

Life-history traits as causes or consequences of social behaviour: why do cooperative breeders lay small clutches?

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ABSTRACT

Cooperatively breeding birds tend to exhibit high adult survival and relatively small clutch sizes. According to the life-history hypothesis for cooperative breeding, high survival creates conditions for philopatry based on difficulties that dispersers face when competing for territories in a landscape with slow territory turnover. However, this hypothesis evokes a puzzle because high fecundity should also lead to problems in territory acquisition because of the large number of competitors for each vacancy. We suggest two reasons for the observed association between small clutch size, high survival rate and cooperative breeding in birds. The first reason is that when survival rate is a better predictor of cooperative breeding than fecundity, a general life-history trade-off between clutch size and survival rate will create the observed association between cooperative breeding and the two life-history characters. Theoretically, a high survival rate is expected to predict cooperative breeding better than fecundity, because a high survival rate increases both habitat saturation and the direct benefits of staying at home. The second reason is that the reproductive value of the first offspring each year is higher than that of subsequent offspring for cooperative breeders (the offspring depreciation hypothesis). This is because these offspring will be able to delay dispersal and gain indirect benefits by helping at home. We show that this, under very general conditions, decreases the optimum clutch size of cooperative breeders below that of non-cooperative breeders.

Keywords: cooperative breeding, clutch size evolution, life-history hypothesis, life-history trade-off, offspring depreciation, survival rate.

INTRODUCTION

In cooperatively breeding birds, not only do parents provide care for the offspring, but also a number of helpers. These helpers are often genetically related to the breeders and are frequently retained offspring (Emlen, 1991; Cockburn, 1998), which delay dispersal to

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remain in the natal territory and to help their parents raise other broods. The reasons for cooperative breeding are still unclear. Empirical studies have focused on ecological explanations for delayed dispersal. Constraining factors such as habitat saturation may limit the opportunities for independent breeding and make delayed dispersal a better option for the young (e.g. Emlen, 1997). Alternatively, the 'benefits of philopatry' theory emphasizes the delayed benefits of staying – for example, inheritance of the territory once the parents are dead (Stacey and Ligon, 1987, 1991). For both alternatives, the benefit of staying at home must exceed the benefit of dispersing, and they can be viewed as 'two sides of the same coin' (Koenig *et al.*, 1992; Komdeur, 1992).

Even though constrained access to breeding habitat clearly influences dispersal decisions, there are several problems with purely habitat-based explanations of cooperative breeding. First, cooperative breeding is not randomly distributed in terms of phylogeny (Russell, 1989; Cockburn, 1996; Arnold and Owens, 1998), suggesting that current ecological conditions cannot fully explain the evolution of cooperative breeding. For example, in Australia, where cooperative breeding is common among birds, it is predominantly exhibited by the Corvida – a clade that originates in Australia – but not by the Passerida, which secondarily invaded Australia (Russell, 1989; Cockburn, 1996). Moreover, species belonging to the Corvida have often retained their cooperative habit outside Australia (Cockburn, 1996). Second, many non-cooperative breeders live in saturated habitats with intense competition for breeding opportunities (Brown, 1969, 1987; Heinsohn *et al.*, 1990; Hatchwell and Komdeur, 2000). Habitat saturation, therefore, becomes a satisfactory explanation of behaviour only if we understand why it arises in a given species and how it influences individual dispersal options. These factors depend on the life history of a species (Kokko and Lundberg, 2001). Consequently, life-history characters have recently attracted attention as determinants of social behaviour (Arnold and Owens, 1998; Hatchwell and Komdeur, 2000; Pen and Weissing, 2000; Kokko and Lundberg, 2001).

