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Can we measure the benefits of help in cooperatively breeding birds: the case of superb fairy-wrens *Malurus cyaneus*?

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Summary

1. Correlational studies of reproductive success are plagued by difficulty over the direction of causation. For example, improved reproductive success with age can result from increased experience or reproductive effort, or selection against low-quality phenotypes that survive poorly. An association between supernumeraries and reproductive success in cooperative breeders can arise either because supernumeraries boost productivity, or productive territories accumulate supernumeraries.

2. Paired comparisons of parents sampled with and without supernumeraries have recently been widely applied to quantify help. However, Dickinson & Hatchwell (2004) have argued that this approach is flawed. They conjectured that those groups that gain supernumeraries are a biased superior sample of those that initially lack supernumeraries, while groups that lose supernumeraries will be a sample of inferior cooperative groups. They predict that these biased comparisons will underestimate the effect of help.

3. This conjecture has neither been explored theoretically, nor empirically tested. We use data from a 19-year study of the superb fairy-wren *Malurus cyaneus* to examine the conjecture and derive predictors of annual reproductive success in this species.

4. We introduce statistical models of reproductive success based on a zero-inflated Poisson link function to identify three strong correlates of reproductive success: high spring rainfall, progress from the first to later years of life, and acquisition of supernumeraries.

5. First year females that died after breeding and those that survived to breed again had similar productivity. As female productivity improves with age, increased reproductive skill or effort is implicated rather than selection against inferior phenotypes.

6. We argue that the Dickinson–Hatchwell conjecture does not constrain paired comparisons in *M. cyaneus*. The dominant male and breeding female gain no immediate fecundity advantage from supernumeraries.

7. Effects on the future survival of dominants are even more difficult, as while helpers could enhance survival of dominants, a territory that facilitates survival should also accumulate philopatric supernumeraries. Males, the philopatric sex, did not survive better on territories with supernumeraries. However, females, the dispersive sex, had higher survival as the number of supernumeraries increased, because helpers allowed them to reduce the costs of reproduction. These data exacerbate the paradox posed by previously reported costs that supernumeraries impose on dominant males.

Key-words: cooperative breeding, helper, reproductive success, zero-inflated Poisson.

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Introduction

The fundamental assumption of many of the hypotheses that attempt to explain the occurrence of cooperative breeding in birds is that the presence of supernumerary birds (so-called helpers) enhances the reproductive success of the dominants they assist. For example, this relationship is necessary for helpers to gain indirect fitness benefits from kin selection (Emlen 1995; Griffin & West 2003), and direct fitness benefits from group augmentation (Kokko, Johnstone & Clutton-Brock 2001). However, there are considerable difficulties in confirming that supernumeraries have a positive effect on productivity (Cockburn 1998; Dickinson & Hatchwell 2004). A simple correlation between the number of supernumeraries and productivity on the territory provides no information because such a correlation is expected if helpers increase productivity, or some territories and/or breeders are of better quality, and hence are more likely to accumulate supernumeraries (Brown *et al.* 1982).

Four approaches to this problem have been suggested. First, experimental removal of supernumeraries is likely to be informative (Brown *et al.* 1982; Mumme 1992), but this approach suffers because removals simultaneously manipulate many additional variables rather than help *per se*, and have the potential to disrupt social relationships within the group profoundly (Dunn & Cockburn 1996; Jamieson & Quinn 1997; Cockburn 1998). Second, in some species it is possible to compare the productivity of groups where supernumeraries provision with those where they do not (Davies & Hatchwell 1992; Magrath & Yezerinac 1997). While this approach is potentially powerful, it is only applicable where supernumeraries often fail to provision, which is rare among cooperatively breeding birds. Third, it has been suggested that statistical models that incorporate the effect of territory and the identity of the breeder as random effects may allow the influence of supernumerary provisioning to be disentangled (Cockburn 1998). These methods offer some promise because other impacts on productivity, such as variation between years in reproductive output, can be explicitly controlled. However, such modelling can be subject to overinterpretation. While small estimates for random effects could be interpreted to indicate that there is no effect of territory or parental quality, these parameters are rarely estimated with the same power that is obtained for fixed effects. For example, sampling at a sufficient intensity to estimate whether there are separate effects of territory and parental ability requires sampling of the same individuals on different territories, which is unlikely to be possible for most study species.

Finally, it has been suggested that a comparison between the productivity of adults with and without supernumeraries allows the effect of help to be detected (Marzluff & Balda 1990; Green *et al.* 1995). The paired comparison approach has been applied with increasing frequency (Caffrey 2000; Legge 2000; Eguchi *et al.* 2002), and often fails to detect a benefit from help. However, this approach was criticized by Dickinson & Hatchwell (2004), who argued that because the comparison is only possible on territories where helper number changes, inference is based on a biased sample. Territories where the number of supernumeraries increase are likely to have been initially more productive than average, while decline in the number of supernumeraries is most likely on unproductive territories. Dickinson & Hatchwell conjecture that this will obscure the effect of help in paired comparisons. The logic of this claim has not been explored, nor has its empirical foundation been tested.

Superb fairy-wrens *Malurus cyaneus* (Ellis, 1782) are particularly interesting as they have been used as a textbook example of the effects of kin selection, based on the discredited approach of identifying a correlation between group size and territory productivity (Brown 1975; Grafen 1984). Not only is this approach conceptually flawed, but molecular dissection of the fairy-wren mating system has revealed extremely high rates of extra-group mating (Mulder *et al.* 1994); therefore, supernumeraries often care for young to which they are completely unrelated, suggesting a limited role for kin selection (Dunn, Cockburn & Mulder 1995). Unfortunately, this species is particularly sensitive to experimental manipulation of the presence of supernumeraries (Mulder & Langmore 1993; Dunn & Cockburn 1996), and all supernumeraries provision young (Dunn & Cockburn 1996), precluding the use of these methods for detecting the effects of help. Here we use data from a long-term study to explore the statistical and paired comparison approaches, in the hope of developing generally applicable methods. We pay particular attention to the Dickinson–Hatchwell conjecture, and introduce new statistical methods for analysing reproductive success.

