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Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird

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In many species mature individuals delay independent reproduction and may help others to reproduce. This behaviour is often explained through ecological constraints, although recently attention has also been paid to the variation in habitat quality. If the quality of vacant habitat influences the fitness trade-off between delaying reproduction and breeding independently, individuals should delay reproduction when conditions for breeding are poor. Yet, no study has experimentally manipulated habitat quality or the conditions experienced during the breeding period to test this assertion conclusively. We report results from an experiment conducted on a colonial cooperative bird with no territory constraints on reproduction. We artificially improved breeding conditions in several colonies of sociable weavers, *Philetairus socius*, through the provision of an easily obtainable and unlimited supply of food. We provide experimental evidence showing that under enhanced conditions some individuals reduce their age at first reproduction, a greater proportion of colony members engage in independent breeding and proportionally fewer birds act as helpers. Hence, these results also provide evidence for a direct influence of reproductive costs on life-history decisions such as age at first reproduction and breeding and helping behaviours.

Keywords: age of first reproduction; cooperative breeding; deferred reproduction; delayed dispersal; food supplementation; habitat quality

1. INTRODUCTION

The age at first reproduction varies widely within and between species (Stearns 1992). Understanding the factors leading to delayed onset of reproduction is particularly important in group-living species since delayed reproduction is considered to be the first step in the evolution of cooperative breeding. First, mature individuals forgo independent breeding. Then, if they remain in the natal territory, conditions allow them to engage in helping (Koenig & Pitelka 1981; Emlen 1982, 1991; Brown 1987). In cooperative breeders, delayed reproduction was initially mainly explained through the ecological-constraints (Koenig & Pitelka 1981; Emlen 1982, 1991; Brown 1987) or benefits-of-philopatry (Stacey & Ligon 1987) hypotheses. However, in a landmark paper published in 1992, Koenig *et al.* combined the two approaches by presenting correlative evidence suggesting that variation in breeding conditions and the associated cost and output of reproduction influence individual decisions regarding whether to delay dispersal or breed independently.

If the cost and likelihood of successful breeding vary in space and time, individuals may delay dispersal and/or independent breeding in response to either the poor quality of available territories, or the severity of the breeding conditions. Some studies have shown that delayed reproduction may ultimately yield higher lifetime reproductive success than breeding in low-quality territories (Stacey & Ligon 1987; Ekman *et al.* 1999, 2001) or when conditions are poor (MacColl & Hatchwell 2002). These results suggest that the cost of breeding under poor conditions could play a role in explaining delayed dispersal or reproduction in cooperative species. However, current evidence of a link between breeding conditions and the decision to breed or to help is only correlative and hence cannot be used to reject alternative hypotheses.

In territorial species, this issue is complicated by the fact that becoming a breeder is necessarily associated with losing the important benefits of remaining in the natal territory (Ekman *et al.* 1999, 2000; Green & Cockburn 2001). By comparison, colonial species, where breeding status can be obtained in the natal colony, present opportunities to control for the effects of dispersal. In contrast to territorial birds, most individuals in a colony have access to nesting sites and experience similar environmental conditions, and dispersal is not a prerequisite for acquiring breeding status. Thus, colonial birds are not necessarily exposed to the risks commonly associated with dispersal, which have been suggested to have a strong influence on the reproductive decisions that are taken by territorial cooperatively breeding birds (e.g. du Plessis 1992).

To investigate the importance of environmental conditions in the decision of whether to breed or help, we manipulated conditions during two breeding seasons in a colonial cooperative bird, the sociable weaver, *Philetairus socius*, by providing an unlimited amount of food under the nest. These weavers are relatively long-lived passerines (sometimes in excess of 10 years; *ca.* 66% annual survival; Covas *et al.* 2002) that inhabit communal thatched nest masses of up to 6 m across, wherein they nest and roost

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throughout the year (Maclean 1973*b*; Covas *et al.* 2002). Contrary to what is expected under the life-history hypothesis (Russell 1989; Arnold & Owens 1998), relatively high longevity in this species does not lead to habitat or nest-site saturation. The colonies often have vacant chambers, and the weavers continuously add material to the nest mass, thus nest sites do not appear to limit independent breeding (Covas 2002; R. Covas and C. Doutrelant, personal observation). Birds frequently become breeders in their natal colony (more than 60%; Covas 2002). Further, availability of mates apparently is not limiting, since the sex ratio in the population does not deviate from parity (Doutrelant *et al.* 2004). Nevertheless, sociable weavers rarely engage in reproduction in the first 2 years of life and will commonly remain with their parents as helpers-at-the-nest, although most colonies also have a variable percentage of non-breeding floaters (up to 30%; Covas 2002).

