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The relationship between ecology and the optimal helping strategy in cooperative breeders

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HIGHLIGHTS

- We investigate the role played by ecology upon the evolution of cooperative breeding.
- We determine the optimal helping strategy under both maternal and offspring control.
- There is an environmental critical point at which helping is preferable to breeding.
- Environments with constraints on being a breeder minimize breeder–auxiliary conflict.

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ABSTRACT

Cooperative breeding is a social system in which certain individuals (auxiliaries) postpone or forgo their own reproduction to help other individuals (breeders). The selective advantage for this behaviour has been considerably debated, but that debate has focused on models that neglect long-term evolutionary dynamics. As a result, there is little theoretical understanding of how system ecology relates to either optimal strategies or the scope for breeder–auxiliary conflict. In this paper, we construct an explicit population model of cooperative breeding when help is under either maternal and auxiliary control, and obtain an ecologically-specific optimal strategy. Our optimal strategy reveals that there is a critical point at which helpers are no longer 'making the best of a bad situation', and are instead exploiting the breeders. The critical value at which this occurs delineates two qualitatively different ecological regimes. We also show that ecologies with constraints upon becoming a breeder, or unappealing aspects of being a breeder (e.g. high breeder mortality), minimize breeder–auxiliary conflict, whereas when there are appealing aspects (e.g. low breeder mortality) and few constraints, breeder–auxiliary conflict is maximized.

1. 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 (Pope, 2000; Griffin and West, 2003; Woxvold and Magrath, 2005; Hodge et al., 2008; Brouwer et al., 2009), yet providing help comes at some cost, such as exposing auxiliaries to greater mortality risks (Reyer, 1984; Rabenold, 1990; Heinsohn and Legge, 1999). 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 (Trivers, 1971; Axelrod and Hamilton, 1981; Brown, 1987; Emlen, 1982a).

While there are many evolutionary explanations for the emergence of cooperative breeding (Emlen, 1982a; Stacey and Ligon, 1991; Arnold and Owens, 1998; Covas and Griesser, 2007), and a large body of modelling work (Emlen, 1982b; Motro, 1993; Pen and Weissing, 2000; McLeod and Wild, 2013), 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 either did so without explicitly accounting for population dynamics (Motro, 1993), an approach that can produce ecologically artificial results (see Pen and Weissing, 2000 for discussion), or by treating the ecology as a static quantity independent of the population dynamics (Kokko et al., 2001). The latter paper by Kokko et al. (2001) found that the ecology, or the 'ecological constraints' (i.e. recruitment success) of the system did not impact the level at which individuals should help, a result which runs counter to some of the more prominent

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evolutionary explanations for cooperative breeding (Brown, 1987; Koenig et al., 1992; Emlen, 1995). As a result, the link between the ecology of the system and the optimal strategy is poorly understood. Additionally, the interplay between the ecology of the system and the optimal strategy should affect the level of conflict between breeders and auxiliaries over allocation of help, with implications for the resilience of the cooperatively breeding system. Theoretical understanding of these issues is prerequisite to the understanding of the evolution of higher level social organization and major evolutionary transitions, such as obligate cooperative breeding.

Previously, we investigated the emergence of cooperative breeding in the face of ecological constraints (McLeod and Wild, 2013). However, the model of that paper was limited in that it did not allow us to investigate the full evolutionary dynamics of cooperative breeding – instead we focused exclusively on the conditions under which a cooperative mutant could invade a selfish population (McLeod and Wild, 2013). The objective of this paper is to extend those results by determining the optimal cooperative breeding strategy and relating it to: (i) the ecology of the system and (ii) the scope for breeder–auxiliary conflict. To do so, we build an ecologically-explicit model upon which we conduct a full adaptive dynamics analysis. The optimal strategy obtained from our model enables us to investigate the role played by ecology. We find that the qualitative effect of the ecology upon the optimal strategy depends upon whether helpers are 'making the best of a bad situation' (Dickinson and Hatchwell, 2004) or whether individuals can generate superior fitness returns from helping rather than breeding. In both cases, we find that the ecology of the system has a strong impact on the optimal helping strategy. We also find that environments characterized by constraints upon breeding (e.g. high mortality, low recruitment) tended to have the lowest conflict between breeders and auxiliaries, whereas environments with weak constraints upon breeding tended to have the highest conflict.

2. Population dynamics

Our model population consists of diploid hermaphrodites experiencing continuously overlapping generations. We focus on hermaphrodites to simplify the evolutionary argument, but our results apply to dioecious species with an evolutionarily fixed pattern of sex allocation. To keep our model tractable, we ignore the joint evolution of sex ratio and auxiliary help but note that evolution of sex allocation in cooperative breeding has been studied elsewhere (Emlen et al., 1986; Pen and Weissing, 2000; Wild, 2006). Individuals in the population are either breeders or auxiliaries, and we denote their densities at time t as B and A, respectively. Newborn individuals immediately become auxiliaries, and remain as such until either they die or they recruit to the breeding class. Breeders produce male gametes (sperm) and female gametes (oocytes) through fair meiosis. Oocyte production occurs at a per-capita rate α and 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 (Koenig and Haydock, 2004).

