ECOLOGICAL CONSTRAINTS INFLUENCE THE EMERGENCE OF COOPERATIVE BREEDING WHEN POPULATION DYNAMICS DETERMINE THE FITNESS OF HELPERS

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Cooperative breeding is a system in which certain individuals facilitate the production of offspring by others. The ecological constraints hypothesis states that ecological conditions deter individuals from breeding independently, and so individuals breed cooperatively to make the best of a bad situation. Current theoretical support for the ecological constraints hypothesis is lacking. We formulate a mathematical model that emphasizes the underlying ecology of cooperative breeders. Our goal is to derive theoretical support for the ecological constraints hypothesis using an ecological model of population dynamics. We consider a population composed of two kinds of individuals, nonbreeders (auxiliaries) and breeders. We suppose that help provided by an auxiliary increases breeder fecundity, but reduces the probability with which the auxiliary becomes a breeder. Our main result is a condition that guarantees success of auxiliary help. We predict that increasing the cost of dispersal promotes helping, in agreement with verbal theory. We also predict that increasing breeder mortality can either hinder helping (at high population densities), or promote it (at low population densities). We conclude that ecological constraints can exert influence over the evolution of auxiliary help when population dynamics are considered; moreover, that influence need not coincide with direct fitness benefits as previously found.

KEY WORDS: Alloparental care, helpers-at-the-nest, inclusive fitness, kin selection, mathematical model, sociality.

In many cooperatively breeding species, nonbreeding individuals (i.e., auxiliary individuals) postpone or forgo their own reproduction to increase the fecundity of others. Cooperative breeders include a taxonomically broad set of species that occur in a wide range of environments (Jennions and MacDonald 1994; Cockburn 1998; Leadbeater et al. 2011; Wong and Balshine 2011). Thus, the help provided by nonbreeding auxiliaries represents one of the most diverse forms of cooperation in nature.

The adaptive significance of auxiliary help is often explained in terms of its direct and indirect fitness benefits (Wiley and Rabenold 1984; Brown 1987; Heinsohn and Legge 1999; Clutton-Brock 2002; Griffin and West 2002). Direct benefits of help accrue through the production of descendant offspring. These are realized, for example, when a helpful auxiliary gains valuable parenting experience (Skutch 1961), or when a helpful auxiliary contributes to the formation of a larger, more productive group that it will inherit at some later date (Wiley and Rabenold 1984; Kokko et al. 2001; Clutton-Brock 2002). Indirect benefits of help accrue through increased production of related, nondescendant offspring. For indirect benefits to play a role in the emergence and maintenance of auxiliary help, helpers must be able to associate with breeding kin (Griffin and West 2002). While both direct and indirect fitness benefits likely promote the evolution of helpful behavior in cooperatively breeding species (Clutton-Brock 2009), we choose to focus on indirect benefits here.
The indirect fitness benefits of auxiliary help can be realized in a number of ways, but the most prominent explanation of how they accumulate is given by the ecological constraints hypothesis (ECH). The ECH proposes that the provision of help by auxiliaries is motivated by the relatively small direct-fitness returns that come from independent breeding attempts. In this way, the ECH views an auxiliary’s decision to postpone independent reproduction to help relatives as simply making the best out of a bad situation (Dickinson and Hatchwell 2004). Importantly, the ECH predicts that the selective advantage of auxiliary help is promoted by the high cost of dispersal, low probability of establishing a breeding territory, and low expected fecundity of independent breeders (Emlen 1982a, b).

While there is substantial empirical evidence to support the ECH (Hannon et al. 1985; Pruett-Jones and Lewis 1990; Komdeur 1992; Dickinson 2004; Schoepf and Schradin 2012), comprehensive theoretical support is lacking. Early theoretical work supported the hypothesis (Emlen 1982b; Motro 1993; Reeve and Ratnieks 1993), but did not embed key ecological features in a population-dynamic context. Consequently, the predictions made by these early models do not necessarily correspond to any ecologically plausible scenario. Pen and Weissing (2000a) were the first to address this limitation by modeling the evolution of cooperative breeding with explicit population dynamics. However, they found that in the absence of other effects, such as territory inheritance, the evolution of cooperative breeding was independent of ecological constraints (Pen and Weissing 2000a). Not only does this result run counter to empirical findings, but also suggests that the indirect fitness effects that feature in the ECH only act to supplement the more important direct fitness benefits associated with territory inheritance. Our goal is to reverse this view of the ECH, and show that ecological constraints alone can influence the emergence of auxiliary help—and ultimately cooperative breeding—when explicit population dynamics are taken into account.

We use a mathematical model to investigate the role played by ecological constraints in the emergence of auxiliary help. We find that the ecological constraints associated with the cost of dispersal, probability of establishment, and independent breeding success all play a role in the emergence of cooperative breeding. As a result, we are able to provide ecologically consistent theoretical support for an explanation of cooperative breeding that is widely used in biology. We also provide interpretations of our results in terms of inclusive fitness and equilibrium population densities to make our predictions amenable to experimental testing.

Model

DYNAMICS OF A SELFISH WILDLIFE TYPE POPULATION

We consider an environment composed of a fixed density of breeding territories, $K$. Each breeding territory can be inhabited by up to one breeding individual, and $X \equiv X(t) \leq K$ denotes the density of breeders in the population at time $t$. Each breeding territory has a variable number of nonbreeding, or auxiliary, individuals associated with it, and we use $Y \equiv Y(t)$ to denote the total density of auxiliaries at time $t$. We initially assume that auxiliaries do not help breeders.

Breeders die at per capita rate $m_X$, and auxiliaries die at per capita rate $m_Y$. Reproduction is sexual, and breeders are outcrossing hermaphrodites. Breeders produce oocytes at per capita rate, $b$, oocytes are immediately fertilized by sperm from a uniform random breeder in the population, and the resulting offspring is immediately counted as an auxiliary on its natal patch. The decision to model breeders as hermaphrodites was made for convenience and our results will apply to dioecious species with an evolutionarily fixed pattern of sex allocation. Treating the model species as outcrossed was intended to reflect the biology of the many cooperatively breeding species that avoid inbreeding (Koenig and Haydock 2004). The decision to have newborn offspring join the auxiliary class was made to keep the dimensionality of the population dynamics as low as possible.

