

August 2013

Ecological Constraints and the Evolution of Cooperative Breeding

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ECOLOGICAL CONSTRAINTS AND THE EVOLUTION OF
COOPERATIVE BREEDING
(Thesis format: Integrated Article)

by

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Graduate Program in Applied Mathematics

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

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Abstract

Cooperative breeding is a social behaviour in which certain individuals will opt to delay or forgo their own reproduction in order to help other individuals. Cooperative breeding is one of the most conspicuous examples of cooperation in nature. However, theoretical understanding of why this behaviour occurs is lacking and contradictory. In this thesis, I examine the role played by ecological constraints on the emergence of cooperative breeding. Contrary to previous results, I find that ecological constraints do matter, provided the population dynamics are properly accounted for. I also examine the long-term evolutionary dynamics of cooperative breeding, and obtain the optimal helping strategy from the perspective of both the helper and breeder. I relate existing emergence theory to the predicted trajectory of the optimal strategy, and examine the role of ecology and ecological constraints upon the optimal helping strategy.

Keywords: Cooperative breeding, adaptive dynamics, invasion analysis

Co-Authorship Statement

Chapter 2 is based upon work co-authored with Dr. Geoff Wild, currently in press. Chapter 3 is based upon work co-authored with Dr. Geoff Wild, currently in preparation for publication.

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Chapter 1

Introduction

1.1 Cooperative breeding

Cooperative breeding is a social system in which certain individuals (auxiliaries) postpone or forgo their own reproduction to help other individuals (breeders). Cooperative breeding has been observed in a diverse array of taxa, spanning a wide variety of environments [1–4], and as such, is one of the most conspicuous examples of cooperation in nature. In general, the help provided by auxiliaries can be categorized as either functioning to increase breeder survival or functioning to increase offspring production, the latter of which can be subdivided as increases to breeder fecundity or increases to survivorship of offspring. Engaging in the helping behaviour comes at a cost, typically paid by the auxiliary: for example, auxiliaries could suffer higher mortality [5, 6], or a reduced likelihood of becoming a breeder [7].

1.1.1 Explanations for cooperative breeding

From a naive interpretation of natural selection, cooperative breeding seems somewhat paradoxical. Since the action of helping comes at a cost to the helper, why would an individual be willing to help? Indeed, it is for this reason that cooperative breeding is one of the most widely studied social behaviours. The explanations for why cooperative breeding occurs can be broadly divided into ultimate and proximate mechanisms. Proximate mechanisms include the potential benefits of helping as a learning mechanism for offspring [8], as part of a social hierarchy [9], or as a pathway to territory inheritance [10, 11], while ultimate mechanisms emphasize the role played by indirect fitness gains [12, 13]. Proximate mechanisms certainly play a role in the emergence and maintenance of cooperative breeding, however, the focus of this thesis will be on ultimate, evolutionary mechanisms.

While there are many evolutionary explanations for the emergence of cooperative breed-

ing, most focus on either ecological features or life history characteristics [12–15]. Life history theory focuses on an array of individual attributes such as reproductive rate, dispersal and longevity [14–16]. On the other hand, ecological explanations focus on various environmental attributes that form ‘ecological constraints’; these arguments are generally known as the *Ecological Constraints Hypothesis* (ECH) [13, 17]. The ECH is arguably the most prominent and empirically well-supported theory of cooperative breeding, particularly in avian species [18–20]. The key attribute of the ECH is that limitations such as insufficient breeding opportunities, low probability of finding a mate, low chance of successful independent reproduction, and high cost of dispersal cause cooperative breeding to be selectively advantageous, promoting its emergence [13, 17].

Of course, many aspects of the life history hypothesis and the ECH are not mutually exclusive, and there exists considerable overlap between the two schools of thought [16]. In particular, both emphasize that helpers are simply helping in order to make the best out of a bad situation [13, 14, 20], and that if given a viable opportunity to breed independently, they would take it. As a result, both theories focus on the evolutionary emergence, rather than the evolutionary maintenance, or long-term evolutionary dynamics of cooperative breeding. However, the general and intuitive nature of the constraints featured in the ECH should make it relatable to the evolutionary maintenance under certain circumstances.

Another shortcoming of existing theory is that in general the focus is on the perspective of the auxiliary (but see [17]). This ignores the potential for the breeder to shape, or otherwise exert some control over, the auxiliary’s behaviour. When this occurs through the interaction of the offspring with its mother, it is known as maternal effects [21]. While forcible retention of auxiliaries by breeders is unlikely [17], breeders could exert control through, for example, maternal hormones [21, 22]. Indeed, Russell and Lummaa [21] provide the example of cooperatively breeding meerkats (*Suricata suricatta*), who have varying levels of cortisol based upon group size, levels which are correlated with the amount individuals help [23]. Russell and Lummaa [21] suggest that cortisol could be transferred to developing foetuses, allowing the mother to control the productivity of her offspring. The concept that breeders could exert some control over offspring behaviour is important because it gives rise to potential breeder-auxiliary conflicts [17, 21, 24]. When the costs of helping are paid asymmetrically by auxiliaries (e.g. helping exposes helpers to higher mortality risks), the level of help that is ‘optimal’ for an auxiliary will likely differ from that which is viewed as ‘optimal’ for the breeder.

1.1.2 Evolutionary models of cooperative breeding

Numerous mathematical models have been used to explain the phenomenon of cooperative breeding primarily by focusing on its evolutionary emergence [25–28]. A common drawback of these models has been a failure to explicitly account for population dynamics, a modelling simplification which can yield unrealistic or inaccurate results [29]. More recent work [29, 30], however, did examine cooperative breeding within a population-explicit context. Leggett et al. [30] examined the emergence of cooperative breeding when helping acted to increase breeder survival. Work by Pen and Weissing [29], looked at the role played by ecological constraints and territory inheritance, when helping served to increase fecundity. Pen and Weissing [29] found that the ecological constraints of the ECH do not matter, provided direct benefits such as territory inheritance had been removed. However, their model violated specific criteria of the ECH [13] (see Chapter 2 for detailed explanation). Moreover, there has been no theoretical work studying the long-term evolutionary dynamics of cooperative breeding within a population-dynamic explicit context, and existing work in general assumes auxiliary control of helping (but see [17]).

In this thesis, I address two of these issues. In Chapter 2, I look at the role played by ecological constraints upon the emergence of cooperative breeding, re-examining the conclusions of Pen and Weissing [29]. I find that ecological constraints do matter when explicit population dynamics are modelled, contrary to previous findings [29]. In Chapter 3, I study the long-term evolutionary dynamics of cooperative breeding, and find the optimal helping strategy. I do so under both maternal and auxiliary control of helping, illustrating the scope for breeder-auxiliary conflict. I then relate the predictions made by the ECH for the emergence of cooperative breeding to the predicted trajectories of the optimal helping strategy. In both chapters, I assume the act of helping increases breeder fecundity, but comes at some cost to the auxiliary (e.g. increased mortality, decreased dispersal). Before I begin, I introduce some important tools that the remainder of the thesis relies upon.

1.2 Inclusive fitness

Inclusive fitness is a tool used to understand causal aspects of social evolutionary behaviours [31–34]. Participants in social behaviours can be labelled as either actors (e.g. helpful auxiliaries) or recipients (e.g. breeders). Inclusive fitness focuses on the perspective of the actor engaging in the behaviour, and as such it represents a method of *actor-centered* accounting [31, 32]. Engaging in a social behaviour has consequences: in particular, the actor pays a cost C , typically in terms of loss of its own reproduction, or direct fitness, and by paying

the cost, the actor confers on another individual (i.e. the recipient) some benefit, \mathcal{B} . Because the process under consideration is an evolutionary one, each of these terms must be weighted by relatedness coefficients between the actor and recipient of a particular action (i.e. \mathcal{R}_1 and \mathcal{R}_2). Relatedness is measured as a statistical probability such that any two individuals in a population selected at random should on average have a relatedness of zero [31–33]. As a consequence, highly related individuals have a positive relatedness, while highly unrelated individuals have a negative relatedness. The reason that relatedness is measured as a statistical measure is that while relatedness is often caused by genealogy, selection is indifferent to the specific causal pathway [32]. Combining the above information allows us to arrive at what is known as *Hamilton's rule*, which can be written

$$\mathcal{R}_1 C < \mathcal{R}_2 \mathcal{B}. \quad (1.1)$$

When the inequality (1.1) is satisfied, the frequency of a behaviour in a population should increase. Of course, Hamilton's rule and inclusive fitness simply represent one accounting methodology, and there are others [34]. However, as inclusive fitness interpretations are often preferred by biologists [35–37], for accessibility this thesis will rely upon them to provide evolutionary context.

1.3 Invasion analysis

An *invasion analysis* is a tool for studying phenotypic evolution. Its purpose is to find what the conditions are for a rare mutant allele, say x' , encoding some novel strategy, to invade (i.e. not go extinct) a monomorphic population of individuals practicing strategy $x \neq x'$. A *monomorphic* population implies genetic and phenotypic homogeneity. The monomorphic population is often referred to as the 'resident' or 'wild-type' population. Moreover, it is assumed that the trait continuously varies.

To illustrate this concept mathematically, suppose the density of the resident population at time t is R , and that the dynamics of the resident population in the absence of mutants can be described as

$$\dot{R} = f(x, R) R, \quad (1.2)$$

where the dot denotes differentiation with respect to time. Let $\bar{R} = n(x)$ be the locally or globally stable ecological equilibrium of (1.2). Then by extending (1.2) to include the mutant,

the resident-mutant population dynamics can be described as

$$\begin{aligned}\dot{R} &= f(x, R; x', M) R, \\ \dot{M} &= f(x', M; x, R) M,\end{aligned}\tag{1.3}$$

where M denotes the density at time t of mutants practicing strategy x' . Now, an invasion analysis supposes that since ecological processes occur on a much shorter time scale than evolutionary processes, it is reasonable to assume that sufficient time has elapsed for the ecological processes to be static. In particular, at the instance that the rare mutant enters the population, the wild-type population is at or near a locally stable ecological equilibrium, \bar{R} . Since the mutant is rare, at the point of invasion we assume $M = 0$. This equilibrium, $(R, M) = (\bar{R}, 0)$, is known as the *mutant-free equilibrium* (MFE). Then, to determine whether or not an invasion succeeds, we need to consider the local asymptotic stability of this equilibrium. If it is unstable, then invasion is possible, whereas if it is stable, the rare mutant will go extinct. The Jacobian evaluated at the MFE for system (1.3) is

$$J_{MFE} = \begin{pmatrix} \bar{R} \frac{\partial f(x, \bar{R}; x', 0)}{\partial R} + f(x, \bar{R}; x', 0) & * \\ 0 & f(x', 0; x, \bar{R}) \end{pmatrix}.$$

Matrix J_{MFE} is triangular (in general, block triangular), so the entry $*$ does not affect the stability of the MFE. Moreover, the real part of the first entry is negative by assumption (because the resident equilibrium is locally asymptotically stable). Therefore, the invasion function, or invasion fitness is

$$\lambda(x', x) = f(x', 0; x, \bar{R}).\tag{1.4}$$

Biologically, (1.4) represents the growth rate of a rare mutant in a wild-type population at or near equilibrium. If we are focused on mutant invasion into a selfish population (i.e. evolutionary emergence; this is the focus of Chapter 2), then we are concerned only with the sign of (1.4). That is, if it is positive, the mutant can invade. If negative, the mutant goes extinct.

If we are focused on predicting an optimal strategy (as in Chapter 3), then it is necessary to treat (1.4) as a function, and the analysis becomes more complicated. First, an equilibrium, or *singular strategy* is a strategy in which the local fitness gradient is equal to zero. Such a strategy can be obtained by solving

$$\left. \frac{\partial \lambda(x', x)}{\partial x'} \right|_{x'=x=x^*} = 0.\tag{1.5}$$

The solution to (1.5) can be either a fitness minimum or fitness maximum. This brings us to

our next definition, an *Evolutionary Stable Strategy* (or ESS; [38, 39]). An ESS is a singular strategy, x^* , with the property that no nearby mutant strategy, say x' , where $x' \neq x^*$, can invade [38, 40]. The specific condition for assessing ESS is

$$\left. \frac{\partial^2 \lambda(x', x)}{\partial x'^2} \right|_{x'=x=x^*} < 0. \quad (1.6)$$

Finally, if (1.5) is a non-linear function there is one remaining notation of stability, which is *convergence stability* [41]. In particular, a singular strategy can be considered convergence stable if selection corrects population-level strategy perturbations. The condition for convergence stability is

$$\frac{d}{dx} \left[\left. \frac{\partial \lambda(x', x)}{\partial x'} \right|_{x'=x} \right]_{x=x^*} < 0. \quad (1.7)$$

Of course, different combinations of (1.6) and (1.7) exist. If a strategy satisfies both (1.6) and (1.7), the strategy is called a *continuously stable strategy* [40, 41]. Such a strategy is viewed as a terminal point of evolution. A strategy that is ESS but not convergence stable is referred to as a ‘Garden of Eden’ strategy; these are believed to be rare in nature. A strategy which satisfies (1.7) but is not ESS is called an evolutionary branching point and is a site of potential genetic polymorphisms or speciation events [42, 43].

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Chapter 2

Ecological constraints and the emergence of cooperative breeding ¹

2.1 Summary

Cooperative breeding is a social 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 in order to make the best of a bad situation. Current theoretical support for the ecological constraints hypothesis is lacking. In this chapter, I formulate a mathematical model that emphasizes the underlying ecology of cooperative breeders. My goal is to derive theoretical support for the ecological constraints hypothesis using an ecologically plausible model of population dynamics. I consider a population composed of two kinds of individuals, non-breeders (auxiliaries) and breeders. I suppose that help provided by an auxiliary increases breeder fecundity, but reduces the probability with which the auxiliary becomes a breeder. My main result is an invasion condition that guarantees the evolutionary success of auxiliary help. I predict that increasing the cost of auxiliary dispersal promotes the evolutionary success of helping, in agreement with verbal theory. I also predict that increasing breeder mortality can either hinder the emergence of help (at high population densities), or promote it (at low population densities). Overall, I conclude that ecological constraints can exert influence over the evolution of auxiliary help when population dynamics are considered explicitly; moreover, that influence need not coincide with direct fitness benefits as previously found.

¹A version of this chapter has been accepted for publication [1].

2.2 Introduction

In many cooperatively breeding species, non-breeding 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 [2–5]. Thus, the help provided by non-breeding auxiliaries represents one of the most conspicuous forms of cooperation in nature.

The adaptive significance of auxiliary help is often explained in terms of its direct and indirect fitness benefits [6–10]. Direct benefits of help accrue through the production of descendant offspring. These are realized, for example, when a helpful auxiliary gains valuable parenting experience [11], or when a helpful auxiliary contributes to the formation of a larger, more productive group that it will inherit at some later date [7, 9, 12]. Indirect benefits of help accrue through increased production of related, non-descendant 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 [10]. While both direct and indirect fitness benefits likely promote the evolution of helpful behaviour in cooperatively breeding species [13], I will 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 fitness returns that come from independent breeding attempts. In this way, the ECH views an auxiliary's decision to postpone independent reproduction in order to help relatives as simply making the best out of a bad situation [14]. 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 [15, 16].

While there is substantial empirical evidence to support the ECH [14, 17–20], comprehensive theoretical support is lacking. Early theoretical work supported the hypothesis [16, 21, 22], 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 [23] 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 [23]. Not only does this result run counter to empirical findings, it 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. The objective of this chapter is to show that ecological constraints alone can influence the emergence of auxiliary help – and ultimately cooperative breeding – when explicit population dynamics are taken into account.

In this chapter, I use a mathematical model to investigate the role played by ecological constraints in the emergence of auxiliary help. I 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, I am able to provide ecologically consistent theoretical support for an explanation of cooperative breeding that is widely used in biology. I provide interpretations of my results in terms of inclusive fitness and equilibrium population densities in order to make the predictions amenable to experimental testing.

2.3 Model

2.3.1 Dynamics of a selfish wild-type population

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 non-breeding, or auxiliary, individuals associated with it, and so let $Y \equiv Y(t)$ denote the total density of auxiliaries at time t . 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 the 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 [24]. 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. A dispersing auxiliary successfully establishes itself as a breeder with probability $(1 - c)$, where $0 \leq c < 1$ is the dimensionless cost of dispersal. I assume that once a breeder is established, it remains to breed on its territory for the duration of its life. Dispersal by breeders would not be adaptive because there is nothing to be gained from leaving a territory that has already been secured.

