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# Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined

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We present quantitative models that unify several adaptive hypotheses for the evolution of cooperative breeding in a single framework: the ecological constraints hypothesis, the life-history hypothesis and the benefits-of-philopatry hypothesis. Our goal is to explain interspecific variation in the occurrence of cooperative breeding in terms of interspecific variation in life-history traits and ecological conditions. We analyse two models, according to whether or not helpers can inherit their parents' territory. Major results are (i) territory inheritance always promotes cooperative breeding; (ii) if territories are not inherited, neither ecological constraints nor variation in life-history traits predict interspecific variation in cooperative breeding; and (iii) if territories are inherited, the mechanism of density regulation is crucial in determining which factors promote cooperative breeding. If density dependence acts on the probability to obtain a free territory or on the survival of dispersers, variation in ecological constraints cannot explain variation in cooperative breeding. Lower adult mortality favours helping, not because it reduces the availability of free territories, but because it enhances the direct benefits of helpers. If density dependence acts on fecundity, lower probability of obtaining a free territory and lower survival of dispersers promote cooperative breeding. In this case, lower adult mortality works against the evolution of helping. We suggest that the difference between birds and social insects in the covariance between cooperative breeding and life-history traits is due to different mechanisms of density regulation that operate in these taxa, and we explain how natural selection on habitat choice might have caused these different mechanisms to operate.

**Keywords:** helping; relatedness; Hamilton's rule; fitness; reproductive value; density dependence

## 1. INTRODUCTION

In cooperatively breeding species, some individuals forgo their own reproduction, at least temporarily, and help raise the offspring of others, usually their close relatives. What are the factors that predispose a species to evolve such behaviour? More specifically we ask: In a comparative analysis, what properties of cooperatively breeding species or their environment would set them apart from non-cooperatively breeding species, argued from a selectionist perspective? In this paper we focus on the conditions that favour cooperative breeding in birds, or at least organisms with a life history similar to that of many birds, because of the wealth of comparative studies on birds (reviews in, for example, Faaborg & Patterson 1981; Koenig & Pitelka 1981; Emlen 1984; Brown 1987; Koenig *et al.* 1992; Arnold & Owens 1998, 1999; Hatchwell & Komdeur 2000). We will discuss the relevance of our results for social insects, which usually have quite different life histories and genetics (Crozier & Pamilo 1996).

Several hypotheses, not mutually exclusive, have been proposed to explain the evolution of cooperative breeding. The most influential hypotheses can be classified according to the following scheme.

- (i) Ecological constraints (EC) hypothesis (Brown 1974; Emlen 1982, 1997; Koenig *et al.* 1992).

- (ii) Life-history (LH) hypothesis (Russell 1989; Cockburn 1996; Arnold & Owens 1998).
- (iii) Benefits-of-philopatry (BP) hypothesis (Stacey & Ligon 1987, 1991).

According to the EC hypothesis, the opportunities for independent breeding are limited or risky because of ecological factors such as low availability of nesting sites, low availability of other resources, or a high risk of mortality during dispersal. The LH hypothesis emphasizes that certain life-history characteristics of a species limit the opportunities for independent breeding. For example, low adult mortality might lead to slow territory turnover, leading to prolonged periods of floating or queuing and a smaller probability to obtain a territory (e.g. Ens *et al.* 1995; Kokko & Sutherland 1998; Pen & Weissing 2000a). Thus, the EC and LH hypotheses both stress that the direct fitness benefits of seeking independent breeding opportunities are too small to outweigh the indirect inclusive fitness benefits of helping relatives. In terms of Hamilton's rule  $rb - c > 0$  (Hamilton 1964), EC and LH hypotheses suppose that the direct costs  $c$  of helping are small relative to the indirect benefit  $b$ , because individuals have little to lose by not dispersing. In contrast, the BP hypothesis emphasizes the long-term direct benefits of staying near the natal nest: short-term losses incurred by not dispersing are compensated by greater long-term direct benefits, in the form of inheritance of the natal territory.

We study these hypotheses by unifying them into a quantitative model. The main objective is to make predictions that can be tested with comparative studies. Our

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models might be useful for three reasons: first, most of the above hypotheses have not been modelled quantitatively, and it is well known that verbal arguments can be quite misleading when the complexities of life histories have to be taken into account. Our models serve to test the logic of such verbal arguments, and to better understand what assumptions are required to make the arguments work. Second, existing models are mostly based on applying Hamilton's rule without using proper fitness measures. It is not so obvious what the benefit  $b$  and the cost  $c$  in Hamilton's rule represent in a life-history context, and most authors rely on ad hoc interpretations. In contrast, we use a reproductive value approach where fitness is derived from explicit population dynamic considerations. Third, existing models do not take into account population dynamic constraints that limit population growth. We explicitly incorporate several mechanisms of density regulation and show that these can have important consequences for the evolution of cooperative breeding.