Materials and methods

SPECIES AND STUDY SITE

We studied fairy-wrens at the Australian National Botanic Gardens in Canberra from 1988 until 2007, encompassing 19 breeding seasons. The first nests are usually initiated in September, and although in most years many birds initiate their final nest in December, the last nests can fledge as late as early March. The study area initially comprised about 30 territories. However, it was expanded through 1991 and 1992 to incorporate between 55 and 90 territories, from which the complete nesting history and performance of offspring is determined by continuous census. Basic field methods are described in Cockburn *et al.* (2003).

Female fairy-wrens are multibrooded, and occasionally rear three broods to independence. Starvation of nestlings is negligible. However, nest predation is high, and females can initiate as many as eight clutches in a season. All females must disperse before the start of their first breeding season in order to gain a breeding vacancy, while males are the most philopatric year-round territorial birds studied thus far (Cockburn *et al.* 2008), with most spending their entire lives on their natal territory, whether or not they inherit the breeding vacancy (Mulder 1995; Cockburn *et al.* 2008). If they do disperse it is to an adjacent territory, and such dispersal is only possible if all males in that territory die. Because females suffer considerable mortality during this pre-breeding dispersal, the adult population is strongly male-biased, and as many as five adult males can occupy a single territory, though dispersal of young females means that there is only one breeding female. The oldest male is dominant, and guards the single breeding female. The supernumerary younger males assist the breeding pair to feed and defend offspring. Like females, males become sexually active at 1 year of age, and supernumerary males can be successful at siring offspring (Double & Cockburn 2003; Dunn & Cockburn 1999).

CURRENCY OF REPRODUCTIVE SUCCESS

Three features of the fairy-wren life history influence the currency used in these analyses: the number of young raised to 4 weeks post-fledging during a breeding season. First, clutch size variation is quite conservative, with the overwhelming majority of broods comprising three or four eggs, so the capacity of supernumeraries to influence output is limited. However, annual productivity could potentially be high as 12 offspring if three broods of four were successfully reared. Re-nesting could potentially be accelerated in the presence of helpers if they freed the female to initiate a new clutch. Second, although nests are highly vulnerable to predators, predation is most likely during the first few days after fledging, as fledglings fly poorly for the first week out of the nest, and are preyed upon heavily by an avian predator, pied currawongs *Strepera graculina* (Shaw, 1790). Finally, some females make long distance dispersal movements several weeks after they are fledged (Mulder 1995), so their fate can no longer be monitored. While these movements usually occur 6–10 weeks after fledging, we have recorded one instance of dispersal at 5 weeks. Hence, we model the seasonal production of young that survive to 4 weeks post-fledging, after predation has declined, but before dispersal is possible.

Analyses included only females that survived for the majority of the breeding season, i.e. until at least 90% of the population had stopped breeding. We excluded from analyses any case where the circumstances of the female (her mate, or the number of supernumeraries) changed during the breeding season. We also excluded cases where we had undertaken interventions that were likely to inflate (caging of nests, $n = 21$) or reduce (addition of a cuckoo egg, $n = 5$) the reproductive success of the female during that season. However, because groups are quite stable, and our interventions were rare, in most seasons our sample for analysis includes at least 90% of breeding females. The major exception was the 1995/96 breeding season, when an epidemic of unknown cause killed many birds during the breeding season, so only 70% of territories were fully sampled. The final sample was 421 females sampled in 927 seasons (mean = 2·20 seasons ± 1·54 SD, maximum = 8).

STATISTICAL MODELLING OF PRODUCTIVITY

Our first approach was to build statistical models of female annual reproductive success. During initial analysis we encountered a problem that has received little attention in the study of life-history ecology, though it is likely to be pervasive. Seasonal productivity ranged from 0 to 9. High values were rare, as is commonly the case for count data, and can be approached in statistical modelling using a Poisson distribution. However, the distribution was bimodal, with the strongest mode at zero reproductive success (Fig. 1). Indeed, females failed to rear any young to independence in 31% (285 of 927) of breeding seasons.

Distributions of this sort are called zero-inflated Poisson (hereafter *ZIP*), and are beginning to attract use in ecology (Welsh *et al.* 1996; Barry & Welsh 2002; Martin *et al.* 2005). In principle, this problem is easily handled if the two modes are discrete, so that no zero values could have arisen through the same processes affecting the positive values, as it is possible to analyse the zeroes and positive values separately. However, if the mean value is low, some of the zeroes will arise from the same sampling process that gives values of 1, 2, 3, etc. Welsh *et al.* (1996) compared a number of methods for dealing with this case, and recommend an approach they called the conditional ZIP model, which we follow here. In brief, this involves initially modelling the occurrence of reproductive failure using a generalized linear model with a logit link and binomial error. The cases where some reproductive success occurred are then modelled in a second generalized linear model with a truncated Poisson distribution. The predictions from the two models can also be combined because there is no covariance between the estimators for the two models. We calculated means, variances and standard errors using a conventional generalized linear model approach using the estimators in Appendix A of Welsh *et al.* (1996, pp. 306–307). We fitted these models in Genstat 9 for Windows using code written by C. Donnelly (Statistical Consultancy Unit, Australian National University).

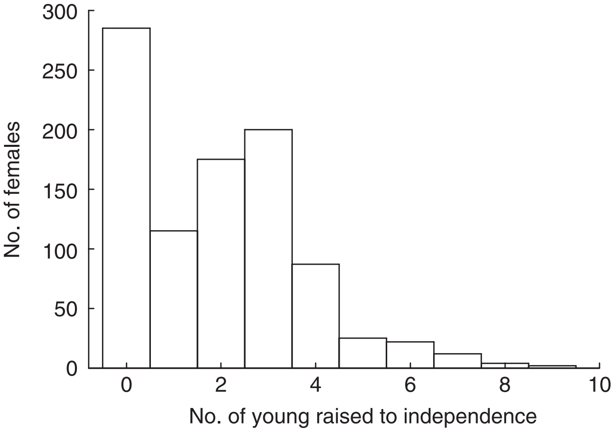

Fig. 1. Variation in the number of young raised to independence during a single breeding season on territories of *M. cyaneus*.

