Evolution of delayed dispersal and subsequent emergence of helping, with implications for cooperative breeding

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ABSTRACT

Cooperative breeding occurs when individuals help raise the offspring of others. It is widely accepted that help displayed by cooperative breeders emerged only after individuals' tendency to delay dispersal had become established. We use this idea as a basis for two inclusive-fitness models: one for the evolution of delayed dispersal, and a second for the subsequent emergence of helpful behavior exhibited by non-breeding individuals. We focus on a territorial species in a saturated environment, and allow territories to be inherited by non-breeding individuals who have delayed dispersal. Our first model predicts that increased survivorship and increased fecundity both provide an incentive to non-breeding individuals to delay dispersal, and stay near their natal territory for some period of time. Predictions from the first model can be well understood by ignoring complications arising from competition among relatives. Our second model shows that effects on relatives play a primary role in the advantage of helping. In addition, the second model predicts that increased survivorship and fecundity promote the emergence of help. Together, our models lead us to conclude that the emergence of cooperative-breeding systems is made easier by life-history features associated with high survivorship and fecundity. We discuss the implications of our conclusions for life-history-based hypotheses of cooperative breeding and social evolution.

1. Introduction

In many cooperatively breeding species, subordinate individuals postpone or even forgo their own reproduction in order to promote the reproductive success of the dominant individuals who occupy breeding territories. Familiar examples include the Florida Scrub Jay (*Aphelocoma coerulescens*), and meerkats (*Suricata suricatta*) (Clutton-Brock, 2002; Cockburn, 1998). Uncovering the adaptive significance of the helpful behavior displayed by these and other cooperative breeders is key to understanding the evolution of animal societies more broadly.

Attempts to explain the selective advantage of cooperative breeding have emphasized a range of complementary influences (Emlen, 1994). Some have focused on the personal fitness benefits of helping, such as delayed reciprocity (Wiley and Rabenold, 1984), and territory inheritance (Stacey and Ligon, 1991). Others have focused on the indirect fitness benefits of raising related but

non-descendant offspring, especially as a response to various environmental constraints (Emlen, 1982a; 1982b; Skutch, 1961).

As plausible as the various explanations for cooperative breeding are, studies in the field have failed to uncover a general effect of species' ecology that is also consistent with the variety of theoretical predictions made (Arnold and Owens, 1998). Consequently, recent research has looked more deeply into the specific life-history features that might promote cooperative breeding (Arnold and Owens, 1998; Beauchamp, 2014). Efforts there have centred on finding evidence, among cooperatively breeding species, for the predominance of similar "K-selected" life-history traits. These traits include high survivorship and low fecundity—traits that are thought to be advantageous in environmentally constrained populations, near carrying capacity. Unfortunately, empirical support for the existing life-history based theories has also been mixed (Hatchwell and Komdeur, 2000).

Despite the lack of empirical support, it seems inappropriate to dismiss life-history-based explanations for cooperative breeding outright, since they are theoretically underdeveloped. That is to say, the explanations are based on generic ideas about life-history evolution, rather than on models tailored for cooperatively breeding species. In this paper, we use simple, yet reasonably compre-

Table 1
Summary of notation used in the main text.

Symbol(s)	Explanation
b	Number of immature offspring produced on a territory during a given time period, and interpreted as fecundity or birth rate.
c, $\hat{c}$	Fraction of dominant vacancies per time period per territory that are contested by related individuals. A hat denotes the equilibrium value of the parameter.
h	Subordinate helping rate.
m_α, $\hat{m}_\alpha$	Number of local dominant vacancies secured by a subordinate. This parameter can also be interpreted as a probability. A hat denotes the equilibrium value of the parameter.
m_β, $\hat{m}_\beta$	Likelihood that a subordinate does not compete successfully for a breeding opportunity as a dominant. Of course, $m_\beta = 1 - m_\alpha$. A hat denotes the equilibrium value of the parameter.
n_α, $\hat{n}_\alpha$	Number of dominant vacancies secured by a disperser. A hat denotes the equilibrium value of the parameter.
$\hat{r}$	Genetic relatedness between two different individuals born on the same territory during the same time period, at equilibrium.
s_α	Survival rate of a dominant individual.
s_β, Δs_β	Survival rate of a subordinate, and the positive change in this rate following receipt of help from a subordinate born in the previous time period.
s_ω, Δs_ω	Survival rate of a disperser, and the negative change in this rate following donation of help to an individual born in the current time period.
v_α	Reproductive value of a dominant individual.
v_β	Reproductive value of a subordinate individual, $v_\beta = s_\omega \hat{n}_\alpha v_\alpha$.
z	The probability that an individual delays its dispersal from its natal territory for one time period for the chance to compete to inherit a dominant position.

hensive, models to capture the evolution of cooperative breeding, with the goal of clearly assessing the influence of basic life-history on the origin of these systems.