Both theory (Pen and Weissing, 2000; Kokko and Lundberg, 2001) and comparative data (Arnold and Owens, 1998) indicate that low adult mortality predisposes species to become cooperative. If adult mortality is low, vacancies become scarce and hence constraints for independent breeding become tighter (Hatchwell and Komdeur, 2000; Kokko and Lundberg, 2001). For helpers, the value of attaining breeder status in the future may also be higher with low adult mortality, as they can then count on a higher lifetime reproductive success once they become breeders (Pen and Weissing, 2000). Furthermore, if offspring mortality is low, the young can expect to survive even a long wait for a vacant territory, which increases the incentive to stay (Rowley and Russell, 1990; Kokko and Johnstone, 1999).

Here we focus on a puzzle inherent in the life-history hypothesis, a puzzle that has, in our view, not been fully appreciated in the field. If the life-history hypothesis functions by making it difficult for juveniles to acquire breeding positions, high fecundity should predispose species to become cooperative and, similarly, to low adult mortality. This is because high fecundity means that there are more competitors for each vacancy, which decreases the opportunities for independent breeding just as much as a long lifespan of the breeders (Pen and Weissing, 2000; Kokko and Lundberg, 2001). However, cooperative breeding in birds is not associated with large clutch sizes, whereas there is a strong association with long lifespan (Arnold and Owens, 1998; Geffen and Yom-Tov, 2000). Furthermore, phylogenetic data also suggest that a cooperative breeding habit precedes an evolutionary reduction in clutch size, so there may be a causal relationship between

behaviour and life-history characters (Arnold and Owens, 1998). Here, we discuss two reasons why cooperatively breeding birds often have small clutches, contrary to the predictions of recent life-history theory (Kokko and Lundberg, 2001). One relates to clutch size evolution before the transition to cooperative breeding takes place; the other relates to clutch size evolution after the transition.

HOW DOES CLUTCH SIZE EVOLUTION INTERACT WITH THE EVOLUTION OF COOPERATIVE BREEDING?

Here, we discuss two mechanisms that predict smaller clutch sizes in cooperative breeders. The first applies before the evolutionary transition to cooperative breeding, by determining which species are predisposed to become cooperative. The second considers clutch size evolution after the transition to cooperation.

Clutch size evolution before the transition to cooperation: across-species life-history trade-offs

The models of Pen and Weissing (2000) and Kokko and Lundberg (2001) derive conditions under which philopatry and cooperation should evolve. In populations limited by territory availability, an increasing density of individuals implies fewer opportunities for dispersers to find vacancies (if philopatric individuals have priority over local resources; see Kokko and Ekman, 2002). Thus, without prior knowledge of the life-history characteristics of cooperatively breeding species, we might predict as strong an association between high fecundity and cooperative habits as that between high adult survival and cooperation. However, in their data set of cooperative breeding birds, Arnold and Owens (1998) found a significant association between survival and the transition to cooperation, but effects on clutch sizes were less clear. There was no association between changes in clutch size and changes in the proportion of cooperative breeders in a family, although there were signs that cooperative breeding leads to a subsequent reduction in clutch size (Arnold and Owens, 1998). Consequently, discussions of the life-history hypothesis have characteristically focused on the effects of long lifespan, which is the trait that shows a clearer association with cooperation (e.g. Hatchwell and Komdeur, 2000).

Across taxa, there is good evidence for trade-offs between fecundity and survival (Stearns, 1992). If both are equally good predictors of cooperative breeding, we would expect no clear covariation between survival and cooperative breeding, or between fecundity and cooperative breeding (area A in Fig. 1). But if high adult survivorship is a stronger selective factor for cooperative breeding than high fecundity, cooperation will evolve in families with highest adult survival. These will then have the lowest clutch sizes because of the general across-species trade-off between survival and fecundity (area B in Fig. 1).

