since one of the intervals is picked randomly. Therefore, it was calculated 10 000 times as well and its distribution compared with the null distribution.

INDIVIDUAL-BASED SIMULATIONS

We performed an individual-based simulation to assess the population consequences of competition for breeding positions, with all parameters drawn from field data. The simulation is based on a probabilistic model where the productivity and frequency of takeovers in each territory depends on its social composition (i.e. the presence of subordinates of either sex). The probabilities of dispersal and death of each nonbreeding individual depend on their status, while those of dominants are conditional on having their dominant position taken over by another individual. All these probabilities are extracted from the individual-based data base described above (see Appendix S1 for details). It is important to note that the model implicitly incorporates density dependence because of the increase in the frequency of takeovers (and consequently, the negative effects in productivity) with the increase in the nonbreeder population.

In a first set of simulations, we did not incorporate environmental stochasticity nor did we assume an upper limit for the number of territories (see Discussion for a full justification). Instead, we considered the IUCN Red List criteria to be the best judgment of extinction risk in a situation where not all risks can be known beforehand. For the Seychelles magpie robin, the IUCN criteria dictate that downlisting occurs when the population has consisted of at least 50 mature individuals for more than 5 years and followed an upward trend during this time (IUCN 2006). We thus make the assumption that the longer it takes a population to grow from the ‘Critically Endangered’ status, the longer it is exposed to extreme danger due to any kind of unaccounted environmental stochasticity or other external factors. In a second set of simulations, we considered environmental stochasticity explicitly by including a range of catastrophic events occurring at different frequencies.

We compared a scenario simulating the real-life situation (*control* scenario) – where subordinates affected demography through competition for breeding positions – with a hypothetical scenario of relaxed territorial conflict (conflict-free scenario), where the effects of subordinates (positive or negative) and the breeding delays associated with takeovers were removed. The populations otherwise obeyed the same rules of reproduction and death as in the real-life scenario (see Appendix S1 for details). From each simulation, we extracted the following emergent properties: time of downlistment to ‘Endangered’, number of breeders, number of juveniles and number of nonbreeding adults present at the time of downlistment. We also calculated the linear growth in population during the 5 years before downlistment. Each scenario was simulated 1000 times.

Results

Dominant individuals were involved in aggressive interactions more often when they had subordinates of their own sex in their territory (Fig. 2a; GLMM, estimate = 1·66 ± 0·41, $P < 0{\cdot}0001$, observation bout as random effect nested within individual, $n = 23$, $\sigma^2 = 1{\cdot}83$) irrespective of the number of subordinates of the opposite sex (estimate = –0·49 ± 0·43, $P = 0{\cdot}255$). Nest disturbance by subordinates was common, as reported before (Komdeur 1996). Long-term data show that the presence of same-sex subordinates increases the probability of the dominant having its position taken over (Fig. 2b) regardless of whether the subordinates are related (GLMM, estimate = 0·587 ± 0·277, $P = 0{\cdot}0338$) or not (GLMM, estimate = 0·342 ± 0·146, $P = 0{\cdot}0197$, see Table S1). Not all takeovers occur within individuals of the same territory. Takeover frequency is also related to the proportion of nonbreeding adults in the whole island population [GLMM, estimate = 2·45 ± 0·93, $P = 0{\cdot}008$, territory ($n = 48$, $\sigma^2 = 0{\cdot}44$) and individual ($n = 146$, $\sigma^2 = 0{\cdot}61$) as random effects].