Biologists have long agreed that the evolution of delayed dispersal of offspring from their natal site is an important first step in the establishment of cooperative-breeding systems (Brown, 1974; Emlen, 1982a; Hatchwell and Komdeur, 2000; Koenig et al., 1992; Kokko and Ekman, 2002; Kokko and Lundberg, 2001). Evidence also suggests that the evolution of delayed dispersal preceded the emergence of helping in certain eusocial insects (Thorne, 1997). Our approach, therefore, is to separate an individual's dispersal decision from its decision to help, in contrast to many previous models (Leggett et al., 2012; McLeod and Wild, 2013; Motro, 1993; Pen and Weissing, 2000; Wild and Koykka, 2014). We implement this approach by constructing and analysing a model for the evolution of delayed dispersal (Model I). Results from this model are then used to inform a second model for the evolution of helping following establishment of delayed dispersal (Model II).

Biologists have also long recognized the importance of genetic relatedness among cooperative breeders (Brown, 1987; Emlen, 1982b). Unlike those who incorporate relatedness into their theory as a fixed parameter (Kokko and Johnstone, 1999; Kokko et al., 2001), we model relatedness as a function of species' population dynamics, which ultimately depends on life-history details. Furthermore, our consideration of relatedness is explicit and allows for inbreeding within groups to build, and so our models differ from recent theoretical work (Koykka and Wild, 2016).

Overall, our models predict that cooperative breeding is promoted as survivorship, or fecundity (or both) is increased. We discuss the implications of our predictions in the final section, paying particular attention to life-history based explanations of cooperative breeding and the evolution of social insects.

2. Model I: delayed-dispersal

It is a challenge to build a simple model of the evolution of delayed dispersal, since so many factors (both ecological and social) come into play (Kokko and Ekman, 2002). Here, we concentrate on building a model that is tractable but still reflects key aspects of relevant biological systems. As the reader will see, this has required us to sometimes balance our interest in biological realism against our need for a set of assumptions that help to keep our models mathematically tractable. For the reader's convenience, we summarize all mathematical notation introduced below in Table 1.
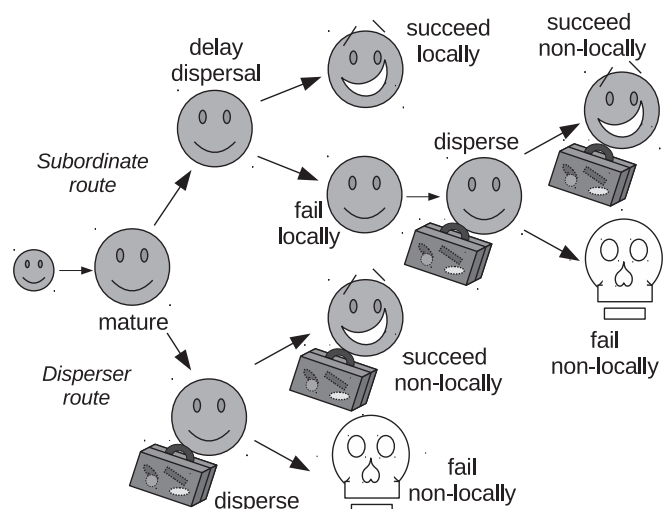

Fig. 1. Cartoon depiction of the possible fate of individuals in our models. Verbal descriptions of events are given in Section 2.1.

2.1. Monomorphic wild-type population

We first consider a genetically monomorphic population of haploid individuals. This "wild-type" population will serve as the backdrop against which we later measure the fitness of mutant individuals. We assume a haploid genetic system because it is simple, and because it mirrors a diploid system with additive interactions between alleles (Johnstone and Cant, 2008).

We track our model wild-type population in discrete time, observing it at the beginning of each time period, e.g. season, year, generation (Fig. 1). Each individual in this population begins its life as one of $b \geq 2$ offspring produced by the two dominant breeders occupying one of a very large number of breeding territories. In keeping with our use of dominant individuals as stand-ins for dominant males and females, respectively, we assume that an offspring inherits all of its genetic material from one or the other dominant on its natal territory, independently, with one-half probability.

As the reader will see, our decision to allow two dominant individuals on a territory means that, in general, genetic lineages experience some degree of inbreeding. In turn, the possibility of inbreeding implies that relatedness among family members is not fixed, but rather can vary in a way that is influenced by the details of the life history. As we have said, this approach to modelling re-