Skew Theory

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Skew Theory

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Synonyms

Optimal skew theory; Reproductive skew theory

Definition

An evolutionary theory attempting to explain the unequal sharing of reproduction among same-sex individuals within social groups.

Introduction

Cooperatively breeding animals vary markedly in reproductive skew, the unequal distribution of direct reproduction among same-sex individuals within social groups. In high-skew groups, such as eusocial ants, honeybees, termites, and meerkats, reproduction is concentrated in one or a few dominant individuals; in low-skew groups, such as some polistine and polybiine wasps and banded mongooses, reproduction is distributed more equitably among group members. Variation in skew frequently occurs both within and across species (Reeve and Ratnieks 1993; Vehrencamp 1983).

Reproductive skew theory aims to predict how members within a social group would partition reproduction in an evolutionarily stable way. To determine the optimal level of skew, it integrates genetic relatedness, ecological constraints on solitary breeding, group-living benefits, and within-group competitive asymmetries into a single theoretical basis (Johnstone 2000; Reeve and Ratnieks 1993). Further, skew models tend to, but not always, assume that each member's payoff of staying in the group should be greater or equal to the payoff of leaving to breed alone or fighting for the sole possession of the nest, thus opening up a new avenue for unraveling the evolution of group size and within-group conflict. Not surprisingly, researchers have boldly claimed that reproductive skew theory may be a good candidate for a general unified theory of social evolution, one that explains all the major features of all social taxa ranging from termite colonies to human societies.

Over two decades, a wide variety of skew models has been devised and the resulting predictions have been tested numerous times. The plethora of model variants with conflicting predictions, however, has attracted considerable skepticism and criticisms (Nonacs and Hager 2011). As a comprehensive literature review over various work and controversies on skew is beyond the aim of this entry, the basic models of reproductive skew and their implications for the humans are presented below.

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Models of Reproductive Skew

Reproductive skew models can be classified into three major classes according to their different assumptions about how reproductive sharing is achieved within a social group: transactional models, compromise models, and synthetic models.

Transactional Models

Transactional models of skew assume that one individual has complete control over the partitioning of reproduction but the individual may "yield" a share of reproduction to other group members in order to maintain group stability (Reeve and Ratnieks 1993). Two types of transactional models exist: concession models and restraint models.

First, the concession model assumes that the dominant individual has full control over the reproductive partitioning within the group. Consider a group of two individuals, a dominant and a subordinate. If the dominant is too greedy and try to monopolize all direct reproduction in the group, the subordinate may choose to leave the group and reproduce solitarily. In response to the subordinate's threat of departure, the dominant may concede just barely enough reproduction to the subordinate as an incentive to stay (Reeve and Ratnieks 1993; Vehrencamp 1983). The minimum share given to the subordinate would decline as (1) the expected reproductive success of a subordinate pursuing the departing option decreases (because, under harsh ecological constraints on solitary breeding, the dominant does not need to "pay" a large staying incentive), (2) the group's overall productivity increases (i.e., the total size of the pie to be divided between the two has expanded), and (3) the genetic relatedness between the dominant and the subordinate increases (the subordinate's indirect fitness payoff from remaining in the group increased).

Second, the restraint model assumes that the dominant only control group membership; that is, it has have the ability to evict the subordinate from the group (Johnstone and Cant 1999). It is the subordinate, however, who is assumed to have complete control over reproductive sharing. The subordinate may still exhibit a form of reproductive restraint in order to avoid ejection from the group; it will thus obtain its maximum share of reproduction that can be tolerated by the dominant. Consequently, the concession and restrain models make exactly opposite predictions about the relationship between the genetic, ecological, and social factors and the level of reproductive skew.

Compromise Models

Compromise models do not incorporate the possibility of group dissolution. In other words, they assume that subordinates could not voluntarily depart the group, nor could the dominant forcefully evict subordinates. Another difference from the transactional models lies in whether any individual is assumed to have full control over the division of reproduction. In compromise models, no individual has complete control. Rather, each group member competes selfishly to gain a higher personal share of reproduction, at a cost to the overall productivity of the group. The partitioning of reproduction is determined by a compromise between the diverging optima of dominant and subordinates (Reeve et al. 1998).