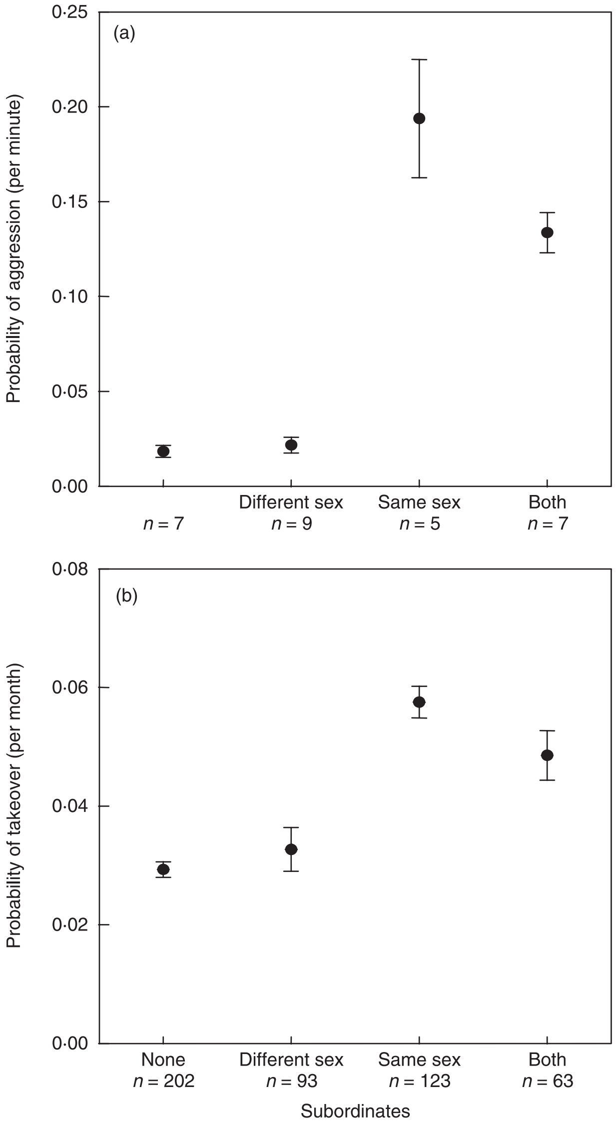

Fig. 2. Effect of adult subordinates on dominant individuals. The presence of same-sex subordinates is associated with (a) higher levels of aggression in dominants, and (b) higher chances of loosing their dominant position. Note the similarity in the pattern of results derived from short-term behavioural observations (a) and long-term individual-history data (b). Bars indicate standard errors. Sample size *n* indicates the number of dominant individuals that contributed to that category (note that a same individual can contribute to several categories if its state changed over time).

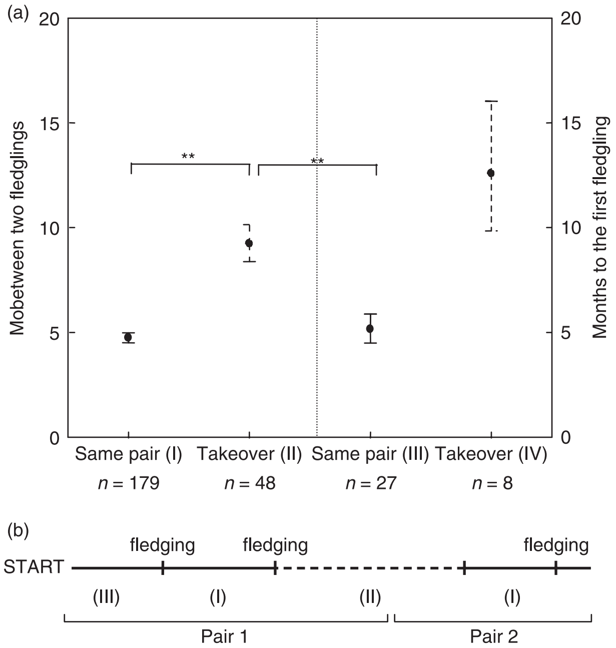

Fig. 3. Effect of territory takeovers on breeding frequency. (a) The left half of the graph shows that the interval between two successful breeding attempts is significantly longer when there is a pair takeover in between. This delay in breeding is also significantly longer than the time between the settling of a new territory by a pair and their first successful breeding attempt, as indicated by the right half of the graph. Bars indicate standard errors. (b) Schematic representation of a territory's timeline illustrating the three first types of intervals considered in the figure above (see text). The fourth type includes intervals where there was a takeover before the production of the first fledging of the territory.