Potentially, a very large number of variables can be included as explanatory variables. However, we had particular a priori interest in some interactions (between climatic variables and age and the presence of supernumeraries), so it was desirable to reduce the number of explanatory variables in order to facilitate the fitting of interaction terms. Exploratory data analysis suggested that some responses to variables of interest were nonlinear. In particular, any change associated with the age of the breeding female was concentrated in the first 3 years of life (Fig. 2a), and statistical modelling repeatedly revealed a strong contrast between the first and second year of life, though no significant differences thereafter. In a similar fashion, any correlations with the number of supernumeraries occurred between the transition from zero to one or more (Fig. 2b). We therefore used dichotomous factors to describe age (1 vs. older) and the presence of supernumeraries (present or not), which facilitated fitting interaction terms. We used a similar approach to find whether the age of the dominant male was influential. However, exploratory analysis and formal modelling suggested male age was not associated with productivity at all, yet it greatly increased the complexity of interaction terms. For simplicity, male age is not included in the analyses reported here. In order to control for environmental effects, we also used exploratory data analysis to identify variables that described weather conditions. The nature of the climate of the study area means that high rainfall during the breeding season is correlated with low temperatures. We have therefore used rainfall from August to November (hereafter spring rainfall) as an indicator of breeding conditions, though any of a

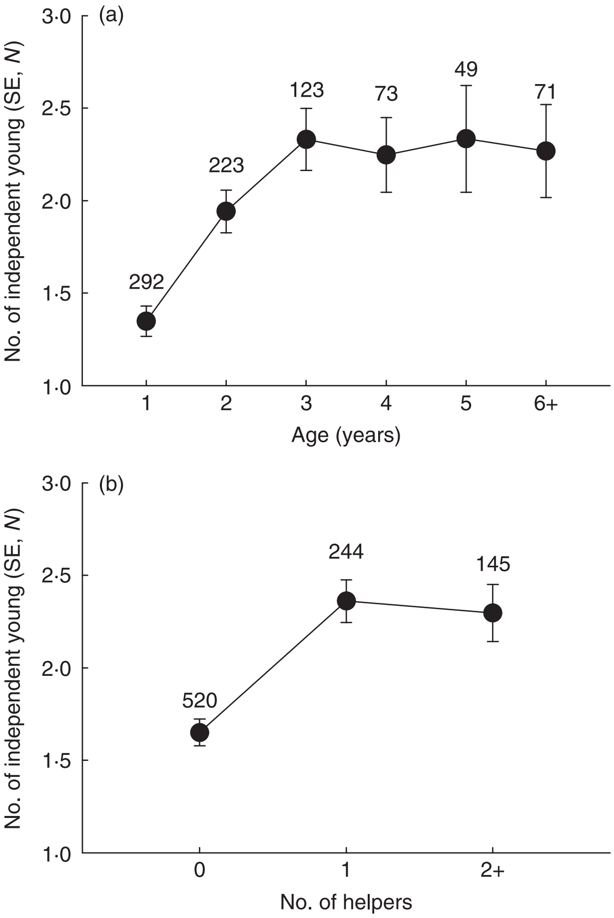

Fig. 2. Annual production of independent young by *M. cyaneus* in relation to: (a) the age of the female; and (b) the number of helpers. Sample sizes are the number of breeding years.

number of correlated weather variables returns similar results, albeit with slightly lower explanatory power. We tested age of the breeding female, presence of supernumeraries, spring rainfall and their interactions. We sequentially discarded nonsignificant terms ($P > 0{\cdot}05$) to obtain a parsimonious model.

CHANGES IN PRODUCTIVITY WITHIN INDIVIDUALS

We also examined how reproductive success changed within individuals, as these comparisons potentially control for consistent effects of territory and/or female quality. We could contrast females whose age changed in consecutive years from 1 to 2 years of age, and where supernumeraries were present in 1 year and not the other. In such contrasts, the influence of environmental conditions is better represented by change in climate between years. Exploratory analysis revealed a dichotomy between abrupt changes between years in spring rainfall (change > 110 mm) and consecutive years where the rainfall was similar (change < 65 mm). These abrupt changes correspond to the well-known alternation between dry years influenced by the El Nino Southern Oscillation, and wet years driven by the converse La Nina phenomenon. We therefore defined three categories of change (wetter: increased by > 110 mm, same: change from –65 to +65 mm, and drier: decreased by > 110 mm).

In order to explore whether differences between 1-year-old and older females reflect selection against 1-year-old female, we initially fitted ZIP models to test whether there was a difference in reproductive success between 1-year-old females that did and did not survive to breed again. In order to explore the Dickinson–Hatchwell conjecture, we fitted ZIP models to distinguish between four classes of breeders that were sampled in two consecutive years. First, some birds remain as unassisted pairs (Neither). Second, some unassisted pairs gain a supernumerary (Increaser). Third, some birds have supernumeraries in both years (Both). Finally, some groups lose their supernumeraries (Decreaser). The data we report here are for 470 transitions for 223 females; 129 (57%) of these females were sampled both with and without helpers.

We then examined the performance of females sampled over 2 years by fitting residual maximum likelihood models (REML) of the change in reproductive success using three factors (climate change, breeder class and age). We included the identity of the breeding female as a random term in these models (inclusion of the male was attempted in exploratory data analysis but lead to negative estimates of the variance component). These models were analysed in *Genstat for Windows* version 9.

Finally, we performed paired comparisons between birds where group size had changed, and where females changed from the first to second year of life.

STATISTICAL MODELLING OF SURVIVAL EFFECTS

We modelled the probability that birds would survive from the end of the breeding season until they were able to initiate breeding in the subsequent breeding season (a clutch was produced on their territory). We fitted generalized linear mixed models with a logit-link function and binomial error where the response variable was to survive or not, and the random term was the identity of the female. We fitted separate models for male and female dominants. Explanatory variables were spring rainfall, number of supernumeraries (initially 0, 1 or 2+) and the age of the dominant (initially 1, 2 or 3+), and the interactions between these terms. A paired comparison approach is not possible in this case as the failure to survive in the first year obviously precludes assessment in the second year.

Results

ANNUAL REPRODUCTIVE SUCCESS

Seasonal productivity increased strongly with both the binomial and truncated Poisson components for spring rainfall, between the first and later years of life of the female, and as territories acquired a supernumerary (all $P < 0{\cdot}002$; Table 1; Fig. 3). There were no interaction effects, though the binomial component of the interaction between female age and the presence of a supernumerary approached significance (Table 1).