Auxiliaries disperse at a per capita rate that is proportional to breeder vacancies, specifically $d(K - X)/K$, where $d$ is the intrinsic rate of dispersal (henceforth, simply “dispersal rate”). A dispersing auxiliary fails to successfully establish itself as a breeder with probability $c$, in which case it is assumed to die. We call $c$ the (dimensionless) cost of dispersal, and we note that $(1 - c)$ represents the probability that a disperser successfully establishes its own breeding territory. We assume that once a breeder is established, it remains to breed on its territory for the duration of its life. This assumption is a reasonable one because, in our model, there is nothing to be gained from leaving a territory that has already been secured.

Combining the assumptions listed above, we can describe the population dynamics using

$$\frac{dX}{dt} = -m_X X + d(1 - c) \frac{K - X}{K} Y,$$
$$\frac{dY}{dt} = -m_Y Y - d \frac{K - X}{K} Y + b X. \quad (1)$$

To simplify our analysis, we nondimensionalize (1) by defining new variables $x = X/K$, $y = Y/K$, $\tau = b t$, $\mu_x = m_X/b$, $\mu_y = m_Y/b$, and $\delta = d/b$. It follows that (1) can be rewritten

$$\dot{x} = -\mu_x x + \delta (1 - c) (1 - x) y,$$
$$\dot{y} = -\mu_y y - \delta (1 - x) y + x, \quad (2)$$

where dots denote differentiation with respect to $\tau$. Nondimensionalization is a standard way mathematicians reduce the number of parameters in dynamical models. Below, we will refer to our new, dimensionless demographic parameters by their original names. That is, we will continue to refer to $\mu_x$ and $\mu_y$ as breeder
and auxiliary mortality rates, respectively, and we will continue to refer to $\delta$ as an intrinsic dispersal rate. However, the reader should be aware that these new rates are dimensionless.

In Appendix A, we use the theory of planar dynamical systems (Perko 1996) to show the model population avoids extinction if and only if

$$R_0 = \frac{\delta(1 - c)}{(\mu_y + \delta) \mu_x} > 1.$$  \hspace{1cm} (3)

The expression on the left-hand side of the inequality in (3) describes the expected lifetime reproductive success of an individual in a low-density population, and is known as the basic reproduction number. The basic reproduction number in our model is the product of (1) the probability of successful establishment as a independent breeder at low population densities, $\delta(1 - c)/(\mu_y + \delta)$, and (2) lifetime reproductive success through both male and female function, weighted by genetic contribution, $(1/2)(2/\mu_x) = 1/\mu_x$.

When inequality (3) holds, the dimensionless population densities tend toward the equilibrium values:

$$x \rightarrow \bar{x} = \frac{R_0 - 1}{R_0 - \delta/(\delta + \mu_y)},$$

$$y \rightarrow \bar{y} = \frac{R_0 - 1}{\mu_y}.$$  \hspace{1cm} (4)

We show in Appendix A that $\bar{x}$ and $\bar{y}$ are globally asymptotically stable equilibrium solutions to (2) when $R_0 > 1$. At equilibrium, the probability with which an auxiliary becomes established as a breeder is given by $\psi = \delta(1 - c)/(1 - \bar{x})/(\mu_y + \delta(1 - \bar{x}))$, and reproductive success as a breeder is $N = 2/\mu_x$. Intuitively, lifetime reproductive success, weighted by genetic contribution at equilibrium is unity, that is, $\psi N/2 = 1$.

**DYNAMICS OF INVASION BY A HELPFUL MUTANT**

We assume that the extent to which an auxiliary helps the breeder on its natal patch is determined at a single, diallelic autosomal locus. An auxiliary homozygous for the selfish, wild-type allele provides no help, whereas an auxiliary carrying the mutant allele helps the breeder on its natal territory by increasing the breeder’s oocyte production. We assume that the mutant allele is not recessive and is rare.

Because the mutant allele is rare, the success of a mutant invasion is determined entirely by the success of heterozygous mutant individuals. Moreover, when the mutant is rare the dynamics of the mutant subpopulation are approximately linear. Assuming the wild-type population is near equilibrium (4), mutant invasion is described by the following linearized system of differential equations:

$$\dot{x}_m = -\mu_x x_m + \delta (1 - c)(1 - \bar{x}) y_m,$$

$$\dot{y}_m = -\mu_y y_m - \delta(1 - \bar{x}) y_m + x_m + \frac{1}{2}z_m,$$

$$\dot{z}_m = -(\mu_x + \mu_y + \delta(1 - \bar{x}))z_m + \frac{1}{2}x_m + \frac{1}{2}y_m.$$  \hspace{1cm} (5)

All notation in this system of equations will be explained in due course, beginning with the variables.

Variables $x_m$ and $y_m$ in equation (5) denote the dimensionless densities of heterozygous breeders and auxiliaries, respectively. The variable $z_m$ denotes the joint density of heterozygous breeders and heterozygous auxiliaries. Although wild-type breeders are associated with heterozygous auxiliaries, the effect of these associations on mutant invasion is captured sufficiently by the equation for $y_m$ because they do not yield a benefit in terms of production of subsequent mutant offspring. Note that the equation for $y_m$ includes an input due to unassisted reproduction by mutant breeders represented by the term $x_m$. To better understand this term recall that the unassisted rate at which a breeder produces offspring through both male and female function is 2. Because half of these offspring are mutants, the total unassisted rate of mutant offspring production is $(1/2) \times 2 = 1$ (Fig. 1), and so the total rate at which mutant offspring are produced without help is $1 \times x_m = x_m$. With this in mind, it makes sense that the inputs in equation (5) associated with reproduction through female function only get weighted by $1/2$.
Equation (5) also contains rescaled parameters \( \bar{\gamma}, \bar{\mu}_y, \) and \( \gamma. \) The parameter \( \gamma \) describes the additive increase in the rate of oocyte output due to the presence of one mutant auxiliary. The parameter \( \bar{\mu}_y \) describes the per capita mortality rate of a heterozygous mutant auxiliary. Finally, the parameter \( \bar{\delta} \) describes the rate at which a mutant auxiliary disperses at low population densities.