## 2. LIFE HISTORY AND ECOLOGY

### (a) *Strategy*

We consider a species where individuals have the choice to stay at the natal nest and become a helper, or to disperse and find a new nest elsewhere. The species is either asexual, or dioecious with males having complete dispersal and females deciding whether to stay or not. Females have a genetically determined strategy  $x \in [0,1]$ , which represents their tendency to become a helper. The population as a whole, the resident population, is monomorphic for helping tendency  $x^*$ . We concentrate on a mutant female with helping tendency  $x \neq x^*$ . As an adult, the female may get help from her previously produced offspring, the probability of which is determined by the average helping tendency  $\bar{x}$  of the female's offspring. The offsprings' helping tendency  $\bar{x}$  may differ from that of the population as a whole because of the relatedness between mother and offspring.

In §3(a), we ask under what conditions a mutant female with helping tendency  $x > 0$  has a selective advantage in a resident population without any helpers, that is, with helping tendency  $x^* = 0$ . We assume that mutations are of small effect, such that  $x > 0$  is small.

### (b) *Demography*

Territory owners or 'breeders' survive from one season to the next with probability  $S_b$  and helpers survive with probability  $S_h$ . The survival probabilities are assumed to be independent of the number of helpers. This assumption simplifies the analysis, but does not affect our main conclusions. Breeders produce  $F$  offspring per season.  $F$  depends on a breeder's expected number of helpers  $\bar{n} = \bar{n}(\bar{x})$ , which is an increasing function of the average helping tendency  $\bar{x}$  of a breeder's offspring. For a small number of helpers, reproductive output can be approximated by

$$F(\bar{x}) = F_0 + h\bar{n}(\bar{x}), \quad (1)$$

where  $F_0$  is reproductive output without helpers and  $h$  is the expected number of extra offspring produced per helper.

Individuals that opt for dispersal pay a survival cost  $k$ ; that is, relative to helpers they survive with probability

$1 - k$  from their season of birth to the next. Dispersers become 'waiters', floating or queuing individuals without a territory, waiting for suitable territories to become available in the future. Waiters survive from one season to the next with probability  $S_w$ . Provided they survive, waiters have a per-capita probability  $\alpha$  of obtaining a territory in a given season. The variables  $k$ ,  $S_w$  and  $\alpha$  may be regarded as representing the 'ecological constraints' on independent breeding. The higher  $k$  and the lower  $S_w$  or  $\alpha$ , the more severe are these constraints.

### (c) *Helping, and then what?*

Helpers remain helpers as long as their mother is still alive. We consider two scenarios of what happens to helpers when they finish their helping 'career'.

#### (i) *No territory inheritance*

When helpers stop helping, they disperse from the natal area and wait for territories to become available. Dispersal is just as costly (survival cost  $k$ ) for helpers as it is for individuals that opt for dispersal in their season of birth. Our main conclusions are robust with respect to small departures from this assumption (i.e. small survival benefits of philopatry). Thus, helpers do not gain any direct benefits from helping, but only indirect benefits by raising related offspring.

The life cycle for this scenario is depicted in figure 1. The figure shows three classes of individuals: helpers (H), waiters (W) and breeders (B). Arrows indicate transitions between classes and the symbols the per-capita contribution per season of one class to another. Equivalently, the transitions between the three classes can be represented by a transition matrix (Caswell 1989), given by

$$A = \begin{bmatrix} S_h S_b & 0 & x S_b F(\bar{x}) \\ (1-k)S_h(1-S_b) & (1-\alpha)S_w & (1-k)(1-xS_b)F(\bar{x}) \\ 0 & \alpha S_w & S_b \end{bmatrix}. \quad (2)$$

The matrix represents the population dynamics of females with strategy  $x$  having offspring with strategy  $\bar{x}$  in a resident population with strategy  $x^*$ . In §3(b) we explain how the matrix is used to derive the fitness consequences of having strategy  $x$ . First we explain the entries of the matrix.

Individuals are counted just before the onset of the breeding season. Mortality of helpers and breeders occurs between breeding seasons. The first column of the matrix represents the per-capita contribution of the class of helpers to the three classes of individuals. The first entry is the probability that a helper is still a helper one season later, which happens if and only if both helper and breeder survive until then, with probability  $S_h S_b$ . The second entry is the probability that a helper is no longer a helper next season, but has dispersed and is waiting for a territory. This happens if the breeder dies (probability  $1 - S_b$ ) and the helper survives (probability  $(1 - k)S_h$ ). The third entry is zero because helpers cannot obtain a territory without waiting at least one season for it first, just like offspring that skip the helping altogether.