Generalized linear models differ in their assumptions concerning the distribution of the error term in the regression model, which can be assessed by examining the distribution of Pearson residuals ((observed values-fitted values)/(standard error of the fitted values)) relative to the fitted values from the model. We contrasted our ZIP models with comparable models based separately on the assumption of Normal, Poisson and Binomial errors. Although one benefit of the ZIP

Table 1. Model estimates for the binomial and truncated Poisson component of zero-inflated Poisson models of seasonal reproductive success in *Malurus cyaneus.* Models for interaction terms refer to the estimate of effects from models also containing main effects (two-way terms) or two-way terms (three-way terms). All main effects were highly significant – denoted by *P*-values in bold

	Binomial				Truncated Poisson			
Model term	Estimate	SE	*t*	*P*	Estimate	SE	*t*	*P*
Rainfall · Help · Female age	0·0012	0·0043	0·29	0·38	0·00097	0·00177	0·54	0·34
Rainfall · Female age	–0·0016	0·002	–0·82	0·29	0·00096	0·00089	0·64	0·32
Rainfall · Help	–0·0014	0·0029	–0·75	0·31	–0·00008	0·00069	–0·11	0·40
Female age · Help	0·67	0·35	1·93	0·06	–0·15	0·13	–1·15	0·21
Female age	0·73	0·16	4·60	**< 0·001**	0·28	0·06	4·45	**< 0·001**
Help	–0·56	0·16	–3·53	**< 0·001**	–0·17	0·05	–3·33	**0·002**
Rainfall	0·004	0·0009	4·39	**< 0·001**	0·0021	0·0003	6·17	**< 0·001**

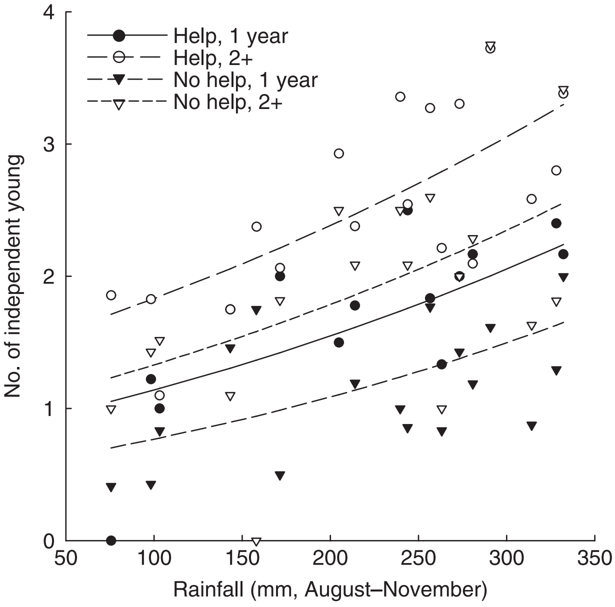

Fig. 3. Means and predictions from models based on a zero-inflated Poisson link function in relation to spring rainfall, and whether the female is in her first year or not, and whether a supernumerary is absent or present on the territory.

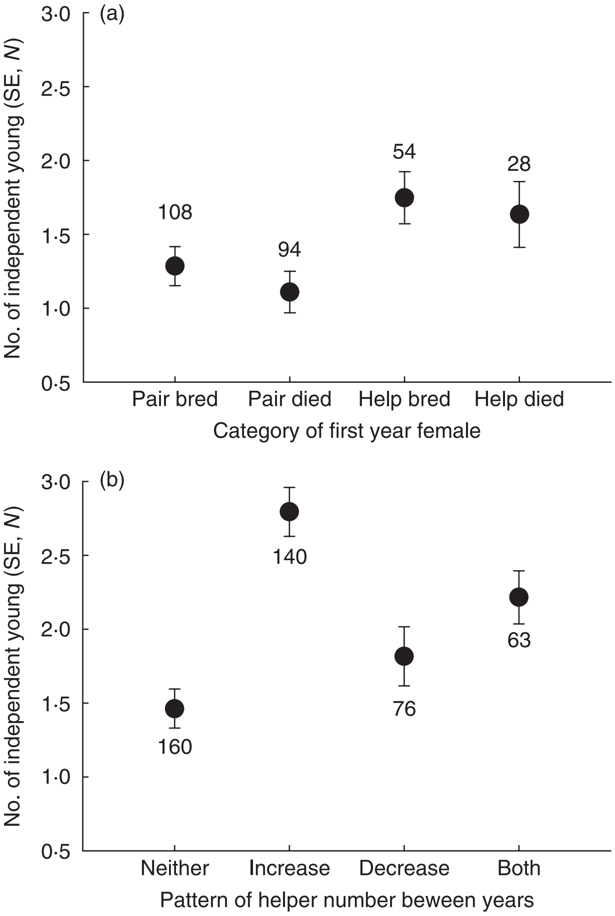

Fig. 4. Model estimates of the production of independent young in: (a) first year females according to whether they survive to breed again; and (b) females according to whether they will remain without a helper (Neither), gain a helper (Increase), lose any helpers (Decrease), or continue to have access to helpers (Both). The values are model estimates, their standard errors, and the number of seasons sampled.

approach, the ability to have different explanatory variables for the Binomial and truncated Poisson responses, does not apply in this case, the ZIP method captured the data well, while the residuals derived from other link functions were highly constrained. However, analyses conducted using the other link functions produced identical conclusions – there were three main effects and no interactions. As already described, these models give little indication of causation. While the effects of rainfall are almost certainly causative, age and supernumerary effects require some care in interpretation.