Recent theoretical developments suggest that high survival can indeed promote cooperation more strongly than high fecundity. High survival has a twofold effect on cooperative breeding. First, as discussed above, it increases habitat saturation (Arnold and Owens, 1998; Hatchwell and Komdeur, 2000; Pen and Weissing, 2000; Kokko and Lundberg, 2001). This is an effect that high survival shares with high fecundity. Second – and importantly because this benefit does not apply for high fecundity – high survival also increases the direct benefits of waiting at home. A long lifespan enables prolonged mutualistic associations

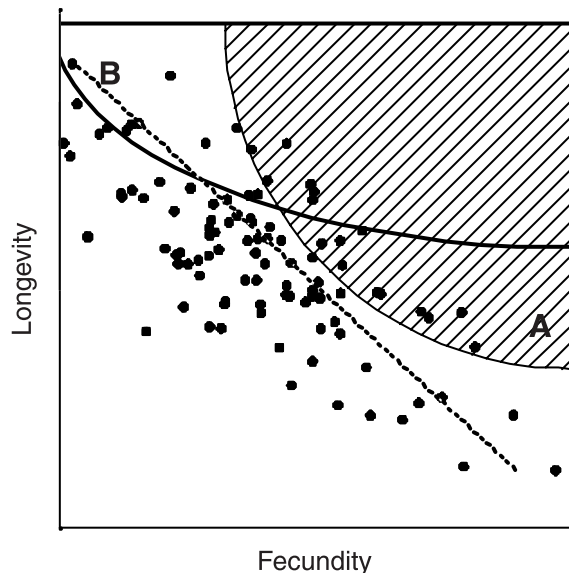


Fig. 1. Hypothetical data for several species showing a trade-off between fecundity and longevity (dotted line). If high fecundity and longevity were equally important predictors of cooperative breeding, cooperative breeding would mainly occur in species within the region A. If, however, longevity predisposes species to become cooperative more strongly than high fecundity, the spectrum of clutch sizes that favours cooperation is much wider in long-lived species (region B). Consequently, points (species) that are predisposed to become cooperative (i.e. fall inside B) tend to be ones with low fecundity.

among kin that improve the chances that a retained offspring survives to obtain a breeding vacancy (Brown, 1987; Ekman *et al.*, 2001). High survival also increases the importance of territory inheritance, so that waiting for one or a few breeding attempts is not a prohibitive cost on lifetime reproductive success (Rowley and Russell, 1990; Kokko and Johnstone, 1999; Ragsdale, 1999). Also, once breeder status has been attained, the reproductive values of breeders are relatively higher in species with longer lifespans (Pen and Weissing, 2000).

Naturally, such effects must always be checked for corresponding increases in the success of dispersers; for example, if survival increases equally in dispersers and philopatric offspring, and if local density does not influence the relative competitiveness of either type of individual when competing for vacancies, lifespan does not necessarily correlate with philopatry (Kokko and Ekman, 2002). Nevertheless, the above list provides a multitude of mechanisms that could account for the pattern in Fig. 1: a combination of stronger importance of lifespan than fecundity on philopatry, and a trade-off between fecundity and survival, predicts that cooperative breeding will tend to evolve in families with small clutch size.

Clutch size evolution after the transition to cooperation: within-species life-history trade-offs

Whether or not a species breeds cooperatively, the fitness gain from offspring does not increase linearly with clutch size. This can be the result of many factors, including food

limitation, which lowers survival of offspring that fledge from large broods (Pettifor *et al.*, 2001). This leads to a concave-down relationship between clutch size F and the reproductive value $v(F)$ of each egg laid. If we model fitness simply as a sum of each year's reproductive value of offspring, then a parent with lifespan $L(F)$ will have fitness $L(F)v(F)F$.

In cooperative breeders, the expression for fitness can become modified in additional ways. For many reasons, the benefits of staying as a helper are not equally large for all retained offspring. For example, breeding success per helper is often highest in small breeding groups (e.g. Walters, 1990; Woolfenden and Fitzpatrick, 1990; Langen and Vehrencamp, 1999). The future prospects of attaining breeder status also decrease for lower-ranking helpers (Field *et al.*, 1999). More generally, it is natural to expect that the reproductive value of dispersers is lower than that of the offspring which stay (Kokko and Lundberg, 2001; Kokko and Ekman, 2002; Ridley and Sutherland, 2002).