The second column represents the per-capita contribution of waiters. The first entry is zero because waiters

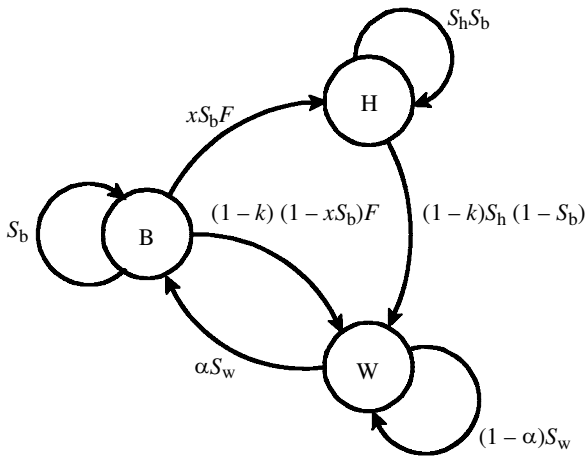


Figure 1. Life cycle when helpers (H) do not inherit the territory of their parents (B) but join the waiters (W) after they stop helping.

do not become helpers. The second entry is the probability that a waiter is still a waiter next season, which happens if she survives (probability  $S_w$ ) and does not find a vacant territory (probability  $1 - \alpha$ ). The third entry is the probability a waiter will be a breeder next season, which happens if she survives (probability  $S_w$ ) and finds a vacant territory (probability  $\alpha$ ).

The third column combines the per-capita contribution of breeders to the next season's population. The first entry is a breeder's offspring that become helpers next year. A breeder's  $F(\bar{x})$  offspring becomes a helper with probability  $xS_b$ ; that is, an offspring becomes a helper with probability  $x$  if its mother survives, with probability  $S_b$ . The second entry represents the offspring that are waiting for a territory next season. An individual offspring does not become a helper with probability  $1 - xS_b$  and survives the dispersal phase with probability  $1 - k$ . The final entry is the probability that a breeder is still a breeder next season because she survived. The referees of this paper remarked that it might be confusing that the helping probability  $x$ , the strategic decision of newborn individuals, appears in the third column, corresponding to the per-capita contribution of breeders. This issue is clarified in Appendix A.

(ii) *Territory inheritance*

In the second scenario for the fate of helpers, they may inherit the territory, which can be considered a direct benefit of philopatry. If  $x$  is sufficiently small, parents have at most one helper. This helper will then inherit the territory with certainty, provided she survives. The life cycle is depicted in figure 2 and the corresponding transition matrix is given by

$$A = \begin{bmatrix} S_h S_b & 0 & x S_b F(\bar{x}) \\ 0 & (1 - \alpha) S_w & (1 - k)(1 - x S_b) F(\bar{x}) \\ S_h(1 - S_b) & \alpha S_w & S_b \end{bmatrix}. \tag{3}$$

(d) *Density dependence*

No population can grow or shrink forever; hence we assume that density dependence acts to keep the resident

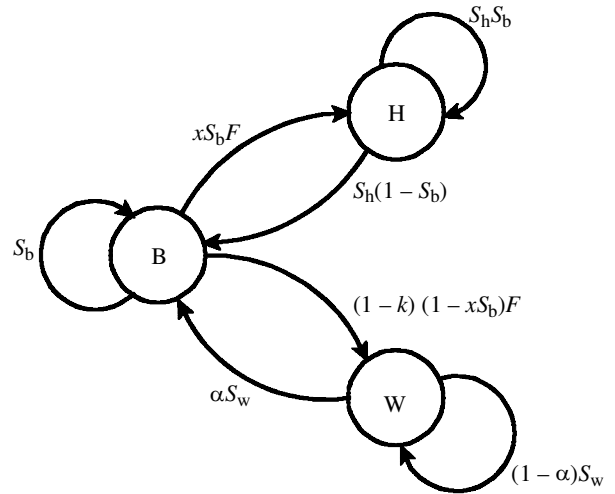


Figure 2. Life cycle when helpers (H) inherit the territory of their parents (B) after the parents die. Helpers do not compete with waiters (W).

population stationary in size. Mathematically, this means that the dominant eigenvalue  $\lambda^*$  of the transition matrix with  $x$  and  $\bar{x}$  replaced by  $x^*$  equals unity. The constraint  $\lambda^* = 1$  implies that the model loses one degree of freedom; that is, one of the model parameters must be removed by expressing it in terms of the remaining model parameters. Choosing which parameter is to be removed from the model reflects an assumption about the specific mechanism of density dependence (Mylius & Diekmann 1995). As we shall see, this choice may have profound consequences for the model predictions.

3. SELECTION

(a) *The direction of selection*

We want to know under what conditions helping behaviour has a selective advantage in a population without helpers. In other words, we ask whether a resident population monomorphic for helping tendency  $x^* = 0$  can be invaded by a rare mutant with helping tendency  $x > 0$ . To answer this question, we analyse the fitness of such a mutant, written as  $W(x, \bar{x}, x^*)$ . This notation expresses the notion that the fitness of a mutant need depend not only on its own helping tendency  $x$  and the population helping tendency  $x^*$ , but also on the average helping tendency  $\bar{x}$  of individuals that interact locally with the mutant.