Combining the assumptions listed above, the population dynamics can be described as

$$\begin{aligned}\frac{dX}{dt} &= -m_X X + d(1-c) \frac{K-X}{K} Y, \\ \frac{dY}{dt} &= -m_Y Y - d \frac{K-X}{K} Y + b X.\end{aligned}\tag{2.1}$$

To simplify the analysis, non-dimensionalize (2.1) by defining new variables $x = X/K$, $y = Y/K$, $\tau = bt$, $\mu_x = m_X/b$, $\mu_y = m_Y/b$, and $\delta = d/b$. It follows that (2.1) can be rewritten

$$\begin{aligned}\dot{x} &= -\mu_x x + \delta(1-c)(1-x)y \\ \dot{y} &= -\mu_y y - \delta(1-x)y + x\end{aligned}\tag{2.2}$$

where dots denote differentiation with respect to τ . System (2.2) always admits a trivial equilibrium solution, $(0, 0)$. I will establish the local behaviour of the system before analyzing the global behaviour. First, define

$$R_0 = \frac{\delta(1-c)}{(\mu_y + \delta)} \frac{1}{\mu_x}.\tag{2.3}$$

The expression given by (2.3) is called the basic reproduction number; it describes the expected lifetime reproductive success of an individual in a low-density population. The basic reproduction number is the product of (a) the probability of successful establishment as a independent breeder at low population densities, $\delta(1-c)/(\mu_y + \delta)$, and (b) lifetime reproductive success through both male and female function, weighted by genetic contribution, $(1/2)(2/\mu_x) = 1/\mu_x$.

Local behaviour

Theorem 2.3.1 *The trivial equilibrium solution to (2.2) 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 $(0, 0)$ can be 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.

If $R_0 > 1$, system (2.2) also admits a positive equilibrium solution (\bar{x}, \bar{y}) . Specifically, this solution is

$$\begin{aligned}\bar{x} &= \frac{R_0 - 1}{R_0 - \delta/(\delta + \mu_y)}, \\ \bar{y} &= \frac{R_0 - 1}{R_0} \frac{1}{\mu_y}.\end{aligned}\tag{2.4}$$

By inspection, this solution exists in the positive quadrant if and only if $R_0 > 1$.

Theorem 2.3.2 *The positive equilibrium is a locally asymptotically stable, proper node whenever it exists.*

Proof The Jacobian evaluated at the positive equilibrium is

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

I assess the local asymptotic stability of the equilibrium again using the Routh-Hurwitz criteria.

The trace of \bar{J} is clearly negative, and so to demonstrate stability it is sufficient 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 the positive equilibrium is locally asymptotically stable.

To show that the positive equilibrium is a proper node, consider the discriminant of the characteristic polynomial of \bar{J} :

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

Since the discriminant is strictly positive, the positive equilibrium is a proper node.

Global behaviour

In this section I focus on the global qualitative behavior of solutions to system (2.2). First, I show boundedness. Equation (2.2) indicates that the $\dot{y} = 0$ isocline can be represented by the curve $C = \frac{x}{\mu_y + \delta(1-x)}$. This curve passes through the origin and the point $(1, 1/\mu_y)$. Moreover, elementary calculus shows that C is increasing on the unit interval. Therefore, consider the open rectangle

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

where $M > 1/\mu_y$ is arbitrary. When it exists, the positive equilibrium solution to (2.2) will belong to the set $\Omega(M)$.

Theorem 2.3.3 *The rectangle $\Omega(M)$ is forward invariant under solutions to (2.2).*

Proof Taking the dot-product of $\langle \dot{x}, \dot{y} \rangle$ (from (2.2)) with vectors that are inward normal to the boundary of $\Omega(M)$ yields:

$$\begin{aligned} \langle \dot{x}, \dot{y} \rangle_{\substack{x=0 \\ 0 < y \leq M}} \cdot \langle 1, 0 \rangle^T &= \delta(1-c)y > 0, \\ \langle \dot{x}, \dot{y} \rangle_{\substack{x=1 \\ 0 < y \leq M}} \cdot \langle -1, 0 \rangle^T &= \mu_x > 0, \\ \langle \dot{x}, \dot{y} \rangle_{\substack{0 < x \leq 1 \\ y=0}} \cdot \langle 0, 1 \rangle^T &= x > 0 \\ \langle \dot{x}, \dot{y} \rangle_{\substack{0 < x \leq 1 \\ y=M}} \cdot \langle 0, -1 \rangle^T &= \mu_y M + \delta(1-x)M - x > (1-x)(1+\delta) \geq 0. \end{aligned}$$

It follows that the rectangle $\Omega(M)$ is forward invariant under solutions to (2.2).

The proof to Theorem 2.3.3 also shows solutions to (2.2) with initial conditions in the closure of $\Omega(M)$ ($cl \Omega(M)$) remain trapped in this compact subset of \mathbb{R}^2 for all dimensionless time $\tau > 0$. This ensures the ω -limit sets of the solutions are non-empty [25]. I now turn to Bendixson's Criteria [25], to rule out the possibility that the ω -limit sets are composed of anything but equilibrium solutions.

Theorem 2.3.4 *The rectangle $\Omega(M)$ contains neither periodic solutions, nor compound separatrix cycles to (2.2).*

Proof Since right-hand side of the system (2.2) is continuously differentiable on $\Omega(M)$, and since $\Omega(M)$ is a simply connected region of \mathbb{R}^2 , Bendixson's Criteria apply. Calculating the divergence of $\langle \dot{x}, \dot{y} \rangle$, I obtain

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

It follows immediately that no periodic solution or separatrix cycle lies entirely in $\Omega(M)$.

It is now possible to demonstrate the limiting behavior of solutions with initial conditions in $\Omega(M)$.

Theorem 2.3.5 *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 non-trivial equilibrium asymptotically.*

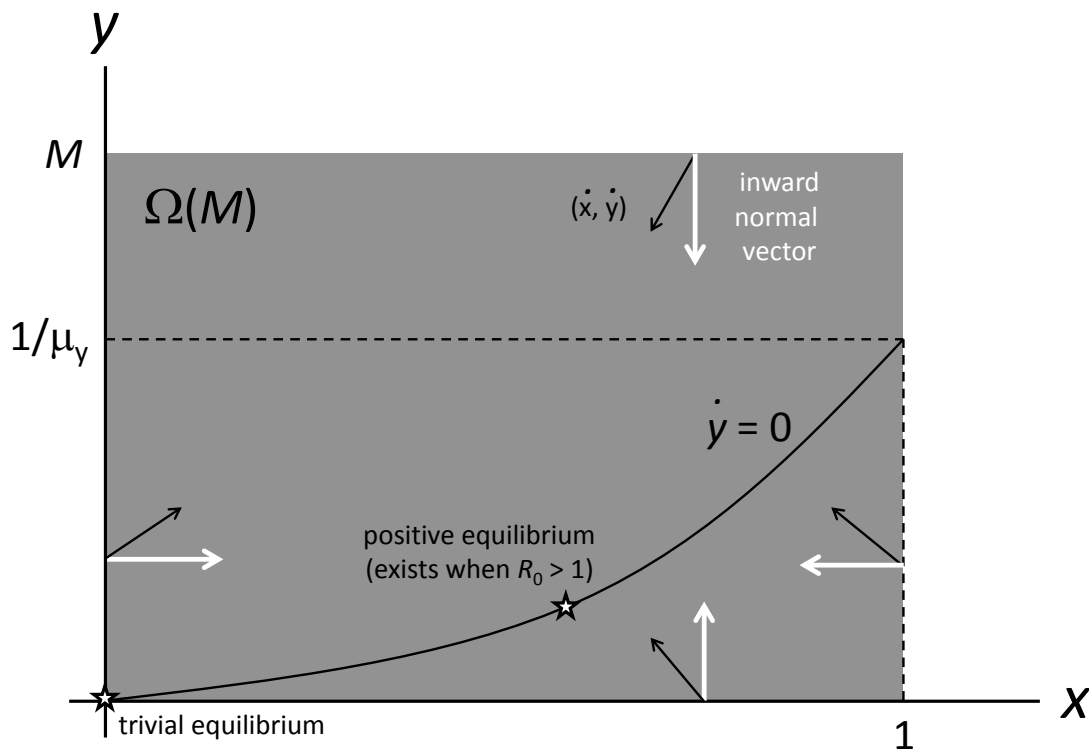


Figure 2.1: A sketch of the rectangle $\Omega(M)$. This region is forward invariant under (2.2); moreover, it contains the positive equilibrium whenever that equilibrium exists.

Proof The right-hand side of (2.2) is continuously differentiable on \mathbb{R}^2 . By Theorem 2.3.3, solutions to (2.2) with initial conditions in $cl\Omega(M)$ are contained in this compact subset of \mathbb{R}^2 . By Poincaré-Bendixson Theorem it follows that the ω -limit set of such a solution is either an equilibrium, a periodic solution, or a separatrix cycle. By Theorem 2.3.4, solutions with initial conditions in $cl\Omega(M)$ must tend toward an equilibrium. When $R_0 \leq 1$ only the trivial equilibrium solution $(0, 0) \in cl\Omega(M)$ exists. It follows that all solutions with initial conditions in $cl\Omega(M)$ must tend toward $(0, 0)$ whenever $R_0 \leq 1$. If $R_0 > 1$, then both the trivial and non-trivial equilibria exist. Like the trivial equilibrium, the non-trivial equilibrium belongs to $cl\Omega(M)$, and no other equilibria occur in this set. Since $R_0 > 1$ implies that the trivial equilibrium is unstable, all solutions with initial conditions in $cl\Omega(M)$ must tend toward the non-trivial equilibrium whenever $R_0 > 1$.

Theorem 2.3.6 (Corollary to Theorem 2.3.5) *If $R_0 \leq 1$, then the trivial equilibrium is glob-*

ally asymptotically stable (GAS), in the sense that solutions with non-negative initial conditions tend to this equilibrium asymptotically. If $R_0 > 1$ the non-trivial equilibrium is GAS in the same way.

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

Therefore, provided $R_0 > 1$, the dimensionless population densities tend toward the equilibrium values:

$$\begin{aligned} x \rightarrow \bar{x} &= \frac{R_0 - 1}{R_0 - \delta/(\delta + \mu_y)}, \\ y \rightarrow \bar{y} &= \frac{R_0 - 1}{R_0} \frac{1}{\mu_y}. \end{aligned} \tag{2.5}$$

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 $\psi N/2 = 1$.

2.3.2 Dynamics of invasion by a helpful mutant

Suppose 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. Furthermore, 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 (3.35), the dynamics of the heterozygous mutant can be described by the equations

$$\begin{aligned} \frac{dX_m}{dt} &= -m_x X_m + \tilde{d}(1 - c)(1 - \bar{x}) Y_m \\ \frac{dY_m}{dt} &= -\tilde{m}_y Y_m - \tilde{d}(1 - \bar{x}) Y_m + bX_m + \frac{1}{2}hZ_m \\ \frac{dZ_m}{dt} &= -(m_x + \tilde{m}_y + \tilde{d}(1 - \bar{x}))Z_m + \frac{1}{2}bX_m + \frac{1}{2}hZ_m, \end{aligned}$$

where X_m and Y_m are mutant breeder and auxiliary densities respectively, Z_m is the density of mutant auxiliaries at breeding sites occupied by mutant breeders (see Appendix A for full

derivation of these equations), and parameters accented 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. Non-dimensionalizing by letting $\tau = bt$, and define $\tilde{\mu}_y = \tilde{m}_y/b$, $\tilde{\delta} = \tilde{d}/b$, and $\gamma = h/b$, then mutant invasion is described by the following linearized system of differential equations:

$$\begin{aligned}\dot{x}_m &= -\mu_x x_m + \tilde{\delta}(1-c)(1-\bar{x})y_m, \\ \dot{y}_m &= -\tilde{\mu}_y y_m - \tilde{\delta}(1-\bar{x})y_m + x_m + \frac{1}{2}\gamma z_m, \\ \dot{z}_m &= -(\mu_x + \tilde{\mu}_y + \tilde{\delta}(1-\bar{x}))z_m + \frac{1}{2}x_m + \frac{1}{2}\gamma z_m.\end{aligned}\tag{2.6}$$

Variables x_m and y_m in equation (2.6) denote the dimensionless densities of heterozygous breeders and auxiliaries, respectively. The variable z_m denotes the density of heterozygous auxiliaries on territories occupied by heterozygous breeders. While these groups can also be formed between wild-type breeders and heterozygous auxiliaries, the effect of such groups on mutant invasion is captured sufficiently by the equation for \dot{y}_m since they do not yield a benefit in terms of production of subsequent mutant offspring. Note that the equation for \dot{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. Since half of these offspring are mutants, the total unassisted rate of mutant offspring production is $(1/2) \times 2 = 1$, 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 (2.6) associated with reproduction through female function only get weighted by $1/2$.

Equation (2.6) also contains re-scaled parameters $\tilde{\delta}$, $\tilde{\mu}_y$, and γ . The parameter γ describes the additive increase in the rate of oocyte output due to the presence of one mutant auxiliary. The parameter $\tilde{\mu}_y$ describes the per-capita mortality rate of a heterozygous mutant auxiliary. Finally, the parameter $\tilde{\delta}$ describes the rate at which a mutant auxiliary disperses at low population densities.

Helping is energetically expensive [8]. To reflect this, assume that the provisioning of help comes at the cost of some combination of higher auxiliary mortality ($\tilde{\mu}_y \geq \mu_y$) and lower auxiliary dispersal ($\tilde{\delta} \leq \delta$). In regards to dispersal, while helpers can disperse at a lower rate than selfish individuals, the model does not force a lower dispersal rate on helpers. In other words, the model allows for dispersal and helping to be treated as independent decisions—a feature that has been advocated elsewhere [12].

In keeping with the ECH, auxiliary help in this 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 [23, 26–28]. Moreover, direct benefits, such as the parenting experience gained by helpful auxiliaries, are neglected so as to focus solely on indirect benefits. Finally, note that auxiliary help is provisioned over a variable period of time, in keeping with assumptions made by previous authors [23].

2.4 Results and Discussion

2.4.1 Invasion fitness

System (2.6) admits a trivial equilibrium solution, which is the so-called mutant free equilibrium (MFE). The stability of the MFE can be determined by using the *next generation matrix method* [29, 30]. In essence, this method involves decomposing a non-singular matrix A , where A is the constant matrix of (2.6), into $A = F - V$, where F and V satisfy three conditions: $F \geq 0$, $V^{-1} \geq 0$, and the spectral bound of $-V$ is $s(-V) < 0$. Provided these conditions are satisfied, then $\rho(FV^{-1}) < 1$ will guarantee that $s(A) < 0$. From a biological perspective, F is generally a matrix containing new additions to the population and V is a matrix containing movement between classes and loss of individuals, however for this chapter I will slightly deviate from the traditional approach and will instead define F as new additions to each class and V as loss of individuals from each class. Importantly, this definition does not alter the validity of the method in any way. Proceeding in this fashion, the decomposition is

$$F = \begin{pmatrix} 0 & \tilde{\delta}(1-c)(1-\bar{x}) & 0 \\ 1 & 0 & \frac{1}{2}\gamma \\ \frac{1}{2} & 0 & \frac{1}{2}\gamma \end{pmatrix}$$

and

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

The fate of the mutant is then determined by the spectral radius of the next-generation matrix,

$$FV^{-1} = \begin{pmatrix} 0 & \frac{\tilde{\delta}(1-c)(1-\bar{x})}{\tilde{\mu}_y + \delta(1-\bar{x})} & 0 \\ \frac{1}{\mu_x} & 0 & \frac{1}{2} \frac{\gamma}{\mu_x + \tilde{\mu}_y + \delta(1-\bar{x})} \\ \frac{1}{2} \frac{1}{\mu_x} & 0 & \frac{1}{2} \frac{\gamma}{\mu_x + \tilde{\mu}_y + \delta(1-\bar{x})} \end{pmatrix},$$

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. While obtaining an explicit condition for $\rho(FV^{-1})$ is possible, in this case it is not easily amenable to biological interpretation. Instead, suppose that selection is weak. That is, the invading strategy only slightly deviates from the resident strategy. Then, obtaining an condition for invasion is easy [31]. To do so, I must consider FV^{-1} in the absence of selection (i.e. when $\tilde{\mu}_y = \mu_y$, $\tilde{\delta} = \delta$, and $\gamma = 0$). In the absence of selection the next-generation matrix becomes

$$F_0V_0^{-1} = \begin{pmatrix} 0 & \psi & 0 \\ \frac{1}{2}N & 0 & 0 \\ \frac{1}{4}N & 0 & 0 \end{pmatrix}.$$

It is trivial to determine that $\rho(F_0V_0^{-1}) = 1$, and that this eigenvalue is associated with the dominant right and left eigenvectors $\mathbf{u} = \langle \psi, 1, 1/2 \rangle^T$ and $\mathbf{v} = \langle N/2, 1, 0 \rangle^T$, respectively. That the dominant eigenvalue in the absence of selection is 1 is expected, as linear approximations are expected to fail in this case.