Helping is energetically expensive (Heinsohn and Legge, 1999). To reflect this, we assume that the provisioning of help comes at the cost of some combination of higher auxiliary mortality \( (\bar{\mu}_y \geq \mu_y) \) and lower auxiliary dispersal \( (\bar{\delta} \leq \delta). \) In regard to dispersal, while we do allow for the possibility that helpers disperse at a lower rate than selfish individuals, our model does not force a lower dispersal rate on helpers. In other words, our model allows for dispersal and helping to be treated as independent decisions—a feature that has been advocated elsewhere (Kokko et al. 2001).

We emphasize that, in keeping with the ECH, auxiliary help in our model is not associated with territory inheritance. Territory inheritance and the associated effects of local kin competition have been studied extensively elsewhere in the context of cooperative breeding and the evolution of helping in general (Taylor 1992; Pen and Weissing 2000a; Wild 2006; Leggett et al. 2012). We also stress that direct benefits, such as the parenting experience gained by helpful auxiliaries, are neglected so we can focus on indirect benefits only. Finally, we note that auxiliary help is provisioned over a variable period of time, in keeping with assumptions made by previous authors (Pen and Weissing 2000a).

**Results**

**INVASION FITNESS**

In Appendix B, we use a standard weak-selection approximation (Taylor and Frank 1996), and the “next-generation tools” presented by Hurford et al. (2010) to show that the fitness of a rare mutant is

\[
W(\gamma) = \frac{\bar{\delta}(1 - c)(1 - \bar{x})}{\bar{\mu}_y + \bar{\delta}(1 - \bar{x})} \frac{1}{2} N \left\{ \frac{1}{2} \bar{\mu}_y + \bar{\mu}_y + \bar{\delta}(1 - \bar{x}) \right\} \gamma / 2. \tag{6}
\]

Here, \( W \) is a function of \( \gamma \) because we assume an unspecified functional relationship between \( \gamma \) and both \( \bar{\mu}_y \equiv \bar{\mu}_y(\gamma) \) and \( \bar{\delta} \equiv \bar{\delta}(\gamma). \) The mutant allele invades when \( W(\gamma) > 1 \) and is eliminated when the inequality is reversed. When \( W(\gamma) = 1, \) selection can neither favor nor eliminate the mutant.

In analogy to \( \Psi N / 2, \) as described previously for wild-type individuals, the first term of (6) is the product of (1) the probability that a mutant auxiliary recruits to the breeding class, \( \bar{\delta}(1 - c)(1 - \bar{x})/(\bar{\mu}_y + \bar{\delta}(1 - \bar{x})), \) and (2) the expected unassisted lifetime fecundity of a mutant breeder, weighted by the probability that any one of the offspring it produces is a mutant, \( N / 2. \) The second term of (6) is the product of (1) the probability that the focal mutant was produced through the female function of its mutant parent, \( 1 / 2, \) and (2) the expected number of mutant offspring the focal mutant helps to produce over the lifetime of one mutant-breeder-mutant-auxiliary association, \( (\gamma / 2)/(\bar{\mu}_y + \bar{\mu}_y + \bar{\delta}(1 - \bar{x})). \) In particular, the second term shows that the focal mutant will direct half of its help to producing non-mutants.

In some cases, the interpretations presented above assume that the mutant is selectively neutral, but any discrepancies this introduces will be of no consequence as we have applied a weak selection approximation.

**INCLUSIVE FITNESS EFFECTS**

Regardless of the genotypic differences that might occur among nestmates, auxiliaries are always helping to raise kin (half-sibs), and so we expect the invasion condition \( W(\gamma) > 1 \) to yield an inclusive-fitness interpretation. In fact, this is precisely what we find.

Let \( C \) be the direct cost of help incurred by the mutant auxiliary, defined as a marginal reduction in reproductive success achieved through independent breeding. Since only half of the future offspring produced by a mutant auxiliary are also expected to be mutants, we expect \( C \) to be weighted by \( r_1 = 1/2. \) Let \( B \) be the indirect benefit associated with auxiliary help, defined as a marginal improvement in the reproductive output realized by the breeder with whom the auxiliary associates. Since one quarter of the offspring produced by said breeder, on average, will also be mutants, we expect \( B \) to be weighted by \( r_2 = 1/4. \) Overall, when the effect of selection is weak the condition \( W(\gamma) > 1 \) becomes

\[
- \frac{1}{2} \frac{\Psi N}{r_1} \frac{\bar{\delta}}{\bar{\mu}_y + \bar{\delta}(1 - \bar{x})} \frac{d(\bar{\mu}_y/\bar{\delta})}{dy} \bigg|_{\gamma = 0} + \frac{1}{4} \frac{1}{\bar{\mu}_y + \bar{\mu}_y + \bar{\delta}(1 - \bar{x})} > 0, \tag{7}
\]

which is Hamilton’s rule (Hamilton 1964), modified for cooperative breeders, \( r_1 C < r_2 B \) (Brown 1987).

**ECOLOGY AND ECOLOGICAL CONSTRAINTS**

Putting inclusive-fitness interpretations aside, the invasion condition (7) simplifies to

\[
\frac{d(\bar{\mu}_y/\bar{\delta})}{dy} \bigg|_{\gamma = 0} < \frac{1}{4} \frac{1}{\bar{\mu}_y} \frac{\bar{\mu}_y}{\bar{\delta}} \frac{1}{1 - c} \frac{\mu_y}{\bar{\mu}_y + \mu_y} = \frac{1}{4} \frac{1}{\bar{\delta}} \text{ expected time spent as an auxiliary,} \tag{8}
\]

where we have used the fact that with weak selection \( \gamma \) is small and \( \bar{\mu}_y \approx \mu_y \) and \( \bar{\delta} \approx \delta. \) Condition (8) shows that the fate of the
rare mutant in our model is influenced by the tension between the expected lifetime of breeder–auxiliary associations (i.e., the time during which indirect benefits can accrue) and the expected time spent as an auxiliary (i.e., the time during which costs associated with increased mortality and decreased dispersal are paid).

