From individual control to majority rule: extending transactional models of reproductive skew in animal societies

Hudson Kern Reeve^{1*} and Robert L. Jeanne²

¹*Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA*

²*Department of Entomology, University of Wisconsin, Madison, WI 53706, USA*

Transactional concession models of social evolution explain the reproductive skew within groups by assuming that a dominant individual completely controls the allocation of reproduction to other group members. The models predict when the dominant will benefit from donating parcels of reproduction to other members in return for peaceful cooperation. Using linear programming methods, we present a 'majority-rules' model in which the summed actions of all society members, each with equal power, completely determine the reproductive share of any single member. The majority-rules model predicts that, despite the diffusion of power, a 'virtual dominant' (a dominant lacking special behavioural power) will emerge and that the reproductive skew will be exactly that predicted if the virtual dominant were to control completely the group's reproductive partitioning. The virtual dominant is the individual to which group members have the maximum average genetic relatedness. This result greatly broadens the applicability of transactional models of reproductive skew to social groups of any size, such as large-colony eusocial insects, and explains why queens in such colonies can achieve reproductive domination without any behavioural enforcement. Moreover, the majority-rules model unifies transactional-skew theory with models of worker policing and even generates a new theory for the cooperation among somatic cells in a multicellular organism.

Keywords: cooperation; dominance; kin selection; reproductive skew; staying incentives; worker policing

1. INTRODUCTION

Transactional models of social evolution explain the distribution of reproduction within animal societies as the result of reproductive payments exchanged among group members (Reeve *et al.* 1998; Johnstone 2000; Reeve & Keller 2001). The power of transactional models lies in their ability to predict precisely the reproductive partitioning within societies as a function of the genetic relatedness among the members of the society, the ecologically driven pay-offs for group living versus solitary breeding and the power asymmetries among group members (Vehrencamp 1983; Reeve & Ratnieks 1993; Reeve *et al.* 1998; Reeve 1998; Johnstone *et al.* 1999; Johnstone 2000; Reeve & Emlen 2000; Reeve & Keller 2001). For example, transactional models predict that a focal individual will cede a greater fraction of reproduction to a partner the lower the genetic relatedness between it and the partner and the greater the personal pay-off of the non-cooperative option for the partner (e.g. the greater the partner's pay-off for leaving the group or for evicting the focal individual from the group; see reviews in Johnstone (2000) and Reeve & Keller (2001)).

The transactional-model predictions have received recent support from studies of insects and vertebrates (Reeve & Keller 2001). These models explain the degree of the monopolization of reproduction by dominants (i.e. the reproductive skew) by assuming that a single individual completely controls the allocation of reproduction to

other group members. This 'individual control' assumption may not apply in large groups, such as many insect societies, or even in small groups with widely spatially distributed resources. In such groups, there may be no individual with complete control of the reproductive partitioning, and the reproductive skew (degree of the monopolization of reproduction by dominants) may be determined instead by competitive 'tugs-of-war' among colony members (Reeve *et al.* 1998), with reproductive sharing resulting when no one party can exert complete reproductive control (for reviews see Johnstone 2000; Reeve & Keller 2001).

However, a previously unexamined possibility is that a 'majority-rules' model applies, i.e. a model in which the summed actions of all society members completely determine the reproductive share of any single individual. Under this view, the collective genetic interests of the group prevail over the genetic interest of any one individual simply owing to the sheer numerical superiority of the collective. We show that the individual-control and majority-rules models (and all intermediate models) are special cases of a general linear programming optimization problem, the solution of which yields the striking prediction that 'virtual dominants' will appear even in large groups. A 'virtual dominant' is an individual who captures a disproportionately large share of the group reproduction despite having no special behavioural power to enforce its reproductive dominance.