Takeovers are often resolved after a period of fighting between the dominant individual and the challenger. This raises the possibility that group composition and takeover risk impact the territory's overall breeding output. Breeding is aseasonal and a single egg is laid per breeding attempt, thus the interval between two successful fledging events can be used as a measure of fledging production. Intervals between two fledglings were classified as *same-pair* intervals when the same parents produced two consecutive fledglings and as *takeover* intervals if there had been a change of at least one member of the pair between the two fledging events. Takeover intervals were significantly longer than same-pair intervals, suggesting a decrease in territory productivity due to dominance takeovers (II in Fig. 3; GLMM on the monthly probability of fledging given the type of interval the month lies in, estimate = –0·83 ± 0·27, $P = 0·002$, territory as a random effect, $n = 43$, $\sigma^2 = 0·009$). This result does not reflect a natural delay that any new dominant would require to start breeding successfully (e.g. due to lack of experience), since newly founded territories did not show this delay (III, estimate = 0·02 ± 0·08; $P = 0·93$) unless a pair takeover occurred (IV in Fig. 3, estimate = –1·23 ± 0·42, $P = 0·003$). The number of male or female subordinates did not influence productivity beyond the takeover effect (all $P > 0·1$, see Table S2).

Although takeovers clearly impact breeding output negatively in the short term, this does not exclude the possibility of longer-term benefits as takeovers bring in new pairs with potentially higher reproductive success. For example, if pair reproductive success declines with time, pair turnover would increase population performance as old pairs get replaced by pairs breeding at a higher rate. We tested for this possibility through pairwise comparisons of the last breeding interval of an old pair (immediately before a turnover interval) with the first interval of the replacement pair (i.e. we compared intervals I of pairs 1 and 2 in Fig. 3). Post-takeover intervals were longer (effect = 3·52 moths, $P < 0·0001$, see Materials and

Methods) than pre-takeover intervals. Furthermore, to test whether these negative effects carried on longer term, we also compared pre-takeover intervals with a randomly picked breeding interval of the new pair. Again, these comparisons showed a significant increase in interval length (effect = 2·00 months, $P < 0{\cdot}0001$, see Materials and Methods). These results indicate that pairs are not replaced in a phase of declining productivity. On the contrary, these results point at yet another likely negative effect of takeovers: replacement by inexperienced pairs. This aspect is not incorporated in our subsequent simulations, thus making them conservative.

We built an individual-based simulation to assess the population consequences of competition for breeding positions, with all parameters drawn from field data. The rate at which populations recover thus emerges from empirically estimated parameters that capture the net effects of social group composition. The simulation uses a probabilistic model where the productivity and frequency of takeovers in each territory depend on its social composition. We simulated two scenarios: (i) *control* populations with the same characteristics as the actual Seychelles magpie robin population, which should recreate the observed rate of population growth, and (ii) hypothetical *conflict-free* populations where subordinates do not create heightened takeover risk and the associated delays in breeding performance. Note that any potential positive effect of sociality is also removed, since parameterization of fecundity and mortality rates is based on solitary pairs and should reflect the net effect of subordinates (see Appendix S1).

In a model with no environmental stochasticity, control populations (initiated with the same population size and structure as the species was in June 1988) correctly predicted the observed growth out of the 'Critically Endangered' status. This change in status (downlistment) occurred significantly earlier in conflict-free populations (32·3 months later on average, Kolmogorov–Smirnov = 0·79, $P < 0{\cdot}0001$; Fig. 4), which translates into a 33% delay since the full implementation of the recovery programme (October 1992). Conflict-free populations were also likely to be in a healthier state at the time of downlistment: they had on average 67·7% more juveniles (Kolmogorov-Smirnov = 0·66, $P < 0{\cdot}001$) and 71·6% higher population growth rates (Kolmogorov–Smirnov = 0·70, $P < 0{\cdot}001$) than control simulations (Table 1), as well as a slight (5·5%) and marginally significant increase in breeder numbers (Kolmogorov–Smirnov = 0·17, $P = 0{\cdot}047$). In simulations that included environmental stochasticity, this translated into a lower probability of extinction of conflict-free populations at low frequencies of catastrophic events (Table 2).