We use the direct fitness approach, developed by Taylor & Frank (1996; see also Frank 1998) to investigate the effect of selection on helping behaviour. A small change in mutant behaviour  $x$  changes the fitness of the mutant according to

$$\Delta W = \frac{\partial W}{\partial x} + r \frac{\partial W}{\partial \bar{x}}, \tag{4}$$

evaluated at  $x = \bar{x} = x^*$ . The first term on the right is the effect of a small change in the actor's helping propensity  $x$  on her fitness, and the second term is the effect on the actor's fitness caused by a correlated change in the amount of help the actor gets herself, as determined by the local helping tendency  $\bar{x}$ . The strength of the correlation is

measured by the relatedness coefficient  $r$  between helpers and their beneficiaries. A positive sign of  $\Delta W$  implies selection in favour of higher  $x$ , and a negative sign selection against higher  $x$ .

**(b) Fitness**

In a class-structured population, condition (4) can be written in the form

$$\Delta W = \sum_{ij} u_j^* v_i^* \left( \frac{\partial a_{ij}}{\partial x} + r \frac{\partial a_{ij}}{\partial \bar{x}} \right)_{x=\bar{x}=x^*}, \tag{5}$$

where  $a_{ij} = a_{ij}(x, \bar{x}, x^*)$  is an element of a transition matrix (the contribution by a class  $j$  individual with strategy  $x$  to class  $i$  individuals in the next season), the  $u_j^*$  are relative frequencies of classes  $j$  in demographic equilibrium, and the  $v_i^*$  are the reproductive values of class  $i$  individuals in the resident population (see, for example, Taylor 1996; Pen & Weissing 2000c). The class frequencies and reproductive values are normalized such that  $\sum_i u_i^* v_i^* = 1$ . If, as in our model, the behaviour of interest is expressed in only class of individuals, say class  $j = k$ , then all terms  $j \neq k$  vanish. The positive constant  $u_k^*$  does not affect the direction of selection and can be ignored. In other words, we can take as a fitness function

$$W(x, \bar{x}, x^*) = \sum_i a_{ik}(x, \bar{x}, x^*) v_i^*. \tag{6}$$

This can be interpreted as the total amount of reproductive value produced by a class  $k$  individual that exhibits the mutant behaviour  $x$  during one time-step, and then switches back to the resident behaviour  $x^*$ .

In our model, the fitness of a mutant female with helping tendency  $x$  is given by

$$W(x, \bar{x}, x^*) = x S_b F(\bar{x}) v_h^* + (1 - k)(1 - x S_b) F(\bar{x}) v_w^* + S_b v_b^*, \tag{7}$$

where  $v_h^*$ ,  $v_w^*$  and  $v_b^*$  are the reproductive values of, respectively, helpers, waiters and breeders in the resident population.

**(c) Reproductive values**

Technically, the reproductive values  $v_j^*$  are the elements of a dominant left eigenvector (e.g. Lancaster 1969) of the matrix  $A^*$  that results from matrices (2) or (3) by replacing  $x$  and  $\bar{x}$  by the resident trait  $x^*$ . In other words, the  $v_j^*$  can be found by solving

$$v_j^* = \sum_i a_{ij}^* v_i^*. \tag{8}$$

Because only the relative reproductive values matter (technically, the direction of the vector is important, not its magnitude), we arbitrarily set one of them to a specific value. Here we set the reproductive value of waiters equal to their expected life-time reproductive success (LRS) of unity, that is,

$$v_w^* = 1. \tag{9}$$

For both matrices (2) and (3) we obtain the same reproductive value for breeders when  $x^* = 0$  (when there are no helpers):

$$v_b^* = \frac{(1 - k)F_0}{1 - S_b}. \tag{10}$$

This is just a breeder’s life expectancy  $1/(1 - S_b)$  multiplied by her yearly number of surviving offspring,  $(1 - k)F_0$ , which is her lifetime reproductive success.

The reproductive value of a helper depends on whether or not the helper obtains direct benefits by inheriting a territory. If a helper does not obtain direct benefits, we calculate  $v_h^*$  from matrix (2), and we get

$$v_h^* = \frac{(1 - k)S_h(1 - S_b)}{1 - S_h S_b}. \tag{11}$$

This again has a clear-cut interpretation:  $1/(1 - S_h S_b)$  is the expected number of seasons that a helper helps her parents, and  $(1 - k)S_h(1 - S_b)$  is the probability that a helper switches to the waiting class. Hence, equation (11) represents the probability that a helper ever becomes a waiter (multiplied by the LRS of unity of a waiter).