In the simple dyadic transactional model of skew called the concessions model, the magnitudes of the staying and peace incentives yielded to a subordinate by a dominant, as well as the conditions under which these incentives are

*Author for correspondence (hkr1@cornell.edu).

given, are obtained by the use of the Hamilton's rule inequality (Reeve & Ratnieks 1993). In particular, an action i is favoured over an action j if

$$A_i - A_j + r(B_i - B_j) > 0, \quad (1.1)$$

where A_i (or A_j) is the personal reproductive output associated with action i (or j), B_i (or B_j) is the corresponding partner's reproductive output and r is the genetic relatedness between the partners. Inequality (1.1) can be expressed equally well as a comparison of the inclusive fitnesses associated with the alternative actions:

$$A_i + rB_i > A_j + rB_j. \quad (1.2)$$

The variables entering into the simple dyadic skew model are:

- (i) x , the expected reproductive output of a solitary potential subordinate (standardized relative to an expected output of 1.0 for a solitary potential dominant);
- (ii) k , the standardized total output of the dyad; and
- (iii) r , the genetic relatedness.

It is usually assumed that $k > 1$ (i.e. the dyad does better than a lone dominant) and that $r < 1$.

Using inequality (1.1), the dyadic model the minimal staying incentive p_s for a subordinate, that is, the fraction of reproduction that the dominant must pay to prevent the subordinate from leaving, can be calculated by finding that fraction of the group reproduction that just makes staying favourable over leaving (Reeve & Ratnieks 1993):

$$p_s = \frac{x - r(k - 1)}{k(1 - r)}. \quad (1.3)$$

Hamilton's rule is also used to determine under what conditions the staying incentive will be donated by dominants. Reeve & Ratnieks (1993) showed that the subordinate will stay and help without being granted any direct reproduction under strong ecological constraints, corresponding to the condition $x < r(k - 1)$. Dominants will yield the staying incentive (1.3) instead of ejecting the subordinate under moderate ecological constraints, corresponding to the condition $r(k - 1) < x < k - 1$. No stable group forms under weak ecological constraints, i.e. $x > k - 1$.

These dyadic-model results could have been obtained by treating the subordinate's staying incentive as the solution to a linear programming problem. The problem is finding the subordinate's staying incentive p_s that maximizes the dominant's inclusive fitness

$$(1 - p_s)k + rp_s k \quad (1.4)$$

(reflecting the fact that the dominant is completely controlling the reproductive partitioning), subject to the linear constraint

$$p_s k + r(1 - p_s)k \geq x + r \quad (1.5)$$

(reflecting the requirement that the subordinate's inclusive fitness if it stays must equal or exceed that if it leaves and breeds solitarily). This approach also yields equation (1.3) for the case $r(k - 1) < x < k - 1$, as previously derived (Reeve & Ratnieks 1993).

This linear programming problem is easily generalized to a group of n individuals. Let K be the total group output (in offspring) if everyone stays in the group (this was represented by k in the original dyadic model). Let $\mathbf{P} = [p_1, p_2, \dots, p_n]$ be the vector describing the reproductive fraction received by each group member, with the group members being indexed by the subscripts. Let $\mathbf{R}_i = [r_{i1}, r_{i2}, \dots, r_{in}]$ be the vector describing the genetic relatedness of the i th group member to the offspring of each of the other group members (including itself). Finally, let $\mathbf{B}_i = [b_{i1}, b_{i2}, \dots, b_{in}]$ be the vector describing the offspring production of each group member if the i th group member leaves the group (or pursues some other personal reproductive option, such as fighting to the death to monopolize group resources). We let the dominant group member, i.e. the one whose inclusive fitness is to be maximized, be represented by the subscript d .

