A general ploidy model for the evolution of helping in viscous populations

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ABSTRACT

There is growing interest in understanding how kin selection drives the evolution of social behaviours in viscous populations. A key result, that has inspired much work on this topic, is the exact cancellation of the genetic relatedness and kin competition effects of dispersal in the simplest models of population viscosity, such that a reduction in the rate of dispersal neither promotes nor inhibits the evolution of helping behaviour. This theoretical result has been demonstrated for populations characterised by haploid, diploid and haplodiploid modes of inheritance. Here we develop a model of general ploidy that recovers these three scenarios as special cases and allows examination of scenarios that have not been considered previously. Specifically, we: clarify the importance of the implicit assumption of monandry in previous models; show that the cancellation result obtains in some models of ploidy but not in others; and reveal that the cancellation result obtains for different reasons in different models of ploidy. The cancellation result therefore hinges upon a population's genetic system as well as its demography.

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1. Introduction

Recent years have seen much interest in the role for demography to mediate social evolution. Of particular interest has been the evolution of helping behaviour in viscous populations. Hamilton (1964, 1971) suggested that indiscriminate helping could be favoured in populations that are characterised by low rates of dispersal, such that individuals tend to be closely related to their neighbours. However, low dispersal also leads to localised competition for resources among kin, and this can reduce selection for helping (Hamilton, 1971; Grafen, 1984; Queller, 1992; Frank, 1998; West et al., 2002). Indeed, Taylor (1992a) showed that – in the simplest scenario of an infinite, inelastic island model (Wright, 1931) – the effects of genetic relatedness and kin competition exactly cancel, such that there is no net impact of the rate of dispersal upon the evolution of helping.

This surprising result has stimulated a great deal of theoretical work, exploring which alterations to the basic model assumptions bring about a decoupling of genetic relatednes and kin competition, such that population viscosity may promote the evolution of helping (reviewed by Lehmann and Rousset, 2010). These include factors such as elastic/unsaturated populations (Taylor, 1992b; Alizon and Taylor, 2008), overlapping generations (Taylor and Irwin, 2000; Irwin and Taylor, 2001), dispersal-dependent behaviour (Perrin and Lehmann, 2001; El Mouden and Gardner, 2008), budding dispersal (Gardner and West, 2006; Lehmann et al., 2006), sex-biased dispersal (Johnstone and Cant, 2008; Gardner, 2010), birth–death versus death–birth demographies (Grafen and Archetti, 2008), reproductive skew (Pen and West, unpublished; Johnstone, 2008) and resource heterogeneity (Rodrigues and Gardner, 2012). Some of these theoretical predictions have been empirically tested using experimental evolution methods (Kümmerli et al., 2009).

Taylor's (1992a) original analysis considered three separate models, concerning haploid, diploid and haplodiploid modes of inheritance. Here, we develop a model of general ploidy (cf. Grafen, 1986, 2006a) that recovers each of these three scenarios as special cases, and allows examination of scenarios not considered by Taylor (1992a). We also relax Taylor's (1992a) implicit assumption of monandry, allowing females to mate with potentially multiple males. This allows an assessment of the robustness of Taylor's (1992a) cancellation result to variation in model assumptions, and helps to illuminate the genetical and demographic reasons for cancellation, both in his original models and also more generally.

2. Model and analysis

2.1. Model

We assume a population comprising an infinite number of patches, in which adult females each produce a large number of offspring. The probability that two randomly chosen juveniles

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that are born in the same patch are maternal siblings is denoted by α, and the probability that two randomly chosen maternal siblings are also paternal siblings is denoted by β. The number of genomes inherited by a juvenile female from her mother is denoted by κ, and the number of genomes she inherits from her father is denoted by λ (Fig. 1). The number of genomes inherited by a juvenile male from his mother is denoted by μ, and the number of genomes he inherits from his father is denoted by ν (Fig. 1).

We allow breeding females to divert resources from maternal care to communal care – i.e. helping behaviour – thereby improving the survival of random juveniles in her patch whilst reducing the survival of her own offspring. Formally, we denote a focal juvenile's probability of survival by $S(x,y)$, where x is the investment into helping made by that juvenile's mother, and y is the average investment into helping made by breeding females in the juvenile's patch. And we define $-c \equiv \partial S/\partial x$, representing the cost of helping for the actor, and $b \equiv \partial S/\partial y$, representing the benefit of helping for the recipient.