Going a step further, inequality (8) can be thought of as an upper bound on the derivative $d(\tilde{\mu}_y/\delta)/d\tilde{y}|_{\tilde{y} = 0}$, which in turn can be understood as the rate at which the immediate costs of mutant behavior are incurred when mutant helping has a small effect on breeder fecundity. In order for cooperative breeding to emerge in our model, these immediate costs cannot exceed the normalized benefit represented by the far right-hand side of (8). It follows that the right-hand side of (8) describes the scope for the emergence of help, and that auxiliary is promoted (resp. hindered) as this side of the inequality is increased (resp. decreased).

Broadly speaking, condition (8) shows the importance of ecological constraints. Specifically, we find that the ecological parameters $c$ and $\mu_x$, that simplified out of Pen and Weissing’s (2000a) condition for the emergence of auxiliary help are present (Fig. 2). At equilibrium the parameter $\mu_x$ can be interpreted as the probability of establishment $\psi$, which is considered to be a key ecological constraint in the ECH (Emlen 1982a). In short, our model reveals that ecological constraints do influence the emergence of cooperative breeding.

Having now established that ecological constraints alone can influence the emergence of cooperative breeding systems, we turn our attention to the specific effects of the ecological parameters found in our model.

**Cost of dispersal**

Differentiating the left-hand side of (8) with respect to the cost of dispersal parameter $c$, while maintaining the basic reproduction number $R_0 > 1$, we find that increasing the cost of dispersal promotes cooperation at a rate proportional to

$$
\frac{1}{4} \left( \frac{\delta}{1 - \mu_x} \right)^2 \mu_x \mu_y (\mu_x + \delta)^2 R_0^2
$$

(recall that $R_0 > 1$ implies $\mu_x < 1 - c$). Line (9) shows that the effect of increasing cost of dispersal is strongest when $R_0 \approx 1$. This finding is also reflected in Figure 3 (top panels), where we see that the effect of increased $c$ is most pronounced as $R_0$ approaches 1 from above. In agreement with the expressions in (4), results show that the pronounced effect of increased cost of dispersal is associated with moderate-to-low occupancy of breeding territories, and moderate-to-low densities of auxiliaries (Fig. 3, middle panel, bottom panel). Therefore, our model predicts that changing the cost of dispersal is likely to have greatest influence on the emergence of auxiliary help in populations exposed to moderate-to-harsh environmental conditions.

**Breeder mortality**

Differentiating the left-hand side of (8) with respect to breeder mortality parameter $\mu_x$, while maintaining the basic reproduction number $R_0 > 1$, yields an expression whose sign is variable. This indicates that changes to breeder mortality can hinder the emergence of auxiliary cooperation in some cases, and promote it in others. Specifically, we find that increasing breeder mortality hinders cooperation when $R_0 > 2\delta/(\delta + \mu_x)$, and promotes cooperation when the inequality is reversed (Fig. 4, top panel).

Biologically speaking $R_0 > 2\delta/(\delta + \mu_x)$ (resp. $R_0 < 2\delta/(\delta + \mu_x)$) corresponds to a population with relatively high (resp. low) densities. As a result, our model predicts that increases
The scope for the emergence of help increases monotonically with the increasing cost of dispersal $c$. The effect exerted by increasing $c$ is weak when territory occupancy rates and population densities are relatively high (i.e., when $c$ is relatively small, and $R_0$ is relatively large). The effect of $c$ is more substantial as occupancy rates and population densities decrease (i.e., as $c$ increases, and $R_0$ approaches 1 from above). In this figure, $\mu_x = \mu_y = 0.1$, and $\delta = 1$, but the same qualitative relationships were observed at all parameter combinations investigated.

in breeder mortality rate will hinder the emergence of cooperation in populations with relatively high population densities, but will promote cooperation in low-density populations (Fig. 4, middle panel, bottom panel).

As previously noted, mutant invasion hinges on the tension between time until a breeding opportunity becomes available, and the benefits that can be accrued through help during that time. Thus, increasing breeder mortality represents a double-edged sword for the emergence of cooperation. Increasing breeder mortality not only reduces the time a helpful auxiliary spends waiting for its own breeding territory, but also reduces the benefit auxiliary help confers on related breeders during the waiting period. When the population is at high densities, waiting times are already so lengthy that benefits associated with their reduction are small in comparison to the concomitant costs associated with reduced time spent helping. When the population is at low densities, the relationship is reversed.

At the equilibrium presented in (4) one can interpret the parameter $\mu_x$ as the probability with which an auxiliary becomes established as a breeder during its lifetime. This interpretation follows from the relation, $\psi N/2 = 1$. Previous work predicts that increasing the probability of establishment will hinder cooperation because larger $\psi$ implies that helping is more costly (i.e., more is being sacrificed by the helpful auxiliary; Emlem 1982b). The fact that increasing $\psi = \mu_x$ can sometimes promote and sometimes hinder the emergence of auxiliary help shows that the relationship between $\psi$ is more complicated than previously thought. In addition, the complications are compounded here because lifetime unassisted fecundity $N = 2/\mu_x$ decreases as $\psi = \mu_x$ increases. Broadly speaking, our result illustrates a key advantage of pursuing ecologically explicit accounts of evolution: these models are able to elucidate the complex interrelationships among ecological parameters, whereas other less explicit models naively treat such quantities as independent.
Figure 4. The scope for the emergence of help is affected by increasing breeder mortality \( \mu_x \) in a nonmonotonic manner. When territory occupancy rates and population densities are large (i.e., when \( \mu_x \) is small and \( R_0 \) large), increasing \( \mu_x \) reduces the scope for help. When territory occupancy rates and population densities are low (i.e., when \( \mu_x \) is large and \( R_0 \) small), increasing \( \mu_x \) increases the scope for help. The qualitative effect of increasing \( \mu_x \) changes when \( R_0 = 2\delta/(\mu_y + \delta) \), of course in those cases where \( 2\delta/(\mu_y + \delta) < 1 \) such a switch does not occur and increasing \( \mu_x \) always inhibits help. In this figure, \( c = 0.4, \mu_y = 0.1, \) and \( \delta = 1, \) but the same qualitative relationships were observed at all parameter combinations investigated.