If a helper inherits her parents’ territory, we calculate  $v_h^*$  from matrix (3), and now we obtain

$$v_h^* = \frac{S_h(1 - S_b)}{1 - S_h S_b} \times \frac{(1 - k)F_0}{1 - S_b}, \tag{12a}$$

$$= \frac{S_h(1 - k)F_0}{1 - S_h S_b}. \tag{12b}$$

This is just the probability that a helper will ever inherit the territory times the LRS of a territory owner.

Because we set  $v_w^* = 1$ , equation (8) represents three equations in two unknowns ( $v_h^*$  and  $v_b^*$ ). We have solved for  $v_h^*$  and  $v_b^*$ , hence that leaves one equation. This equation is the same for both matrices, and it represents a ‘compatibility requirement’ which is equivalent to our assumption that the resident population is stationary ( $\lambda^* = 1$ ):

$$\frac{\alpha S_w}{1 - (1 - \alpha)S_w} = \frac{1 - S_b}{(1 - k)F_0}. \tag{13}$$

The left-hand side is the probability that a waiter ever obtains a territory. The right-hand side is the inverse of the LRS of a breeder, so we see that the LRS of unity of a waiter is its probability of ever obtaining a territory multiplied by the LRS of a breeder. With the help of equation (13), we will judge later how comparative predictions are affected by the mechanism of density dependence. Suppose, for example, that density dependence acts via the availability of breeding sites. In this case, the chance of obtaining a territory,  $\alpha$ , will decrease with an increasing density of competitors for breeding sites. When a stationary population has been reached through these density-dependent effects, equation (13) has to be satisfied; that is,  $\alpha$  has to satisfy the relationship

$$\alpha = \frac{(1 - S_w)(1 - S_b)}{S_w[(1 - k)F_0 - (1 - S_b)]}. \tag{14}$$

Likewise, if density dependence acts on reproductive output (fecundity and/or juvenile survival), then  $F_0$  has to satisfy

$$F_0 = \frac{(1 - S_b)[1 - (1 - \alpha)S_w]}{(1 - k)\alpha S_w}. \quad (15)$$

#### 4. RESULTS

The direction of selection on  $x$  in a population without helpers is found by applying equation (4) to equation (7) and setting  $x^* = 0$ :

$$\Delta W = S_b F_0 [v_h^* - (1 - k)v_w^*] + rh\bar{n}'(0)(1 - k)v_w^*, \quad (16)$$

a prime denoting differentiation. Here we have used  $F'(0) = h\bar{n}'(0)$ . To evaluate  $\Delta W$ , we need an expression for the mean number  $\bar{n}$  of helpers per breeder as a function of the helping tendency.  $\bar{n}$  can be derived from the distribution  $(u_h^*, u_w^*, u_b^*)$  of helpers, waiters and breeders in demographic equilibrium. Technically, this distribution corresponds to a dominant right eigenvector of the matrix  $A$ , but it can easily be derived as follows. In demographic equilibrium, the number of helpers  $u_h^*$  has to satisfy

$$u_h^* = S_h S_b u_h^* + \bar{x} S_b F(\bar{x}) u_b^*, \quad (17)$$

i.e. it is given by  $S_h S_b u_h^*$ , the number of helpers in the previous season that go on helping, plus  $\bar{x} S_b F u_b^*$ , the number of newly produced helpers. Because the expected number of helpers per parent is given by  $\bar{n} = u_h^*/u_b^*$ , we obtain from equation (17)

$$\bar{n}(\bar{x}) = \frac{\bar{x} S_b F_0}{1 - S_b(S_h + h\bar{x})}. \quad (18)$$

Differentiation of this expression yields

$$\bar{n}'(0) = \frac{S_b F_0}{1 - S_h S_b}. \quad (19)$$

The resemblance of equation (16) to Hamilton's rule  $rb - c > 0$  (Hamilton 1964) becomes apparent if we rewrite equation (16) in the form (up to the factor  $S_b F_0$ )

$$\Delta W = -c + rb, \quad (20)$$

where

$$c = (1 - k)v_w^* - v_h^*, \quad (21a)$$

$$b = \frac{h(1 - k)v_w^*}{1 - S_h S_b}. \quad (21b)$$

The term  $c$  is the difference in reproductive value  $v_w^*$  of a waiter, discounted by the probability  $1 - k$  that it survives the dispersal phase, and the reproductive value  $v_h^*$  of a helper. Hence,  $c$  represents the direct fitness cost of helping rather than dispersing. The term  $b$  also has a simple interpretation: it is the extra number of surviving offspring  $(1 - k)h$  produced per helper per season, multiplied by the expected number of seasons a helper helps,  $1/(1 - S_h S_b)$ . Hence,  $rb$  represents the indirect fitness benefits of helping.