The linear programming problem of finding the stable distribution of reproduction among all n members of a stable group when the d th individual (the dominant) has complete reproductive control then becomes: find the $\mathbf{P} = \mathbf{P}^*$ that maximizes the dot product $\mathbf{K}\mathbf{R}_d \cdot \mathbf{P}$ ($= Kr_{d1}p_1 + Kr_{d2}p_2 + \dots + Kr_{dn}p_n$, i.e. the dominant's inclusive fitness if everyone stays in the group) subject to the n linear constraints $\mathbf{K}\mathbf{R}_i \mathbf{P} \geq \mathbf{R}_i \mathbf{B}_i$ (the condition for each group member to do better by staying in the group rather than leaving or pursuing other selfish options) for $i = 1, 2, \dots, n$, together with the constraint that $\sum p_i = 1$. This general formulation encompasses both 'concessions' and 'restraint' transactional models of skew if the dominant is defined as the individual controlling reproductive shares; in the restraint model, the dominant may yield reproduction to avoid being ejected from the group (for reviews see Johnstone 2000; Reeve & Keller 2001). This linear programming problem usually will have to be solved numerically with solution methods such as the simplex algorithm (Dantzig 1998), although analytical results have been obtained for special cases such as three-member groups (Johnstone *et al.* 1999) or n -member groups with homogeneous relatedness and identical staying incentives for subordinates (Reeve & Emlen 2000).

2. THE MAJORITY-RULES MODEL OF REPRODUCTIVE SKEW

Next, we consider the majority-rules model, in which reproductive control, i.e. control over the resources critical for reproduction, is diffuse and an individual's actual resource share, hence its reproductive share, is determined entirely by the aggregate actions of the remaining group members and little or not at all by the individual's own actions. In other words, the entire aggregation of all group members other than a given individual effectively behaves like a completely controlling dominant with respect to that individual. There need not be any coordinated joint action or coalition-mediated behaviour by the aggregate: the individual's reproductive share may be determined simply by the statistically averaged flows of reproductively valuable resources within the group, with an individual's attempts to modify the flow of resources to itself being nearly overwhelmed by the summed actions of the numerous other group members.

Remarkably, such a majority-rules model, when cast as a linear programming problem, predicts that a ‘virtual dominant’, i.e. a dominant lacking any special behavioural power, can emerge in the society, and that the resulting partitioning of reproduction will be identical to that predicted by a transactional skew model in which the virtual dominant has complete behavioural control over reproduction. Moreover, the majority-rules model will be seen to sit at one extreme in a continuum of models differing in the assumed variance in behavioural control among group members, with the original complete-control models sitting at the other extreme.

We begin by modelling the dynamics of the flows of reproductively valuable resources among group members. We make the simple assumption that each group member (actor) attempts to alter a recipient’s fraction of reproduction p with an intensity that varies directly with the product of the actor’s individual power, denoted by a weighting coefficient a , and the slope dI/dp , which describes how that actor’s inclusive fitness I changes as the recipient’s fraction of reproduction changes. In other words, the effect of an actor on the reproductive share of another group member depends both on the actor’s power and on the actor’s inclusive fitness change for changing that share. We then assume that the overall change over time in the recipient’s fraction of reproduction is equal to the sum of the effects of all the group members; additionally, we assume that actors have knowledge of their expected relatednesses to other group members. Mathematically, then, the rate of change in the fraction of reproduction p_j going to the j th individual, dp_j/dt , is equal to

$$\frac{dp_j}{dt} = a_1 \frac{dI_1}{dp_j} + a_2 \frac{dI_2}{dp_j} + \dots + a_n \frac{dI_n}{dp_j} = \sum_{i=1}^n a_i \frac{dI_i}{dp_j}. \quad (2.1)$$

The i th actor’s inclusive fitness is equal to $Kr_{i1}p_1 + Kr_{i2}p_2 + \dots + Kr_{in}p_n$ (K is the total group output). This can be rewritten as

$$I_i = Kr_{ik}p_k + Kr_{i,k}(1 - p_k), \quad (2.2)$$

where r_{ik} is the actor’s mean relatedness to the k th individual’s offspring and $r_{i,k}$ is the actor’s mean relatedness to the offspring of all group members other than the k th group member (which will depend on precisely how the reproduction is divided up among these other group members). The derivative of this inclusive fitness with respect to p_k is just $K(r_{ik} - r_{i,k})$, so equation (2.1) for the k th group member becomes

$$\frac{dp_k}{dt} = K \sum_{i=1}^n a_i (r_{ik} - r_{i,k}) = K \left(\sum_{i=1}^n a_i r_{ik} - \sum_{i=1}^n a_i r_{i,k} \right). \quad (2.3)$$