Assuming weak selection, the mutant invades whenever

$$\mathbf{v}^T FV^{-1} \mathbf{u} > \mathbf{v}^T \mathbf{u} \Leftrightarrow \frac{1}{2}N \frac{\tilde{\delta}(1-c)(1-\bar{x})}{\tilde{\mu}_y + \tilde{\delta}(1-\bar{x})} + \frac{1}{4} \frac{\gamma}{\mu_x + \tilde{\mu}_y + \tilde{\delta}(1-\bar{x})} > 1, \quad (2.7)$$

and is eliminated whenever the inequality is reversed. In analogy to $\psi N/2$ as described previously for wild-type individuals, the first term of (2.7) is the product of (a) the probability that a mutant auxiliary recruits to the breeding class, $\tilde{\delta}(1-c)(1-\bar{x})/[\tilde{\mu}_y + \tilde{\delta}(1-\bar{x})]$, and (b) 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 (2.7) is the product of (a) the probability that the focal mutant was produced through the female function of its mutant parent, $1/2$, and (b) the expected number of mutant offspring the focal mutant helps to produce during the time spent as a productive helper, $(\gamma/2)/[\mu_x + \tilde{\mu}_y + \tilde{\delta}(1-\bar{x})]$. 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 because I have applied a weak selection approximation.

2.4.2 Inclusive fitness effects

Regardless of the genotypic differences that might occur among nestmates, auxiliaries are always helping to raise kin (half-siblings), and so it is expected that the invasion condition will

yield an inclusive-fitness interpretation. When the effect of selection is weak, a Taylor expansion of the left-hand side of (2.7) about $\gamma = 0$, and assuming $\tilde{\delta} \equiv \tilde{\delta}(\gamma)$, $\tilde{\mu}_y \equiv \tilde{\mu}_y(\gamma)$ with $\tilde{\delta}(0) = \delta$ and $\tilde{\mu}_y(0) = \mu_y$, gives

$$1 + \left(\frac{1}{\delta} \frac{\mu_y}{\mu_y + \delta(1 - \bar{x})} \frac{d\tilde{\delta}}{d\gamma} \Big|_{\gamma=0} - \frac{1}{\delta} \frac{\delta}{\mu_y + \delta(1 - \bar{x})} \frac{d\tilde{\mu}_y}{d\gamma} \Big|_{\gamma=0} + \frac{1}{4} \frac{1}{\mu_x + \mu_y + \delta(1 - \bar{x})} \right) \gamma$$

to first-order in γ . Note that to simplify the previous line the relation $\frac{1}{2}\psi N = 1$ was used. Substituting the approximation back into the invasion condition (and using the quotient rule), then when the effect of selection is weak, invasion occurs if

$$- \underbrace{\frac{1}{2}}_{\mathcal{R}_1} \underbrace{\psi N \frac{\delta}{\mu_y + \delta(1 - \bar{x})} \frac{d(\tilde{\mu}_y/\tilde{\delta})}{d\gamma} \Big|_{\gamma=0}}_C + \underbrace{\frac{1}{4}}_{\mathcal{R}_2} \underbrace{\frac{1}{\mu_x + \mu_y + \delta(1 - \bar{x})}}_B > 0 \quad (2.8)$$

which is Hamilton's rule [32], modified for cooperative breeders, $\mathcal{R}_1 C < \mathcal{R}_2 B$ [6]. The first term in (2.8) is the marginal reduction in reproductive success through independent breeding incurred by the mutant auxiliary ($C > 0$), weighted by the relatedness between the auxiliary and its potential offspring ($\mathcal{R}_1 =$ probability that any offspring produced by the focal mutant auxiliary would also be a mutant). The second term in (2.8) corresponds to the marginal benefit of auxiliary help ($B > 0$), weighted by the relatedness between the helpful auxiliary and the offspring produced via help ($\mathcal{R}_2 =$ probability of the event that the mutant auxiliary was born on the territory occupied by its mutant parent, and that any offspring it helps to raise on that territory is also a mutant). Regardless of the interpretation used, the invasion condition (2.8) can be rewritten as

$$\frac{1/(\mu_x + \mu_y + \delta(1 - \bar{x}))}{1/(\mu_y + \delta(1 - \bar{x}))} > 4 \delta \frac{d(\tilde{\mu}_y/\tilde{\delta})}{d\gamma} \Big|_{\gamma=0} \quad (2.9)$$

or equivalently,

$$\frac{1}{4} \frac{1}{\delta} \frac{\mu_y}{(1 - \frac{\mu_x}{1-c})\mu_x + \mu_y} > \frac{d(\tilde{\mu}_y/\tilde{\delta})}{d\gamma} \Big|_{\gamma=0} \quad (2.10)$$

where I have relied on the fact that with weak selection γ is small and $\tilde{\mu}_y \approx \mu_y$ and $\tilde{\delta} \approx \delta$. Condition (2.9) shows that the model predicts that the fate of the rare mutant is influenced by the tension between the expected amount of time spent as a productive helper (numerator, left-hand side), and the expected time spent as an auxiliary (denominator, left-hand side). Condition (2.10) shows the importance of ecological constraints. Specifically, it is clear that the ecological parameters such as cost of dispersal, c , and breeder mortality, μ_x , that simplified out of Pen and Weissing's [23] condition for the emergence of auxiliary help are present. Moreover, at equilibrium the parameter μ_x can be interpreted as the probability of establishment ψ (this is

because $1 = (1/2) \psi N = (1/2) \psi (2/\mu_x) = \psi (1/\mu_x)$, which is considered to be a key ecological constraint of the ECH [15]. In short, the model reveals that ecological constraints do influence the emergence of cooperative breeding.

Inequalities (2.9) and (2.10) also show that the invasion condition can be thought of as an upper bound on the rate at which the immediate costs of mutant behavior are incurred when mutant helping has a small effect on breeder fecundity. It follows that cooperation is promoted (resp. hindered) as the upper bound is increased (resp. decreased). I now investigate the specific effects of the ecological components of the model.

2.4.3 Cost of dispersal

Differentiating the left-hand side of (2.10) with respect to cost of dispersal, c , and maintaining $R_0 > 1$, it is clear that increasing the cost of dispersal promotes cooperation at a rate proportional to

$$\frac{1}{4} \frac{1}{\left(1 - \frac{\mu_x}{1-c}\right) \mu_x + \mu_y} \frac{\delta}{\mu_y + \delta} \frac{\mu_y}{\mu_y + \delta} \frac{1}{R_0^2} \quad (2.11)$$

(recall that $R_0 > 1$ implies $\mu_x < 1 - c$). Line (2.11) shows that the effect of increasing c is strongest when $R_0 \approx 1$. This finding is also reflected in Figure 2.2 (top panel) where the effect of increased c is most pronounced as R_0 approaches 1 from above. In agreement with the expressions in (3.35), my results show that the pronounced effect of c is associated with moderate-to-low occupancy of breeding territories, and moderate-to-low densities of auxiliaries (Figure 2.2, middle panel, bottom panel). Therefore the 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.

2.4.4 Breeder mortality

Differentiating the left-hand side of (2.10) with respect to the breeder mortality parameter, μ_x , and maintaining $R_0 > 1$, 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, increasing breeder mortality hinders cooperation when $R_0 > 2\delta/(\delta + \mu_y)$, and promotes cooperation when the inequality is reversed (Figure 2.3, top panel).

Biologically speaking $R_0 > 2\delta/(\delta + \mu_y)$ (resp. $R_0 < 2\delta/(\delta + \mu_y)$) corresponds to a population with relatively high (resp. low) densities. As a result, the model predicts that increases in breeder mortality rate will hinder the emergence of cooperation in populations with relatively

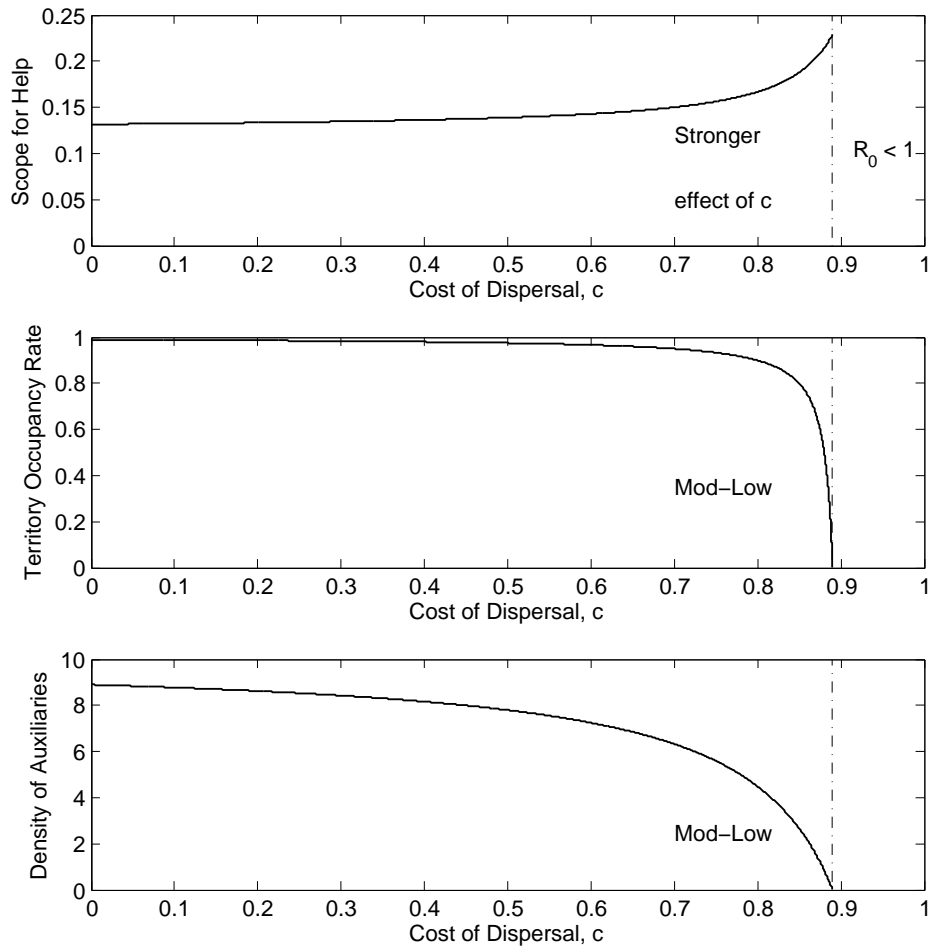


Figure 2.2: The scope for the emergence of help increases monotonically with the increasing cost of dispersal c . The effect exerted by increasing c is weak when territory occupancy rates and population densities are relatively high (i.e. when c is relatively small, and R_0 is relatively large). The 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.

high population densities, but will promote cooperation in low-density populations (Figure 2.3, 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 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 (3.35) the parameter μ_x can be interpreted 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, since larger ψ implies that helping is more costly (i.e. more is being sacrificed by the helpful auxiliary) [16]. The fact that increasing $\psi = \mu_x$ can sometimes promote and sometimes hinder the emergence of auxiliary help shows that the relationship between ψ 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, these results illustrate a key advantage of pursuing ecologically explicit accounts of evolution: these models are able to elucidate the complex interrelationships among ecological parameters, where other less explicit models naively treat such quantities as independent.

2.4.5 Auxiliary mortality and dispersal

(2.10) cannot be used to study the effect of changes in auxiliary mortality rate, μ_y , and dispersal rate, δ , because μ_y and δ appear on both sides of the inequality. Therefore, we must collect all terms in μ_y and δ on one side of the invasion condition. For clarity and convenience, I 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

$$\frac{1}{4} \frac{\delta}{(1 - \frac{\mu_x}{1-c})\mu_x + \mu_y} > - \left. \frac{d\tilde{\delta}}{d\gamma} \right|_{\gamma=0}. \quad (2.12)$$

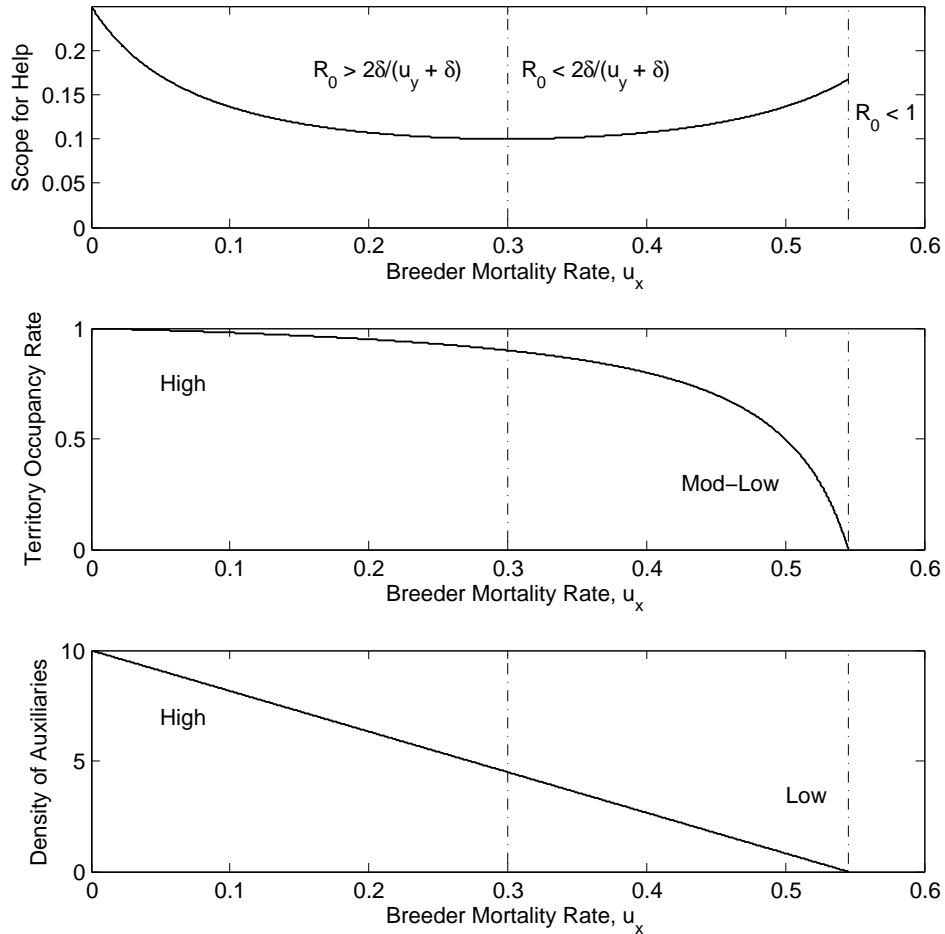


Figure 2.3: The scope for the emergence of help is affected by increasing breeder mortality μ_x in a non-monotonic manner. When territory occupancy rates and population densities are large (i.e. when μ_x is small and R_0 large), increasing μ_x reduces the scope for help. When territory occupancy rates and population densities are low (i.e. when μ_x is large and R_0 small), increasing μ_x increases the scope for help. The qualitative effect of increasing μ_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 μ_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.