Following social interaction, adult females die, and all juveniles surviving to adulthood mate at random within their patch. After mating, the males die and the females either disperse with probability d to another patch or else remain with probability $1-d$ in their natal patch. Following dispersal, females compete within patches for breeding opportunities, returning the population to the beginning of the lifecycle. Model notation is summarised in Table 1.

Taylor's (1992a) model is recovered by setting $\alpha=1/n$ (that is, there are n breeding females per patch, each having the same fecundity; our model keeps the number of breeding females
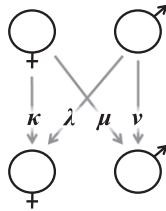

Fig. 1. A general model of ploidy. Daughters inherit κ genomes from their mother and λ genomes from their father, and sons inherit μ genomes from their mother and ν genomes from their father. Hence, females are $(\kappa+\lambda)$-ploid whilst males are $(\mu+\nu)$-ploid.

implicit, and allows for any degree of reproductive skew) and $\beta=1$ (that is, monandry; our model allows females to mate with potentially multiple males). Moreover, Taylor's (1992a) haploidy model is recovered by setting $\kappa=1$, $\lambda=0$, $\mu=0$ and $\nu=0$; his diploidy model is recovered by setting $\kappa=1$, $\lambda=1$, $\mu=1$ and $\nu=1$; and his haplodiploidy model is recovered by setting $\kappa=1$, $\lambda=1$, $\mu=1$ and $\nu=0$.

2.2. Evolution of helping

We determine how natural selection operates upon indiscriminate helping behaviour, using the neighbour modulated fitness approach of Taylor and Frank (1996; see also Taylor, 1996; Frank, 1997, 1998; Rousset, 2004; Taylor et al., 2007). This yields a condition for natural selection to favour helping:

$$-c(c_f p_d + c_m p_s) + b(c_f p_f + c_m p_m) - (1-d)^2(b-c)(c_f p_f + c_m p_m) > 0, \quad (1)$$

where c_f and c_m are the class reproductive values (Fisher, 1930; Taylor, 1996; Grafen, 2006a) of females and males, respectively; and p_d, p_s, p_f and p_m are the coefficients of consanguinity (Bulmer, 1994) between an adult female and her daughter, her son, a random juvenile female from her patch, and a random juvenile male from her patch, respectively (see Appendix for details).

Inequality (1) yields a simple inclusive fitness interpretation (Hamilton 1964, 1970). First, helping reduces the survival of the actor's offspring by an amount c, and the actor values her offspring by an amount $c_f p_d + c_m p_s$. Second, helping increases the survival of random juveniles on the actor's patch by an amount b, and the actor values these juveniles by an amount $c_f p_f + c_m p_m$. Third, to the extent that competition is local—i.e. $(1-d)^2$, the probability that two females competing for breeding opportunities within a patch are both native to that patch (Frank, 1998; Gardner and West, 2006)—the net increase $b-c$ in the survival of local juveniles leads to a competitive displacement of juveniles who were born on the actor's patch, and the actor values them by an amount $c_f p_f + c_m p_m$.

Inequality (1) may be rearranged to the form $c/b < A$, where A defines the potential for helping (cf. Gardner, 2010), i.e. the value that an adult female places on the survival of a random juvenile in her patch, relative to the value that she places on the

Table 1
A summary of model notation.

Symbol	Definition
α	Probability that two random juvenile patch mates are maternal siblings
β	Probability that two random maternal siblings are paternal siblings
κ	Number genomes in daughter that came from mother
λ	Number of genomes in daughter that came from father
μ	Number of genomes in son that came from mother
ν	Number of genomes in son that came from father
d	Rate of dispersal
S	Probability of juvenile survival
x	Helping strategy of focal juvenile's mother
y	Average helping strategy among breeding females in focal juvenile's patch
z	Average helping strategy among breeding females in population
b	Survival benefit of helping
c	Survival cost of helping
m	Male
f	Female
d	Focal female's daughter
s	Focal female's son
f	Random juvenile female in focal female's patch
m	Random juvenile male in focal female's patch
c_X	Class reproductive value of class X $\in$ (m,f)
p_Y	Consanguinity of focal female to social partner Y $\in$ (d,s,f,m)
A	Potential for helping