The most well-known variant of this category, i.e., the tug-of-war model of Reeve et al. (1998), assumes that the dominant's higher competitive ability renders it more efficient in converting its selfish effort to an increased personal share of reproduction. The evolutionarily stable level of skew is solved by finding the selfish efforts of dominants and subordinates in a way that the inclusive fitness of each is simultaneously maximized. The tug-of-war model yields different predictions from those of transactional models. The subordinate's reproductive share at equilibrium would decline as the subordinate's relative competitive ability decreases, but it will be quite insensitive to the genetic relatedness between the competitors. Ecological constraints, which were assumed away from the outset, would not affect the division of reproduction.

Synthetic Models

Synthetic models integrate the possibility of both group dissolution and incomplete control into a single framework. Each group member may exchange reproductive payments to each other in order to maintain group stability, while simultaneously engaging in a tug-of-war competition over the remaining portion of reproduction (Johnstone 2000; Reeve and Shen 2006). Initial models, however, have been harshly criticized for theoretical shortcomings. For instance, it has been formally proved that a mixed strategy that involves both a tug-of-war and reproductive payments is unstable to invasion by a mutant "nicer" strategy that competes less strongly and gives a lesser reproductive payment (Cant and Johnstone 2009). Recent synthetic models attempt to overcome the stability problems of previous analyses, taking seriously the threat of departure/eviction or the power of negotiation.

Skew Theory Applied to Humans

Given that reproductive skew theory aspires to be a unified science of social evolution, it may be fruitfully utilized to elucidate the foundations of human sociality. Summers (2005) applied the classical concession model to the development of social stratification among human males. Recall that the concession model predicts that when group productivity benefits are greater, when the prospects for solitary breeding are lower, and when group members are more closely related, the level of skew within a group will be higher. Summers (2005) suggested that, since our divergence from the chimpanzee lineage, early hunter-gatherer societies were largely egalitarian (i.e., low level of skew) via the collective suppression of a self-assertive dominant individual by a group of subordinates. Around 10,000 years ago, strong ecological constraints on solitary dispersal, combined with the economically storable nature of agricultural crops, led to the formation of despotic preindustrial societies (i.e., high level of skew). For example, the harsh environments surrounding the Nile Valley made possible the development of extreme despotism in ancient Egypt. In the same vein, Betzig (2014) emphasized the role of ecological constraints in shaping despotic civilizations in Mesopotamia, Egypt, India, and China. Kings and emperors collected as many as 100,000 fertile women, whose children were supported by thousands of eunuchs ("sterile castes"). About 500 years ago, modern egalitarian societies emerged, the reason of which was attributed to the relaxation of ecological constraints, i.e., the discovery of two nearly empty continents (Betzig 2014).

In addition to human societies, the reproductive skew framework has been applied to analyze the extended human family. A growing body of evidence indicates that humans have evolved as a cooperatively breeding species, in which care and provisioning from family members from other than mothers were essential for child survival. Cant and Johnstone (2008) applied the tug-of-war model to understand reproductive conflicts between women of different generations. If female dispersal predominantly occurred in ancestral humans, there would be relatedness asymmetries between a mother and her son's wife in the extended family. Although the mother is related to the offspring of the daughter-in-law, the daughter-in-law, by contrast, is completely unrelated to the mother-in-law's offspring. Under these circumstances, the evolutionarily stable solution is for the old mother to commit to zero reproduction and allow the daughter-in-law to monopolize reproduction, leading to the evolution of menopause in human females. Empirical studies that tested Cant and Johnstone's (2008) reproductive conflict model, however, have yielded mixed results.

Conclusion

Models of reproductive skew predict how reproductive conflict among same-sex individuals within a group will be resolved at evolutionary equilibrium, depending upon various factors such as grouping benefits, ecological constraints, genetic relatedness, group size, and competitive ability. The bewildering array of skew models, however, has recently met serious criticisms based on both theoretical and empirical grounds. Nonacs and Hager (2011) reviewed dozens of empirical studies across diverse animal taxa, concluding that that neither relatedness nor competitive ability affected skew within a group. It thus remains to be seen whether skew theory lucidly captures the true causes underlying the evolution of sociality. Nonetheless, skew theory has already done an important contribution on the study of cooperative breeding and reproductive conflict. For instance, the theory has rightfully highlighted that the possibility of group dissolution via departure/eviction has a great influence on how within-group conflict is resolved (Cant and Johnstone 2009). It is apparent that the studies of human kinship would also benefit by making full use of skew framework.

Cross-References

- ▶ Cooperative Breeding
- ▶ Inclusive Fitness
- ▶ Game Theory
- ▶ Menopause

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