In contrast to the indirect benefits of helping, which are the same for both scenarios, the direct costs of helping obviously depend on the future prospects of a helper. When helpers do not inherit the territory, the direct cost of helping is obtained by substituting the reproductive values  $v_w^* = 1$  and equation (11):

$$\text{direct cost without inheritance} = \frac{(1 - k)(1 - S_h)}{1 - S_h S_b}. \quad (22)$$

This expression is always positive.

For the scenario where a helper inherits the territory, the direct cost of helping is obtained by using equation (12b):

$$\text{direct cost with inheritance} = \frac{(1 - k)[1 - S_h(F_0 + S_b)]}{1 - S_h S_b}. \quad (23)$$

This expression can be negative for sufficiently large  $F_0$  and/or  $S_b$ .

The direction of selection on helping is determined by the sum of direct and indirect fitness effects. For the scenario where helpers do not inherit the territory, helping is favoured by selection if

$$rh > 1 - S_h. \quad (24)$$

For the scenario where helpers inherit the territory, helping is favoured if

$$rh > 1 - S_h(F_0 + S_b). \quad (25)$$

One conclusion is immediately obvious: the right-hand side of equation (25) is always smaller than the right-hand side of equation (24). This is because the LRS of a breeder,  $F_0/(1 - S_b)$ , must be larger than unity in a stationary population. Moreover, the right-hand side of equation (25) may be negative, in contrast to the right-hand side of equation (24). We thus have our first comparative prediction.

**Comparative prediction 1:** The occurrence of cooperative breeding is positively related to territory inheritance by helpers. When helpers inherit the territory, philopatry can even evolve if  $rh$  is negative, i.e. if the 'helpers' do not help at all or if they are unrelated to the breeders.

According to the EC hypothesis, the parameters  $k$ ,  $S_w$  and  $\alpha$  are important because they determine the chances of independent breeding, whereas according to the LH hypothesis, survival  $S_b$  of breeders is important because it determines territory turnover rate. We see that none of these parameters appear in condition (24); hence they should not affect the occurrence of cooperative breeding when territories are not inherited. In other words, in the absence of 'benefits of philopatry', the EC and LH hypotheses do not make different interspecific predictions. We therefore predict the following.

**Comparative prediction 2:** In the absence of territory inheritance by helpers, neither ecological constraints on independent breeding nor adult survival affect the occurrence of cooperative breeding.

Ecological constraints are not important here because the reproductive value of a waiter always equals unity, regardless of the severity of the constraints. This makes intuitive sense: the smaller the probability that a disperser ever obtains a territory, the larger must be the reward for those that eventually do obtain a territory, because fewer individuals will be the progenitors of the next generation.

If there are benefits of philopatry in the form of territory inheritance, then the predictions depend strongly on the mechanism of density regulation. We see that the ecological constraint parameters  $k$ ,  $S_w$  and  $\alpha$  do not appear in condition (25); hence if density dependence acts on any one of these parameters, the condition remains unchanged and we can conclude that ecological constraints do not affect the predictions. In that case higher adult survival  $S_b$  increases the likelihood that helping evolves, as predicted by the LH hypothesis. However, the reason is not because of higher territory turnover, as claimed by the LH hypothesis, but rather because of the higher direct benefits once a helper has inherited the territory. We predict the following.

Comparative prediction 3: If helpers inherit territories and density dependence acts on the cost of dispersal or on survival of waiters or on the probability to find an empty territory, then (i) ecological constraints on independent breeding do not affect the occurrence of cooperative breeding; and (ii) adult survival is positively related to the occurrence of cooperative breeding.

If density dependence acts via reproductive output  $F_0$  or the survival probabilities of breeders  $S_b$ , then the ecological constraints parameters  $k$ ,  $S_w$  and  $\alpha$  enter, indirectly, again in the criterion (25) for the evolution of helping. If, for example, density dependence acts via reproductive output, then  $F_0$  has to satisfy equation (15) in a stationary population. Inserting equation (15) into condition (25) reveals that now the right-hand side depends on the ecological constraints parameters. It is easy to show that the right-hand side of equation (25) decreases with the ecological constraint parameters  $k$ ,  $S_w$  and  $\alpha$ , and, contrary to the LH hypothesis, increases with adult survival  $S_b$ . This gives the fourth prediction.

Comparative prediction 4: If helpers inherit territories and density dependence acts on reproductive output, then (i) ecological constraints on independent breeding are positively related to the occurrence of cooperative breeding; and (ii) adult survival is negatively related to the occurrence of cooperative breeding.

## 5. DISCUSSION

We have constructed and analysed several models to obtain a better understanding of some of the selective forces that may explain why in some species there is cooperative breeding and in others there is not. We have summarized our findings in four comparative predictions, which predict correlations and syndromes of correlations between life-history traits or ecological factors and the occurrence of cooperative breeding.