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

$$\frac{1}{4} \frac{\mu_y}{(1 - \frac{\mu_x}{1-c})\mu_x + \mu_y} > \left. \frac{d\tilde{\mu}_y}{d\gamma} \right|_{\gamma=0}. \quad (2.13)$$

In the first case, increasing μ_y clearly decreases the left-hand side of the invasion condition (2.12). Consequently, increases to auxiliary mortality inhibit the emergence of cooperation. In the second case, increasing μ_y increases the left-hand side of the invasion condition (2.13), and so higher auxiliary mortality promotes cooperation. Returning to (2.12), it is clear that increasing δ increases the threshold for invasion of helping to occur. Changes to δ have no impact in (2.13).

In general, it can be expected that $\tilde{\delta}$ and $\tilde{\mu}_y$ could trade off with γ in any number of ways. Hence, increasing δ and μ_y will have a variable effect on mutant invasion—one that depends on the nature of the trade-off.

2.5 Concluding Remarks

The ECH is an empirically well-supported explanation for the adaptive significance of cooperative breeding [14, 17–20]. 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 [16, 21, 22]. 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 [23]. This more recent result suggests that ecological constraints are of secondary importance to other explanations.

In this Chapter, I present an explicit account of population dynamics, and use that account to derive an ecologically reasonable measure of helper fitness. The model purposefully neglects local factors such as territory inheritance, and direct benefits of helping such as gained parenting experience, in order to focus solely on the importance of ecological constraints.

My 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, μ_x . Ecological constraints can influence the emergence of cooperative breeding without additional direct-fitness benefits like territory inheritance. In particular, I find that increased cost of dispersal acts as an incentive for auxiliary help, as originally suggested by Emlen [15, 16]. Changes to breeder mortality (equivalently, probability of establishment ψ , at equilibrium) have a variable effect that depends on the tension between the expected time spent as a productive helper on

the one hand, and expected time spent in the auxiliary class on the other hand. Lastly, I find that other life history parameters, such as auxiliary dispersal rate (δ) and auxiliary mortality rate (μ_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.

I was able to frame my qualitative results concerning ecological constraints in terms of the occupancy rate of breeding territories (\bar{x}), and the density of auxiliaries (\bar{y}). These results indicate that the cost of dispersal exerts greatest influence in populations with low-to-moderate occupancy rates, and low-to-moderate auxiliary densities. They also predict that increases to μ_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 ψ , N , and \bar{x}) 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 my 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) in order to exert influence over the emergence of auxiliary help. This conclusion differs from conclusions made by other theoretical treatments of cooperative breeding that have incorporated population dynamics. The model proposed by Pen and Weissing [23] 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, my model did not explicitly consider a “waiter” stage. Instead it 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 my model could affect helpful and selfish auxiliaries differently, and were not fated to cancel out of the calculations. Since “waiters” or “floaters” are simply dispersers that have not yet secured a breeding territory [33], my 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. I chose to ignore many features of the biology of cooperative breeders (e.g. parenting ex-

perience, local competitive effects, territory inheritance, issues concerning variable levels of promiscuity) in order to focus on the ECH. Granted, some assumptions were made in order to keep the model as simple as possible. In particular, I chose to model cooperative breeders as hermaphrodites with an evolutionarily fixed pattern of sex allocation. While the consequences of cooperative breeding for the evolution of sex allocation and the sex ratio are well understood [27, 34, 35], the joint evolution of auxiliary help and sex allocation are not. In my model, the parent who produces an offspring (auxiliary) through female function receives help. This suggests that if I was to track the evolution of sex allocation strategies I 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 the main conclusion that ecological constraints exert a principal – rather than supplementary – influence on the emergence of cooperative breeding.

One key limitation of my work is that it does not address possible changes in breeder behaviour with increasing help. In many cooperatively breeding birds, for example, breeders reduce their workload as helpers take on some of the burden [36–38]. Adaptive changes like these would certainly detract from the size of the benefit required for auxiliary help to emerge, but should not affect my main conclusion.

A second key limitation of my 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 I was able to ensure population dynamics could be described in two dimensions which made a powerful set of mathematical results available. Future work will go beyond the emergence of auxiliary help, and consider the maintenance of help.

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Chapter 3

Evolutionary dynamics of cooperative breeding

3.1 Summary

Cooperative breeding is a social system in which certain individuals (auxiliaries) postpone or forgo their own reproduction to help other individuals (breeders). The evolutionary motivation for this behaviour has been considerably debated, but the debate has focused on models that neglect long-term evolutionary dynamics. As a result, there is little theoretical understanding of how emergence theory relates to the maintenance of cooperative breeding and optimal strategies, how optimal strategies relate to ecology, and the scope for breeder-auxiliary conflict, particularly when costs are paid by auxiliaries (i.e. helping causes higher mortality). In this chapter, I use an adaptive dynamics approach to explicitly model the long-term evolution of cooperative breeding when help is under either maternal or auxiliary control. I then use the Ecological Constraints Hypothesis (ECH), a well-known theory for the emergence of cooperative breeding, to provide context for the predicted trajectory of the optimal strategy. I find that the predictions made by the ECH for the effect of ecology upon the emergence of helping can be related to the effect of ecology upon the optimal strategy – provided helpers are ‘making the best of a bad situation’. When fitness returns from helping are sufficiently large, the motivation for helping changes, and the ECH does not apply.

3.2 Introduction

Cooperative breeding is a social system in which certain non-breeding individuals (i.e. auxiliaries) postpone or forgo their own reproduction to help breeding individuals. In many species,

auxiliary help increases breeder fecundity [1–5], yet providing help comes at some cost, such as exposing auxiliaries to greater mortality risks [6–8]. Why an individual would opt to help another instead of behaving selfishly represents a fundamental question of biology, and as a result, has been studied extensively [9–12].

While there are many evolutionary explanations for the emergence of cooperative breeding [10, 12–14], and a large body of modelling work [15–18], very little has been done on the long-term evolution of cooperative breeding, that is, what constitutes an optimal helping strategy, rather than what conditions promote the emergence of helping. The few models that have considered optimal strategies [16], did so without explicitly accounting for population dynamics, an approach that can produce misleading or ecologically unrealistic results [17]. As a consequence, there are many unanswered questions about the evolution of cooperative breeding. In particular: i) what is the range of ecological conditions and optimal strategies that can be explained by extending existing emergence theory, ii) what the relationship between the ecology and the optimal strategy is, and iii) because costs are often asymmetrically paid by auxiliaries, the scope for breeder-auxiliary conflict [15, 19]. Theoretical understanding of these questions is prerequisite to the understanding of the evolution of higher level social organization and transitions to more complicated breeding systems, such as obligate cooperative breeding.

Clearly, existing theory for the emergence of helping should, under certain conditions, be able to predict the optimal strategy and the maintenance of cooperative breeding. As such, existing emergence theory should provide context for the long-term evolutionary dynamics of cooperative breeding. Arguably the most prominent evolutionary explanation for the emergence of cooperative breeding is the Ecological Constraints Hypothesis, or ECH [9, 10, 15]. The ECH argues that the decision to help is motivated by constraints on independent breeding, specifically: a high cost of dispersal, a low probability of securing a breeding territory, and low expected fecundity as an independent breeder [10, 15]. The ECH emphasizes that auxiliaries help in order ‘make the best of a bad situation’, and if given a viable opportunity, would breed independently [20]. While helpers may initially help in order to ‘make the best of a bad situation’, it is not necessarily true that this will persist with escalating levels of help, or that the constraints will facilitate higher levels of help in the same way that they are predicted to promote the emergence. Moreover, there is considerable scope for maternal-auxiliary conflict: if the auxiliaries bear the brunt of the costs of helping (e.g. increased mortality), then there should exist a discrepancy between the optimal level of help under auxiliary control versus maternal control [15, 19, 21]. Despite these drawbacks, the general and intuitive nature of the constraints of the ECH makes them useful measures to contextualize the evolutionary dynamics of cooperative breeding.

The objective of this chapter is to determine the optimal cooperative breeding strategy and relate it to: i) the scope for breeder-auxiliary conflict, ii) the ecology of the system, and iii) the ECH. To do so, I consider a population consisting of breeders and auxiliaries, and suppose that by helping, auxiliaries increase breeder fecundity. I use an explicit population dynamic model on which I conduct a full evolutionary analysis. I investigate the role played by the ecology and the ecological constraints of the ECH [10, 15] upon the optimal strategy. I find that provided helpers are ‘making the best of a bad situation’ [20], the predictions of the ECH for the emergence of cooperative breeding can explain the trajectory of the optimal strategy. However, my analysis reveals that there exists a critical value at which helping yields equivalent fitness returns to breeding: above this value, helpers are no longer simply ‘making the best of a bad situation’ and the predicted relationship between the ECH and optimal level of help breaks down.

3.3 Wild-type population

The model population consists of diploid hermaphrodites experiencing continuously overlapping generations. I focus on hermaphrodites to simplify the analysis, but my results will apply to dioecious species with an evolutionarily fixed pattern of sex allocation. Individuals in the population are classified as either breeders or auxiliaries, and I denote their densities at time t as B and A , respectively. Breeders produce male gametes (sperm) and female gametes (oocytes) through fair meiosis. I assume that breeder production of oocytes occurs at a per-capita rate α . Each oocyte is fertilized independently by a uniform random breeder in the population. The assumption that the population is outcrossed is intended to mimic cooperatively breeding species who avoid inbreeding [22].

While there are many forms of cooperative breeding [23, 24], I assume that cooperation in my population occurs in a ‘kin neighbourhood’ system [20, 23, 24]. Kin neighbourhoods are opportunistic, flexible aggregates of individuals in which helpers tend to associate with specific groups of breeders, rather than with their natal site [24]. Kin neighbourhood systems represent a substantial proportion of cooperatively breeding birds [23, 24], and in avian species these loose affiliations are often referred to as ‘clans’ or ‘coteries’ [24–26]. Using a ‘kin neighbourhood’ system will reduce the dimensionality of the model and make the mathematics more tractable.

Because the focus is kin neighbourhood cooperative breeding, I suppose that auxiliaries are imprinted on the phenotype of their ‘mother’. Since each type of ‘mother’ is comprised of identical individuals, on average each individual mother can expect the same amount of help as other mothers of the same type, and so helping is evenly allocated within phenotype. A key

component of this assumption is that I do not model a class of ‘waiter’ or ‘floater’ auxiliaries as has been done elsewhere [17, 27]. While certain species do develop ‘waiter’ classes, it is not essential to the emergence or evolution of cooperative breeding [28]. Help provided by auxiliaries increases breeder oocyte production at an additive rate $h \geq 0$ ($h = 0$ corresponds to a selfish population).

Density-dependent fecundity can act as a limitation to population growth in cooperatively breeding species [1, 3], so I assume that oocytes instantaneously develop into auxiliaries at a density-dependent per capita rate of $\frac{\kappa_1}{\kappa_1 + A}$ where κ_1 is a positive parameter. I suppose the environment can only support a limited density of breeders, hence auxiliaries recruit to the breeding class at a per-capita rate of $\frac{d\kappa}{\kappa + B}$, where d and κ are positive parameters. In keeping with the ECH [10], I allow dispersal to come at a cost, c , therefore successful recruitment occurs with probability $(1 - c)$. Upon successful recruitment, an individual remains a breeder for the remainder of their life. Helping is a costly behaviour [8]. To account for this, I let the per-capita rate of auxiliary mortality be a strictly increasing function of h , that is $\mu(h)$, a trade-off in many cooperatively breeding species [6, 7]. Finally, breeders die at a per-capita rate of m_B . To reduce the number of parameters in the model, I non-dimensionalize by letting $\tau = \alpha t$ and then define new non-dimensionalized parameters as $b = h/\alpha$, $\mu_B = m_B/\alpha$, and $\nu = d/\alpha$. Therefore, the monomorphic wild-type population dynamics can be described as

$$\begin{aligned} \dot{B} &= -\mu_B B + \frac{(1-c)\nu\kappa}{\kappa+B}A, \\ \dot{A} &= -\mu(b)A + \frac{\kappa_1}{\kappa_1+A}(B+bA) - \frac{\nu\kappa}{\kappa+B}A, \end{aligned} \quad (3.1)$$

where dots denote differentiation with respect to τ . We are only interested in non-negative solutions of (3.1). System (3.1) always admits a trivial equilibrium, $(0, 0)$. Denote the expected life-time reproductive success (LRS), or basic reproduction number, of an individual at low-densities as

$$R_0 = \frac{(1-c)\nu}{\mu(b) + \nu} \left(\frac{b}{(1-c)\nu} + \frac{1}{\mu_B} \right). \quad (3.2)$$

The basic reproduction number, R_0 , is the product of i) the probability of successful establishment as a independent breeder at low population densities, $\nu(1-c)/(\mu(b) + \nu)$, and ii) lifetime reproductive success through both male and female function, weighted by genetic contribution, $(1/2)(2b/((1-c)\nu) + 2/\mu_B)$. From the quantity given by (3.2), I can make the following statement about the trivial equilibrium:

Theorem 3.3.1 *The trivial equilibrium solution to (3.1) is locally asymptotically stable whenever $R_0 < 1$, and unstable whenever $R_0 > 1$.*

Proof The Jacobian evaluated at the trivial equilibrium is

$$J_0 = \begin{pmatrix} -\mu_B & (1-c)\nu \\ 1 & -(\mu(b) + \nu) + b \end{pmatrix},$$

and I assess local asymptotic stability of $(0, 0)$ by using the Routh-Hurwitz criteria. For stability, we require that $\text{Tr } J_0 = -(\mu_B + \mu(b) + \nu) + b < 0$, and $\det J_0 = \mu(b) + \nu - b - \frac{(1-c)\nu}{\mu_B} > 0$. It is clear that the limiting condition is $\det J_0 > 0$. This can be rearranged such that if $R_0 < 1$ then the equilibrium is stable. Therefore, the trivial equilibrium is stable when $R_0 < 1$, and unstable whenever $R_0 > 1$.

Now, note that there are no possible solutions to (3.1) where either $\bar{B} = 0$ or $\bar{A} = 0$ and $\bar{A} \neq 0$ or $\bar{B} \neq 0$. Therefore, suppose that $\bar{B} \neq 0$ and $\bar{A} \neq 0$, then $\bar{A} = \frac{\mu_B}{(1-c)\nu\kappa} \bar{B} (\kappa + \bar{B})$, and \bar{B} is the roots of the cubic polynomial

$$\frac{\mu(b)}{\kappa(\mu(b) + \nu)} \bar{B}^3 + \left(1 + \frac{\mu(b)}{\mu(b) + \nu}\right) \bar{B}^2 + \left(\kappa - \frac{(1-c)\nu\kappa_1 b - \mu(b)}{\mu(b) + \nu} \frac{1}{\mu_B}\right) \bar{B} - \kappa_1 \kappa \frac{\nu(1-c)}{\mu_B} (R_0 - 1).$$

Theorem 3.3.2 *When $R_0 > 1$, there is a unique, positive non-trivial equilibrium, (\bar{B}, \bar{A}) .*

Proof Suppose we rewrote the cubic polynomial (3.3) as $a_0 \bar{B}^3 + a_1 \bar{B}^2 + a_2 \bar{B} + a_3$. Then if $R_0 > 1$, $a_3 < 1$. Since a_0 and a_1 are strictly positive, irrespective of whether or not a_2 is positive or negative, if $R_0 > 1$ there is only one sign change amongst the ordered coefficients of the polynomial (3.3). Therefore, by Descartes' rule of signs, if $R_0 > 1$, there is a unique, positive root of (3.3), and hence only one positive non-trivial equilibrium of (3.1).

I now establish that (3.1) is a biologically well-behaved model.