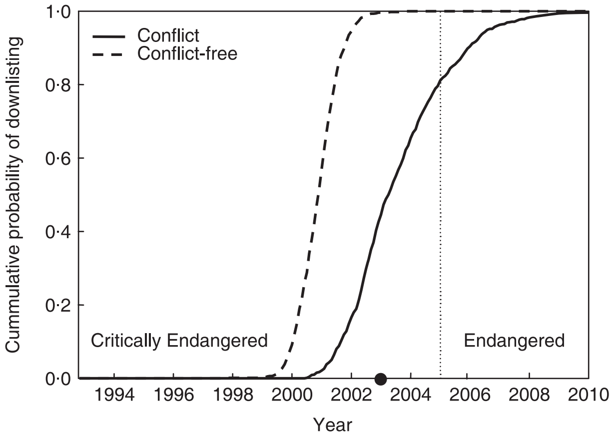

Fig. 4. Simulated times to recovery of the Seychelles magpie robin. Cumulative probability of the Seychelles magpie robin meeting the criteria for being downlisted from Critically Endangered, as calculated by simulation of 1000 populations. The solid line corresponds to the *control* scenario. The dashed line represents the *conflict-free* scenario. The *x*-axis starts at the time of full implementation of the species' recovery programme. The actual date when the species met the IUCN criteria to be downlisted is indicated by the solid circle and the end of the data by the vertical dotted line. Asterisks indicate a significant difference with respect to the control scenario at the 0.05 (*) and 0.001 (***) levels.

Discussion

Much of conservation biology deals with understanding how populations grow when they have been driven to low sizes. Since the boundary between extinction and safety can be extremely sensitive to small changes in vital rates, it is increasingly realized that behaviour can play a large role in shaping extinction risk (e.g. Vucetich, Peterson & Waite 1997; Sutherland & Norris 2002; Ridley, Komdeur & Sutherland 2004; Le Galliard *et al.* 2005). So far, the attention of conservation biologists to behaviour has largely concentrated on identifying maladaptive behaviours in novel environmental conditions (Reed 1999; Schlaepfer, Runge & Sherman 2002). It is well accepted that social species are more vulnerable to extinction when low population sizes constrain their social behaviour, creating an Allee effect (Reed 1999; Stephens, Sutherland & Freckleton 1999). Less appreciated is the fact that individual behaviour evolves to maximize relative rather than absolute fitness (Haldane 1932; Wright 1969). This has the profound

Table 1. Demographic parameters of the simulated populations at their respective times of downlistment. Means ± standard errors are displayed. Asterisks indicate a significant difference with respect to the control scenario

	Population size	No. of breeders	No. of juveniles	Growth trend†
Control	123·87 ± 1·65	63·85 ± 0·85	24·50 ± 0·56	0·95 ± 0·03
No conflict	166·47 ± 2·20***	67·00 ± 0·94*	41·08 ± 0·74***	1·63 ± 0·03***

†Slope of the linear regression between population size and time (over the previous 5 years to downlisting).

Table 2. Summary of the GLM for the probability of species extinction given the magnitude and frequency of catastrophic events simulated. Asterisks indicate significance at the 0.001 (***) and 0.01 (**) levels

	Estimate	SE	*Z* value	*P* value
(intercept)	1·001	0·756	1·323	0·186
Magnitude of catastrophe (mortality)	4·585	0·592	7·745	< 0·001***
Period of catastrophe	–1·539	0·269	–5·710	< 0·001***
Conflict	–0·468	0·938	–0·499	0·617
Conflict × period	0·664	0·255	2·601	0·009**

consequence that natural selection can promote behaviours that are detrimental at the population level, yielding the theoretical prediction that it can even increase the chances of extinction (Dieckmann & Ferrière 2004; Parvinen 2005).

Our results show that a behaviour that can be considered highly advantageous to the individual – that is, attempt to take over a territory for breeding – can result in a significant delay in species recovery and a higher extinction probability. The delay, which meant on average a 33% longer time to reach the criteria for loosing its 'Critically Endangered' status, occurred despite the fact that our simulations were parameterized with data from an intensively managed population, showing a healthy rate of recovery. These results hold when random environmental catastrophes are simulated, although it would be interesting to further explore how conflict affects population resilience to environmental stochasticity affecting different stages of the life history.

Helping by young related subordinates, by means of chick feeding, is known to occur in the Seychelles magpie robin, and one could expect a positive effect of helper subordinates on population performance. By extracting productivity and survival probabilities of dominants with and without subordinates directly from the data, our model accounts for any possible positive effect of helper subordinates. The net effect of subordinate presence, however, was clearly negative, indicating conflict has a stronger effect in population dynamics than helping. This is consistent with the results in Table S1, where negative subordinate effects are equally significant regardless of whether dominant and subordinate were related.