Under these conditions, the fitness gain from the first few offspring annually produced – who will be able to delay dispersal – will be higher than the fitness gain from subsequent offspring. Everything else being equal, therefore, the fitness gain from fecundity (F) increases steeply at low values of F and then at a lower rate as additional offspring have to disperse to become floaters or join low-ranking positions in other groups. This is called 'offspring depreciation' by Ridley and Sutherland (2002). For a non-cooperative breeder, the gain should not increase as steeply at low values of F , as these offspring disperse and do not interact with each other. We illustrate this using the following model.

Assume that the value of a brood of size F equals $v(F)F$ in a non-cooperative breeder, as before. For a cooperative breeder, we introduce a rank factor f_r , which additionally modifies the success of offspring according to their rank r , so that the fitness gain from the first few offspring – who can choose their preferred option, disperse or stay at home – is steeper than that of the last offspring from a large brood. The rank factor f_r therefore decreases with r , but for our argument it is unimportant whether this is interpreted as a higher value of first offspring in cooperative breeders compared with non-cooperative breeders (first offspring enjoy philopatric benefits; $f_r > 1$ for small r) or a lower value of offspring from large broods (dispersing offspring are constrained; $f_r < 1$ for large r). For our argument, it is sufficient that f_r decreases with rank – that is, philopatric offspring are, within a species, better off than dispersing offspring.

The fitness to be maximized is the product of the parent's lifespan L and the value of its annual offspring production. This holds true regardless of how density dependence shapes the future of offspring, as long as increasing density affects each offspring equally (Kokko and Ekman, 2002). Fitness thus equals $L(F)v(F)F$ for non-cooperative breeders and $L(F)v(F)\sum_{r=1}^F f_r$ for cooperative breeders.

Therefore, everything else being equal, the relatively high value of the first few offspring for cooperative breeders means that they will have an optimal clutch size equal to or smaller than that of the non-cooperative breeders (Fig. 2).

The results shown in Fig. 2 hold independently of two additional variations. First, arguing that the overall value of offspring is lower in cooperative species (e.g. because they obtain breeding positions rarely) or, alternatively, higher (e.g. because alloparenting increases chick survival rate) than in non-cooperative species, only means that all the f_r are multiplied by the same factor (compare curves C_1 and C_2 in Fig. 2a). This merely scales the y axis of Fig. 2 and hence has no effect on the solution of optimal clutch size (Fig. 2b; see also Pen and Weissing, 2000, on the scaling of offspring values in cooperative breeders). Second, help may lighten the load of parents so that they may achieve a higher longevity for