Now, equation (2.3) must always be greater than zero if the k th group member is the one with the maximum value of

$$\sum_{i=1}^n a_i r_{ij}, \quad (2.4)$$

i.e. expression (2.4) is a maximum when $j = k$. The proof is as follows: $\sum a_i r_{i,k}$ is equal to

$$\sum_{i=1}^n a_i r_{i,k} = \sum_{i=1}^n a_i \sum_{\substack{j=1 \\ j \neq k}}^n r_{ij} f_j = \sum_{\substack{j=1 \\ j \neq k}}^n f_j \sum_{i=1}^n a_i r_{ij}, \quad (2.5)$$

where

$$f_j = \frac{p_j}{\sum_{\substack{l=1 \\ l \neq k}}^n p_l}$$

is a fraction that sums to 1.0 across all group members other than the k th group member. Consequently, the right-hand side of equation (2.5) is just a weighted average of $\sum a_i r_{i,j}$ for all group members other than the k th member. By assumption, each of these values cannot exceed $\sum a_i r_{i,k}$ and thus their mean must be less than $\sum a_i r_{i,k}$. As a result, $\partial p_k / \partial t > 0$, and the k th individual will receive an increasing reproductive share (at the expense of others) over time and will become a ‘virtual dominant’ in the above sense—its reproductive share will be limited only by the linear constraints $KR_i \cdot P \geq R_i \cdot B_i$ that represent the minimal incentives, e.g. staying incentives, for other group members to cooperate. In other words, the k th individual in the group will be a dominant in the sense that, despite having little or no reproductive control, it will dominate reproduction in exactly the way predicted by the ‘complete control’ transactional models; as in these models, the dominant’s reproduction is limited only by the requirement to pay out incentives for cooperation to the other group members. The important implication is that behavioural reproductive control by a dominant is not required for transactional models to make the correct quantitative predictions about the reproductive partitioning within a group.

We can substitute for a_i in equation (2.4), a fractional ‘power’ $\pi_i = a_i / \sum a_i$ that determines the degree to which the i th individual’s inclusive fitness is maximized (with $\sum \pi_i = 1$). The virtual dominant is then the individual for which $\sum \pi_i r_{i,k}$ is the greatest. (If more than one individual has the maximum value, then either they should divide the reproduction equitably or (perhaps more likely) their exact shares will be determined by their powers relative to each other.) The traditional transactional model of reproductive skew is the special case in which the dominant’s power is one ($\pi_d = 1$) and everyone else’s power is zero. The majority-rules model results in the special case when everyone has equal power, i.e. $\pi_i = 1/n$ for every individual i . In intermediate cases, some individuals have more power than others, but no one has complete power.

3. THE IDENTITY OF THE VIRTUAL DOMINANT

Who will be the virtual dominant? Under the majority-rules model, $\pi_i = 1/n$ for all individuals, so the virtual dominant will be the individual with the maximum value of $(\sum r_{ij})/n$, i.e. the individual whose offspring have the maximum mean relatedness to all group members (including itself). Even if powers are unequal, reproductive dominance should be determined less by an individual’s intrinsic competitive ability and more by aggregate group interests as group size increases, since individual power will approach zero relative to the

Table 1. Virtual dominants in a variety of social groups.
(As predicted, parents are usually the virtual dominants in large-colony eusocial Hymenoptera (Wilson 1971; Michener 1974), the exceptions occurring in some single-queen colonies in which the queen is mated few times ($m < 2$, e.g. honeybees; Ratnieks 1988) or in multiple-queen societies in which inter-queen relatedness r is low (Crozier & Pamilo 1996; Bourke 1997). Parents are typically also the virtual dominants in termite societies, with workers usually inbreeding as secondary reproductives only when the parents die (Shellman-Reeve 1997). The model of germ cells as virtual dominants assumes ‘infinite alleles’, i.e. that there is a relatedness of 1.0 between two cells at a given locus only if there have been no mutations in their cell lineages since they diverged from an ancestral cell.)