Theorem 3.3.3 *The system given by (3.1) is positive and bounded.*

Proof For positivity, I calculate the dot-product of system (3.1) with vectors that are inward normal to the axes of the positive quadrant

$$\left\langle \dot{B}, \dot{A} \right\rangle_{\substack{B=0 \\ A>0}} \cdot \langle 1, 0 \rangle^T = (1-c)\nu A > 0, \quad (3.3)$$

$$\left\langle \dot{B}, \dot{A} \right\rangle_{\substack{B>0 \\ A=0}} \cdot \langle 0, 1 \rangle^T = B > 0. \quad (3.4)$$

It follows immediately that positivity is satisfied. To prove boundedness, I do so by contradiction. Suppose $B(\tau)$ becomes unbounded. Then when $\tau \rightarrow \infty$, $\dot{B} > 0$, and so $\mu_B B <$

$(1 - c)v\kappa/(\kappa + B)A$. If true, I can construct an upperbound for \dot{A} , \dot{A}^u , as

$$\dot{A} = -\mu(b)A + \frac{\kappa_1}{\kappa_1 + A}(B + bA) - \frac{(1 - c)v\kappa}{\kappa + B}A, \quad (3.5)$$

$$< -\mu(b)A + \frac{\kappa_1}{\kappa_1 + A}(B + bA) - \mu_B B, \quad (3.6)$$

$$< -\mu(b)A + B + b\kappa_1 - \mu_B B = \dot{A}^u. \quad (3.7)$$

Solving \dot{A}^u , I obtain

$$A^u(\tau) = \frac{\int [B(\tau) + b\kappa_1 - \mu_B B(\tau)] e^{\mu(b)\tau} d\tau + A_0}{e^{\mu(b)\tau}}. \quad (3.8)$$

Since $\mu(b) > 0$, $\lim_{\tau \rightarrow \infty} e^{\mu(b)\tau} = \infty$. Therefore, if the numerator of (3.8) remains finite, then $\lim_{\tau \rightarrow \infty} A^u(\tau) \rightarrow 0$ which implies that $B(\tau)$ is bounded, a contradiction. Suppose instead that the numerator of (3.8) becomes unbounded. Then by l'Hospital's rule

$$\lim_{\tau \rightarrow \infty} A^u(\tau) = \frac{B(\tau) + b - \mu_B B(\tau)}{\mu(b)} \quad (3.9)$$

So $A^u(\tau) < \frac{B(\tau)+b}{\mu(b)}$. Using this upperbound of A^u in \dot{B} :

$$\dot{B} = -\mu_B B(\tau) + \frac{(1 - c)v\kappa B(\tau) + b}{\kappa + B(\tau)} \frac{b}{\mu(b)}, \quad (3.10)$$

$$< -\mu_B B(\tau) + \frac{v\kappa}{\mu(b)} + \frac{bv}{\mu(b)}, \quad (3.11)$$

with solution

$$B(\tau) \leq \frac{1}{\mu_B} \left(\frac{v\kappa}{\mu(b)} + \frac{bv}{\mu(b)} \right) + e^{-\mu_B \tau} B_0 \quad (3.12)$$

which is finite. So $B(\tau)$ cannot become unbounded. Suppose $B(\tau)$ is bounded and $A(\tau)$ becomes unbounded. This implies that as A becomes large

$$\dot{A} = -\mu(b)A + \frac{\kappa_1}{\kappa_1 + A}(B + bA) - \frac{v\kappa}{\kappa + B}A \quad (3.13)$$

$$< -\mu(b)A + b = \dot{A}^u \quad (3.14)$$

and this has solution $A^u(\tau) = \frac{b}{\mu(b)} + A_0 e^{-\mu(b)\tau}$ which is bounded, so I again arrive at a contradiction. Therefore the system is bounded.

Now, define the following open rectangle,

$$\Omega(M) = \{(A, B) \in \mathbb{R}^2 \mid 0 < B < M, 0 < A < M\}, \quad (3.15)$$

where $M > 0$ is arbitrary. It is apparent that $\Omega(M)$ is an open, simply connected region of \mathbb{R}^2 . Then by Theorem 3.3.3, all solutions of (3.1) in $\Omega(M)$ are positive and bounded, which is also the proof to the following theorem.

Theorem 3.3.4 *The rectangle $\Omega(M)$ is forward invariant under solutions to (3.1).*

Remark My proof to Theorem 3.3.4 also shows solutions to (3.1) with initial conditions in the closure of $\Omega(M)$, $cl\Omega(M)$, remain trapped in this compact subset of \mathbb{R}^2 for all dimensionless time $\tau > 0$. This ensures the ω -limit sets of the solutions are non-empty [29].

Theorem 3.3.5 *The rectangle $\Omega(M)$ does not contain any periodic solutions to (3.1).*

Proof To demonstrate the absence of periodic solutions in $\Omega(M)$, I will use Dulac's criteria [29]. Define $g(B, A) = \frac{1}{AB}$. Then calculating the divergence of $\langle g \cdot \dot{B}, g \cdot \dot{A} \rangle$, I obtain

$$\begin{aligned} \operatorname{div}(g \cdot \dot{B}, g \cdot \dot{A}) &= \operatorname{div}\left(-\frac{\mu_B}{A} + \frac{(1-c)\nu\kappa}{(\kappa+B)B}, -\frac{\mu(b)}{B} + \frac{1}{A} \frac{\kappa_1}{\kappa_1+A} - \frac{\nu\kappa}{(\kappa+B)B}\right) \\ &= -\left(\frac{(1-c)\nu\kappa(\kappa+2B)}{((\kappa+B)B)^2} + \frac{1}{A^2} \frac{\kappa_1}{(\kappa_1+A)^2} (\kappa_1+2A)\right) < 0. \end{aligned} \quad (3.16)$$

As $\Omega(M)$ is an open, simply connected subset of \mathbb{R}^2 and the right-hand side of (3.1) is continuously differentiable, because (3.16) does not change signs in $\Omega(M)$, by Dulac's criteria there are no periodic orbits in $\Omega(M)$ [29].

I now can address the limiting behaviour of solutions with initial conditions in $\Omega(M)$.

Theorem 3.3.6 *If $R_0 > 1$, trajectories of solutions with non-negative initial conditions tend to the unique non-trivial equilibrium, \bar{B}, \bar{A} within $\Omega(M)$.*

Proof I have demonstrated that the trajectories are bounded for arbitrarily large M , that there are no periodic solutions in $\Omega(M)$, and that when $R_0 > 1$ the trivial equilibrium is unstable. Moreover, provided $R_0 > 1$, there exists a unique, non-trivial equilibrium in $\Omega(M)$. Therefore, by Poincaré-Bendixson Theorem [29] as $\tau \rightarrow \infty$ the trajectories must converge to this non-trivial equilibrium in the interior of $\Omega(M)$.

Let $\phi = \frac{\nu\kappa}{\kappa+B}$. Then when the population is at equilibrium, an individual expects to recruit to the breeding class with probability $\psi = \frac{(1-c)\phi}{\mu(b)+\phi}$, while its expected reproductive success as a breeder is the sum of its unassisted and assisted reproduction, $N = N_A + N_U$, where $N_U = \frac{\kappa_1}{\kappa_1+A} \frac{2}{\mu_B}$ and $N_A = \frac{\kappa_1}{\kappa_1+A} \frac{2b}{\mu_B} \frac{\bar{A}}{B}$. In the monomorphic, wild-type population, N_A and N_U are comprised of equal parts male and female reproductive function. It follows that the expected LRS of a wild-type individual at equilibrium, weighted by genetic contribution to offspring, is $\frac{1}{2} \psi N = 1$.

3.4 Evolutionary dynamics

I now look for the optimal helping strategy, which I will denote b^* . Because the mutant allele is initially rare, the success of a mutant invasion is determined entirely by heterozygous individuals. Moreover, while rare, the dynamics of the mutant subpopulation are approximately linear. Let A_{ij} denote the density of auxiliaries with i copies of the mutant allele produced by the female function of a breeder with j copies of the same allele (i.e. i helping j), and let B_1 denote the density of heterozygous breeders.

Suppose a mutant enters the wild-type population which is at the wild-type ecological equilibrium. Assume the mutation is initially rare, is not recessive, and occurs at a single, diallelic autosomal locus. I do not consider behaviour mutations: if the mutant is an auxiliary and is the only mutant in the population, it must be helping a wild-type breeder, because both of its parents must be wild-type (i.e. the mutant must have originated from a spontaneous germline mutation). Denote the wild-type strategy as $b_0 = h/\alpha \geq 0$, and let the strategy employed by heterozygous individuals be $b_1 \neq b_0$.

In general, models of cooperative breeding have assumed that the level of help is under auxiliary control [17, 18] (but see [15]); however it is likely that breeders have at least some say in the amount of help that auxiliaries provide [15]. While forcible retention of helpers by breeders is unlikely [15], breeders could exert control through, for example, maternal hormones [19, 30]. In what follows, I consider the cases of auxiliary and maternal control of helping. Under auxiliary control, the rate at which an auxiliary helps is determined by its genotype, whereas under maternal control, the rate at which the auxiliary helps is determined by the genotype of the breeder which it imprints upon.

For the moment, suppose helping is under auxiliary control. Then the invasion dynamics of the mutant can be described using the non-dimensionalized linearized system of differential

equations

$$\begin{aligned}
\dot{B}_1 &= -\mu_B B_1 + \frac{(1-c)\nu\kappa}{\kappa + \bar{B}} (A_{10} + A_{11}), \\
\dot{A}_{01} &= -\mu(b_0) A_{01} - \frac{\nu\kappa}{\kappa + \bar{B}} A_{01} + \frac{1}{2} \frac{\kappa_1}{\kappa_1 + \bar{A}} (B_1 + b_0 A_{01} + b_1 A_{11}), \\
\dot{A}_{11} &= -\mu(b_1) A_{11} - \frac{\nu\kappa}{\kappa + \bar{B}} A_{11} + \frac{1}{2} \frac{\kappa_1}{\kappa_1 + \bar{A}} (B_1 + b_0 A_{01} + b_1 A_{11}), \\
\dot{A}_{10} &= -\mu(b_1) A_{10} - \frac{\nu\kappa}{\kappa + \bar{B}} A_{10} + \frac{1}{2} \frac{\kappa_1}{\kappa_1 + \bar{A}} \left(1 + b_0 \frac{\bar{A}}{\bar{B}}\right) B_1.
\end{aligned} \tag{3.17}$$

Because the mutant is rare, I am interested in the stability of the mutant-free equilibrium (MFE). As before, the MFE entails the wild-type population being at or near the non-trivial equilibrium, \bar{A} and \bar{B} , while $A_{01} = A_{10} = A_{11} = B_1 = 0$. The Jacobian evaluated at the MFE is:

$$J_{MFE} = \begin{pmatrix} -\mu(b_0) - \phi + \frac{1}{2}b_0\vartheta & \frac{1}{2}b_1\vartheta & 0 & \frac{1}{2}\vartheta \\ \frac{1}{2}b_0\vartheta & -\mu(b_1) + \frac{1}{2}b_1\vartheta - \phi & 0 & \frac{1}{2}\vartheta \\ 0 & 0 & -\mu(b_1) - \phi & \frac{1}{2}\vartheta + \frac{1}{2}b_0\vartheta\frac{\bar{A}}{\bar{B}} \\ 0 & (1-c)\phi & (1-c)\phi & -\mu_B \end{pmatrix}$$

where I have let $\vartheta = \frac{\kappa_1}{\kappa_1 + \bar{A}}$. To determine stability, I will use *Next Generation Theorem* [31, 32]. Briefly, this approach involves decomposing matrix J into matrices F and V where F represents the inputs to the system while V represents movement between classes and mortality, such that $J = F - V$. Then the MFE is stable if the spectral radius of the matrix, $\rho(FV^{-1})$, is less than 1. Following this logic, FV^{-1} is equal to

$$\begin{pmatrix} \boxed{\begin{matrix} \frac{1}{2} \frac{b_0}{\phi + \mu(b_0)} \vartheta & \frac{1}{2} \frac{b_1}{\phi + \mu(b_1)} \vartheta + \frac{1}{2} \frac{1}{\mu_B} \vartheta \psi_m & \frac{1}{2} \frac{1}{\mu_B} \vartheta \psi_m \\ \frac{1}{2} \frac{b_0}{\phi + \mu(b_0)} \vartheta & \frac{1}{2} \frac{b_1}{\phi + \mu(b_1)} \vartheta + \frac{1}{2} \frac{1}{\mu_B} \vartheta \psi_m & \frac{1}{2} \frac{1}{\mu_B} \vartheta \psi_m \\ 0 & \frac{1}{2} \left(\frac{1}{\mu_B} + \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) \vartheta \psi_m & \frac{1}{2} \left(\frac{1}{\mu_B} + \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) \vartheta \psi_m \end{matrix}} & \begin{matrix} \frac{1}{2} \frac{1}{\mu_B} \vartheta \\ \frac{1}{2} \frac{1}{\mu_B} \vartheta \\ \frac{1}{2} \left(\frac{1}{\mu_B} + \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) \vartheta \end{matrix} \\ 0 & 0 & 0 & 0 \end{pmatrix} \tag{3.18}$$

where $\psi_m = \frac{(1-c)\phi}{\mu(b_1) + \phi}$. The matrix (3.18) is block triangular, and the magnitude of one of its eigenvalues is clearly less than one. Therefore, I am only concerned with the eigenvalues of the highlighted 3×3 block. The characteristic polynomial of this block is $\lambda(\lambda^2 + A_1\lambda + A_2)$ where

$$-A_1 = \frac{(1-c)\phi}{\mu(b_1) + \phi} \vartheta \left(\frac{1}{\mu_B} + \frac{1}{2} \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) + \vartheta \frac{1}{2} \frac{b_1}{\mu(b_1) + \phi} + \vartheta \frac{1}{2} \frac{b_0}{\mu(b_0) + \phi}, \tag{3.19}$$

$$A_2 = \frac{1}{2} \frac{(1-c)\phi}{\mu(b_1) + \phi} \vartheta \left(\frac{1}{\mu_B} + \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) \vartheta \left(\frac{1}{2} \frac{b_1}{\mu(b_1) + \phi} + \frac{1}{2} \frac{b_0}{\mu(b_0) + \phi} \right). \tag{3.20}$$

From the form of the characteristic polynomial, it is clear that one eigenvalue is 0, and hence I

need only assess the magnitude of the roots of $\lambda^2 + A_1\lambda + A_2$. If M is a 2×2 matrix then the preceding expression is its characteristic polynomial; moreover $-A_1 = \text{Tr } M$ and $A_2 = \det M$.

Theorem 3.4.1 *All eigenvalues of M are less than one in absolute value if and only if $|\text{Tr } M| < \det M + 1$.*

Proof To prove this, I use the Jury Conditions. These state that the necessary and sufficient conditions for the absolute value of all eigenvalues of a 2×2 matrix to be less than one is that $\det M < 1$ and $|\text{Tr } M| < \det M + 1$. Let $P_0 = \frac{1}{2}\vartheta\frac{b_0}{\mu(b_0)+\phi}$, $P_1 = \frac{1}{2}\vartheta\frac{b_1}{\mu(b_1)+\phi}$. When $b_1 > b_0$, $\det M < 1$ can be rearranged to give

$$(P_0 + P_1) \frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N < 1. \quad (3.21)$$

Likewise, $|\text{Tr } M| < \det M + 1$ can be rearranged to give

$$\begin{aligned} \vartheta \frac{(1-c)\phi}{\mu(b_1) + \phi} \left(\frac{1}{\mu_B} + \frac{1}{2} \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) + P_0 + P_1 &< [P_0 + P_1] \frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N + 1, \\ \Leftrightarrow (P_0 + P_1) \left(1 - \frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N \right) + \vartheta \frac{(1-c)\phi}{\mu(b_1) + \phi} \left(\frac{1}{\mu_B} + \frac{1}{2} \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) &< 1. \end{aligned} \quad (3.22)$$

Based upon how I have arranged (3.21) and (3.22), it is clear that if the left-hand side of (3.22) is always larger than the left-hand side of (3.21), then $|\text{Tr } M| < \det M + 1$ must be the limiting condition. It follows that for $|\text{Tr } M| < \det M + 1$ to be the condition, it is sufficient that

$$\begin{aligned} 1 - \frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N &> \frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N, \\ \Leftrightarrow 1 = \frac{1}{2} \frac{(1-c)\phi}{\mu(b_0) + \phi} N &> \frac{1}{2} \frac{(1-c)\phi}{\mu(b_1) + \phi} N, \end{aligned}$$

which is true because $\mu(b_1) > \mu(b_0)$. Now consider the case when $b_1 < b_0$. If $b_1 < b_0$, then $\frac{(1-c)\phi}{\mu(b_1)+\phi} \vartheta \frac{1}{\mu_B} > \frac{(1-c)\phi}{\mu(b_0)+\phi} \vartheta \frac{1}{\mu_B}$ so $P_1 < P_0$ otherwise there is no evolutionary trade-off. Then it follows that $P_0 + P_1 < 2P_0 < 1$, and $\det M < 1$ can be rearranged to give

$$\frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N < \frac{1}{P_0 + P_1}. \quad (3.23)$$

Likewise, $|\text{Tr } M| < \det M + 1$ can be rearranged such that

$$\begin{aligned}
& \frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N + \frac{1}{2} \vartheta \frac{(1-c)\phi}{\mu(b_1) + \phi} \frac{1}{\mu_B} + P_1 + P_0 < \frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N (P_0 + P_1) + 1, \\
& \Leftrightarrow \frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N [1 - P_0 - P_1] < 1 - P_0 - P_1 - \frac{1}{2} \vartheta \frac{(1-c)\phi}{\mu(b_1) + \phi} \frac{1}{\mu_B}, \\
& \Leftrightarrow \frac{\frac{1}{4}(1-c)\phi}{\mu(b_1) + \phi} N < 1 - \frac{\frac{1}{2} \vartheta \frac{(1-c)\phi}{\mu(b_1) + \phi} \frac{1}{\mu_B}}{1 - P_0 - P_1}. \tag{3.24}
\end{aligned}$$

Notice that the left-hand side of (3.23) and the left-hand side of (3.24) are identical, yet the right-hand side of (3.24) is always smaller than the right-hand side of (3.23), therefore $|\text{Tr } M| < \det M + 1$ is the limiting condition. It follows that the invasion function under auxiliary control is $|\text{Tr } M| < \det M + 1$.