**Auxiliary mortality and dispersal**

We cannot use (8) to study the effect of changes in auxiliary mortality rate \( \mu_y \) and dispersal rate \( \delta \) because these parameters appear on both sides of the inequality. Therefore, we must collect all terms in \( \mu_x \) and \( \delta \) on one side of the invasion condition. For clarity and convenience, we do this by focusing on each trade-off independently. First, suppose that helping decreases the dispersal rate of auxiliaries. In this case, the invasion condition is

\[
\frac{1}{4} \left( 1 - \frac{\mu_x}{1 - c} \right) \mu_x + \mu_y > -\frac{\delta}{\mu_y} \Bigg|_{\gamma = 0}. \tag{10}
\]

Second, in the event that help increases auxiliary mortality, the invasion condition is

\[
\frac{1}{4} \left( 1 - \frac{\mu_x}{1 - c} \right) \mu_x + \mu_y > \frac{d\mu_y}{d\gamma} \Bigg|_{\gamma = 0}. \tag{11}
\]

In the first case, increasing the auxiliary mortality rate \( \mu_y \) clearly decreases the left-hand side of the invasion condition (10). Consequently, increases to auxiliary mortality inhibit the emergence of cooperation. In the second case, increasing auxiliary mortality \( \mu_y \), in turn, increases the left-hand side of the invasion condition (11), and so higher auxiliary mortality promotes cooperation. Returning to (10), we see that increasing the dispersal rate, \( \delta \), increases the threshold for invasion of helping to occur. Changes to \( \delta \) have no impact in (11).

In general, we expect that mutant dispersal rate \( \tilde{\delta} \) and the rate at which mutant auxiliaries die \( \tilde{\mu}_y \) could trade-off with \( \gamma \) in any number of ways. Hence, increasing \( \delta \) and \( \mu_y \) will have a variable effect on mutant invasion—one that depends on the nature of the trade-off.

**Discussion**

The ECH is an empirically well-supported explanation for the adaptive significance of cooperative breeding (Hannon et al. 1985;
Pruett-Jones and Lewis 1990; Komdeur 1992; Dickinson 2004; Schoepf and Schradin 2012). By contrast, theoretical support for the hypothesis is equivocal. Early theoretical work that supported the ECH treated key ecological parameters as fixed quantities, effectively neglecting the ecological underpinnings of the natural systems in which cooperative breeding occurs (Emlen 1982b; Motro 1993; Reeve and Ratnieks 1993). More recent work has taken ecological dynamics into consideration, and has found that the emergence of auxiliary help is independent of the ecological constraints featured in the ECH, when auxiliary territory inheritance is absent (Pen and Weissing 2000a). This more recent result suggests that ecological constraints are of secondary importance to other explanations.

We present an explicit account of population dynamics, and we use that account to derive an ecologically reasonable measure of helper fitness. We purposefully neglect local factors, such as territory inheritance, and direct benefits of helping, such as gained parenting experience, to focus solely on the importance of ecological constraints.

Our main result is an invasion condition that can be expressed in terms of quantities that relate directly to the ECH—specifically, cost of dispersal $c$ and breeder mortality $\mu_x$. We find that ecological constraints can influence the emergence of cooperative breeding without additional direct-fitness benefits, such as territory inheritance. In particular, we find that increased cost of dispersal acts as an incentive for auxiliary help, as originally suggested by Emlen (1982a, b). Changes to breeder mortality (equivalently, probability of establishment $\psi_x$, at equilibrium) have a variable effect that depends on the tension between the expected lifetime of breeder–auxiliary associations, on the one hand, and expected time spent in the auxiliary class, on the other hand. Lastly, we find that other life-history parameters, such as auxiliary dispersal rate $(b)$ and auxiliary mortality rate $(\mu_y)$, influence the emergence of cooperation; however, the effect of those parameters will depend heavily on the nature of the fitness costs of increased helping.

We framed our qualitative results concerning ecological constraints in terms of the occupancy rate of breeding territories ($\tilde{\chi}$), and the density of auxiliaries ($\tilde{\gamma}$). Our results indicate that the cost of dispersal $c$ exerts greatest influence in populations with low-to-moderate occupancy rates and low-to-moderate auxiliary densities. We also predict that increases to breeder mortality $\mu_x$ will inhibit the emergence of auxiliary help in populations with high territory occupancy rate and high breeder densities, and promote the emergence of auxiliary help as occupancy rates and auxiliary densities fall. Lastly, the complicated relationship among key ecological constraints featured in the ECH (particularly the probability of establishment $\psi$, unassisted lifetime reproductive success $N$, and territory occupancy rate $\tilde{\chi}$) indicates that the ECH is better framed in terms of more basic ecological features (e.g., mortality rates, or even birth rates when appropriate). Of course, what basic ecological features one accounts for will depend on what species is under consideration, and constraints beyond those accounted for here (e.g., constraints like spatial or temporal variability in habitat quality or food availability) will play a role, in general.

The main conclusion our analysis points to is that ecological constraints do not need to “piggy-back” on other features of a species’ biology (e.g., territory inheritance or indeed any other feature that supplies helpers with a direct fitness benefit) to exert influence over the emergence of auxiliary help. This conclusion differs from conclusions made by other theoretical treatments of cooperative breeding that have—like us—incorporated population dynamics. The model proposed by Pen and Weissing (2000a) assumed that helpful and selfish auxiliaries alike had to pass through the same intermediary stage (a “waiter” or “floater” stage) before breeding could occur. Individuals were influenced by ecological constraints during the “waiter” stage, and since “waiting” occurred regardless of the level of help offered by an auxiliary, ecological constraints acting during that period of the life history necessarily cancelled from the invasion condition. By contrast, our model did not explicitly consider a “waiter” stage. Instead our model assumed that the life history of a helpful auxiliary diverged from that of a selfish auxiliary until such time as recruitment to the breeder class occurred. As a result, ecological constraints in our model could affect helpful and selfish auxiliaries differently, and were not fated to cancel out of our calculations. Since “waiters” or “floaters” are simply dispersers that have not yet secured a breeding territory (Koenig et al. 1992), our model does implicitly deal with these types of individuals. Indeed, the cost of dispersal $c$ could be interpreted as a mortality rate suffered while “waiting” or “floating”.