If factors affecting breeding conditions influence reproductive decisions (Koenig *et al.* 1992), we predicted that colonies that received supplemental food would have: (i) a higher proportion of the colony members breeding; (ii) fewer helpers per nest (as potential helpers would engage in independent reproduction); and (iii) a lower age at first breeding. Our results verify these predictions, thus confirming the importance of breeding conditions for reproductive decisions.

2. MATERIAL AND METHODS

(a) *Study area and species*

The sociable weaver is a colonial, cooperatively breeding passerine endemic to the semi-arid savannahs of southern Africa (Maclean 1973*a*; Mendelsohn & Anderson 1997). Sociable weavers weigh *ca.* 28.5 g, and the sexes are indistinguishable in the field. They feed on insects, seeds and other plant products (Maclean 1973*c*). These weavers build very large communal nests, usually in *Acacia erioloba* trees, in which they roost and breed. The nest mass is maintained and occupied by the whole colony throughout the year. Sociable weavers inhabit a highly fluctuating environment where rainfall has a strong impact on reproduction, influencing clutch size, fledging success and the duration of the breeding season (leading to up to nine continuous months of breeding in a good-rainfall year, or no breeding in a dry year; Covas *et al.* (2002). Nest predation is the main cause of reproductive failure, with more than 70% of the clutches falling prey to snakes (Covas 2002). The proportion of nests with helpers may vary greatly between years. In our study population, *ca.* 30% of nests had one or two helpers in the first season, while in the second season 82% of the nests had between one and three (exceptionally four or five) helpers (Covas 2002). Helpers are mainly offspring of previous years, but unrelated birds may also help (Covas 2002; Doutrelant *et al.* 2004). One-year-old helpers may be male or female, but older or unrelated helpers are normally male (Doutrelant *et al.* 2004). Microsatellite analyses suggest that these helpers do not contribute to genetic paternity (C. Doutrelant, R. Covas, A. Caizergues and M. du Plessis, unpublished data). In addition, most colonies also have a variable percentage of floaters (Covas 2002).

The food-supplementation experiment was conducted during the breeding seasons of September 1999–April 2000 and September 2000–January 2001. These two seasons experienced contrasting rainfall conditions, with totals of 525 mm in the first year (25% above average rainfall) and 360 mm in the second year (20% below average rainfall), resulting in conspicuous differences in both reproductive effort and success (Covas 2002). The study took place at Benfontein Game Farm near Kimberley in the Northern Cape Province, South Africa. The study site comprises open *Acacia* savannah dominated by *Stipagrostis* grass. The area supports approximately 24 sociable weaver colonies, each comprising 10–200 birds. The birds in 15–20 of these colonies have normally been captured and ringed twice every year since 1993, and since 1998 all fledglings and adults have been ringed with unique colour combinations (see Covas *et al.* 2002), including a specific colour for each colony to help to identify immigrants.

(b) *Food-supplementation experiment*

Food-supplemented colonies were provided with a daily portion of mixed canary seed (millet and red rape) throughout the breeding season. Feeding stations were replenished early every morning with 0.5–1.5 kg of seed, depending on colony size, to provide an unlimited supply of food. The seed was scattered on the ground under the colonies and was readily taken by the birds. Colonies were randomly divided into treatments (i.e. food supplemented: eight colonies of 37 ± 40 individuals; number of colonies, $n = 10$) and controls (10 colonies of 39 ± 19 individuals; $n = 8$). Each colony was used only once in the experiment, i.e. a colony that was used as either a control or a treatment in the first year was excluded from the experiment altogether in the second year. Colony size was determined by mist-netting at the beginning of each season (Covas *et al.* 2002) and no significant immigration occurred afterwards (see § 3). All colonies were visited every 4–7 days, and nest contents were inspected for the initiation of new clutches. The nests were marked with plastic sheep ear-tags with an individual number. Hides were placed 2–5 m away from colonies to allow observation for a total of 2–6 h over several days, to identify the colour rings of all individuals attending a given nest, and to locate any immigrants. The proximity of the hides did not hinder birds from continuing with their normal activities.