Obviously we have neglected other factors that might also be important for the evolution of helping behaviour (Cockburn 1998). For example, we have assumed that offspring remaining near the natal nest always help (constant positive  $h$  in equation (1)). In reality, offspring may face two decisions: to stay at home or not, and if staying at home, to help or not. With the methods used in this paper, it would be relatively straightforward to analyse selection on  $h$ , the amount of help provided per helper, given trade-offs between helping and survival and

between helping and being tolerated by group members. Other potentially important factors we have neglected: there may be disadvantages associated with territory inheritance if this leads to inbreeding. There may be conflicts over who reproduces. There may be inherent advantages to group living. There are plenty of ideas, and it is a challenge to incorporate these into quantitative models.

### (a) *Comparative empirical evidence*

We stress once more that our analysis has focused on the species level, i.e. our model parameters represent average values for a given population. Even if our model predicts no interspecific correlation between cooperative breeding and ecological constraints, variation of cooperative breeding within a species might well be associated with ecological constraints. Thus, the experimental evidence that individual decisions whether to become a helper or not depend on territory availability (e.g. Pruett-Jones & Lewis 1990; Komdeur 1992) does not contradict our predictions.

Our predictions did not take into account that there may be correlations between different life-history traits and/or ecological factors. For example, according to condition (24), in the absence of territory inheritance by helpers, survival  $S_b$  of breeders should not affect selection pressures on helping, but higher survival  $S_h$  of helpers should make helping more likely. It seems quite possible that  $S_b$  and  $S_h$  are positively correlated between species, in which case  $S_b$  should also be positively related to the occurrence of cooperative breeding, contrary to prediction 2. This kind of problem applies to all models attempting to make comparative predictions. Nevertheless, comparative analyses can circumvent this problem by carefully controlling for correlations between explanatory variables.

Two recent articles by Arnold & Owens (1998, 1999) present phylogenetic analyses of the factors that correlate with the presence or absence of cooperative breeding in birds. They find that ecological constraints do not correlate with the occurrence of cooperative breeding, whereas adult mortality is negatively correlated with cooperative breeding. This syndrome of correlations corresponds precisely to our prediction 3. Arnold & Owens (1998, 1999) suggest that the mechanism by which low adult mortality might promote cooperative breeding is the slow territory turnover in such species, limiting the opportunities for independent breeding. Our analysis suggests that this mechanism is unlikely to be the causal factor. Rather, the enhanced direct benefits associated with low adult mortality appear to be a crucial factor selecting for cooperative breeding.

Prediction 3 makes the specific assumptions of territory inheritance by helpers and a mechanism of density regulation acting on territory availability. Both assumptions are supported by the available evidence: territory inheritance is widespread among cooperatively breeding birds (Emlen 1997) and territory availability is an important limiting factor in birds (Hanski 1982).

### (b) *Comparison with other models*

There are very few quantitative models for the evolution of cooperative breeding. Most models are of the verbal kind (e.g. Emlen 1982, 1997; Stacey & Ligon 1987, 1991). The quantitative models that come closest to our

models are the models of reproductive skew (e.g. Reeve & Ratnieks 1993). These models attempt to explain the division of reproduction within cooperatively breeding groups. As a special case, they consider under what conditions individuals become helpers without getting a share of group reproduction, just as we assume here. However, apart from a notable exception, these skew models assume non-overlapping generations and are therefore not applicable to birds. The exception is a recent model by Kokko & Johnstone (1999) who correctly point out that earlier models ignore one of the main reasons why subordinates (helpers) might remain in the group: future prospects. Their model assumes that a single helper takes over the territory after the territory owner has died, just as in the scenario of territory inheritance considered here. Kokko & Johnstone's (1999) model predicts that high survival of adults may facilitate selection for helping. However, according to their model, if survival of breeders is higher than that of helpers, the opposite is also possible. In contrast, according to our condition (25) higher survival of breeders should either always facilitate helping or always select against helping regardless of the relative survival probabilities of helpers and breeders, but depending on the mechanism of density regulation. In essence, their result is based on the fact that the probability of ever inheriting the territory (the first factor in the right-hand side of equation (12a)) may decrease with the survival  $S_b$  of breeders. However, our analysis shows that the smaller chance of taking over is compensated by the higher lifetime reproductive success once a helper has taken over (the second factor in equation (12a)). The discrepancy arises because of two important differences between our models. First, their model quantifies fitness in a more ad hoc manner, instead of using reproductive values that are derived from population dynamic considerations. Second, in our model the probability that a breeder gets a helper depends on the strategic helping tendency of the breeder herself (because her strategy is correlated with the strategies in her local environment, due to non-zero relatedness) and of the helping tendency of others. In Kokko & Johnstone's (1999) model the probability that a breeder gets a helper is a constant, decoupled from the strategies of individuals. At first sight this might seem to make our model more complicated, but the results are actually simpler. This is typical in these kinds of models (Pen & Weissing 2000b).