There are many aspects of cooperative breeding not addressed by the work presented here. We chose to ignore many features of the biology of cooperative breeders (e.g., parenting experience, local competitive effects, territory inheritance, issues concerning variable levels of promiscuity) to focus on the ECH. Granted, some assumptions were made because we wished to keep the model as simple as possible. In particular, we chose to model cooperative breeders as hermaphrodites with an evolutionarily fixed pattern of sex allocation. Although the consequences of cooperative breeding for the evolution of sex allocation and the sex ratio are well understood (Emlen et al. 1986; Pen and Weissing 2000b; Wild 2006), the joint evolution of auxiliary help and sex allocation are not. In our model, the parent who produces an offspring (auxiliary) through female function receives help. This suggests that if we were to track the evolution of sex allocation strategies, we would find bias toward investment in female function (or, for a dioecious species, possibly a female-biased sex ratio). Nevertheless, allowing sex allocation or the sex ratio to evolve should not affect our main conclusion that ecological
constraints exert a principal—rather than supplementary—
influence on its emergence.

One key limitation of our work is that it does not address possible changes in breeder behavior with increasing help. In many cooperatively breeding birds, for example, breeders reduce their workload as helpers take on some of the burden (Hatchwell 1999; Heinsohn 2004; Russell et al. 2008; Santos and Macedo 2011). Adaptive changes like these would certainly detract from the size of the benefit required for auxiliary help to emerge, but should not affect our main conclusion.

A second key limitation of our work is that it only predicts when auxiliary help will emerge—it does not predict the ultimate level at which such help will be provisioned. By focusing on emergence only, we were able to ensure population dynamics could be described in two dimensions which made a powerful set of mathematical results available to us (the theory of planar dynamical systems; see Appendix A). Future work will go beyond the emergence of auxiliary help, and consider the maintenance of help.

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**Appendix A**

**WILD-TYPE DYNAMICS**

**Local results**

In this section, we consider the dimensionless dynamics of a selfish, wild-type population given by system (2) of the main text. Recall that we are only interested in nonnegative solutions to (2).

System (2) of the main text always admits a trivial equilibrium solution, $(0, 0)$. System (2) also admits a positive equilibrium solution $(\bar{x}, \bar{y})$ (equation 4 in the main text) if and only if $R_0 = \frac{Rc}{\mu_r + \delta} > 1$. This subsection is devoted to describing the behavior of solutions to (2) in a small neighborhood around $(0, 0)$ and $(\bar{x}, \bar{y})$, respectively.

Claim 1. The trivial equilibrium solution to (2) is locally asymptotically stable whenever $R_0 < 1$, and unstable whenever $R_0 > 1$.

**Proof.** The Jacobian evaluated at the trivial equilibrium is

$$J_0 = \begin{pmatrix} -\mu_x & -\delta(1-c) \\ 1 & -(\mu_y + \delta) \end{pmatrix},$$

and local asymptotic stability of $(0, 0)$ is assessed by applying the Routh–Hurwitz criteria to this matrix.

It is clear that the trace of $J_0$ is negative. If $R_0 < 1$, then $\delta(1-c) < \mu_x(\mu_y + \delta)$, which implies $\det J_0 > 0$, and it follows that $(0, 0)$ is locally asymptotically stable. If $R_0 > 1$, then $\delta(1-c) > \mu_x(\mu_y + \delta)$, which implies $\det J_0 < 0$, and it follows that $(0, 0)$ is unstable. □

Remark 1. It can also be shown that $J_0$ has two distinct real eigenvalues, given by the formula,

$$\frac{-(\mu_x + \mu_y + \delta) \pm \sqrt{(\mu_x + \mu_y + \delta)^2 - 4 \det J_0}}{2} = \frac{-(\mu_x + \mu_y + \delta) \pm \sqrt{(\mu_x - (\mu_y + \delta))^2 + 4\delta(1-c)}}{2}.$$  

The claim that the eigenvalues are distinct follows from the fact that the discriminant in the previous line is positive.

In the proof to Claim 1, we saw that $\det J_0 < 0$ whenever $R_0 > 1$ (they are, in fact, equivalent statements). In this case, we can also assert that $J_0$ has one positive eigenvalue, and one negative eigenvalue. Thus, $(0, 0)$ is a saddle whenever $R_0 > 1$. We also saw that $R_0 < 1$ implies that the equilibrium $(0, 0)$ is locally asymptotically stable. The fact that the eigenvalues of $J_0$ are real, then, tells us that $(0, 0)$ is a stable node whenever $R_0 < 1$.

Claim 2. The positive equilibrium is a locally asymptotically stable, proper node whenever it exists.

**Proof.** The Jacobian evaluated at the positive equilibrium is

$$\bar{J} = \begin{pmatrix} -\mu_x - \delta(1-c)\bar{y} & \delta(1-c)(1-\bar{x}) \\ 1 + \delta\bar{y} & -(\mu_y + \delta(1-\bar{x})) \end{pmatrix}$$

$$= \begin{pmatrix} -\frac{\delta(1-c) - \mu_x}{\mu_y} & \frac{\mu_y}{(1-c) - \mu_x} \\ \frac{\mu_x(1-c) - \mu_x}{\mu_y + \delta} & -\frac{\mu_y}{(1-c) - \mu_x} \end{pmatrix}.$$

We assess the local asymptotic stability of the equilibrium, here, again using the Routh–Hurwitz criteria.

The trace of $\bar{J}$ is clearly negative, and so to demonstrate stability we need only to show $\det \bar{J} > 0$. If the positive equilibrium exists, then $R_0 > 1$ which implies $\delta(1-c) > \mu_x(\mu_y + \delta)$. It follows that $\det \bar{J} > 0$, and we conclude that the positive equilibrium is locally asymptotically stable.

