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A kin-selection approach to the resolution of sex-ratio conflict between mates

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Abstract

We investigate an instance of conflict between mates over the sex ratio of their brood. We construct a kin-selection model for the evolution of the sex ratio assuming local resource competition (LRC) among females. We explore two basic scenarios: (a) the case where parents make simultaneous sex-ratio decisions (the simultaneous allocation model); and (b) the case where parental sex-ratio decisions occur one after the other (the sequential allocation model). In the simultaneous investment model, resolution of the conflict between mates depends on the extent to which relative paternal contribution influences the brood sex ratio. In the sequential allocation model, fathers determine primary sex-ratio through fertilization bias; then mothers modify the paternal sex-ratio decision by adjusting the level of investment of some resource that contributes to offspring survival. Under the sequential model, a compromise is always achieved; however this compromise favours one perspective or the other, depending on the extent to which maternal investment influences offspring survival.

Keywords: Conflict; Direct fitness; Kin selection; Sex ratio; LRC

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1. Introduction

Fisher (1930) argued that parents who bias their production of offspring toward the rarer sex enjoy a selective advantage. This frequency-dependent advantage means that, on average, parents should invest equally in sons and daughters, producing brood sex-ratios that are unbiased.

It has long been known that Fisher's argument for the evolution of unbiased sex ratios relies on a few tacit assumptions (Hamilton, 1967). In particular, Fisher assumed that competition for the resources necessary for reproduction does not occur among same-sex relatives. When this assumption is violated we say there exists *local competition for reproductive resources* (LCRR); and in this case some form of sex-ratio bias is often advantageous. For example, selection favours female-biased sex ratios when related males compete with one another for mates (called *local mate competition*, LMC; Hamilton, 1967; Taylor and Bulmer, 1980); whereas selection favours male-biased sex ratios when related females compete with one another for nesting sites (called *local resource competition*, LRC; Clark, 1978; Silk, 1984; Taylor, 1994). In general, sex-ratio bias under LCRR favours the sex that is less likely to engage in local competition, i.e. the 'less competitive sex' (Wild and Taylor, 2004).

Sex-ratio evolution under LCRR is easily understood using the related notions of kin selection and inclusive fitness (Hamilton, 1964). From a parent's perspective, over-production of the less competitive sex provides a net benefit to relatives (e.g. sons/daughters, nieces/nephews). In other words, sex-ratio bias toward the less competitive sex will add to an individual's inclusive fitness, and so is favoured by kin-selection.

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The extent of sex-ratio bias under LCRR will depend on the level of relatedness between a parent and its social group; and sometimes, the degree of relatedness is different between members of a mated pair. In these cases, the optimal level of sex-ratio bias depends on which parental perspective (mom or dad) is considered, and we say that parents are in *conflict* over the sex ratio. Under LRC, for instance, mothers—not fathers—are more closely related to the average member of their social group. Mothers, therefore, prefer to increase the extent of male-bias in brood sex ratios.

Sex-ratio conflict between mates, at least for LMC models, has been discussed extensively in the literature (see Courteau and Lessard, 2000 and references therein). Still, the manner by which such conflicts come to be resolved remains to be seen. Using a simple model of LRC, Lessells (1998) has argued that the end result of these sex-ratio conflicts must be investment in only one sex of offspring by one mate, with compensatory investment in offspring of the opposite sex by its partner. Lessells' model, however, falls short of a careful inclusive fitness account of the problem.

In this paper, we investigate the sex-ratio conflict that exists between mates under LRC. We choose LRC models of sex-ratio evolution because they involve an outbreeding population. Relative to LMC models, then, LRC models appear straightforward. We adopt the *direct fitness approach* to contructing kin-selection models, introduced by Taylor and Frank (1996). This approach approximates the evolutionary dynamics described by the famous Price equation (Price, 1970), under the assumption that selection is weak (Taylor, 1988).

Our main findings describe the resolution of sex-ratio conflict (a) when parents make simultaneous sex-ratio decisions (the simultaneous allocation model); and (b) when parental sex-ratio decisions are sequential (the sequential allocation model). In particular, our sequential model posits a scenario in which fathers always make a sex-ratio decision before mothers.

Under the simultaneous allocation model, resolution of the conflict depends on the extent to which relative paternal contribution influences the brood sex ratio. Under the sequential allocation model, a compromise is always achieved, and this compromise favours one perspective or the other, depending on the extent to which parental investment influence offspring survival. The contrast between the two models highlights the importance of accounting for the biological details of conflict resolution in a theoretical setting.

2. Models

2.1. A framework

Our main interest is the co-evolution of two *sex-ratio behaviours* (phenotypes). The proportion of paternal investment made in sons, we call the *paternal sex-ratio behaviour*. Similarly, the proportion of maternal investment made in sons, we call the *maternal sex-ratio behaviour*.

We consider a diploid organism, and we suppose that sex-ratio behaviours are separate quantitative traits—controlled by separate autosomal loci. We will assume that both males and females possess the genetic information coding for both paternal and maternal sex-ratio behaviour. Later, we assume that this information is silent in one sex or the other. In addition, our phenotypic approach to the problem will assume that the genetic covariance between paternal and maternal sex-ratio behaviours is zero.

We assume an infinite population undergoing discrete, non-overlapping generations. We assume further that the population is divided into many patches of finite size, with each patch able to support N mated pairs. In order to set up the direct fitness argument presented in a later section, the model will be described with reference to one particular offspring (male or female, chosen at random). We call this offspring the *focal offspring*.

We will need the following notation:

- x_m, the paternal sex-ratio behaviour exhibited by the father of the focal offspring;
- x_f, the maternal sex-ratio behaviour exhibited by the mother of the focal offspring;
- y_m, the average paternal sex-ratio behaviour exhibited on the focal offspring's natal patch (i.e. the *focal patch*);
- y_f, the average maternal sex-ratio behaviour exhibited on the *focal patch*;
- z_m, the *resident* paternal sex-ratio behaviour;
- z_f, the *resident* maternal sex-ratio behaviour.

The interpretation of sex-ratio behaviours will require that they take values between zero and one.

Our approach is rooted in game theory. We will allow x_m and x_f—and so y_m and y_f also—to describe deviant or 'mutant' behaviour. However, we assume that mutants are rare, and that the population is otherwise fixed at the resident behaviours z_m and z_f.

We explore three separate cases, each defined by who controls the parental sex-ratio behaviours. In the first case, a father controls both his behaviour and that of his mate (i.e. paternal control of the sex ratio). In the second case, a mother controls both her behaviour and that of her mate (i.e. maternal control of the sex ratio). The final case assumes that a father controls paternal sex-ratio behaviour, and that a mother controls maternal sex-ratio behaviour. Conflict occurs in this last case only.

2.2. Life cycle

The hypothetical life cycle is outlined below. Following birth, the life cycle proceeds as follows: (a) parental