Journal of Animal Ecology 2008, **77**, 430–438 doi: 10.1111/j.1365-2656.2007.01351.x

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*

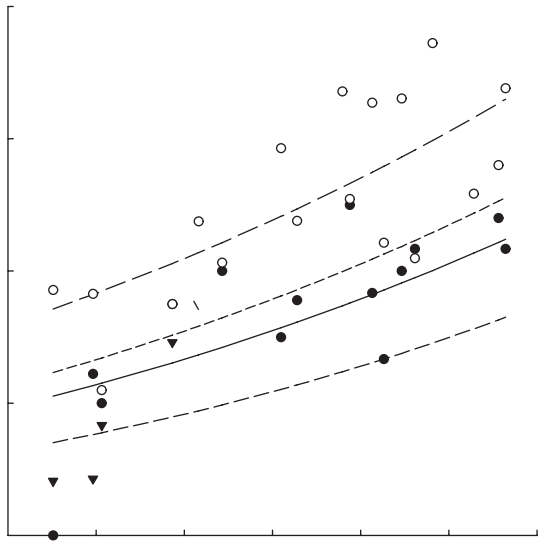
number of correlated weather variables returns similar results, albeit with slightly lower explanatory power. We tested age of the breeding female, presence of supernumeraries, spring rainfall and their interactions. We sequentially discarded nonsignificant terms ($P > 0{\cdot}05$) to obtain a parsimonious 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 Ge4itat7f (aWitd4)29(ws49606/Cs6 cs 0 0 0faly10348144-0.01 0.02sc5.6ca0.03 Tc [23.0.60a-0-348144-0.01 verараso9.oduc-87 715Timate betwee08ecutiveFina3

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**



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; $t = 0{\cdot}69$,

$P = 0{\cdot}33$). 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; $\chi^2 = 7{\cdot}0$, d.f. = 3, $P = 0{\cdot}07$; truncated Poisson effect; $F_{3,343} = 3{\cdot}48$, $P = 0{\cdot}02$). 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 $\chi^2 = 9{\cdot}5$, d.f. = 1, $P = 0{\cdot}002$), and where rainfall increased between years ($\chi^2 = 49{\cdot}2$, d.f. = 2, $P << 0{\cdot}001$). However, there was no effect of gain or loss of a supernumerary ($\chi^2 = 2{\cdot}6$, d.f. = 3, $P = 0{\cdot}45$), 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 $0{\cdot}48 \pm 0{\cdot}16$ SE. ($n = 154$) more young to independence in their second year of life (paired $t = 2{\cdot}97$, $P = 0{\cdot}003$), 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 $0{\cdot}63 \pm 0{\cdot}26$ SE ($n = 41$) young, or 46% (paired $t = 2{\cdot}41$, $P = 0{\cdot}02$).

Paired comparison tests on the effect of gaining or losing a supernumerary among older birds revealed that overall there was no effect ($-0{\cdot}31 \pm 0{\cdot}23$ SE; $n = 139$; paired $t = -1{\cdot}34$, $P = 0{\cdot}18$, 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 ($-0{\cdot}15 \pm 0{\cdot}41$ SE, $n = 54$, paired $t = -0{\cdot}35$; $P = 0{\cdot}73$).

SURVIVAL EFFECTS

It is also possible that the primary benefit of the presence of a supernumerary occurs through load-lightening, which

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 (eed a)22(gain had)]T
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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.