Our analyses and simulation required a series of simplifications that may make our estimate of the effect of conflict conservative. In the statistical analyses, we only considered the immediate effect of having subordinates in the territory on takeover rates. This does not account for any likely cumulative effect of having subordinates in a territory for extended periods, since we did not include duration of subordinate presence in the analysis. Our data on the Seychelles magpie robin stem from an intensively managed population, showing a healthy rate of recovery. Even so, the rate of recovery was considerably slowed down by conflict, which indicates that competition for breeding habitat can significantly hamper population growth even if actual extinction is avoided. Slow recovery obviously heightens extinction risk during the period when small populations are most vulnerable, a general principle which was confirmed by our simulations with environmental variability. This highlights the importance of studying the population consequences of behavioural responses to management.

These results suggest that strategies of conflict mitigation through management could significantly increase population performance in the Seychelles magpie robin, as well as other territorial and social species. For example, in our study species, managers have occasionally removed particularly disruptive subordinates from their territories and used them for establishing populations on new islands, where empty habitat allows them to establish as breeders without causing any disruption. Supplementary feeding schemes should also take our results into account. In other species, it has been shown that it can increase conflict for territories near feeding sites and reduce overall productivity (Carrete, Donázar & Margalida 2006).

Extreme forms of disruption associated with competition for dominance are not uncommon (Arcese *et al.* 1992; Häcklander & Arnold 1999; Whitman *et al.* 2004), and their consequences for population dynamics in experimental populations are starting to be explored in experimental settings (Le Galliard *et al.* 2005; Andreassen & Gundersen 2006). Our results show that social conflict can have significant population consequences in the wild, and implies that knowledge of such behavioural processes can improve our understanding of population dynamics and management.

Acknowledgements

We wish to thank all the people who have monitored the species since 1988 and to Nature Seychelles, Cousine Island Ltd., the Royal Society for Nature Conservation and the Island Conservation Society for allowing work on their islands and facilitating data. Thanks to J. Azolan, E. Quilindo, D. Haggens, Q. Haggens and D. Freminot for help in the field and to R. Bristol, J. Souyave, J. Henwood, J. Samuel, M. Betts and S. Barclays for logistic support. C. Mateman performed the molecular sexing. M. D. Jennions, D. J. Kotze and R. B. O'Hara provided statistical advice. S. R. Beissinger, K. R. Foster, J. M. McNamara, W. J. Sutherland, J. Harwoed and the LEED::ANTZZ discussion group provided comments on different drafts of the manuscript. This work was funded by the Academy of Finland.

References

Andreassen, H.P. & Gundersen, G. (2006) Male turnover reduces population growth: an enclosure experiment on voles. *Ecology*, **87**, 88–94.

Arcese, P., Smith, J.N.M., Hochachka, W.M., Rogers, C.M., & Ludwig, D. (1992) Stability, regulation, and the determination of abundance in an insular song sparrow population. *Ecology*, **73**, 805–822.

Bourke, A.F.G. & Franks, N.R. (1995) *Social Evolution in Ants*. Princeton University Press, Princeton, New Jersey.

Breslow, N.E. & Clayton, D.G. (1993) Approximate inference in generalized linear mixed models. *Journal of the American Statistical Association*, **88**, 9–25.

Carrete, M., Donázar, J.A. & Margalida, A. (2006) Density-dependent productivity depression in Pyrenean bearded vultures: implications for conservation plans. *Ecological Applications*, **16**, 1674–1682.

Collar, N.J. & Andrew, P. (1988) *Birds to Watch: The ICBP World-Checklist of Threatened Birds*. International Council for Bird Preservation, Cambridge, UK.

Courchamp, F., Grenfell, B. & Clutton-Brock, T. (1999) Population dynamics of obligate cooperators. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 557–563.

Dieckmann, U. & Ferrière, R. (2004). Adaptive dynamics and evolving biodiversity. *Evolutionary Conservation Biology* (eds R. Ferrière, U. Dieckmann & D. Couvet), pp. 188–228. Cambridge University Press, Cambridge, UK.

Frank, S.A. (1998) *Foundations of Social Evolution*. Princeton University Press, Princeton, New Jersey.

Frank, S.A. (2007) All of life is social. *Current Biology*, **17**, R648–R650.

Gretton, A. (1993) Ecology of the Seychelles magpie robin *Copsychus sechellarum*. *Proceedings of the VIII Pan-African Ornithological Congress*, pp. 165–172.