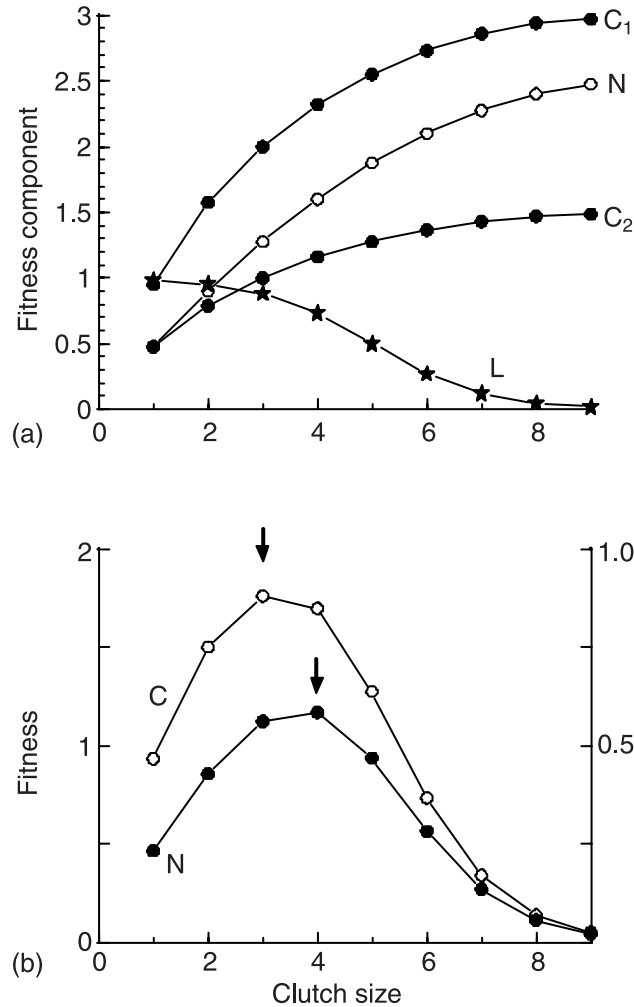


Fig. 2. Selection towards smaller clutch sizes in cooperative breeders. (a) The first few offspring produced have a higher reproductive value than the rest in cooperative breeders, whereas each surviving offspring is equally valuable in non-cooperative breeders. Hence, the relation of fitness gain is more concave-down in cooperative breeders (C_1 or C_2) than in non-cooperative breeders (N). The figure also shows a hypothetical relationship between clutch size and longevity (L) of the parent that cares for the clutch. (b) Fitness, $LFv(F)$ (for non-cooperative breeders) or $Lv(F)\sum f_r$, for the examples in (a), showing that the optimal clutch size (marked with arrow) is lower for the cooperative breeder, C, than the non-cooperative breeder, N. Solutions for both C_1 and C_2 are indicated by the curve C, with the axis on the left giving values for C_1 and the axis on the right giving values for C_2 . This shows that the reduction in optimal clutch size under cooperation only depends on the concave-down versus linear shapes in (a) and not on the absolute value of offspring. Parameters used to produce the examples: $v(F) = 0.5 - 0.025F$; $f_r = 2, 1.5, 1.2, 1.1$ for $r = 1, 2, 3, 4$; and $f_r = 1$ for $r \geq 5$ for species C_1 . For species C_2 , each f_r equals 50% of the corresponding value for species C_1 . Longevity equals $L(F) = 1 - \{1 + \exp[-(F - 5)]\}^{-1}$.

a certain clutch size (Crick, 1992; Hatchwell, 1999). If help increases longevity with the same factor independent of clutch size, helping again merely scales the y axis and does not alter the optimal solutions.

If fecundity F is treated as a continuous variable, we could build the following generalized model, which shows that our argument holds for a very general class of longevity–fecundity relationships $L(F)$, offspring values $v(F)$ and rank functions f_r . Let $L(F)$ be longevity as a continuous function of fecundity F . Let another continuous function $g(F)$ correspond to the fitness gain from producing F offspring [$g(F)$ thus replaces the sum $v(F) \sum_{r=1}^F f_r$ for cooperative breeders, or $v(F)F$ for non-cooperative breeders]. The value function of a cooperative breeder ($g_C(F)$) should be more concave-down than the value function of a non-cooperative breeder ($g_N(F)$), because of the different reproductive value of helpers and dispersers, which gives $g_C(F)$ a steeper increase at low values. We can use a modifier function $a(F)$ to describe this, and write $g_C(F) = g_N(F)a(F)$, where $a(F)$ is a function for which $a(F) > 0$ and $da/dF < 0$. $a(F)$ must be chosen so that $g_C(F) < F$. Optimal fecundity of a non-cooperative breeder obeys $d(g_N L)/dF = 0$; we use F_N^* to denote the value of F that satisfies this condition. For the cooperative breeder, the corresponding optimal fecundity F_C^* must satisfy

$$da/dF g_N L + a(F) d(g_N L)/dF = 0 \quad (1)$$

As da/dF is negative, the second term of the left-hand side of equation (1) must be positive at the equilibrium. Since $a(F) > 0$, we also have $d(g_N L)/dF > 0$ at $F = F_C^*$. This implies that the optimum for the cooperative breeder has a fecundity value F_C^* at which the non-cooperative breeder would still benefit from an increase in fecundity. Hence, a cooperative breeder should, under very general conditions, be less fecund than a non-cooperative breeder.