We assume that cooperation in our population occurs in a 'kin neighbourhood' setting (Dickinson and Hatchwell, 2004; Cockburn, 2006; Hatchwell, 2009). 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 (Hatchwell, 2009). In avian species these loose affiliations are often referred to as 'clans' or 'coteries' (Dickinson et al., 1996; Emlen, 2004; Hatchwell, 2009). Because we focus on kin neighbourhoods, auxiliaries in our model are imprinted on the phenotype of their 'mother'. As each 'mother' phenotype is comprised of identical individuals, available help is allocated evenly within each type of breeder phenotype. Help provided by auxiliaries increases breeder oocyte production at an additive rate $h \geq 0$ ($h=0$ corresponds to a selfish population). Helping is a costly behaviour (Heinsohn and Legge, 1999). To account for this, we let the per-capita rate of auxiliary mortality be a strictly increasing function of h, that is $\mu(h)$ with the condition that $\mu'(h) > 0$, a trade-off in many cooperatively breeding species (Reyer, 1984; Rabenold, 1990).

As density-dependent fecundity is present in some cooperatively breeding species (Woxvold and Magrath, 2005; Brouwer et al., 2009), we assume that oocytes instantaneously develop into auxiliaries at a density-dependent per capita rate of $\rho/(\rho+A)$ where ρ is a positive parameter. Similarly, we assume that the environment can only support a limited density of breeders, so auxiliaries recruit to the breeding class at a per-capita rate of $d\kappa(\kappa+B)$, where d and κ are positive parameters. We emphasize that the explicit dependence of auxiliary recruitment upon breeder density links the ecology of our model to the population dynamics, an approach which differs from the previous work (Kokko et al., 2001). Upon successful recruitment, individuals remain breeders until death, which occurs at a per-capita rate of m_B.

To reduce the number of parameters in the model, we let $\tau = \alpha t$ and then define new non-dimensionalized parameters: $b = h/\alpha$, $\mu_B = m_B/\alpha$, and $\nu = d/\alpha$. It follows that the monomorphic wild-type population dynamics can be described as

$$\begin{aligned} \dot{B} &= -\mu_B B + \frac{\nu\kappa}{\kappa+B}A, \\ \dot{A} &= -\mu(b)A + \frac{\rho}{\rho+A}\left(1+b\frac{A}{B}\right)B\pi - \frac{\nu\kappa}{\kappa+B}A, \end{aligned} \tag{1}$$

where dots denote differentiation with respect to τ and π denotes the randomly selected 'male' breeder who fertilizes the oocytes produced by the focal breeder B; in a monomorphic population this is simply $\pi = B/B$, and the equation simplifies accordingly. System (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

$$R_0 = \frac{\nu}{\mu(b)+\nu}\left(\frac{b}{\nu}+\frac{1}{\mu_B}\right). \tag{2}$$

The basic reproduction number, R_0, is the product of (i) the probability of successful establishment as a independent breeder at low population densities, $\nu/(\mu(b)+\nu)$, and (ii) lifetime reproductive success through both male and female functions, weighted by genetic contribution, $(1/2)(2\,b/\nu+2/\mu_B)$. While the nonlinearities in (1) prevent us from obtaining an analytic expression for the non-trivial equilibrium, in Appendix A we show that provided $R_0 > 1$, there exists a unique, non-trivial equilibrium to (1), which we will denote $(\overline{B},\overline{A})$ (i.e. $\overline{B},\overline{A} > 0$); moreover, this non-trivial equilibrium is globally asymptotically stable; we will refer to this equilibrium as the ecological equilibrium.

Let $\phi = \nu\,\kappa/(\kappa+\overline{B})$, and let $\vartheta = \rho/(\rho+\overline{A})$. Then when the population is at ecological equilibrium, an individual expects to recruit to the breeding class with probability $\psi = \phi/(\mu(b)+\phi)$, while its expected reproductive success as a breeder is the sum of its unassisted and assisted reproduction, $N = N^u + N^a$, where $N^u = N_f^u + N_m^u = \vartheta(2/\mu_B)$ and $N^a = N_f^a + N_m^a = \vartheta(2\,b/\mu_B)(\overline{A}/\overline{B})$. It follows that the expected LRS of a wild-type individual at ecological equilibrium, weighted by genetic contribution to offspring, is $(1/2)\psi\,N = 1$.

Because all individuals in the wild-type population are genetically and phenotypically identical, (1) describes the dynamics of