EFFECTS ON PRODUCTIVITY WITHIN INDIVIDUALS OF HELP, AGE AND CLIMATE

In order to dissect the problem of causality further we first considered whether the increase in productivity with age could be affected by selection against low-quality females that failed to survive through the first year. In contrast to this prediction, females that survived had similar fecundity in their first year to females that only bred once (Fig. 4a; binomial effect; $t = -1{\cdot}84$; $P = 0{\cdot}07$; truncated Poisson effect; $t = 0{\cdot}69$,

Table 2. Significance of interaction terms for a model of the change in reproductive success in *M. cyaneus* in relation to changes in climate, age and helper number. Because climate and helper number factors contain several terms, the individual coefficients are not presented. Main effects are described in the text and presented in Fig. 5

Term	Wald χ^2	d.f.	*P*
Rainfall change · Helper change · Female age	4·26	6	0·64
Helper change · Female age	0·60	3	0·89
Rainfall change · Female age	3·50	2	0·17
Helper change · Rainfall change	10·32	6	0·11

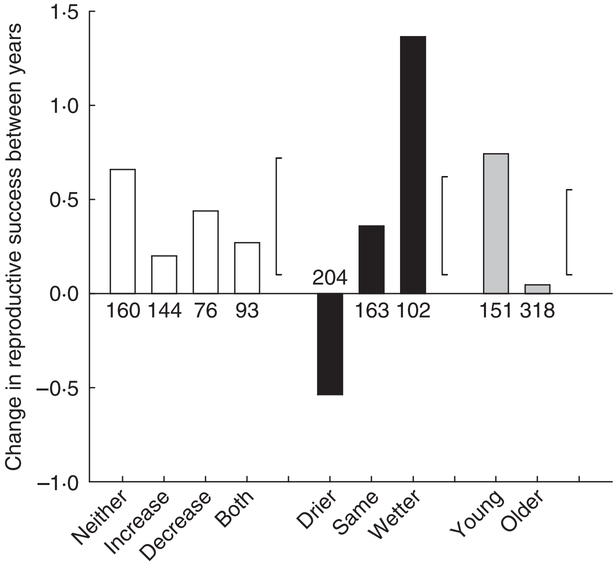

Fig. 5. Predictions of general linear mixed models of the change in reproductive success between years in relation to: (a) whether helper number changes; (b) whether spring rainfall changes; and (c) whether the transition is between the first two years or between later years of life. The bars to the right of each set of histograms represent twice the standard error of the difference for the bars to the left. The effect of change in helper number was not significant but the predictions from a model including this variable are included for illustrative purposes. Sample sizes are the number of seasons sampled.

$P = 0·33$). In order to examine the plausibility of the Dickinson–Hatchwell conjecture, we also fitted ZIP models of the first of paired years of reproduction to test for differences between the Neither, Both, Increaser and Decreaser cases. The difference between the categories was primarily associated with the truncated Poisson effect (Binomial effect; $\chi^2 = 7·0$, d.f. = 3, $P = 0·07$; truncated Poisson effect; $F_{3,343} = 3·48$, $P = 0·02$). As predicted by Dickinson & Hatchwell (2004), reproduction was lowest for Neither, but contrary to expectations, was highest for Increaser rather than Both (Fig. 4b).

In our model of the change between years (Table 2; Fig. 5), improvement was greatest for birds where the change was between first and later years of life (Wald $\chi^2 = 9·5$, d.f. = 1, $P = 0·002$), and where rainfall increased between years ($\chi^2 = 49·2$, d.f. = 2, $P << 0·001$). However, there was no effect of gain or loss of a supernumerary ($\chi^2 = 2·6$, d.f. = 3, $P = 0·45$), nor any interactions (Table 2).

We then used paired comparison tests to contrast performance of individual females in the first and second years of their life. Overall, females reared on average 0·48 ± 0·16 SE. ($n = 154$) more young to independence in their second year of life (paired $t = 2·97$, $P = 0·003$), but this effect was most pronounced if rainfall was similar or improved. For the case where rainfall was similar between the 2 years the increase was 0·63 ± 0·26 SE ($n = 41$) young, or 46% (paired $t = 2·41$, $P = 0·02$).

Paired comparison tests on the effect of gaining or losing a supernumerary among older birds revealed that overall there was no effect (–0·31 ± 0·23 SE; $n = 139$; paired $t = –1·34$, $P = 0·18$, noting that the probability estimate is for the significance of a negative value), with increases in productivity instead primarily associated with improved spring rainfall. For the case where rainfall was similar between the 2 years the estimate was once again negative but not significantly so (–0·15 ± 0·41 SE, $n = 54$, paired $t = –0·35$; $P = 0·73$).

SURVIVAL EFFECTS

It is also possible that the primary benefit of the presence of a supernumerary occurs through load-lightening, which should manifest itself as increased post-breeding survival. In models of the probability that females would die before the next breeding season, there was no effect of any of the interaction terms (Table 3). The probability that females

Table 3. Model estimates from a generalized linear mixed model analysis of survival of dominant female and male *Malurus cyaneus.* Models for interaction terms refer to the estimate of effects from models containing main effects (two-way terms) or two-way terms (three-way terms). The one significant effect is denoted by *P*-value in bold. Significance tests are Wald χ^2

	Females				Males			
Model term	Estimate	SE	χ^2	*P*	Estimate	SE	χ^2	*P*
Rainfall · Help · Age	0·00039	0·005	0·29	0·94	–0·037	0·023	2·55	0·11
Rainfall · Age	–0·0039	0·0023	2·83	0·09	0·0016	0·0036	0·19	0·66
Rainfall · Help	–0·0024	0·0022	1·15	0·28	–0·0020	0·0021	0·92	0·34
Age · Help	–0·20	0·39	0·28	0·60	–0·77	0·82	0·89	0·35
Age	0·16	0·17	0·94	0·33	0·12	0·23	0·28	0·60
Rainfall	–0·0017	0·0010	2·75	0·10	–0·0001	0·0011	0·01	0·92
Help	0·55	0·16	12·1	**< 0·001**	0·02	0·15	0·02	0·89
Constant	–1·27	0·13			–0·85	0·11		