The skew models and the verbal models all predict that ecological constraints on independent breeding opportunities should have a strong positive effect on the occurrence of cooperative breeding. In contrast, our analysis suggests that ecological constraints should correlate with cooperative breeding only under the specific assumptions of prediction 4: helpers inherit the territory and density dependence acts via reduced fecundity or reduced juvenile survival. The difference is due to our explicit assumption of a stationary population. Earlier models kept all parameters constant, thereby implicitly presupposing an exponentially growing or declining population. In reality, one or several of the model parameters will be functions of population density, a fact that can have important evolutionary implications (Mylius & Diekmann 1995). This is illustrated by our model where different scenarios of density dependence lead to quite opposite predictions (3

and 4). Hence, by neglecting density regulation, one would arrive at the wrong conclusion that helping behaviour should always be associated with ecological constraints.

### (c) *Birds versus social insects*

We have been taxonomically biased in applying our models primarily to birds. Models for the evolution of eusociality in insects (Queller 1989; Gadagkar 1990, 1991) have led to the conclusion that a high risk of dispersal or delayed maturity of solitary foundresses are an important prerequisite for selection to favour helping behaviour. Indeed, comparative studies support this conclusion (Gadagkar 1991). Should not our comparative predictions also apply to (social) insects? Not necessarily. Insects often have life histories that differ in a number of crucial aspects from the life histories of birds. In particular, the bivoltine life history of many social insects may have generated unique selection pressures that have been important for the evolution of eusociality (Stubblefield & Charnov 1986; Crozier & Pamilo 1996). More importantly, the differences in life histories of birds and insects will certainly be reflected in the mechanism of density regulation. According to predictions 3 and 4, whether or not ecological constraints should promote cooperative breeding depends crucially on the mechanism of density regulation. The differences between birds and insects in the correlation between ecological constraints and cooperative breeding could therefore be explained if it were true that in birds territory availability is a limiting factor, whereas in insects fecundity or juvenile survival limits population growth. The evidence seems to support this (Hanski 1982). Moreover, there are good theoretical reasons to suppose that natural selection might cause density dependence to act on territory availability more readily in birds than in insects. Elsewhere, we have shown that selection on habitat choice causes higher adult survival to favour a higher minimal acceptable territory quality (Pen & Weissing 2000a). Because mortality rates in insects are generally much higher than in birds, high quality territories are more likely to be a limiting resource in birds than in insects.

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## APPENDIX A

Here we justify the use of the transition matrix (2).

It is helpful to think of a season or year as being composed of two consecutive parts. The first part starts before the breeding season. At this point there are three classes of individuals in the population: helpers, waiters and breeders (see figure 1). We store their numbers in the column vector  $\mathbf{n} = (n_h, n_w, n_b)$ . During the first part of the season, reproduction and mortality take place. During reproduction, each female produces  $F(\bar{x})$  surviving offspring,  $\bar{x}$  being the average helping tendency of the female's previous offspring. Reproduction yields an extra class of individuals, the juveniles, of which there are  $\tilde{n}_j$ , say. After mortality there are  $\tilde{n}_h$  helpers,  $\tilde{n}_w$  waiters



and  $\tilde{n}_b$  breeders left. Thus, at the end of the first part of the season there are four classes of individuals, and we keep track of them in the column vector  $\tilde{\mathbf{n}} = (\tilde{n}_h, \tilde{n}_w, \tilde{n}_b, \tilde{n}_j)$ , which is given by  $\tilde{\mathbf{n}} = \mathbf{B}\mathbf{n}$ , where

$$\mathbf{B} = \begin{bmatrix} S_h & 0 & 0 \\ 0 & S_w & 0 \\ 0 & 0 & S_b \\ 0 & 0 & F(\bar{x}) \end{bmatrix}. \quad (\text{A1})$$

In the second part of the season, individuals can switch between classes. Waiters can become breeders or not, helpers can stay helpers or become waiters, and a juvenile (the 'actor' class in the terminology of Taylor & Frank (1996)) becomes a helper or a waiter, determined by its individual helping tendency  $x$ . After the switching between classes we are at the beginning of the next season, and there are again three classes of individuals, counted in the vector  $\mathbf{n}' = (n'_h, n'_w, n'_b) = \mathbf{C}\tilde{\mathbf{n}}$ , where

$$\mathbf{C} = \begin{bmatrix} S_b & 0 & 0 & xS_b \\ (1-k)(1-S_b) & 1-\alpha & 0 & (1-k)(1-xS_b) \\ 0 & \alpha & 1 & 0 \end{bmatrix}. \quad (\text{A2})$$

Combining the two parts of the season, the change in the number of helpers, waiters and breeders from one season to the next is determined by the product  $\mathbf{CB}$  of the above matrices, which is the matrix  $\mathbf{A}$  in equation (2) in §2(c)(i).

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