By rearranging $|\text{Tr } M| < \det M + 1$, the mutant can invade provided

$$\lambda(b_1, b_0) = \psi_M \left(\frac{2}{\mu_B} + \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) + \left(\frac{b_1}{\mu(b_1) + \phi} + \frac{b_0}{\mu(b_0) + \phi} \right) \left(1 - \frac{1}{4} \psi_M N \right) > \psi \frac{2}{\mu_B}. \tag{3.25}$$

If $b_0 = 0$, (3.25) reduces to the condition for a helpful mutant to invade a selfish population when helping is under auxiliary control. Let $b_0 = 0$, and assume weak selection. Then performing a Taylor expansion of (3.25), and ignoring terms higher than first order, the condition for invasion can be simplified to

$$-\frac{1}{\mu(0) + \phi} \left. \frac{d\mu(b_1)}{db_1} \right|_{b_1=0} + \frac{1}{4} \frac{\kappa_1}{\kappa_1 + \bar{A}} \frac{1}{\mu(0) + \phi} > 0. \tag{3.26}$$

I note the similarities between (3.26) and the condition obtained in the previous chapter (also see [18]). The most important difference between the two is that time spent as a productive helper, in this model $\frac{1}{\mu(0) + \phi}$, is no longer dependent upon breeder mortality, which in turn increases the benefits of helping. In [18] and the previous chapter, helpers were associated with a site rather than a breeder phenotype. When helpers are associated with a particular site, then death of the breeder ends the period for which the auxiliary can be a productive helper. On the other hand, if the auxiliary is associated with a breeder phenotype rather than a site, in the event of a breeder death the auxiliary can shift its help to another breeder in the group. This difference functions to promote the emergence of cooperative breeding, as expected [24].

Now, suppose that auxiliary help is under maternal control. To obtain the condition for invasion under maternal control, notice that in (3.17), whenever b_i or $\mu(b_i)$ is present, it is multiplied by A_{ij} . If I swap each instance of b_i or $\mu(b_i)$ with $i = j$, I obtain the linearized dynamics of a mutant population when the helping strategy is dictated by maternal phenotype.

This slightly modifies the matrix FV^{-1} , (3.18), used for auxiliary control, specifically:

$$\left(\begin{array}{ccc|c} \frac{1}{2} \frac{b_1}{\phi + \mu(b_1)} \vartheta & \frac{1}{2} \frac{b_1}{\phi + \mu(b_1)} \vartheta + \frac{1}{2} \frac{1}{\mu_B} \vartheta \psi_M & \frac{1}{2} \frac{1}{\mu_B} \vartheta \psi & \frac{1}{2} \frac{1}{\mu_B} \vartheta \\ \frac{1}{2} \frac{b_1}{\phi + \mu(b_1)} \vartheta & \frac{1}{2} \frac{b_1}{\phi + \mu(b_1)} \vartheta + \frac{1}{2} \frac{1}{\mu_B} \vartheta \psi_M & \frac{1}{2} \frac{1}{\mu_B} \vartheta \psi & \frac{1}{2} \frac{1}{\mu_B} \vartheta \\ 0 & \frac{1}{2} \left(\frac{1}{\mu_B} + \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) \vartheta \psi_M & \frac{1}{2} \left(\frac{1}{\mu_B} + \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) \vartheta \psi & \frac{1}{2} \left(\frac{1}{\mu_B} + \frac{b_0 \bar{A}}{\mu_B \bar{B}} \right) \vartheta \\ \hline 0 & 0 & 0 & 0 \end{array} \right). \quad (3.27)$$

The matrix (3.27) is block triangular, and the characteristic polynomial of the highlighted block is $\lambda(\lambda^2 + A_1\lambda + A_2)$, where

$$\text{Tr } M = -A_1 = \frac{1}{2} + \frac{1}{2} \vartheta \frac{(1-c)\phi}{\mu(b_1) + \phi} \left(\frac{1}{\mu_B} + \frac{b_1 \bar{A}}{\mu_B \bar{B}} \right) + \frac{b_1}{\mu(b_1) + \phi} \vartheta, \quad (3.28)$$

$$\det M = A_2 = \frac{1}{2} \vartheta \frac{b_1}{\mu(b_1) + \phi}. \quad (3.29)$$

Using the Jury Conditions to determine stability, it is apparent by inspection that $|\text{Tr } M| < \det M + 1$ is the limiting condition. It follows that the invasion condition can be written as

$$\lambda(b_1, b_0) = \frac{(1-c)\phi}{\mu(b_1) + \phi} \frac{\kappa_1}{\kappa_1 + \bar{A}} \left(\frac{1}{\mu_B} + \frac{b_1 \bar{A}}{\mu_B \bar{B}} \right) > 1. \quad (3.30)$$

Like (3.25), if $b_0 = 0$, (3.30) reduces to the condition for a helpful mutant to invade a selfish population when helping is under maternal control. Moreover, (3.30) has a simple biological interpretation: if the expected LRS of a rare mutant in a wild-type population at equilibrium is greater than that of its average wild-type counterpart (that is, $\frac{1}{2}\psi N = 1$ or right-hand side of (3.30)), the mutant will avoid extinction and invade.

3.4.1 Optimal strategy

I now look for the optimal helping strategy, or singular strategy [33], b^* . This can be obtained by differentiating either (3.25) or (3.30) with respect to b_1 , then setting $b_1 = b_0 = b^*$. Following some trivial reductions using the relation $\frac{1}{2}\psi N = 1$, the optimal strategy can be implicitly written as

$$-\frac{1}{2} \frac{\partial}{\partial b_1} \left[\frac{(1-c)\phi}{\mu(b_1) + \phi} \frac{\kappa_1}{\kappa_1 + \bar{A}} \frac{\zeta}{\mu_B} \right]_{b_1=b_0=b^*} = \mathcal{R}_2 \frac{\partial}{\partial b_1} \left[\frac{\kappa_1}{\kappa_1 + \bar{A}} \frac{b_1}{\mu(b_1) + \phi} \right]_{b_1=b_0=b^*}, \quad (3.31)$$

where under auxiliary control, $\mathcal{R}_2 = \frac{1}{4}$ and $\zeta = 2$, while under maternal control, $\mathcal{R}_2 = \frac{1}{2}$, and $\zeta = 1$. From (3.31), it is clear that there exists scope for breeder-auxiliary conflict over the allocation of help. In particular, under maternal control, the costs of helping are always less

because the mutant breeder pays a smaller price as it is enlisting the helpers as opposed to being one of the helpers. As a result, breeders always want more help than the amount that auxiliaries are comfortable providing. This is intuitive: auxiliaries in my model pay the costs, and so while a breeder treats auxiliaries equally, the auxiliary favours itself over its siblings [21, 39].

Of course, (3.31) represents a point at which the local fitness gradient is zero, and does not necessarily correspond to a fitness maximum [33]. To determine whether (3.31) is, for example, a terminal point of evolution or a branching point, one must consider higher order effects. In Appendix B, I derive the conditions for the optimal strategies of (3.31) to be an evolutionarily stable strategy (ESS) [33, 35] and a convergence stable strategy [36]. Because these quantities are not easily amenable to biological interpretation, I do not analyze them further. However, one of the necessary (but not sufficient) conditions for (3.31) to be an ESS is that $\mu(b)$ must be a strictly accelerating function of b , so in what follows I assume this is true (recall that $\mu(b)$ is also strictly increasing with b in order for there to exist a trade-off).

3.5 Ecology and ecological constraints

I now consider the interaction between the optimal strategies and the ecology of the system, which I relate to the constraints of the ECH, specifically: the cost of dispersal, c , and the probability of successfully recruiting to the breeder class, ψ [10]. The other key ecological constraint is expected fecundity as an independent breeder [10]. In an established cooperatively breeding population, an individual can expect to generate indirect fitness benefits as an auxiliary, benefits which on average are equivalent to expected assisted fecundity as a breeder. Critically, to realize these benefits, an auxiliary does not need to become a breeder. Hence, if helping returns escalate, this can provide incentive to remain an auxiliary. Therefore, rather than using the original ecological constraint of the ECH, expected fecundity as an independent breeder, $\frac{2}{\mu_B} \frac{\kappa_1}{\kappa_1 + \bar{A}}$, I instead use the difference between unassisted and assisted fecundity (i.e. $N_U - N_A$). Denoting this value as \hat{N} , or the relative expected fecundity an individual receives as an independent breeder, in my model this is: $\hat{N} = \frac{\kappa_1}{\kappa_1 + \bar{A}} \left(\frac{2}{\mu_B} - \frac{2b}{\mu_B} \frac{\bar{A}}{\bar{B}} \right)$. Notice that if the focus is on emergence, then $b = 0$, and the constraint is identical to the one originally formulated in the ECH.

3.5.1 Cost of dispersal

The ECH predicts that the emergence of cooperative breeding is promoted when the cost of dispersal is increased. Since increasing the cost of dispersal reduces the likelihood of establishment as a breeder, it is expected that it should have a similar effect on the promotion of

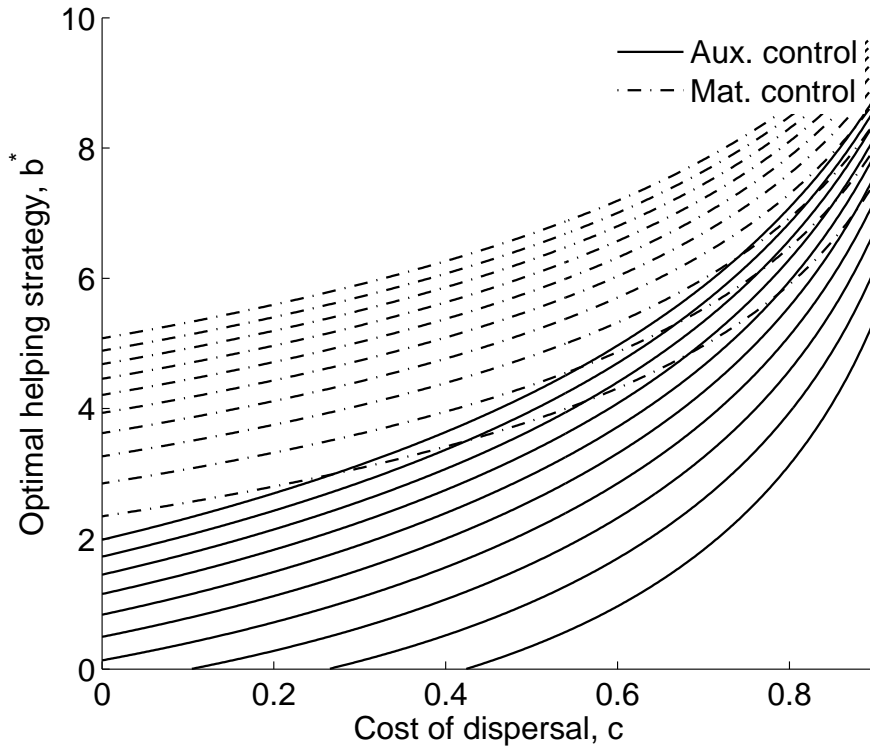


Figure 3.1: Effect of the cost of dispersal, c , on the predicted optimal strategy, b^* . Dashed lines correspond to the scenario when helping is under maternal control, while solid lines correspond to when the helping is under auxiliary control. Each line represents a different value of breeder mortality, μ_B , from $\mu_B = 0.2$ to $\mu_B = 0.7$ in evenly spaced increments. Larger values of μ_B yielded larger predicted values of b^* . In this figure $\kappa = \kappa_1 = 1.0$, $\nu = 2.5$, and $\mu(b) = 0.1 + 0.1b + 0.02b^2$, but the same qualitative relationships were observed at all parameter combinations and functional forms of $\mu(b)$ investigated, provided $\mu(b)$ was strictly increasing and accelerating with b .

higher levels of help; in fact, in my model cost of dispersal is predicted to uniformly increase the optimal helping strategy under both breeder and auxiliary control (Fig. 3.1). Indeed, this result agrees with my results from the previous chapter (see also [18]).

3.5.2 Density-dependent effects

In my model, I have two density-dependent effects: density-dependent recruitment to the breeder class and density-dependent fecundity. The parameters controlling the magnitude of these two density-dependent interactions are κ and κ_1 , respectively. When κ (resp. κ_1) is small, breeder recruitment (resp. fecundity) is strongly affected by the density of breeders (resp. auxiliaries), whereas when κ (resp. κ_1) is large, breeder recruitment (resp. fecundity) is weakly

affected by density of breeders (resp. auxiliaries).

To understand the effect of varying κ and κ_1 upon (3.31), note that

$$\mathcal{R}_2 \frac{b^*}{\mu(b^*)} = \frac{1}{2} \frac{\zeta(1-c)}{\mu_B}, \quad (3.32)$$

is a particular solution to (3.31). To demonstrate this, simply substitute into (3.31) and reduce – explicit values of \bar{A} and \bar{B} are not needed for this particular case. The particular solution given by (3.32) admits a biological interpretation. Suppose we wanted to determine which life-history stage yields greater fitness returns, that is, who would an individual rather be, an auxiliary or breeder? To answer this question, we need to consider the fitness of a breeder independently of an auxiliary, and vice-versa. Doing so requires ignoring any assisted fecundity a breeder can expect and any movement between classes. Then, the left-hand side (LHS) of (3.32) represents the expected indirect fitness gains from helping, while the right-hand side (RHS) is the expected direct fitness gains as an unassisted breeder reduced by cost of dispersal. In both cases, these values are weighted by genetic relatedness to the new individuals produced, measured as a statistical probability. Therefore, when the LHS of (3.32) is greater than the RHS, an individual generates more indirect fitness returns as an auxiliary than direct fitness returns as a breeder; whereas if the converse is true, an individual generates more direct fitness returns as a breeder.

Of course, it is important to note that as solutions deviate from (3.32), different aspects of the ecology come into play (i.e. κ , κ_1 , and equilibrium population values). I have simplified the interpretation by focusing on the comparison between $\mathcal{R}_2 \frac{b^*}{\mu(b^*)}$ and $\frac{1}{2} \frac{\zeta(1-c)}{\mu_B}$. This is why, for example, if the idealized direct benefits I have given here (i.e. $\frac{1}{2} \frac{\zeta(1-c)}{\mu_B}$) exceed the idealized indirect benefits (i.e. $\mathcal{R}_2 \frac{b^*}{\mu(b^*)}$) the actual results are not as simple as the optimal level of helping should be $b^* = 0$. The dilemma for the individual away from (3.32) should be viewed as something akin to a constrained optimization problem – individuals are attempting to maximize (3.32) subject to a number of constraints, which are not known in the absence of explicit solutions to \bar{A} and \bar{B} .

