



## Anniversary Essay

Unity and disunity in the search for a unified reproductive skew theory<sup>☆</sup>H. Kern Reeve<sup>a,\*,†</sup>, Sheng-Feng Shen<sup>b,1,†</sup><sup>a</sup> Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, U.S.A.<sup>b</sup> Biodiversity Research Center, Academia Sinica, Taipei, Taiwan

## ARTICLE INFO

## Article history:

Received 22 March 2013  
 Initial acceptance 29 March 2013  
 Final acceptance 4 April 2013  
 Available online 16 May 2013  
 MS. number: AAE-13-00256

## Keywords:

competition  
 cooperation  
 dominance  
 group formation  
 reproductive share  
 reproductive skew theory  
 society

Sandra Vehrencamp's (1983) *Animal Behaviour* paper provided a rigorous mathematical foundation for understanding reproductive partitioning within animal societies by focusing on the limits to reproductive competition over reproductive shares among group members. The central idea is that the degree of inequity in reproductive shares is limited by the option of group members to leave the group and reproduce elsewhere. This central idea has been retained in extensions of her model, and unification of these extensions with rival models has been developed to accommodate new data and alternative starting assumptions. Although some criticism has been directed towards skew theory, as presented both in the original Vehrencamp model and in subsequent syntheses, we show that many of these criticisms have been misguided. Synthetic skew theory, with Vehrencamp's model as its cornerstone, stands as our most general and complete, yet still largely untested, framework for understanding the evolutionary forces shaping the evolution of reproductive partitioning in animal societies.

© 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd.

The origin and foundation of inequality in human societies has been a key question of interest in the social sciences for centuries. Inspired by studying an unusual cooperatively breeding bird species, the groove-billed ani, *Crotophaga sulcirostris*, in which reproduction is shared relatively equally among unrelated breeders, Vehrencamp (1983) insightfully identified the partitioning of reproduction among group members as a key, but poorly understood, feature of animal societies. She further developed a formal game-theoretical model, incorporating ecological, genetic and social parameters, to explain the evolution of despotic versus egalitarian societies (for a brief history of skew theory, see Vehrencamp 2009). However, Vehrencamp's (1983) paper, was largely untested for nearly a decade (only 37 citations during 1983–1991; Google Scholar database), perhaps because empiricists were still becoming familiar with the melding of kin selection theory and game theory that formed the core of the theory. In early 1990s, several papers (Reeve 1991; Reeve & Ratnieks 1993; Keller & Reeve 1994;

Johnstone et al. 1999) streamlined Vehrencamp's original model, added the possibility of lethal fighting, and coupled it to a model of group formation to form an exact 'optimal skew model' for small groups. The simplified model made quantitative predictions about how genetic relatedness and ecological factors, such as ecological constraints and grouping benefits, jointly influence the biasing of reproduction among same-sex individuals within social groups (known as 'reproductive skew') and also the stability of these groups. With the high aim of providing a unifying general framework to bridge the gaps among researchers studying different social taxa, these papers focused on directing researchers to investigate the common genetic and ecological factors shaping animal societies (Keller & Reeve 1994). Optimal skew theory has since received intense theoretical and empirical attention.

Nevertheless, despite the initial success, the development of the simple optimal skew model also generated some strong scepticism, particularly centering on two issues. First, the 'complete control assumption' of the original optimal skew model (i.e. that dominant members of a society completely control reproduction of subordinates), seemed unrealistic for many species (Clutton-Brock 1998; Packer et al. 2001; Haydock & Koenig 2002; Port & Kappeler 2010). Second, as the number of models being developed increased, the sets of model predictions also quickly increased, with the unfortunate effect of dizzying, and even frustrating, field workers. Even worse, empirical studies were often not

<sup>☆</sup> In honour of Sandra L. Vehrencamp (1983) 'A model for the evolution of despotic versus egalitarian societies' (31, 667–682).

\* Correspondence: H. K. Reeve, Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, U.S.A.

E-mail address: [hkr1@cornell.edu](mailto:hkr1@cornell.edu) (H. K. Reeve).

<sup>1</sup> E-mail address: [shensf@sinica.edu.tw](mailto:shensf@sinica.edu.tw) (S.-F. Shen).

<sup>†</sup> Equal contributions by both authors.

able to experimentally distinguish among these models, due to the logistical difficulty of assessing their assumptions and testing their discriminating predictions. As a result, many researchers considered reproductive skew a topic in which empirical studies lagged seriously behind a rapid proliferation of theoretical models (Magrath & Heinsohn 2000; Davies et al. 2012), generating strong resistance against publication of more model variations and even calls to suspend testing of the theory. A proper assessment of the value of Vehrencamp's contribution requires that we critically examine specific recurring criticisms of skew theory below. However, we first describe how the extensions and alternatives to Vehrencamp's original idea have been recently integrated to give rise to a promising 'synthetic' theory.