Grimm, V., Revilla, E., Groenveld, J., Kramer-Schadt, S., Schwager, M., Tews, J., Wichmann, M.C. & Jeltsch, F. (2005) Importance of buffer mechanisms for population viability analysis. *Conservation Biology*, **19**, 578–580.

Häcklander, K. & Arnold, W. (1999) Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). *Behavioral Ecology*, **10**, 592–597.

Haldane, J.B.S. (1932) *The Causes of Evolution*. Harper and Brothers, London.

Hunt, W.G. (1998) Raptor floaters at Moffat's equilibrium. *Oikos*, **82**, 191–197.

Iguchi, K. & Hino, T. (1996) Effect of competitor abundance on feeding territoriality in grazing fish, the ayu *Plecoglossus altivelis*. *Ecological Research*, **11**, 165–173.

IUCN (2006) *2006 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland.

Kokko, H. & Sutherland, W.J. (1998) Optimal floating and queuing strategies: consequences for density dependence and habitat loss. *American Naturalist*, **152**, 354–366.

Komdeur, J. (1996) Breeding of the Seychelles magpie robin *Copsychus sechellarum* and implications for its conservation. *Ibis*, **138**, 485–498.

Le Galliard, J.-F., Fitze, P.S., Ferrière, R. & Clobert, J. (2005) Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences, USA*, **102**, 18231–18236.

López-Sepulcre, A. & Kokko, H. (2005) Territorial defense, territory size and population regulation. *American Naturalist*, **166**, 317–329.

Norris, K. & McCulloch, N. (2003) Demographic models and the management of endangered species: case study of the critically endangered Seychelles magpie robin. *Journal of Applied Ecology*, **40**, 890–899.

Parvinen, K. (2005) Evolutionary suicide. *Acta Biotheoretica*, **53**, 241.

Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-effects models in S and S-PLUS*. Springer-Verlag, New York.

Rankin, D.J. & López-Sepulcre, A. (2005) Can adaptation lead to extinction? *Oikos*, **111**, 616–619.

Reed, J.M. (1999) The role of behavior in recent avian extinctions and endangerments. *Conservation Biology*, **13**, 232–241.

Ridley, J., Komdeur, J., & Sutherland, W.J. (2004) Incorporating territory compression into population models. *Oikos*, **105**, 101–108.

Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. (2002) Ecological and evolutionary traps. *Trends in Ecology & Evolution*, **17**, 474–480.

Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185–190.

Sutherland, W.J. & Norris, K. (2002) Behavioural models of population growth rates: implications for conservation and prediction. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **357**, 1273–1284.

Thorsen, M., Shorten, R., Lucking, R. & Lucking, V. (2000) Norway rats (*Rattus norvegicus*) on Fregate Island, Seychelles: the invasion; subsequent eradication attempts and implications for the island's fauna. *Biological Conservation*, **96**, 133–138.

Veiga, J.P. (2004) Replacement female house sparrows regularly commit infanticide: gaining time or signaling status? *Behavioral Ecology*, **15**, 219–222.

Vucetich, J.A., Peterson, R.O. & Waite, T.A. (1997) Effects of social structure and prey dynamics on extinction risk in gray wolves. *Conservation Biology*, **11**, 957–965.

Watson, J., Warman, C., Todd, D. & Laboudallon, V. (1992) The Seychelles magpie robin *Copsychus sechellarum*: ecology and conservation of an endangered species. *Biological Conservation*, **61**, 93–106.

Whitman, K., Starfield, A.M., Quadling, H.S. & Packer, C. (2004) Sustainable trophy hunting of African lions. *Nature*, **428**, 175–178.

Williams, G.C. (1966) *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton University Press, Princeton, New Jersey.

Wright, S. (1969) *Evolution and the Genetics of Populations. Vol. 2. The Theory of Gene Frequencies*. University of Chicago Press, Chicago, Illinois.

Young, A.J. & Clutton-Brock, T. (2006) Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. *Biology Letters*, **2**, 385–387.

Received 2 April 2008; accepted 12 August 2008
Handling Associate Editor: Bill Gurney

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Description of the individual-based model simulating recovering Seychelles magpie robin populations.

Table S1. Effect of social environment on breeder takeover

Table S2. Effect of breeder takeover on territory productivity