DISCUSSION

We have suggested two reasons why cooperative breeders tend to have small clutch sizes, despite the theoretical prediction that high fecundity should make competition for breeding sites more intense. First, theory predicts that both fecundity and high survival can promote cooperation, but high survival does that more strongly. Bearing across-species life-history trade-offs in mind, this means that cooperative species tend to be those that have high survival and, consequently, small clutch sizes.

Second, even if certain species are not predisposed to cooperative breeding by virtue of their life history, the transition to social behaviour may have further repercussions on optimal clutch sizes. Offspring may delay dispersal because it is difficult to obtain a breeding position elsewhere (Emlen, 1997); because being a helper brings about indirect fitness benefits superior to direct fitness obtained elsewhere (Komdeur, 1994a); because staying at home improves survival and offers prospects to vie for nearby breeding opportunities (Brown and Brown, 1984; Zack and Stutchbury, 1992; Ekman *et al.*, 2000); or any combination of these effects. Whatever the form of the benefits, however, they are not equally large for all retained offspring. For example, the first helpers often increase the group's breeding success much more than additional ones (e.g. Walters, 1990; Woolfenden and Fitzpatrick, 1990; Langen and Vehrencamp, 1999) and too many helpers may even be deleterious (Komdeur, 1994b). The indirect fitness gain is therefore highest for the first helpers. The prospects of territorial inheritance are similarly reduced for lower-ranking

subordinates (Field *et al.*, 1999). More generally, whenever some individuals stay at home and others disperse, the reproductive value of dispersers should not exceed that of those remaining at home – otherwise all should disperse (Kokko and Lundberg, 2001; Kokko and Ekman, 2002).

We have shown that this stronger differentiation in reproductive value among offspring of cooperative breeders means that the optimum clutch size is reduced (due to the ‘offspring depreciation’ effect; Ridley and Sutherland, 2002). Cooperative breeding, once established, can thus act as a selective force behind the evolution of a further decreasing clutch size, as confirmed in birds by Arnold and Owens (1998). Our model is meant to be conceptual. It is therefore simple and does not track the fates of offspring and their interactions explicitly, but it serves to make the important point that behavioural interactions among individuals can be linked to life-history evolution. Traditionally, these have been considered separately. For example, it has been suggested that small clutch sizes and cooperative breeding in Australian passerines have evolved to enable breeding under conditions of low annual increment in resources and low seasonality (Ford *et al.*, 1988). As we show, these factors may not be independent.

Here, we have shown that one factor (high survival) may explain the distribution of cooperative breeding better than another (high fecundity), even though theory based purely on territory acquisition prospects (Hatchwell and Komdeur, 2000; Pen and Weissing, 2000; Kokko and Lundberg, 2001) would predict that both are equally important because both make breeding habitat constraints more severe. This suggests that the life-history hypothesis is incomplete if it is based solely on rates of territory turnover. It is probably premature to state whether the phylogenetic importance of high adult survival is mainly due to life-history trade-offs (hypothesis 1) or an adaptive reduction in clutch sizes due to the offspring depreciation effect (hypothesis 2). We note, however, that Arnold and Owens’ (1998) interpretation of their data, where reductions in clutch size follow the transition to cooperation, supports the latter alternative.

ACKNOWLEDGEMENTS

We thank Kathryn Arnold and Andrew Cockburn for discussions and for their insightful comments on this manuscript. Ido Pen, Jo Ridley and an anonymous referee provided further helpful comments. Funding was provided by the European Commission (to R.H.), the Royal Society (to H.K.) and the Academy of Finland (to H.K.).

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