Informally, an equilibrium is a *node* if each nearby solution is either eventually attracted to it, or initially repelled by it along a well-defined tangent line. If every ray through the equilibrium is tangent to some nearby solution in this way, the equilibrium itself is a *proper node*. To show that the positive equilibrium is a proper node, we consider the discriminant of the characteristic polynomial of $\bar{J}$:

$$\left(\frac{\delta(1-c) - \mu_x}{\mu_y}\right)^2 + \left(\frac{1-c}{1-c} - \frac{\mu_y}{(1-c) - \mu_x}\right)^2 - 2\delta(1-c)$$

$$+ 4\mu_x(\mu_y + \delta) = \left(\frac{\delta(1-c) - \mu_x}{\mu_y} - \frac{\mu_y}{(1-c) - \mu_x}\right)^2$$

$$+ 4\mu_x(\mu_y + \delta).$$

Since the discriminant is strictly positive, we can conclude that the positive equilibrium is a proper node. □

**Global results**

In this section, we focus on the global qualitative behavior of solutions to system (2) from the main text. The first step in our discussion will be to show that the solutions to (2) that interest us can be bounded.

Let us consider the $\dot{y} = 0$ isocline. Equation (2) from the main text indicates that the $\dot{y} = 0$ isocline can be represented by the curve $C = \frac{1}{\mu_r + \delta}$. This curve passes through the origin and the point $(1, 1/\mu_r)$. Furthermore, elementary calculus shows that $C$ is increasing on the unit interval. Our observations about $\dot{y} = 0$ provide a basis for constructing the following open rectangle,

$$\Omega(M) = \{(x, y) \in \mathbb{R}^2 | 0 < x < 1, 0 < y < M\},$$

where $M > 1/\mu_x$ is arbitrary. Note that, when it exists, the positive equilibrium solution to (2) will belong to the set $\Omega(M)$.

If we compute the dot product of $(\bar{x}, \bar{y})$ (equation 2 of the main text) and those vectors that are inward normal to the
boundary of $\Omega(M)$, then we find the following:

\[
\begin{align*}
\langle \dot{x}, \dot{y} \rangle_{x = 0} & \cdot (1, 0)^T = \delta (1 - c) y > 0, \\
0 < y & \leq M \\
\langle \dot{x}, \dot{y} \rangle_{x = 1} & \cdot (-1, 0)^T = \mu_x > 0, \\
0 < y & \leq M \\
\langle \dot{x}, \dot{y} \rangle_{0 < x \leq 1} & \cdot (0, 1)^T = x > 0 \\
y & = 0 \\
\langle \dot{x}, \dot{y} \rangle_{0 < x \leq 1} & \cdot (0, -1)^T = \mu_x M + \delta (1 - x) M - x \\
y & = M
\end{align*}
\]

The dot products above prove the following claim.

**Claim 3.** The rectangle $\Omega(M)$ is forward invariant under solutions to (2).

**Remark 2.** Our proof to Claim 3 also shows solutions to (2) with initial conditions in the closure of $\Omega(M)$, denoted $\mathcal{C}^\ell(\Omega(M))$, remain trapped in this compact subset of $\mathbb{R}^2$ for all dimensionless time $t > 0$. This observation is key, as it ensures the $\omega$-limit sets of the solutions are nonempty, by Theorem 3.2.1 of Perko (1996).

The $\omega$-limit sets of solutions to planar systems of differential equations (i.e., two-dimensional systems like line 2 from the main text) are either equilibrium solutions, periodic solutions, or compound separatrix cycles (Perko 1996). We now turn to Bendixson’s Criteria (Theorem 3.9.1 and Remark 3.9.1 of Perko (1996)) to rule out the possibility that $\omega$-limit sets are composed of anything but equilibrium solutions.

**Claim 4.** The rectangle $\Omega(M)$ contains neither periodic solutions to (2), nor compound separatrix cycles.

**Proof.** Because right-hand side of system (2) from the main text is continuously differentiable on $\Omega(M)$, and because $\Omega(M)$ is a simply connected region of $\mathbb{R}^2$, Bendixson’s criteria apply. We calculate the divergence of $\langle \dot{x}, \dot{y} \rangle$ to find

\[
\text{div} \langle \dot{x}, \dot{y} \rangle = -\mu_x - \delta (1 - c) y - \mu_y - \delta (1 - x) < 0.
\]

If follows immediately that no periodic solution or separatrix cycle lies entirely in $\Omega(M)$. Our conclusion then follows from the fact that $\Omega(M)$ is forward invariant under (2).

We are now able to prove an important claim about the limiting behavior of solutions with initial conditions in $\Omega(M)$.

**Claim 5.** If $R_0 \leq 1$, then solutions with initial conditions in $\Omega(M)$ tend to the trivial equilibrium asymptotically, whereas if $R_0 > 1$ solutions with initial conditions in $\Omega(M)$ tend to the nontrivial equilibrium asymptotically.

**Proof.** The right-hand side of (2) from the main text is continuously differentiable on $\mathbb{R}^2$. By Claim 3 solutions to (2) with initial conditions in $\mathcal{C}^\ell(\Omega(M))$ are contained in this compact subset of $\mathbb{R}^2$. By the Poincaré–Bendixson Theorem, it follows that the $\omega$-limit set of such a solution is either an equilibrium, a periodic solution, or a separatrix cycle. By Claim 4 above, $\Omega(M)$ (indeed $\mathcal{C}^\ell(\Omega(M))$) contains neither periodic solutions nor separatrix cycles, and so solutions with initial conditions in $\mathcal{C}^\ell(\Omega(M))$ must tend toward an equilibrium. When $R_0 \leq 1$ only the trivial equilibrium solution $(0, 0) \in \mathcal{C}^\ell(\Omega(M))$ exists. It follows that all solutions with initial conditions in $\mathcal{C}^\ell(\Omega(M))$ must tend toward $(0, 0)$ whenever $R_0 \leq 1$. If $R_0 > 1$, then both the trivial and nontrivial equilibria exist. Like the trivial equilibrium, the nontrivial equilibrium belongs to $\mathcal{C}^\ell(\Omega(M))$, and no other equilibria occur in this set. Because $R_0 > 1$ implies that the trivial equilibrium is unstable, all solutions with initial conditions in $\mathcal{C}^\ell(\Omega(M))$ must tend toward the non-trivial equilibrium whenever $R_0 > 1$.

**Claim 6.** (Corollary to Claim 5). If $R_0 \leq 1$, then the trivial equilibrium is globally asymptotically stable (GAS), in the sense that solutions with nonnegative initial conditions tend to this equilibrium asymptotically. If $R_0 > 1$, the nontrivial equilibrium is GAS in the same way.

