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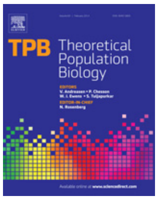

Sex allocation and the emergence of helping in cooperatively breeding species

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ABSTRACT

In cooperative breeding systems individuals invest in the reproductive success of others. In this paper, we study the emergence of cooperative breeding systems in which reproductively active breeders receive investment from reproductively non-active helpers. Our goal is to understand how the division of an investment between male and female components of breeder fitness (i.e. the helper sex-allocation strategy) influences the emergence of cooperative breeding itself. Using mathematical models, we arrive at expressions for the inclusive-fitness advantage of helpful behaviour that generalize previous work. These expressions assume an ecologically stable environment, and that breeders make evolutionarily stable sex-allocation decisions. We find that, when breeders are extremely resource limited, the sex-allocation strategy used by a helper can be a key determinant in the success of helpful alleles. This finding, however, is restricted to cases in which helpers have access to intermediate levels of resources. Surprisingly, when helpers can make only a small investment in a recipient the division of the investment matters only very little to advantage of help. By contrast when resources are extremely abundant, we obtain the unsurprising result that the manner in which resources are allocated has little influence on the emergence of help. When breeders have access to intermediate levels of resources we find increasing relatedness can, in certain cases, inhibit the emergence of help. We also find that increasing the amount of resources available to a breeder can impede help as well. Both of these counter-intuitive results are mediated by evolutionary responses in breeder sex allocation.

1. Introduction

In a cooperative-breeding system, certain individuals promote the reproductive success of their neighbours, sometimes incurring large personal fitness costs as a result. In extreme cases, reproductive skew is high, and helpful individuals must postpone or even forgo their own reproduction to attend to offspring produced by a dominant breeder or breeding pair (Griffin and West, 2003).

Helping among cooperatively breeding individuals is known to influence the evolution of other social traits. In particular, sex allocation – the manner in which resources are divided between male and female components of reproductive fitness – is known to be affected by help (Emlen et al., 1986; Pen and Weissing, 2000a; Griffin et al., 2005; Wild, 2006). This influence is commonly observed as a sex-ratio bias in cooperatively breeding species, with investment favouring the more helpful sex.

Although the effect of helpful behaviour on sex allocation is quite well understood, the same cannot be said for the effect that sex allocation has on the emergence of helpful behaviour. What little we do know about the influence sex allocation has on helping in cooperative-breeding systems has come from studies by Taylor (1992) and Johnstone and Cant (2008). Using kin-selection models, both sets of authors outlined mathematical conditions for the advantage of helping among reproductively active neighbours. Sex allocation decisions did not factor into the conditions they developed, simply because any increase (resp. decrease) in investment made in a given sex was balanced by a decrease (resp. increase) in the reproductive value of that sex. Importantly, Johnstone and Cant (2008) did find that sex-specific patterns of *dispersal* could influence the emergence of helping. Consequently, changes to sex allocation could influence helping indirectly by changing evolutionarily stable dispersal rates (e.g. see Wild and Taylor, 2004).

At first glance, then, it might seem reasonable to expect sex allocation to play only an indirect role in the emergence of cooperative breeding. However, none of the work that could support such an expectation (i.e., Taylor, 1992; Johnstone and Cant, 2008) allowed

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the donor itself to influence the allocation of its investment. Given that donor and recipient can have different social-evolutionary perspectives in general (e.g. as in social insects: Trivers and Hare, 1976), it seems more reasonable to expect sex allocation could be "tuned" to maximize the donor's incentive to help. In other words, a direct role for sex allocation in the emergence of help ultimately appears plausible, despite the conclusions of previous studies.

In order to outline how sex allocation might directly influence the emergence of cooperative breeding systems, we generalized two recent models (Wild and Koykka, 2014) to include variable investment in male/female components of reproductive success and inbreeding. Our models assume a high-degree of reproductive skew, in the sense that they track the invasion of an allele that leads one individual to delay its own chance at reproduction in order to improve the reproductive success of another.

As expected, we can easily identify a direct role for sex allocation in the emergence of cooperative breeding. Specifically, we find that conditions for the advantage of help can be made more/less stringent by altering the way in which a donor divides its investment between the male and female components of recipient fitness. More importantly, we show *why* one should expect such dependence to occur: selection on breeder allocation implies that maximum advantage is achieved by a helper who allocates its resources like resource-unlimited breeders. Finally, we evaluate how competition among kin can alter this basic result, and the consequences of following what parent does for the emergence of help.

The sections that follow describe our models and results in three parts. The first part details the population dynamics that underlie our evolutionary argument. In the second part we determine the evolutionarily stable (ES) sex-allocation strategy used by a breeder in the absence of help. And in the third part we develop the conditions for the advantage of help offered to a breeder with ES sex allocation.