Returning to density-dependent effects, when (3.32) is satisfied, b^* is independent of both κ and κ_1 . However, if this equality is violated, qualitatively different behaviours of b^* with respect to varying κ and κ_1 are generated depending upon what side of (3.32) (i.e. whether LHS is larger than RHS or vice-versa) we are on. In the event κ_1 becomes large, that is, fecundity is only weakly constrained by the density of auxiliaries, (3.1) reduces to

$$\begin{aligned} \dot{B} &\approx \mu_B B + \frac{(1-c)\nu\kappa}{\kappa+B} A, \\ \dot{A} &\approx \mu(b) A + B + b A - \frac{\nu\kappa}{\kappa+B} A. \end{aligned} \quad (3.33)$$

System (3.33) can be solved for explicit equilibrium solutions, in particular, the non-trivial equilibrium, \bar{A} and \bar{B} , is:

$$\begin{aligned}\bar{B} &\approx \kappa \frac{\mu(b) + \nu}{\mu(b) - b} (R_0 - 1), \\ \bar{A} &\approx \frac{\mu_B}{(1-c)\kappa\nu} \bar{B} (\kappa + \bar{B}).\end{aligned}\tag{3.34}$$

Substituting these into (3.31) and solving the differential equation shows that as κ_1 becomes large, the solutions converge to (3.32) (Fig. 3.2). On the other hand, if κ becomes large, that is, breeder recruitment is only weakly constrained by the density of breeders, the approximate solutions to \bar{A} and \bar{B} , obtained similarly to (3.35) are:

$$\begin{aligned}\bar{B} &\approx \frac{\nu(1-c)\kappa_1}{\mu_B} (R_0 - 1), \\ \bar{A} &\approx \frac{\mu_B}{(1-c)\nu} \bar{B}.\end{aligned}\tag{3.35}$$

and when these are substituted into (3.31), the solution of the differential equation is

$$\mu(b^*) = \left(\frac{\zeta(1-c)\nu}{\mu_B} + \frac{\mathcal{R}_2}{\mathcal{R}_1} b^* \right) \mu_0 - \nu\tag{3.36}$$

where μ_0 is the death rate of selfish auxiliaries. If $\mu_0 = \frac{\mu_B}{\zeta(1-c)}$, then the solution is simply (3.32). Therefore, as κ increases, solutions converge to the curves specified by this equation (Fig. 3.2). Of course, the behaviour of the differential equation given by (3.31) when κ and κ_1 are not large and we are away from the solution given by (3.32) differs, but for all functional forms of $\mu(b)$ that were strictly increasing and accelerating, I found qualitatively similar results to those plotted in Figure 3.2.

To understand the biological interpretation of these results, observe that for a fixed value of breeder mortality, μ_B , cost of dispersal, c , and functional form of $\mu(b)$, the relationship given by (3.32) is driven by b^* : it is this value that the individual manipulates to maximize the more valuable fitness return (i.e. LHS or RHS of (3.32)). Suppose indirect fitness benefits gained as a helper surpass the direct fitness benefits gained as a breeder (LHS greater than RHS of (3.32)). Then the focus of the individual is upon increasing the level of help, b^* , in order to maximize the LHS of (3.32) (that is, $\mathcal{R}_2 \frac{b^*}{\mu(b^*)}$). When the effect of density-dependence upon fecundity increases (κ_1 decreases), less individuals are produced per unit of help, so it is necessary to increase the level of help to compensate. Similarly, when recruitment becomes increasingly independent of breeder density, or κ increases, individuals recruit to the breeder class at a higher rate, meaning less time is spent as an auxiliary, and individuals are thus motivated to increase the level of help, despite the associated greater risks. Now, suppose that the RHS of

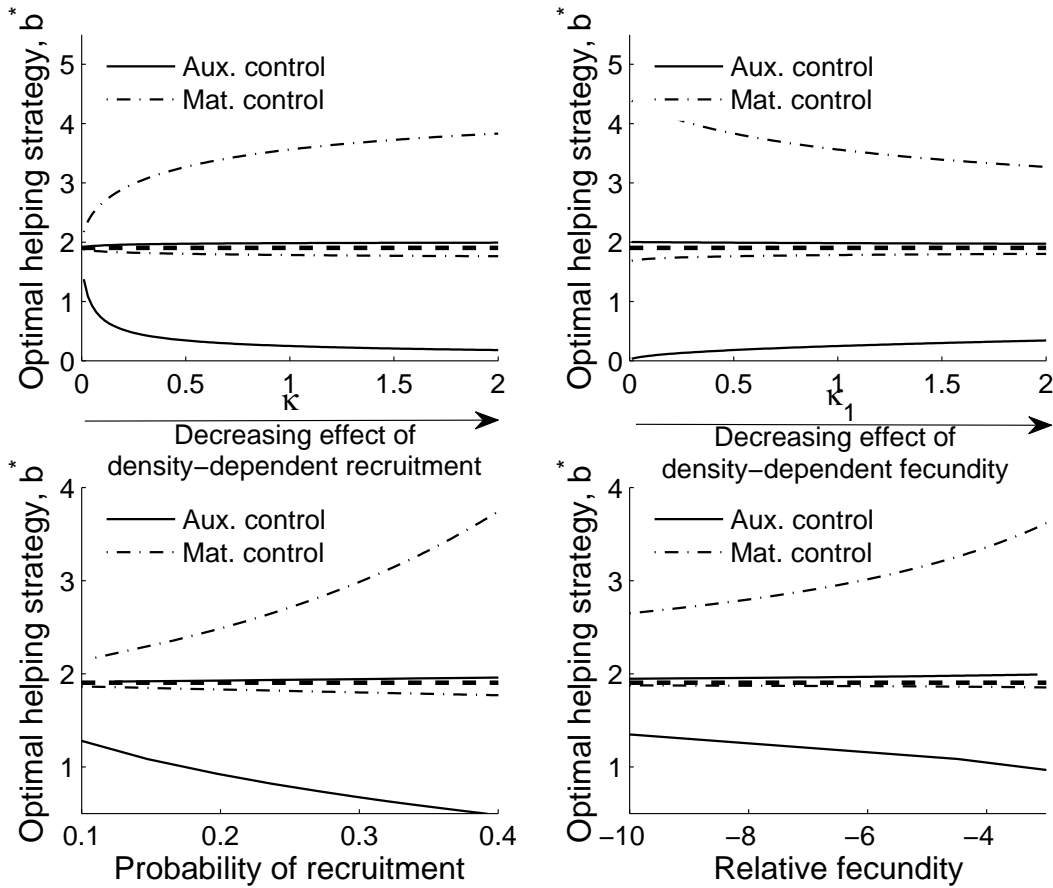


Figure 3.2: Effect of density-dependent breeder recruitment, κ , density-dependent fecundity, κ_1 , probability of recruitment, ψ , and relative fecundity, \hat{N} , on the predicted optimal strategy, b^* . Dashed curves correspond to the optimal strategy under maternal control, solid curves to the optimal strategy under auxiliary control. Heavy-set dashed straight line represents the critical solution, (3.32), at which the behaviour of system changes changes. For all values above this line, $\mathcal{R}_2 \frac{b^*}{\mu(b^*)} > \frac{1}{2} \frac{\zeta(1-c)}{\mu_B}$, while below, the inequality is reversed. Both solutions above the line use $\mu_B = 0.95$, while below $\mu_B = 0.2$. The remaining parameter values for κ and κ_1 plots were $\kappa = 1$ or $\kappa_1 = 1$ depending on which was fixed, $\nu = 1.5$, and $c = 0.1$, and $\mu(b) = 0.18 + 0.06b + 0.05b^2$. The same qualitative relationships were observed at all parameter combinations and functional forms of $\mu(b)$ investigated, provided $\mu(b)$ was strictly increasing and accelerating with b .

(3.32) is greater. Then the focus of an individual is on decreasing the level of help provided to reduce its mortality risk as an auxiliary. If fecundity is strongly constrained by density (κ_1 is small), then an individual wants to decrease the level of help provided so as not to pay the same cost on a depreciating return. If recruitment is weakly effected by breeder density (κ large), the constraints on becoming a breeder are reduced, and an individual is motivated to decrease the amount of help it provides to reduce the chance of dying before becoming a breeder.

Importantly, the qualitative behaviour around $\mathcal{R}_2 \frac{b^*}{\mu(b^*)} = \frac{1}{2} \frac{\zeta(1-c)}{\mu_B}$ directly impacts the effect of two of the ecological constraints upon the optimal strategy, specifically: probability of securing an independent breeding opportunity, ψ , and the difference between unassisted and assisted fecundity, \hat{N} . The ECH predicts that increasing expected fecundity as an independent breeder, \hat{N} , and increasing probability of recruitment, ψ , should hinder the emergence of helping [10]. I found that when the expected indirect fitness gains as an auxiliary are less than the expected direct fitness gains as a breeder (LHS < RHS of (3.32)), that is, helpers are making the best of a bad situation [20], the constraints act to decrease the optimal level of helping (Fig. 3.2), as predicted by the ECH. However, when the situation is reversed, and indirect fitness gains as an auxiliary exceed the direct fitness gains as a breeder (LHS > RHS of (3.32)), an individual has sufficient incentive as an auxiliary that they are no longer simply making the best of a bad situation. That is, cooperative breeding is no longer an evolutionary puzzle, and individuals are motivated to help out of their own self interest. When this occurs, the constraints ψ and \hat{N} have the opposite effect on optimal level of help (Fig. 3.2), that is, an increasing probability of recruitment means that auxiliaries will opt to help at higher levels, despite the associated increase in mortality, because increasing ψ means less time spent as an auxiliary. Similarly, increasing expected relative fecundity, \hat{N} , compels auxiliaries to help at higher levels, because the cost of doing so is minimized.

Breeder mortality

Finally, my results illustrate that under both maternal and auxiliary control, increasing breeder mortality μ_B promoted higher levels of helping (see Fig. 3.1 and Fig. 3.2). While high breeder mortality, μ_B , does result in high population turn-over, the benefits of becoming a breeder are tempered by the corresponding reduction in life-time fecundity as a breeder. Hence, it is often more prudent for the auxiliary to invest in helping, despite the costs, a result that has been predicted elsewhere [10]. This result emphasizes an important point: considering auxiliary and breeder mortality as independent processes facilitates direct analysis of their individual effects rather than focusing on an all encompassing quality such as ‘long-lived’ without partitioning life span into stage structured components. This is particularly true when the risks associated with helping (e.g. higher mortality) are confined to a single stage (e.g. helping as an auxiliary

does not effect the mortality risk as a breeder).

Of course, the magnitude of the breeder mortality parameter resulted in qualitatively different relationships between the constraints, ψ and \hat{N} , and the optimal strategy b^* , depending upon what side of (3.32) we are on (Fig. 3.2). That breeder mortality can have such a qualitatively divergent effect upon the optimal strategy, depending upon the ecology, was also observed in the previous chapter when the focus was on evolutionary emergence of cooperative breeding (see [18]).

3.6 Concluding remarks

In this chapter, I modelled the evolutionary dynamics of cooperative breeding by using an explicit model of population dynamics. I supposed that auxiliaries provided help at a level $b \geq 0$, which had an additive effect upon increasing breeder fecundity, but doing so increased the helpers mortality, $\mu(b)$, which I assumed was a strictly increasing (and accelerating) function of b . I considered both auxiliary and maternal control over the helping strategy auxiliaries employed, and was able to obtain the optimal strategy, b^* . My analysis revealed that breeders always want auxiliaries to help at higher levels than that which they would prefer.

While throughout this chapter I assumed that either auxiliaries or breeders had perfect control over what strategy was employed, in reality it is likely far more complex. My decision to focus on the extremes was for illustrative purposes of the scope for conflict. My maternal-auxiliary conflict arose from a purposefully simplified mechanism to ensure analytic tractability of my model, but other, more complex, maternal-auxiliary conflicts are likely to exist. For example, if the production of oocytes comes at a cost to the breeder in the form of higher mortality, than a breeder may be inclined to suppress helping in some instances. On the other hand, if auxiliary help functioned to improve offspring survival, rather than boosting fecundity, load-lightening could come into play [40], but this would require a different model.

I related the results of my model for the optimal strategy to the constraints of the ECH argued to promote cooperative breeding [9, 10, 15]. I found that the cost of dispersal, c , performed as predicted by the original ECH [10]. That is, the higher the cost of dispersal, the higher the optimal level of help, b^* . The other two primary constraints, specifically, probability of recruiting to the breeder class, ψ , and what I called expected relative fecundity as an independent breeder, \hat{N} , had a more complicated relationship. I found that the predictions of the ECH about the effect of the constraints ψ and \hat{N} upon the promotion of the emergence of helping can be extended to predict the optimal strategy – provided helpers are ‘making the best of a bad situation’ [20]. However, my results showed that if the indirect fitness gains of an auxiliary exceed the direct fitness gains of an unassisted breeder, the motivation for helping changes,

and helpers are no longer trying to make the best of a bad situation. Instead, auxiliaries are motivated to escalate the level of help, despite the increased mortality risks, as the objective is no longer becoming a breeder. As a result, the constraints of the ECH have the converse effect: increasing the probability of recruitment, ψ and expected relative fecundity, \hat{N} , served to increase the optimal level of help.

By assuming auxiliaries were imprinted upon a phenotype rather than associated with a specific site, I created conditions that enhanced the evolution of cooperation [24]. The critical difference is that when auxiliaries associate with a specific site, the amount of time spent as a productive helper is dependent upon breeder mortality [18]. When the association is with a phenotype, if the breeder dies, the helper can simply switch to helping another breeder in the group. However, I would argue that the same qualitative results should be expected irrespective of whether or not the association is with a site or a phenotype.

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Chapter 4

Summary and future work

4.1 Summary of thesis

Cooperative breeding is a social behaviour in which certain individuals (i.e. auxiliaries) postpone or forgo reproduction to help breeding individuals. Because the act of helping comes at some cost [1], why an individual would opt to cooperate rather than behave selfishly is almost paradoxical when viewed from the perspective of the theory of natural selection, and as a result has been studied extensively.

While there are a number of evolutionary explanations for the emergence of cooperative breeding [2–5], one of the most prominent is the Ecological Constraints Hypothesis (ECH) [2, 3, 6]. The ECH proposes that helping is motivated by ecological limitations, or ecological constraints, upon independent breeding. These constraints are: a high cost of dispersal, a low probability of recruitment to the breeder class, and low expected fecundity as an independent breeder [2]. While the ECH has empirical support [7, 8], theoretical support is lacking, as the models that have agreed with it failed to properly account for population dynamics [6, 9, 10]. The one model which did explicitly account for population dynamics by Pen and Weissing [11], found that provided confounding factors such as territory inheritance were removed, the ECH was insufficient to predict the emergence of cooperative breeding.

In Chapter 2, I revisited the effect of ecological constraints upon the emergence of cooperative breeding. By using an explicit population model, I was able to show that ecological constraints alone are sufficient to drive the emergence of cooperative breeding, contrary to results found elsewhere [11]. The reason my results contradicted those of Pen and Weissing [11] is because their model equally exposed individuals to the ecological constraint, irrespective of whether or not they chose to help, something which my model did not do. To make my results accessible to biologists, I interpreted the condition for the emergence of cooperative breeding in terms of inclusive fitness [12]. Because of the explicit nature of my model, I was also able to

obtain novel results about the effect of breeder mortality. Specifically, changing breeding mortality alters the expected time an auxiliary can serve as a productive helper, but also the amount of time spent in the auxiliary class. Therefore, in some circumstances breeder mortality can promote cooperation, and in others, hinder it.

Despite the large number of explanations for the emergence of cooperative breeding, little has been done on the long-term evolutionary implications, or what constitutes an optimal strategy. The few models that have looked at optimal strategies [6, 9], did so without considering population dynamics, an approach that can lead to ecologically unrealistic or misleading results [11]. As a result, it is not known when existing theory for the emergence can or cannot be used to predict the escalation of help, nor what the effect of ecology is upon optimal strategies. Moreover, because the cost of helping is often paid asymmetrically by auxiliaries, the long-term evolution of cooperative breeding has the potential for breeder-auxiliary conflict over what the optimal strategy should be [6, 13], yet little has been done to examine this from a theoretical perspective (but see [6]).