**Proof.** The claim follows from the fact $\Omega(M)$ was constructed using an arbitrarily large $M > 1/\mu_y$.

**Appendix B**

**MUTANT INVASION**

In this section, we develop a condition for a rare, helpful mutant to invade the wild-type population when the wild-type population is at equilibrium $(\bar{x}, \bar{y})$. In this case the dynamics of the heterozygous mutant can be described by the equations

\[
\begin{align*}
\frac{dX_m}{dt} &= -m_x X_m + d(1 - c)(1 - \bar{x}) Y_m \\
\frac{dY_m}{dt} &= -m_y Y_m - d(1 - \bar{y}) Y_m + b X_m + \frac{1}{2} h Z_m \\
\frac{dZ_m}{dt} &= -(m_x + m_y + d(1 - \bar{x})) Z_m + \frac{1}{2} b X_m + \frac{1}{2} h Z_m,
\end{align*}
\]

where $X_m, Y_m, Z_m$ are mutant breeder and auxiliary densities, respectively, $Z_m$ is the density of mutant auxiliaries attending mutant breeders (i.e., joint density of mutant breeders and mutant auxiliaries), and parameters accentuated by a tilde are the mutant analogs to the wild-type counterparts. The parameter $h$ is the rate at which helping increases the oocyte production by a breeder. If
we nondimensionalize as described in the main text, and define \( \tilde{\mu}_y = \tilde{m}_y/b, \tilde{\delta} = \tilde{d}/b, \) and \( \gamma = h/b, \) then we obtain system (5) from the main text.

System (5) of the main text admits a trivial equilibrium solution. The stability of that solution can be determined by using “Next-Generation-Matrix” method described by Hurford et al. (2010). We write the right-hand side of (5) as the product of a matrix and a vector, then we decompose the matrix as \( F - V \) where

\[
F = \begin{pmatrix}
0 & \tilde{d}(1-c)(1-\tilde{x}) \\
\tilde{\mu}_x & 0 & 0 \\
1 & 0 & 1/2 \gamma \\
1 & 0 & 1/2 \gamma
\end{pmatrix}
\]

describes the rate at which new additions are made to each class, and

\[
V = \begin{pmatrix}
\mu_x & 0 & 0 \\
0 & (\tilde{\mu}_y + \delta(1-\tilde{x})) & 0 \\
0 & 0 & (\mu_x + \tilde{\mu}_y + \delta(1-\tilde{x}))
\end{pmatrix}
\]

describes the rate at which individuals leave particular classes. The fate of the mutant is then determined by the spectral radius of the next-generation matrix,

\[
FV^{-1} = \begin{pmatrix}
0 & \frac{\delta(1-c)(1-\tilde{x})}{\tilde{\mu}_y + \delta(1-\tilde{x})} & 0 \\
\frac{1}{\mu_x} & 0 & \frac{1}{2} \mu_x + \tilde{\mu}_y + \delta(1-\tilde{x}) \\
\frac{1}{2} \mu_x & 0 & \frac{1}{2} \mu_x + \tilde{\mu}_y + \delta(1-\tilde{x})
\end{pmatrix}
\]
denoted \( \rho(FV^{-1}). \) If \( \rho(FV^{-1}) > 1, \) the helpful mutant allele invades the population, and if \( \rho(FV^{-1}) < 1, \) it tends toward extinction.

When selection is weak, we can arrive at a very simple expression for \( \rho(FV^{-1}). \) To develop this expression, though, we must consider \( FV^{-1} \) in the absence of selection, that is, when \( \tilde{\mu}_y = \mu_y, \tilde{\delta} = \delta, \) and \( \gamma = 0. \) In the absence of selection the next-generation matrix becomes

\[
F_0V_0^{-1} = \begin{pmatrix}
0 & \psi & 0 \\
1/2N & 0 & 0 \\
1/N & 0 & 0
\end{pmatrix},
\]

where expressions for \( \psi \) and \( N \) are given in the main text. It is easy to determine that \( \rho(F_0V_0^{-1}) = 1, \) and that this eigenvalue is associated with dominant right and left eigenvectors \( u = (\psi, 1/2, 1)^T \) and \( v = (N/2, 1, 0)^T, \) respectively. Assuming weak selection, then, the mutant invades whenever

\[
v^T F_0V_0^{-1} u > v^T u \iff 1 + \frac{1}{2} \frac{\delta(1-c)(1-\tilde{x})}{\tilde{\mu}_y + \delta(1-\tilde{x})} + \frac{\gamma}{4 \mu_x + \tilde{\mu}_y + \delta(1-\tilde{x})} > 1,
\]

and is eliminated whenever the inequality is reversed. The left-hand side of the second inequality presents an expression identical to that found in equation (6) of the main text. A Taylor expansion of the left-hand side of the inequalities found in the previous line (about \( \gamma = 0, \) and assuming \( \tilde{\delta} = \hat{\delta}(\gamma), \tilde{\mu}_y = \hat{\mu}_y(\gamma) \) with \( \hat{\delta}(0) = \delta \) and \( \hat{\mu}_y(0) = \mu_y \) gives

\[
1 + \frac{1}{\hat{\delta}} \frac{\mu_y}{\mu_y + \hat{\delta}(1-\tilde{x})} \frac{d\hat{\delta}}{d\gamma} |_{\gamma=0} + \frac{1}{4 \mu_x + \hat{\mu}_y + \hat{\delta}(1-\tilde{x})} \gamma
\]

to first order in \( \gamma. \) Note that to simplify the previous line, we have used \( \frac{1}{2} \psi \hat{N} = 1. \) Substituting the approximation back into the invasion condition (12) (and using the quotient rule), we see that invasion occurs when

\[
-\frac{\hat{\delta}}{\mu_x + \hat{\delta}(1-\tilde{x})} \frac{d(\hat{\mu}_y/\hat{\delta})}{d\gamma} |_{\gamma=0} + \frac{1}{4 \mu_x + \mu_y + \hat{\delta}(1-\tilde{x})} > 0,
\]

which is the inequality (7) from the main text.