(c) *Statistical methods*

We used backwards deletion models in GLIM 3.77. Normally distributed variables (adult and yearling body masses) were analysed using general linear modelling. Proportion data (proportion of birds breeding per colony) were analysed assuming a binomial distribution. Helper numbers, which had a Poisson distribution, were analysed with PROC GENMOD in SAS v. 8, also using backwards deletion. The following explanatory variables were included in all models: ‘treatment’ (control or food supplemented), ‘year’ (1999 or 2000), ‘colony size’ and the interaction ‘treatment × colony size’. A final model was selected after sequentially excluding all non-significant terms, with the significance of terms being determined by the change in deviance after the term was removed from the model. To analyse differences in yearling breeding activity between control and food-supplemented colonies we used Fisher’s exact test, which deals with the zero-cell phenomenon (Siegel & Castellan 1988). Possible differences in immigration into control and food-supplemented colonies were analysed using a χ^2-test.

3. RESULTS

Both adult and yearling body masses were higher in food-supplemented colonies than in control colonies in

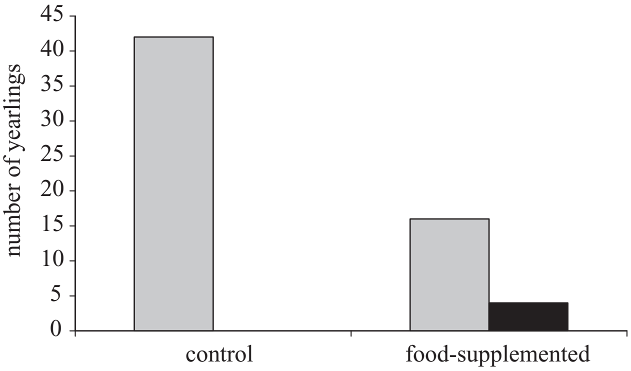

Figure 1. Yearlings' breeding activity in control and food-supplemented colonies. The food supplementation caused a significant increase in the number of 1-year-olds breeding. Grey bars, did not breed; black bars, bred.

Table 1. Generalized linear model of the factors associated with the proportions of birds breeding in control and food-supplemented colonies.
(The analyses were conducted on 18 colonies over two breeding seasons.)

model term	χ^2	d.f.	p
treatment	9.850	1	0.002
year	0.326	1	0.57
colony size	0.049	1	0.82
treatment × year	2.956	1	0.09

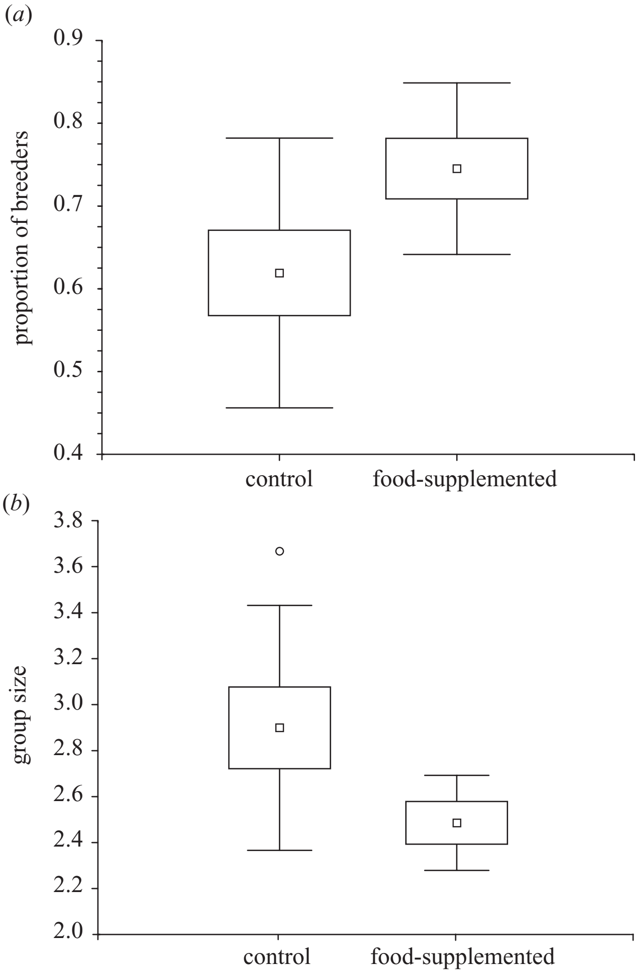

Figure 2. Variations in (*a*) the proportion of breeders and (*b*) the average group size (number of birds attending a nest) in response to the food-supplementation experiment. Small squares denote means, boxes denote standard errors and vertical lines denote standard deviations. The circle is an outlier.