In Chapter 3, I examined the full evolutionary dynamics of cooperative breeding using a population explicit model and the tools of adaptive dynamics. I was able to relate and extend the predictions made by the ECH for the emergence of cooperative breeding to the expected optimal strategy. In particular, I showed that provided helpers are making the best of a bad situation [14], the constraints featured in the ECH can be used to predict the expected optimal strategy similar to how the ECH intended them for emergence. However, when fitness returns as an auxiliary exceed those of a breeder, the constraints of the ECH predicted to hinder the emergence of helping function instead act to facilitate higher levels of optimal strategies. When this occurs, cooperative breeding is not much of an evolutionary puzzle as cooperation is actually motivated by self-interest. Throughout this chapter, I juxtaposed the case in which helping was under auxiliary control and the case in which helping was under maternal control, providing the scope for breeder-auxiliary conflict. I found that breeders always want auxiliaries to provide help at a level higher than that which auxiliaries prefer, a result similar to that found for scenarios involving dispersal [15, 16].

4.2 Future work

4.2.1 Breeder-auxiliary conflict

In Chapter 3, I looked at a simple breeder-auxiliary conflict. Part of the simplicity was because the costs were paid solely by the auxiliary. This contributed to the breeder always wanting auxiliaries to help at a higher level than that which the auxiliaries were willing to provide.

However, there are other, more complicated potential trade-offs that could yield different results. For example, suppose that the rate at which a breeder produced oocytes dictated its mortality rate. In such a scenario, increases in auxiliary help would hasten the death of the breeder, and as such, it is possible that in some circumstances, a breeder would opt to suppress helping. Eviction is present in some cooperatively breeding species [17], so it is possible that this conflict is a motivating factor in breeder eviction of helpful auxiliaries. An interesting concept would be if territory inheritance were included in the model, as then the auxiliaries could have the additional motivation to help at higher levels because the demise of their parents would facilitate their own succession.

Another potential conflict could arise if I instead had explicitly modelled parental care. To do so, I would have to add a third stage to the population, such that when individuals are born, they enter an ‘offspring’ stage, during which breeder care and help by auxiliaries would increase survivorship or accelerate maturation. Individuals would have to pass through this maturation stage in order to become auxiliaries; once an auxiliary they could become a potential helper. Obviously, providing care would come at a cost for both breeders and auxiliaries, and so if breeders expect auxiliaries to help, they may lower the amount of care they provide in response. This phenomenon is called ‘load-lightening’ and is present in many cooperatively breeding avian species [18–20] and should yield considerable range for breeder-auxiliary conflicts.

4.2.2 Co-evolution of helping and the sex-ratio

In many cooperatively breeding species, there is a sex-ratio bias towards the more helpful sex [21]. The idea behind this behaviour is that helpers repay part of the cost of their production by helping, which reduces the net cost of their production [22–24]. While a number of models have examined the evolution of sex-ratios in cooperatively breeding populations [25, 26], no work has been done on the co-evolution of helping and sex-ratio. As a result, the evolution of sex-ratio bias in emerging cooperatively breeding systems is poorly understood from a theoretical perspective, and this has led to some confusion about what ecological conditions will promote or suppress sex-ratio and helping co-evolution [24]. Modification of one of the models used in this thesis to allow for the evolution of a second trait controlling sex would allow one to address this topic.

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Appendix A

Derivation of mutant equations

In what follows I explain the derivation of the mutant equations from the main text. I use all previously defined parameters, details of which are provided in the main text and are thus omitted here for brevity.

Suppose there are two types of individuals, wild-type and heterozygous. Because the mutant is rare, there are no homozygous mutant individuals and so I do not consider them here. Suppose there is some large number, n , territories in the environment. Each territory contains some variable number of auxiliaries, and has a single breeding site which can be either occupied or unoccupied. Let $I_i^{(j)}(t)$ denote the status of a breeder of type j ($j = 0$ if wild-type, $j = 1$ if heterozygous) on patch i at time t , that is, if a breeder of type j is present, then $I_i^{(j)}(t) = 1$. Otherwise, $I_i^{(j)}(t) = 0$. Similarly, let $J_i^{(j)}(t) \geq 0$ denote the number of auxiliaries of type j ($j = 0$ if wild-type, $j = 1$ if heterozygous) present on patch i at time t . Suppose a small increment of time Δt has elapsed. We now want to know the expected number and type of breeders and auxiliaries on patch i at time $t + \Delta t$.

First, the expected status of a heterozygous breeder on patch i at time $t + \Delta t$ after some simplification is

$$\frac{E[I_i^{(1)}(t + \Delta t) | S] - I_i^{(1)}(t)}{\Delta t} = -m_x I_i^{(1)}(t) + \left(1 - I_i^{(0)}(t) - I_i^{(1)}(t)\right) \frac{(1-c)\tilde{d}}{n} \sum_{k=1}^n J_k^{(1)}(t) + O(\Delta t), \quad (\text{A.1})$$

where I have divided through by Δt and let S denote the state of the n patches at time t .

Likewise, the expected number of heterozygous auxiliaries on the i -th patch at time $t + \Delta t$ is

$$\begin{aligned} \frac{E[J_i^{(1)}(t + \Delta t) | S] - J_i^{(1)}(t)}{\Delta t} &= -\tilde{m}_y J_i^{(1)}(t) - J_i^{(1)}(t) \frac{\tilde{d}}{n} \sum_{k=1}^n (1 - I_k^{(0)}(t) - I_k^{(1)}(t)) \\ &+ (b + h J_i^{(1)}(t)) \left(I_i^{(0)}(t) \frac{\sum_k I_k^{(1)}(t)}{\sum_k (I_k^{(0)}(t) + I_k^{(1)}(t))} + \frac{1}{2} I_i^{(1)}(t) \right) + O(\Delta t). \quad (\text{A.2}) \end{aligned}$$

Now, in order to have a closed system of differential equations describing the mutant population dynamics, I must also keep track of the cross products $I_i^{(1)}(t) J_i^{(1)}(t)$ and $I_i^{(0)}(t) J_i^{(1)}(t)$ and their expected values at time $t + \Delta t$ (notice that $I_i^{(1)}(t) I_i^{(1)}(t) = I_i^{(1)}(t)$ by definition). After some trivial reduction and dividing through by Δt , the cross products can be formulated as

$$\begin{aligned} \frac{E[I_i^{(1)}(t + \Delta t) J_i^{(1)}(t + \Delta t) | S] - I_i^{(1)}(t) J_i^{(1)}(t)}{\Delta t} &= - (m_x + \tilde{m}_y) I_i^{(1)}(t) J_i^{(1)}(t) \\ &+ J_i^{(1)}(t) (1 - I_i^{(0)}(t) - I_i^{(1)}(t)) \frac{(1 - c) \tilde{d}}{n} \sum_k J_k^{(1)}(t) + \frac{1}{2} (b + h J_i^{(1)}(t)) I_i^{(1)}(t) \\ &- I_i^{(1)}(t) J_i^{(1)}(t) \frac{\tilde{d}}{n} \sum_k (1 - I_k^{(0)}(t) - I_k^{(1)}(t)) + O(\Delta t), \quad (\text{A.3}) \end{aligned}$$

and

$$\begin{aligned} \frac{E[I_i^{(0)}(t + \Delta t) J_i^{(1)}(t + \Delta t) | S] - I_i^{(0)}(t) J_i^{(1)}(t)}{\Delta t} &= - (m_x + \tilde{m}_y) I_i^{(0)}(t) J_i^{(1)}(t) \\ &+ J_i^{(1)}(t) (1 - I_i^{(0)}(t) - I_i^{(1)}(t)) \frac{(1 - c) \tilde{d}}{n} \sum_k J_k^{(1)}(t) - I_i^{(0)}(t) J_i^{(1)}(t) \frac{\tilde{d}}{n} \sum_k (1 - I_k^{(0)}(t) - I_k^{(1)}(t)) \\ &+ \frac{1}{2} (b + h J_i^{(1)}(t)) I_i^{(0)}(t) \frac{\sum_k I_k^{(1)}(t)}{\sum_k (I_k^{(0)}(t) + I_k^{(1)}(t))} + O(\Delta t). \quad (\text{A.4}) \end{aligned}$$

The reader might be confused as to why the death of the breeder and the death of an auxiliary appear to have the same magnitude of effect, other than the different per-capita rate constants. The reason is that because the derivation is reliant upon initial and final states, which after reduction yields the same answer. To see this, if I write out the change in state in full, the

probability a breeder dies is

$$m_x \Delta t I_i^{(j)}(t) \left(\left[I_i^{(j)}(t) - 1 \right] J_i^{(1)}(t) - I_i^{(j)}(t) J_i^{(1)}(t) \right) = -m_x \Delta t I_i^{(j)}(t) J_i^{(1)}(t), \quad (\text{A.5})$$

whereas the probability an auxiliary dies is

$$\tilde{m}_y \Delta t J_i^{(1)}(t) \left(I_i^{(j)}(t) \left[J_i^{(1)}(t) - 1 \right] - I_i^{(j)}(t) J_i^{(1)}(t) \right) = -\tilde{m}_y \Delta t I_i^{(j)}(t) J_i^{(1)}(t), \quad (\text{A.6})$$

where the term in the round brackets is the change in state. Hence, all that distinguishes the two is the per-capita multiplier rate. Now, let $X_m(t) = \sum_i \frac{I_i^{(1)}(t)}{n}$, $X(t) = \sum_i \frac{I_i^{(0)}(t)}{n}$, $Y_m(t) = \sum_i \frac{J_i^{(1)}(t)}{n}$, $Y = \sum_i \frac{J_i^{(0)}(t)}{n}$, $Z_m(t) = \sum_i \frac{I_i^{(1)}(t) J_i^{(1)}(t)}{n}$, and $\tilde{Z}_m(t) = \sum_i \frac{I_i^{(0)}(t) J_i^{(1)}(t)}{n}$. Then summing the previous equations from $i = 1, \dots, n$, dividing through by n and taking the limit as $\Delta t \rightarrow 0$, I obtain

$$\begin{aligned} \dot{X}_m &= -m_x X_m + \tilde{d} (1 - c) (1 - X - X_m) Y_m, \\ \dot{Y}_m &= -\tilde{m}_y Y_m - \tilde{d} (1 - X - X_m) Y_m + \frac{1}{2} (b X + h \tilde{Z}_m) \frac{X_m}{X + X_m} + \frac{1}{2} (b X_m + h Z_m), \\ \dot{Z}_m &= -(m_x + \tilde{m}_y) Z_m + (Y_m - \tilde{Z}_m - Z_m) (1 - c) \tilde{d} Y_m + \frac{1}{2} (b X_m + h Z_m) - Z_m \tilde{d} (1 - X - X_m), \\ \dot{\tilde{Z}}_m &= -(m_x + \tilde{m}_y) \tilde{Z}_m + (Y_m - \tilde{Z}_m - Z_m) (1 - c) \tilde{d} Y_m + \frac{1}{2} (b X + h \tilde{Z}_m) \frac{X_m}{X + X_m} - \tilde{Z}_m \tilde{d} (1 - X - X_m), \end{aligned}$$

where dots denote differentiation with respect to time t . When the mutant is rare and the population is at the wild-type equilibria, $X = \bar{X}$, and we ignore higher order terms of X_m and Y_m . Then, this system can be non-dimensionalized and linearized about the MFE to give the system in the main text. \tilde{Z}_m is omitted from that version because the eigenvalue associated with it is always strictly negative.

Appendix B

Higher-order evolutionary dynamics

B.1 Evolutionary stability

The optimal strategies given in the main text represent regions of phenotype space where the local fitness gradient is equal to zero. To determine whether they are fitness minima or maxima requires checking the Evolutionary Stable Strategy (ESS) condition [1, 2]. An ESS strategy is a strategy which satisfies

$$\left. \frac{\partial^2 \lambda(b_1, b_0)}{\partial b_1^2} \right|_{b_1=b_0=b^*} < 0. \quad (\text{B.1})$$

Recall that $\lambda(b_1, b_0)$ is the invasion function. Following the procedure steps in (B.1), the strategy for maternal control is ESS provided

$$\left. \frac{d^2 \mu(b)}{db^2} \right|_{b=b^*} > 0 \quad (\text{B.2})$$

That is, provided the costs of helping accelerate with increasing help, the singular strategy is stable under maternal control. On the other hand, when help is under auxiliary control, the optimal strategy is ESS provided

$$0 < -\frac{1}{2} \frac{\partial^2}{\partial b_1^2} \left[\frac{(1-c)\phi}{\mu(b_1) + \phi} \frac{2}{\mu_B} \right]_{b_1=b_0=b^*} + \frac{1}{8} \left. \frac{d^2 \mu(b_1)}{db_1^2} \right|_{b_1=b^*} \frac{b^*}{(\mu(b^*) + \phi)^2} \quad (\text{B.3})$$

In this case, it is a necessary, but not sufficient, condition for (B.2) to hold. Because (B.3) does not hold for all $\mu(b)$ satisfying (B.2), maternally control is stable over a larger region of ecological space. There is a second condition required to ensure that (3.31) is a terminal point of evolution; this is given by the so-called convergence stability condition [3]. Convergence

stability is often of interest because there exist stability conditions under which a singular strategy is an evolutionary branching point [2], however, as I assumed random mating, speciation is not possible in my model [4].

B.2 Convergence stability

For convergence stability, we require that

$$\frac{d}{db_0} \left[\frac{\partial \lambda(b_1, b_0)}{\partial b_1} \Big|_{b_1=b_0} \Big|_{b_0=b^*} \right] < 0. \quad (\text{B.4})$$

Proceeding in this fashion for auxiliary control of helping, and after substituting $b_1 = b_0$ into the first derivative, I obtain

$$\frac{\partial \lambda}{\partial b_1} \Big|_{b_1=b_0} = \frac{1}{\mu(b_0) + \phi} \left(\frac{1}{4}T - \frac{d\mu(b_0)}{db_0} \left(1 - \frac{3}{4}T \frac{(1-c)\phi b_0 \bar{A}}{\mu(b_0) + \phi \mu_B \bar{B}} \right) \right) \quad (\text{B.5})$$

Define

$$\zeta = \frac{1}{4}T - \frac{d\mu(b_0)}{db_0} \left(1 - \frac{3}{4}T \frac{(1-c)\phi b_0 \bar{A}}{\mu(b_0) + \phi \mu_B \bar{B}} \right) \quad (\text{B.6})$$

By definition of the optimal strategy, $\zeta|_{b_0=b^*} = 0$. Therefore for CSS we are only concerned with the sign of $\frac{d\zeta}{db_0}|_{b_0=b^*}$. That is

$$\begin{aligned} \frac{d\zeta}{db_0} \Big|_{b_0=b^*} &= - \frac{d^2\mu(b_0)}{db_0^2} \Big|_{b_0=b^*} + 12 \frac{d\mu(b_0)}{db_0} \Big|_{b_0=b^*}^3 \frac{(1-c)\phi}{(\mu(b^*) + \phi)^2 \mu_B} \\ &+ 3 \frac{d\mu(b_0)}{db_0} \Big|_{b_0=b^*}^2 \frac{b^*}{(\mu(b^*) + \phi)^2} \frac{(1-c)\phi}{\kappa + \bar{B}} \frac{d\bar{B}}{d\bar{b}_0} \Big|_{b_0=b^*} - 4 \frac{d\mu(b)}{db} \Big|_{b=b^*} \frac{1}{\kappa_1} \frac{d\bar{A}}{d\bar{b}_0} \Big|_{b_0=b^*} \end{aligned} \quad (\text{B.7})$$

If this is satisfied, and (B.3) is not, then branching is possible.

Now, consider maternal control. Proceeding as above, I obtain

$$\frac{d}{db_0} \left[\frac{\partial \lambda(b_1, b_0)}{\partial b_1} \Big|_{b_1=b_0} \Big|_{b_0=b^*} \right] = - \frac{1}{\mu(b^*) + \phi} \left(\frac{d^2\mu(b_0)}{db_0^2} \Big|_{b_0=b^*} + \frac{\kappa_1}{(\kappa_1 + \bar{A})^2} \frac{d\bar{A}}{d\bar{b}_0} \Big|_{b_0=b^*} \right). \quad (\text{B.8})$$

Obviously $\frac{d\bar{A}}{d\bar{b}}$ is strictly increasing. Therefore, all accelerating functions of $\mu(b)$ satisfy the

convergence stability condition. Branching is possible if $\mu(b)$ is decelerating and

$$-\left. \frac{d^2\mu(b_0)}{db_0^2} \right|_{b_0=b^*} > \frac{\kappa_1}{(\kappa_1 + \bar{A})^2} \left. \frac{d\bar{A}}{db_0} \right|_{b_0=b^*}. \quad (\text{B.9})$$

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