2. Population dynamics

Although we extend Wild and Koykka (2014), the population dynamics that underlie our model follow theirs closely. We begin by considering a population whose individuals do not engage in any form of helpful behaviour. These individuals are diploid, sexual, and (for mathematical convenience) simultaneous hermaphrodites.

There are two different kinds of individuals in a genetically monomorphic population: breeders and floaters. Breeders are reproductively active individuals. Each breeder is associated with one breeding territory, and no two breeders share territories. By contrast, floaters are not reproductively active, though they are reproductively capable. Floaters are not associated with any breeding territory.

We census the population at discrete, evenly-spaced points in time. Let $F(t)$ and $B(t)$ denote the number of floaters and breeders, respectively, censused at the beginning of time step t. Following census, each breeder produces one viable oocyte with probability $p_♀$. If viable, the oocyte is fertilized by some breeder in the population. With probability ϕ self-fertilization occurs, and with probability $1-\phi$ fertilization is accomplished by a uniform random breeder in the population. The resulting offspring becomes either a breeder or a floater in the next time step depending on the specific model scenario (*No Territory Inheritance* or *Territory Inheritance*, described below).

Each breeder survives from one time step to the next with probability s_b. When a breeder survives, it retains its breeding territory, and any offspring produced by that breeder disperses to become a floater. When a breeder dies, one of two things can occur. In our *No Territory Inheritance* (NTI) Model, we assume that offspring dispersal precedes all breeder mortality events. In this case offspring cannot fill a vacancy left by a dead parent; instead, offspring disperse to become floaters, and vacated territories simply vanish. In our *Territory Inheritance* (TI) Model, we assume that all breeder mortality events precede offspring dispersal. In this case, an offspring will fill a vacancy left by a dead parent rather than dispersing to become floaters. Territory inheritance is an important incentive for helping in cooperative-breeding systems (Stacey and Ligon, 1991). More importantly (as the reader will see) the TI model will allow us to consider the effects of competition among kin, whereas the NTI model will not.

Floaters survive from one season to the next with probability s_f. A fraction of the floaters that survive become breeders; the remaining fraction stay in the floater class. The probability that a surviving floater becomes a breeder is modelled as $1/(1+aB(t))$ for some constant $a>0$, which is essentially Beverton–Holt density dependent competition (Britton, 2003). This is a decreasing function of the number of breeders $B(t)$, and so reflects an important kind of ecological constraint faced by cooperative breeders (Emlen, 1982a,b).

The size of the population in the long-run is determined by a particular combination of parameters. This combination is called *the basic reproduction number* ($\mathcal{R}_0$), and in this model it describes the expected number of newly established breeding territories produced on an established breeding territory when population densities are low. For the NTI Model we have $\mathcal{R}_0 = p_♀ s_f/(1-s_b)$, and for the TI Model we have $\mathcal{R}_0 = p_♀ s_f s_b/((1-s_b)(1-p_♀))$ (Wild and Koykka, 2014). It can be shown that, when $\mathcal{R}_0 < 1$, the population tends to extinction over time, but when $\mathcal{R}_0 > 1$ the numbers of breeders and floaters in the population, respectively, tend to positive steady-state values (Wild and Koykka, 2014, see Appendix A). We disregard the marginal case $\mathcal{R}_0 = 1$, here, and assume that $\mathcal{R}_0 > 1$.

3. Breeder's ES sex allocation

In this section we use the population dynamics above to develop an inclusive-fitness argument for the ES sex-allocation strategy used by a breeder in the absence of help. Our results hold for both the NTI Model and the TI Model, and they can be verified using more formal invasion analyses (Courteau and Lessard, 2000, see Appendices C–F). We use the population dynamic models (seen in Appendix A) to determine whether sex allocation strategies are evolutionarily stable. Alongside this more formal approach, the inclusive-fitness argument is used to explain the invasion condition biologically.

We treat the sex-allocation strategy used by a breeder as a continuous trait. The trait determines the fraction of resources a breeder devotes to reproduction through male function, and is controlled at a single autosomal locus. There are two alleles at the locus in question, namely resident and mutant, with additive effects on the trait. Additivity allows us to think of a resident as having one sex-allocation strategy, α, and of a mutant as having another sex-allocation strategy, β (Taylor and Frank, 1996)

We suppose that each breeder has k_b resources (e.g., measured in terms of calories) to allocate to either male or female reproductive function. Allocation to female function costs $c_♀$ (e.g., measured as calories per unit of function), and allocation to male function costs $c_♂$. It follows that a breeder using strategy $X = \alpha, \beta$ is able to "purchase" $k_b(1-X)/c_♀$ units of female reproductive function, and $k_b X/c_♂$ units of male reproductive function.

Until now, the probability with which a breeder produced a viable oocyte has been treated as a constant, $p_♀$. In addition, all breeders had been assumed to compete on an equal basis for (non-self) fertilizations; a breeder's relative competitive ability is $p_♂$. Now, we treat $p_♀$ and $p_♂$ as a function of $k_b(1-X)/c_♀$