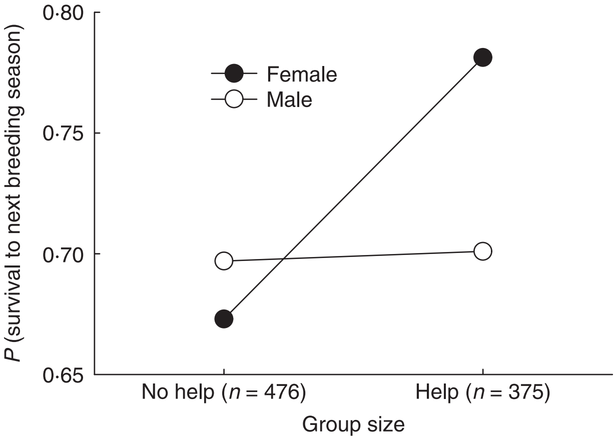

Fig. 6. Effect of the presence of supernumerary *M. cyaneus* on the probability of surviving from the end of the breeding season until eggs are laid on the territory in the following breeding season. Sample sizes denote the number of breeding seasons.

would die was affected by neither age ($\chi^2 = 0{\cdot}9$, d.f. = 1, $P = 0{\cdot}33$), nor rainfall ($\chi^2 = 2{\cdot}8$, d.f. = 1, $P = 0{\cdot}10$), but the risk of mortality was 50% higher for females without a supernumerary on the territory (Fig. 6; $\chi^2 = 12{\cdot}3$, d.f. = 1, $P < 0{\cdot}001$; mortality risk: unassisted females = 0·33, females with a supernumerary present = 0·22). By contrast, there were no terms that predicted the survival of dominant males (Table 3). Most important, there was no effect of the presence of supernumeraries on male survival (Fig. 6; $\chi^2 = 0{\cdot}02$, d.f. = 1, $P = 0{\cdot}89$).

Discussion

Statistical models of annual reproductive success in the cooperatively breeding superb fairy-wren *Malurus cyaneus* identified three strong positive correlates: spring rainfall, the age of the breeding female, and the presence of supernumeraries on the territory. However, analysis of changes within females suggest that while the effect of female age is causative, the effect of help by supernumeraries is not. Instead, high-quality breeders and/or territories are likely to accumulate philopatric supernumeraries. However, supernumeraries do provide a deferred benefit, increased likelihood that the breeding female will survive to breed again. This effect is likely to be causative because increased survival is not observed in the philopatric sex, contrary to predictions of the hypothesis that characteristics of the territory rather than help *per se* promote survival.

REPRODUCTIVE SUCCESS

Statistical models suggest that reproductive success is correlated with spring rainfall, an increase in age, and the presence of at least one supernumerary. The effect of rainfall is easily understood in this case. The study periods encompassed some of the most severe drought conditions recorded in south-eastern Australia, and these clearly restricted virtually every aspect of the reproduction of the fairy-wrens, almost certainly by reducing the availability of food.

Three hypotheses are commonly invoked to explain age-related increases in reproductive success in birds (Curio 1983; Saether 1990; Forslund & Pärt 1995). First, some aspect of parental skill could increase with experience or maturation, such as foraging ability and habitat selection (e.g. Pärt 2001), or co-ordination with other group members (Nevoux, Weimerskirch & Barbraud 2007). Second, because the residual reproductive success of birds declines with age, increased risk-taking may be favoured as age advances, though this could be countered if low-quality individuals incur fewer reproductive costs (e.g. Pärt, Gustafsson & Moreno 1992). Finally, the elimination of low-quality individuals through selection may lead to homogeneous high-quality individuals at advanced ages (e.g. Cam & Monnat 2000; Mauck, Huntington & Grubb 2004). The latter hypothesis is not supported in this case, as first year females that survived to breed again had similar productivity to those that did not, and individual females on average increased their success by 50% from year to year. Hence the effect of age is likely to be causative.

The residual reproductive success hypothesis does not predict that the effects of age will be concentrated between the first and second year of life in birds that can breed for nine breeding seasons. Hence, some aspect of experience is implicated. The absence of an interaction between rainfall and breeding output contrasts with several studies that have reported the poor performance of young birds is exacerbated by severe environmental conditions (e.g. Laaksonen, Korpimäki & Hakkarainen 2002; Bunce, Ward & Norman 2005). This suggests that foraging ability may be less important in determining differences between first and older birds than experience at nest location and construction, as vulnerability to predators may be a more important determinant of output than foraging ability (e.g. Komdeur 1996). None the less, birds of all ages gain a considerable advantage from improved rainfall (Fig. 5).

Our analyses of the consequences of help are more complicated. The initial statistical modelling revealed a positive association between help and productivity, while paired comparisons of females with and without help suggest that this is not due to help *per se*. In addition, the productivity of birds influences the likelihood that helper numbers will change (Fig. 4b), as predicted by both the Dickinson–Hatchwell conjecture and the hypothesis that high-quality territories will be more likely to recruit supernumeraries. Can these alternatives be distinguished? Dickinson & Hatchwell (2004) have argued the association between productivity and the likelihood that helper number will change precludes the use of paired comparisons to control for female/territory effects of help. However, their underlying logic is not clear, as detection of an effect of help is only impossible if there are some individuals that are so superior that they derive no further benefit from help, and another subclass that are so poor that they would gain no benefit from help. Indeed, a logical corollary is that if large proportions of birds undergo changes in group size, as occurs in our data (129 of 223; 57%), the population would eventually reorganize so that birds with supernumeraries would gain no benefit from their presence, while birds that were incompetent at reproduction would be unassisted. This of course exacerbates the unreliability of mean values, and hence reduces even further the ability to interpret the correlations detected in the statistical models as causative. It is less clear that paired comparisons are undermined. For example, in the fairy-wren data, the Decreaser class has intermediate productivity to the Neither or Both class (Fig. 4). It could be argued that Both–Decreaser equals the component due to environmental/female quality, and Decreaser–Neither equals the effect attributable to help. Hence, we predict further decline equivalent to Decreaser–Neither once the helper is no longer present, but there is no change in our data (Fig. 4).