## THE MODEL AND ITS EXTENSIONS

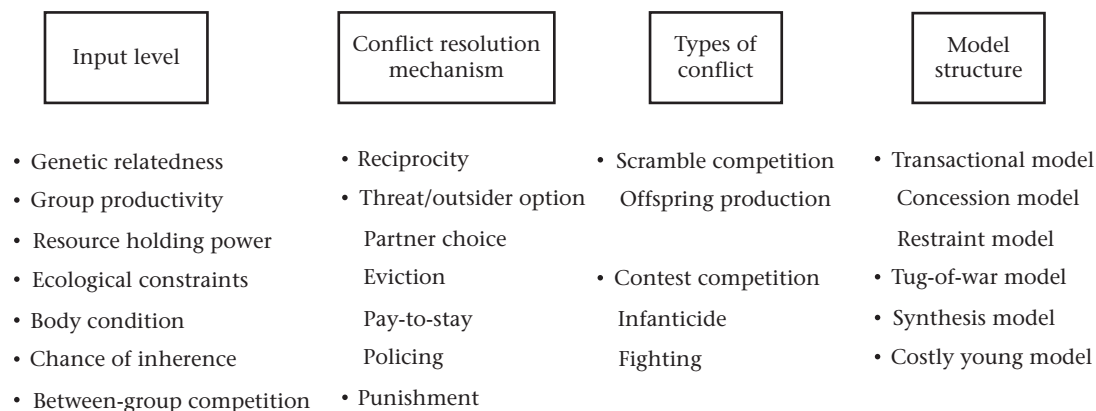
Vehrencamp's key idea is that a dominant member of an animal society may have to concede some reproduction to subordinates to prevent subordinates from leaving the group and breeding alone. Equivalently, the dominant could be seen as having to 'pay' subordinates as part of a reproductive transaction to secure the subordinates' cooperation. Most of the initial extensions of existing skew models were built on this transactional framework. What varied in these early extensions was who did the paying (e.g. dominant versus subordinate) and what the payment was designed to prevent (e.g. leaving versus lethal fighting). Nevertheless, it has been argued that any single one of these models is not enough to encompass the diverse forms of animal societies (Nonacs & Hager 2010; Port & Kappeler 2010). However, as the number of models increase, the number of different sets of predictions also increases (as does the likelihood of overlap in the predictions of two or more models), making it difficult for empiricists to develop tests that maximally discriminate among models.

To help navigate through the maze of models in developing efficiently discriminating tests, we propose a hierarchical approach, which distinguishes four levels of properties of reproductive skew theory: (1) the input level: the ultimate selective drivers of reproductive skew, such as ecological constraints, group benefits, genetic relatedness and individuals' competitive abilities; (2) the conflict structure: the forms of the social conflict being examined, including contest competition (e.g. infanticide) and scramble competition (e.g. races in offspring production within communally breeding species); (3) the conflict resolution mechanism (e.g. reciprocity, threat and punishment); and (4) the model structure: the theoretical framework used to integrate the first three levels (e.g. transactional: Vehrencamp 1983; Reeve 1991; Reeve & Ratnieks 1993; Keller & Reeve 1994; tug-of-war: Reeve et al. 1998; costly

young: Cant 1998; Cant & Johnstone 1999; Shen et al. 2011; Fig. 1). Selection of the appropriate model structure is often the difficult step, due to model multiplicity, but is aided by recent attempts to combine prior models into a unifying, synthetic theory that predicts the precise conditions under which each model should apply, and also delineates the transition zones among them (Reeve & Shen 2006; Cant & Johnstone 2009; Shen & Reeve 2010). In the following sections, we use this hierarchical approach (Fig. 1) to review existing models. We then show that, by clearly distinguishing between forms of social conflict and conflict resolution mechanisms, empiricists can better choose the appropriate level at which to conduct observational and/or experimental tests of the applicability of rival models of reproductive skew and within-group conflict.

### The Transactional Models

The biological picture envisioned by Vehrencamp's (1983) original transactional model was that dominant members of a group have complete control over the subordinates' reproductive shares. If the dominant does not have complete control, then dominants and subordinates may mutually compete, which can affect their combined reproductive shares. If there is a benefit to grouping, dominants will yield some reproduction to the subordinates as an incentive to stay. However, if the subordinate's share is less than that obtained from breeding solitarily, the subordinate can choose to fight for complete control of the group's resources or simply leave the group (Reeve & Ratnieks 1993; Keller & Reeve 1994). Thus, there are two key components of the simplest transactional model structure: (1) dominants' complete control of reproduction and (2) the effect of subordinates' outside options on the strategy of dominants and subordinates. The conflict resolution mechanism is implemented by the subordinates' mechanism to prevent cheating, such as punishment (Reeve & Nonacs 1992; Shen & Reeve 2010). The 'complete control' assumption simply means that the dominant makes the first 'move' to decide its own share of reproduction, which in turn automatically determines a subordinate's share of reproduction. The subordinate can then decide to accept the dominant's offer and stay in the group, or take an outside option, such as leaving the group or fighting the dominant. This sequential decision process of the transactional model has long been acknowledged and even clearly described in Maynard Smith's classic game theory book (Maynard Smith 1982, pp.137–139). Similar sequential-game solutions are widely used as a mechanism for resolution in other types of conflict in evolutionary biology (Maynard Smith 1982; Johnstone & Grafen 1992). The subordinate's signalling of the option to leave the group or fight can be viewed as



**Figure 1.** Summary of the hierarchical components of studying reproductive skew and within-group conflict (see text for details).

Download English Version:

<https://daneshyari.com/en/article/10970717>

Download Persian Version:

<https://daneshyari.com/article/10970717>

[Daneshyari.com](https://daneshyari.com)