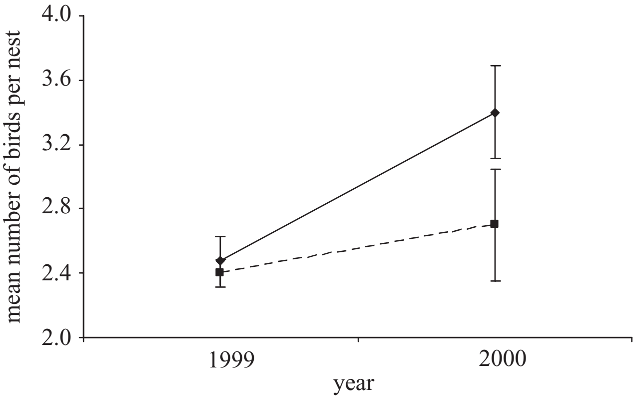

Figure 3. Average group sizes in control (diamonds; solid line) and food-supplemented (squares; broken line) colonies in 1999 and 2000. There was a significant interaction between treatment and year, with a stronger effect of food supplementation in 2000, when the number of nests with helpers in the population was higher (see § 3).

the drier year (interaction of treatment and year: adults $F = 11.53$, d.f. = 1,352, $p < 0.001$; yearlings $F = 8.75$, d.f. = 1,84, $p = 0.004$), indicating a positive effect of food supplementation on body condition.

Food supplementation resulted in a significant increase in the breeding activity of 1-year-old birds: four out of twenty yearlings (20%) bred in food-supplemented colonies, whereas none did so in the control colonies ($n = 42$) (Fisher's exact test: $p = 0.009$; figure 1). One of these yearlings was helping at its parents' nest at the beginning of the season; the other three were presumably floating. Two of these birds paired with resident birds and two with immigrants. The proportion of birds breeding (maximum number of birds breeding in a colony in a given year divided by the total number of birds present in the colony during that year) increased in food-supplemented colonies (binomial model: $\chi^2 = 9.85$, d.f. = 1, $p = 0.002$; table 1). Factors 'year' and 'colony size' were non-significant. There was, however, a non-significant tendency for the proportion of birds breeding in control colonies in the second year to decrease, presumably reflecting the drier conditions experienced that year (interaction of 'treatment' with 'year': $\chi^2 = 2.956$, d.f. = 1, $p = 0.09$). The increase in breeding activity in food-supplemented colonies was not caused by immigration, since immigration into treatment colonies was identical to that into control colonies ($\chi^2 = 0.69$, d.f. = 1, $p = 0.79$; power = 1; Faul & Erdfeler 1992). The number of helpers per nest was lower in food-supplemented colonies ($F = 11.89$, d.f. = 1,10, $p = 0.006$; figure 2*b* and table 2). This effect was particularly strong in the second year of manipulation (interaction between treatment and year: $F = 8.06$,

Table 2. Generalized linear model of the factors associated with the mean group size in control and food-supplemented colonies.
(The analyses were conducted on 14 colonies over two breeding seasons. The data were corrected for underdispersion by using the DSCALE option in PROC GENMOD (SAS v. 8), which fixes the scale parameter at a value of 1 in the estimation procedure.)

model term	*F*	d.f.	*p*
treatment	11.89	1,10	0.006
year	18.14	1,10	0.002
colony size	0.03	1,10	0.874
treatment × year	8.06	1,10	0.018

d.f. = 1,10, $p = 0.018$; figure 3) when there were more helpers in the population owing to the generally high production of young allowed by the good conditions experienced in the previous year. In 1999 only 30% of nests had helpers compared with 80% in 2000 ('year' effect on group size: $F = 18.14$, d.f. = 1,10, $p = 0.002$). Thus, group size increased less sharply in food-supplemented than in control colonies.

4. DISCUSSION

Our results provide compelling experimental evidence that variation in breeding conditions affects reproductive decisions, including age of first reproduction. Food supplementation resulted in an increase in the number of birds breeding, a reduced number of helpers and increased yearling breeding activity. The influence of breeding conditions (or habitat quality) on the decision of whether or not to breed has been strongly suggested by correlative studies, but we are aware of no other study that has confirmed this link experimentally.

Breeding conditions also affected helping behaviour, since the average number of birds attending a nest decreased in food-supplemented colonies. This was particularly true in the second year, when group size increased markedly in control but not in food-supplemented colonies. Although the increase in the number of breeders would lead us to expect a decrease in the number of helpers, this might not be inevitable, since most colonies have a variable percentage of floaters (Covas 2002), which should be at least as likely to respond to the food supplementation as are the helpers. Nevertheless, the lower number of helpers in food-supplemented colonies suggests that at least some of the extra breeders would normally have acted as helpers.

