



## Parental care, cost of reproduction and reproductive skew: A general costly young model

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### SUMMARY

Understanding the mechanisms by which animals resolve conflicts of interest is the key to understanding the basis of cooperation in social species. Conflict over reproductive partitioning is the critical type of conflict among cooperative breeders. The costly young model represents an important, but underappreciated, idea about how an individual's intrinsic condition and cost of reproduction should affect the resolution of conflict over the distribution of reproduction within a cooperatively breeding group. However, dominant control in various forms and fixed parental care (offspring fitness dependent solely on total brood size) are assumed in previous versions of costly young models. Here, we develop a general costly young model by relaxing the restrictive assumptions of existing models. Our results show that (1) when the complete-control assumption is relaxed, the costly young model behaves very differently from the original model, and (2) when the fixed parental care assumption is relaxed, the costly young–costly care model displays similar predictions to the tug-of-war model, although the underlying mechanisms causing these similar patterns are different. These results, we believe, help simplify the seemingly divergent predictions of different reproductive skew models and highlight the importance of studying the group members' intrinsic conditions, costs of producing young, and costs of parental care for understanding breeding conflict resolution in cooperatively breeding animals.

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### 1. Introduction

Reproductive skew refers to the partitioning of reproduction among same-sex individuals within social groups and has been identified as a major dimension along which animal societies vary (Sherman et al., 1995; Vehrencamp, 2000). The development of the simple modeling framework of skew theories with their general predictions has stimulated many theoretical and empirical studies in diverse taxa (reviews in Reeve and Keller, 2001; Johnstone, 2000; Magrath et al., 2004). Two major kinds of reproductive skew models, based on different conflict resolution mechanisms, are transactional models and tug-of-war models. In transactional models (Emlen, 1982; Keller and Reeve, 1994; Reeve and Ratnieks, 1993; Vehrencamp, 1980; Vehrencamp, 1983), a single dominant individual is assumed to fully control both group membership and the fraction of total group reproduction obtained by the subordinate breeder. The dominant breeder maximizes its own fraction of reproduction at the expense of the subordinate, but yields just

enough reproduction to the subordinate to make it favorable for the subordinate to stay in the group. In tug-of-war models, on the other hand, no individual has complete control of the reproductive partitioning, and the reproductive skew is determined instead by competitive 'tugs-of-war' among group members (Reeve et al., 1998). Each group member is assumed to decide what fraction of the group's resources to expend in increasing its share of the group reproduction, and the share each group member receives depends on the ratio of these selfish investments.

Many empirical studies have focused on distinguishing the transactional and tug-of-war models, especially on testing the "complete-control" assumption of the transactional model (Cant, 2000; Clutton-Brock, 1998; Haydock and Koenig, 2002; Packer et al., 2001). These authors have argued that it is unlikely for a dominant individual to exert complete control over others' reproduction and therefore have embraced the tug-of-war model as being more applicable to their findings. The recent development of the bordered tug-of-war model (or incomplete-control transactional model) has relaxed the complete-control assumption of the transactional model (Reeve and Shen, 2006; Shen and Reeve, 2010). This theoretical advance shows that the complete-control assumption is not necessary for the transactional type of conflict resolution mechanism to occur and that evidence of incomplete

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control does not automatically prove the pure tug-of-war to be operating. For example, in subsocial beetles, *Parastizopus armaticeps*, no overt aggression was observed between communally laying females, which does not fit the tug-of-war model unless the competition is non-aggressive, i.e. exploitative. Reproduction was shared between closely related females, but reproductive share was closely correlated with individual body condition and not determined by social suppression. Therefore, the transactional model also does not seem to apply (Heg et al., 2006). It is clear that additional conflict resolution mechanisms besides the transactional and tug-of-war mechanisms should be incorporated into skew theory.

The costly young model represents another important, but overlooked, idea of how an individual's intrinsic condition and cost of reproduction could affect the distribution of reproduction within social groups (Cant, 1998; Cant and Johnstone, 1999). However, various forms of dominant control are assumed in different versions of costly young models. In Cant's (1998) original model, Alpha sets her optimal brood size first and then adjusts again after Beta makes her decision according to Alpha's first move. As the author correctly points out, this gives Alpha an advantage and imposes constraints on Beta for seeking her own optimal production of young. In the subsequent model (Cant and Johnstone 1999), Alpha is assumed to have complete control over the distribution of reproduction, such that both Alpha and Beta produce the brood sizes that maximize Alpha's inclusive fitness; or Alpha yields a minimum proportion of reproduction to retain Beta in the group, as assumed in the standard transactional model (Vehrencamp 1983, Reeve and Ratnieks 1993). In addition, the amount of parental care in a brood is assumed to be fixed in the original costly young model, which means that offspring fitness depends solely on total brood size and group members do not adjust their parental care based on brood size and their shares of reproduction. Here, we first relax the assumption of complete control of the costly young model and explore how asymmetric cost of producing young affects reproductive skew, and second, we develop a costly young–costly care model to include the possibility of flexible parental care. Our results show that (1) when the complete-control assumption is relaxed, the predictions of the new costly young model become very different from the original model and (2) when the fixed parental care assumption is relaxed, the costly young–costly care model generates similar predictions to the tug-of-war model, although the underlying mechanisms causing these similar patterns are different. These results help identify the similarities and key differences between different models and simplify the seemingly divergent predictions of different reproductive skew models.