In addition, the Dickinson–Hatchwell argument trivializes the complex process of acquisition and loss of supernumeraries. Loss can occur on successful territories because death or dispersal to neighbouring vacancies outweighs recruitment. In turn, recruitment depends not just on productivity, but on production of the philopatric sex, which is not guaranteed because the number of independent young is so low that often only daughters will be reared. By contrast, in *M. cyaneus* an increase in the number of supernumeraries is most likely for (1) older females, which have greater productivity, and hence more likely to recruit helpers than 1 year olds, and (2) when drought breaks, when reproductive success increases sharply. It is because helper number increases after rain that the productivity of Increasers exceeds that for the Both class. However, despite the high productivity of Increasers, there is no evidence of a production threshold, as their average performance is less than rearing a single brood to independence. Hence, a further effect of help should be detectable, but does not occur. Thus while dissection into the four classes envisaged by the Dickinson–Hatchwell conjecture is a useful step in analysis, we do not believe their argument that the paired comparison method will not reveal helper effects if they are present. In the case of *M. cyaneus*, there is no evidence that acquisition or loss of a supernumerary leads to gain or reduction in productivity, so we argue that the correlation between group size and productivity is likely to be a consequence of greater recruitment of supernumeraries where the quality of the territory or female is high. However, it will prove interesting to apply these methods to examine the situation in other species where the relativities between the four classes are different, as this may allow novel insights.

By contrast, our analyses reveal a hitherto unreported correlation between the presence of supernumeraries and the subsequent survival of the female. Effects of helpers on future reproductive success are plausible, as many cooperative breeders use the presence of helpers to reduce the amount of parental care (load-lightening), rather than increase productivity (Hatchwell 1999). This is particularly true where nestling starvation is rare (Hatchwell 1999), as in the case in fairy-wrens. However, detecting effects on survival is notoriously difficult to interpret, as load-lightening could lead to improved survival, but territories where survival is enhanced should also accumulate philopatric helpers. Alternative approaches are difficult, as paired comparisons are confounded where death is one of the outcomes, and experiments that increase mortality are questionable ethically. There is also the possibility that highly localized density-dependent competition between group members could cause reduced survival (Cockburn *et al.* 2003; Brouwer *et al.* 2006). However, because we have detected enhanced survival in females, which are never philopatric, and no benefit for males, the philopatric sex, we believe that our results are best interpreted as evidence of a causative improvement of survival.

The fact that females rather than dominant males gain a survival benefit is surprising, because dominant males reduce provisioning in the presence of a helper more than females (Dunn & Cockburn 1996). Our earlier analyses had suggested that males may use load-lightening to increase the rate of extra-group courtship displays (Green *et al.* 1995). However, subsequent work revealed that additional courtship during the breeding season is unlikely to increase extra-group parentage (Green *et al.* 2000), which instead is based on courtship outside the period of parental provisioning (Dunn & Cockburn 1999; Double & Cockburn 2003).

A possible reason for the greater sensitivity of female survival is that males provision at a much lower rate than they can potentially achieve (MacGregor & Cockburn 2002), and are largely insensitive to the needs of the brood (Dunn & Cockburn 1996). By contrast, female provisioning responds strongly to brood size and nestling age (Dunn & Cockburn 1996), and it may be the costs of this sensitivity that allows females to benefit from load-lightening. However, it is more likely that the difference arises because females are exclusively responsible for some components of investment, and hence the unique beneficiaries of any reduction in those components. In particular, females reduce the size of the eggs they lay when they have helpers, yet this reduced investment is fully compensated by the increased food delivery that occurs at nests with helpers (Russell *et al.* 2007). Females thus use helpers to obtain future benefits rather than to enhance current reproductive benefits.

These analyses exacerbate the paradox posed by the balance between cost and benefits experienced by dominant male fairy-wrens that tolerate helpers. Our previous work has identified three severe costs to dominant males of the presence of a supernumerary. Females with helpers increase the allocation of paternity to extra-group males, so the addition of a single helper reduces within-group paternity (Mulder *et al.* 1994; Dunn & Cockburn 1999). In addition, females are often unrelated to the supernumerary males, and in these circumstances allow the supernumerary about one-quarter of the young that are sired within-group (Cockburn *et al.* 2003). Third, if the dominant male is sufficiently attractive to solicit visits from extra-group females, he is vulnerable to parasitism by the helper (Double & Cockburn 2003). The results we report here suggest that these costs are not compensated by increased fecundity or survival. In dramatic contrast, the female gains two substantial benefits from the presence of helpers. First, constraints on unrestricted mate choice are alleviated, so she is free to allocate paternity among a large pool of potential sires (Mulder *et al.* 1994). Second, females without helpers have a 50% greater chance of death between breeding seasons compared with those that were assisted by a supernumerary.

Collectively, these observations raise the problem of why males tolerate helpers. The absence of female supernumeraries is in part a consequence of aggression by the dominant female, suggesting expulsion of supernumeraries is feasible. Why this does not occur is perhaps the greatest unresolved problem in understanding the remarkable social and mating system of these birds.

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References

Barry, S.C. & Welsh, A.H. (2002) Generalized additive modelling and zero inflated count data. *Ecological Modelling*, **157**, 179–188.

Brouwer, L., Richardson, D.S., Eikenaar, C. & Komdeur, J. (2006) The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. *Journal of Animal Ecology*, **75**, 1321–1329.

Brown, J.L. (1975) *The Evolution of Behavior*. WW Norton, New York.

Brown, J.L., Brown, E.R., Brown, S.D. & Dow, D.D. (1982) Helpers: effects of experimental removal on reproductive success. *Science*, **215**, 421–422.

Bunce, A., Ward, S.J. & Norman, F.I. (2005) Are age-related variations in breeding performance greatest when food availability is limited? *Journal of Zoology*, **266**, 163–169.

Caffrey, C. (2000) Correlates of reproductive success in cooperatively breeding western American crows: if helpers help, it's not by much. *Condor*, **102**, 333–341.

Cam, E. & Monnat, J.Y. (2000) Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *Journal of Animal Ecology*, **69**, 380–394.

Cockburn, A. (1998) Evolution of helping behaviour in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, **29**, 141–177.

Cockburn, A., Osmond, H.L., Mulder, R.A., Green, D.J. & Double, M.C. (2003) Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus*. *Journal of Animal Ecology*, **72**, 189–202.

Cockburn, A., Osmond, H.L., Mulder, R.A., Green, D.J. & Double, M.C. (2008) Demography of male reproductive queues in cooperatively breeding fairy-wrens *Malurus cyaneus*. *Journal of Animal Ecology*, **77**, doi: 10.1111/j.1365-2656.2007.01335.x.

Curio, E. (1983) Why do young birds reproduce less well? *Ibis*, **125**, 400–404.