Sociable weavers inhabit a highly variable environment, and the numbers of breeders and helpers fluctuate naturally between years, with higher numbers of birds breeding in years of good rainfall. However, under natural conditions, even in a year of above-average rainfall, breeding by yearlings remained extremely rare (0.6%; $n = 164$; Covas 2002). This indicates that food levels alone are not sufficient to explain variations in breeding behaviour. In fact, in addition to providing an energy supplement, our experiment also reduced the energetic costs and survival risks associated with foraging. This assertion was supported by a reduction in the time spent away from the colony (R. Covas and C. Doutrelant, unpublished data) and an increase in adult and yearling body masses in the drier year. Thus our experiment contributed to a general facilitation of the reproductive process. This is likely to have a positive influence on breeding decisions of potential breeders by lowering the overall cost of reproduction. Hence, our results provide experimental support for a link between reproductive costs and breeding decisions, in agreement with life-history theory (Williams 1966; Stearns 1992; Charlesworth 1994) and correlative studies (Emlen 1990; Koenig *et al.* 1992; Komdeur *et al.* 1995; Ekman *et al.* 2001; MacColl & Hatchwell 2002). In addition, we show that these costs may also influence the expression of helping behaviour. These results may explain why a number of species will delay independent reproduction and engage in helping at the nest when only poor-quality habitat is available (e.g. Komdeur *et al.* 1995; Macedo & Bianchi 1997) or when breeding conditions are poor (Emlen 1990; MacColl & Hatchwell 2002). However, they also raise the question of why delayed reproduction and helping behaviour are restricted to a particular set of species when in fact most species experience variation in breeding conditions.

Cooperative breeders are most common in the tropics and Southern Hemisphere (Arnold & Owens 1999; Cockburn 2003), where survival of passerines is typically higher and fecundity lower (Lack 1968; Ghalambor & Martin 2001). This life-history pattern has led to the hypothesis that long occupancy of suitable territories leads to slow territory turnover and thus promotes delayed dispersal and reproduction in these species (the life-history hypothesis; Russell 1989; Arnold & Owens 1998). Several recent models that explore the evolution of delayed dispersal are based on this premise (Pen & Weissing 2000; Kokko & Lundberg 2001), even though delayed reproduction and cooperative breeding also occur in species with no spatial constraints on reproduction (Emlen 1990; Baglione *et al.* 2002*a*,*b*; Covas 2002).

It is possible to envisage an alternative explanation to the high-survival-leads-to-habitat-saturation hypothesis, *viz.* species with high survival may be more likely to defer breeding. It has been shown that, in species with low fecundity and high longevity, even a small reduction in survival may lower the number of breeding attempts in life, thus considerably reducing lifetime reproductive success (Goodman 1974; Clutton-Brock 1988; Charlesworth 1994). As a corollary of this, it has recently been shown that when faced with an artificial life-threatening risk during reproduction, individuals from species with high survival and low fecundity reacted by changing their behaviour to reduce risks to themselves, whereas individuals from low survival–high fecundity species would expose themselves to a higher risk to decrease the risk to their offspring (Ghalambor & Martin 2001; Martin 2002). Reducing the risks associated with breeding activity might be particularly important for young individuals for two reasons: they probably incur disproportionately high costs of breeding through reduced survival, as suggested in two recent studies (Tavecchia *et al.* 2001; Orell & Belda 2002), and they may experience comparatively lower reproductive output (Green 2001; Magrath 2001). Thus, long-lived cooperative (or non-cooperative) species should be particularly reluctant to breed in suboptimal habitats or under suboptimal conditions, as indicated by several correlative studies (Emlen 1990; Koenig *et al.* 1992; Komdeur *et al.* 1995; Frederiksen & Bregnballe 2001; Ekman *et al.* 2001). This hypothesis is supported by our results in sociable weavers: in a species with no spatial constraints on breeding, when the overall costs of reproduction were reduced by the provision of an easily obtainable food supplement, we were able to lower their age at first independent breeding and to increase the proportion of individuals breeding in any given season.

Hence, delayed reproduction in long-lived cooperative species may be a selected life-history trait and not only a proximate response to habitat saturation or quality (see also Langen 2000). From this standpoint, habitat quality or environmental constraints should play an important role at the proximate level, but species' survival prospects should determine the threshold required for breeding. This should be expected regardless of whether the species is a cooperative or pair breeder. In fact, reproductive decisions of cooperative and non-cooperative birds have largely been studied separately, while life-history trade-offs are common to all species. This leaves us with another unanswered question: why has cooperative breeding not evolved more often among other long-lived groups? For example, in the tropics survival is typically high and the climate is relatively invariable, allowing the maintenance of year-round territories. However, these species seem to be predominantly pair rather than cooperative breeders. Cockburn (2003) might well be justified in stating that the issue of why some clades develop into pair breeders and others into cooperative groups may require a new theory.

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