## 2. The model

### 2.1. The costly young model with incomplete-control modification

In this section, we relax the complete control assumption of the original costly young model (Cant and Johnstone, 1999). For ease of comparison with previous models, the original costly young model equations are used (with slight modifications) but solved differently by simultaneously considering the optimal brood size from both Alpha's and Beta's perspectives. Following Cant and Johnstone (1999), we consider a two-person model without dominance. Two group members, referred to as Alpha and Beta, both contribute to a communal brood, and we ask how reproduction will be partitioned between them. Alpha produces  $n$  offspring and Beta produces  $f$  offspring. The total brood size is denoted  $t$  ( $=n+f$ ). We assume that an individual offspring's fitness,  $s(t)$ , declines linearly with brood size,  $t$ , so that  $s(t)=1-kt$ , where  $k$  is a

measure of the sensitivity of offspring prospects to increasing brood size ( $0 < k < 1$ ). The total productivity of a brood of size  $t$  is  $T(t) = t(1-kt)$ .

In this original costly young model, the per capita fitness of offspring is assumed to be determined by a parameter,  $k$ , which implicitly assumes that offspring fitness is not affected by parental care or parental care is at a fixed level (Fig. 1). We will relax this assumption in the later section. Producing young and providing parental care to the offspring entail an accelerating fitness cost (sensu Cant and Johnstone, 1999; Trivers, 1972) to the individual parent. We thus assume that the cost of producing  $n$  young is equal to  $en^2$ , where  $e$  is a constant describing the extent to which current reproductive effort affects future reproduction (we use this particular function for reasons of tractability; other accelerating cost functions yield qualitatively similar results). We can find the optimum brood size for a single breeder by maximizing  $F(n)$ , the net benefit of producing  $n$  young.  $F(n)$  is given by

$$F(n) = n(1-kn) - en^2 \quad (2)$$

Solving for  $n$ , a single female's optimal brood size, we obtain

$$\hat{n} = \frac{1}{2(k+e)} \quad (3)$$

The direct fitness  $F(n)$  of a female breeding solitarily can be obtained by substituting Eq. (3) into Eq. (2), which is

$$F(n) = \frac{1}{4}(e+k)[2-(e+k)^2] \quad (4)$$

Next, we consider what happens when two females contribute to a joint brood by finding expressions for the inclusive fitness payoff to Alpha and Beta as functions of  $n$  and  $f$ . The cost of producing  $n$  and  $f$  young are  $ae n^2$  and  $ef^2$  for Alpha and Beta, respectively, where  $a$  is a constant between 0 and 1 to express the greater efficiency, or lower cost, of reproduction for Alpha relative to Beta, which may be caused by differences in body condition, experience, or resource access. Combining all the preceding

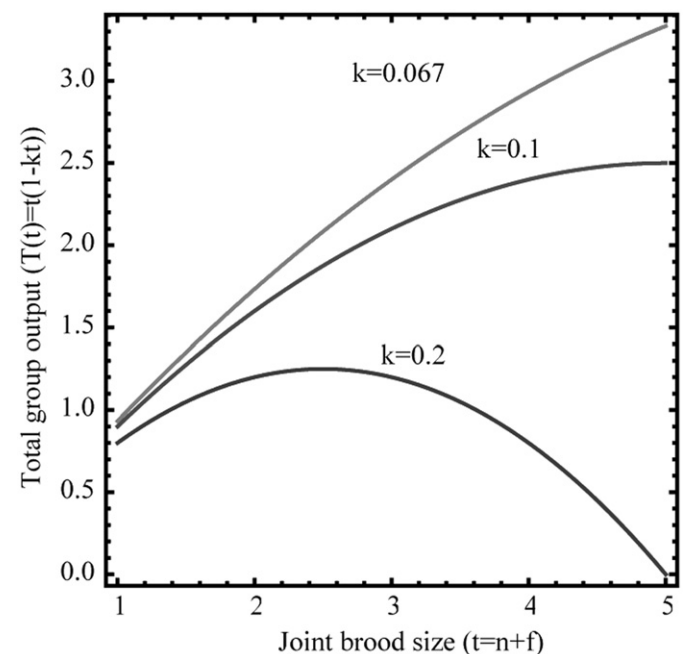


Fig. 1. The relationship between brood size and total group productivity. In the original costly young model, parameter  $k$  determines the shape of the brood size–productivity function. In the later section, we will allow levels of parental care,  $d$  and  $s$ , to affect group productivity.

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