Davies, N.B. & Hatchwell, B.J. (1992) The value of male parental care and its influence on reproductive allocation by male and female dunnocks. *Journal of Animal Ecology*, **61**, 259–272.

Dickinson, J.L. & Hatchwell, B.J. (2004) Fitness consequences of helping. *Ecology and Evolution of Cooperative Breeding in Birds* (eds W.D. Koenig & J.L. Dickinson), pp. 48–66. Cambridge University Press, Cambridge.

Double, M.C. & Cockburn, A. (2003) Subordinate superb fairy-wrens (*Malurus cyaneus*) parasitize the reproductive success of attractive dominant males. *Proceedings of the Royal Society of London B*, **270**, 379–384.

Dunn, P.O. & Cockburn, A. (1996) Evolution of male parental care in a bird with almost complete cuckoldry. *Evolution*, **50**, 2542–2548.

Dunn, P.O. & Cockburn, A. (1999) Extrapair mate choice and honest signaling in cooperatively breeding superb fairy-wrens. *Evolution*, **53**, 938–946.

Dunn, P.O., Cockburn, A. & Mulder, R.A. (1995) Fairy-wren helpers often care for young to which they are unrelated. *Proceedings of the Royal Society of London B*, **259**, 339–343.

Eguchi, K., Yamagishi, S., Asai, S., Nagata, H. & Hino, T. (2002) Helping does not enhance reproductive success of cooperatively breeding *Rufous vanga* in Madagascar. *Journal of Animal Ecology*, **71**, 123–130.

Emlen, S.T. (1995) An evolutionary theory of the family. *Proceedings of the National Academy of Sciences USA*, **92**, 8092–8099.

Forslund, P. & Pärt, T. (1995) Age and reproduction in birds: hypotheses and tests. *Trends in Ecology and Evolution*, **10**, 374–378.

Grafen, A. (1984) Natural selection, kin selection and group selection. *Behavioural Ecology: an Evolutionary Approach*, 2nd edn (eds J.R. Krebs & N.B. Davies), pp. 62–84. Blackwell Scientific Publications, Oxford.

Green, D.J., Cockburn, A., Hall, M.L., Osmond, H.L. & Dunn, P.O. (1995) Increased opportunities for cuckoldry may be why dominant male fairy-wrens tolerate helpers. *Proceedings of the Royal Society of London B*, **262**, 297–303.

Green, D.J., Osmond, H.L., Double, M.C. & Cockburn, A. (2000) Display rate by male fairy-wrens (*Malurus cyaneus*) during the fertile period of females has little influence on extra-pair mate choice. *Behavioral Ecology and Sociobiology*, **48**, 438–446.

Griffin, A.S. & West, S.A. (2003) Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science*, **302**, 634–636.

Hatchwell, B.J. (1999) Investment strategies of breeders in avian cooperative breeding systems. *American Naturalist*, **154**, 205–219.

Jamieson, I.G. & Quinn, J.S. (1997) Problems with removal experiments designed to test the relationship between paternity and parental effort in a socially polyandrous bird. *Auk*, **114**, 291–295.

Kokko, H., Johnstone, R.A. & Clutton-Brock, T.H. (2001) The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London Series B*, **268**, 187–196.

Komdeur, J. (1996) Influence of age on reproductive performance in the Seychelles warbler. *Behavioral Ecology*, **7**, 417–425.

Laaksonen, T., Korpimäki, E. & Hakkarainen, H. (2002) Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. *Journal of Animal Ecology*, **71**, 23–31.

Legge, S. (2000) The effect of helpers on reproductive success in the laughing kookaburra. *Journal of Animal Ecology*, **69**, 714–724.

MacGregor, N.A. & Cockburn, A. (2002) Sex differences in parental response to begging nestlings in superb fairy-wrens. *Animal Behaviour*, **63**, 923–932.

Magrath, R.D. & Yezerinac, S.M. (1997) Facultative helping does not influence reproductive success or survival in cooperatively breeding white-browed scrubwrens. *Journal of Animal Ecology*, **66**, 658–670.

Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J. & Possingham, H.P. (2005) Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters*, **8**, 1235–1246.

Marzluff, J.M. & Balda, R.P. (1990) Pinyon jays: making the best of a bad job by helping. In: *Cooperative Breeding in Birds* (eds P.B. Stacey & W.D. Koenig), pp. 199–237. Cambridge University Press, Cambridge.

Mauck, R.A., Huntington, C.E. & Grubb, T.C. (2004) Age-specific reproductive success: evidence for the selection hypothesis. *Evolution*, **58**, 880–885.

Mulder, R.A. (1995) Natal and breeding dispersal in a co-operative, extra-group-mating bird. *Journal of Avian Biology*, **26**, 234–240.

Mulder, R.A. & Langmore, N.E. (1993) Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour*, **45**, 830–833.

Mulder, R.A., Dunn, P.O., Cockburn, A., Lazenby-Cohen, K.A. & Howell, M.J. (1994) Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proceedings of the Royal Society of London B*, **255**, 223–229.

Mumme, R.L. (1992) Do helpers increase reproductive success: an experimental analysis in the Florida scrub jay. *Behavioral Ecology and Sociobiology*, **31**, 319–328.

Nevoux, M., Weimerskirch, H. & Barbraud, C. (2007) Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. *Journal of Animal Ecology*, **76**, 159–167.

Pärt, T. (2001) The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenanthe oenanthe*. *Animal Behaviour*, **62**, 379–388.

Pärt, T., Gustafsson, L. & Moreno, J. (1992) Terminal investment and a sexual conflict in the collared flycatcher (*Ficedula albicollis*). *American Naturalist*, **140**, 868–882.

Russell, A.F., Langmore, N.E., Cockburn, A., Astheimer, L.B. & Kilner, R.M. (2007) Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science*, **317**, 941–944.

Saether, B.-E. (1990) Age-specific variation in reproductive performance of birds. *Current Ornithology* (ed. D.C. Powers), Vol. 7, pp. 251–283. Plenum Press, New York.

Welsh, A.H., Cunningham, R.B., Donnelly, C.F. & Lindenmayer, D.B. (1996) Modelling the abundance of rare species: statistical models for counts with extra zeros. *Ecological Modelling*, **88**, 297–308.

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