kind of group	majority class	mean relatedness of majority class to the progeny of		virtual dominant
hymenopteran mother queen (Q) with m matings + daughter workers (W)	W	Q $1/4$ (males) $(2 + m)/4m$ (females)	W $(2 + m)/8m$ (males) $(2 + m)/8m$ (females)	Q if $m > 2$ W if $m < 2$ (males) Q (females)
n singly mated hymenopteran queens (Qs) related by r + daughter workers (W) (equal matriline representation)	W	Qs $[1 - r(n - 1)]/4n$ (males) $[3 - r(n - 1)]/4n$ (females)	W $[13 - r(n - 1)]/8n$ (males) $[3 - r(n - 1)]/8n$ (females)	Qs if $n > 1 + 1/r$ W if $n < 1 + 1/r$ (males) Qs (females)
termite primary pair (P) + workers (W) (unrelated primaries with inbreeding coefficient F)	W	P $(1 + F)/2$	W (inbreeding secondary reproductives) $(1 + F)/4$	P
cells in a multicellular organism ^a	S	S (different tissues) $(1 - u)^{2N} \approx e^{-2uN}$	G $(1 - u)^N(1 - u)^{N'} \approx e^{-u(N + N')}$	G

^a S, mature somatic cells with N cell divisions since zygote formation; G, germ cells, which have $N' \ll N$ cell divisions since zygote formation; u , mutation probability per cell division.

summed powers of all group members. This hypothesis explains patterns of dominance in large versus small groups of primates such as macaques, in which individual power determines dominance in small groups, but the aggregate relatedness of group members to other group members determines dominance in larger groups (Dunbar 1988, pp. 227–228). Similarly, it explains why reproductive dominance reflects the individual queen’s, not the collective workers’, genetic interests in the small multi-queen colonies of social paper wasps (Queller *et al.* 1997) but reflects the collective workers’ interests in the large multi-queen colonies of neotropical swarm-founding wasps (Jeanne 1991; Hastings *et al.* 1998).

In a large hymenopteran colony, the mother queen will usually be the virtual dominant (table 1). Given that workers are numerically predominant and control colony resource-allocation decisions, the mean relatedness of group members to the offspring of a single queen inseminated equally by m males is $1/4$ for male offspring and $(2 + m)/4m$ for female offspring, whereas the mean relatedness of group members to the offspring of a worker is $(2 + m)/8m$. Thus, according to the majority-rules model, the mother queen should be the virtual dominant with regard to both female and male offspring if $m > 2$; if $m < 2$, one or more workers should be the virtual dominant with respect to male offspring (table 1). The latter prediction is the same as the ‘worker-policing theory’ (Ratnieks 1988; Ratnieks & Visscher 1989), which now can be seen as a special case of the majority-rules model of reproductive skew. Thus, the generalized transactional

model (which now includes the majority-rules model) unifies reproductive-skew theory and worker-policing theory, and extends the latter, as well as providing a rigorous general explanation for why parents are usually the virtual dominants in large cooperative groups where individual control is difficult or impossible. The majority-rules model also explains the reproductive dominance exhibited by parents in termite societies, with secondary reproductives (inbreeding siblings) arising only when the parents disappear (Shellman-Reeve 1997) (table 1). In such groups, the pattern of relatedness between workers and parents dictates that parents should be virtual dominants and completely monopolize reproduction; when the parents disappear, however, multiple pairs can become virtual dominants as multiple pairs will have the same mean relatedness to the worker aggregate.

Finally, the general model may even illuminate the apparent role of primordial germ cells as ‘virtual dominants’ within many multicellular organisms such as insects and vertebrates (table 1). Germ cells in these organisms differentiate from other embryonic cells very early in development (Gilbert 1991), so on average many fewer cell divisions will separate germ cells and mature somatic cells than will separate mature somatic cells of different tissues. Thus, germ cells will tend to exhibit fewer cumulative replication-associated mutations than will somatic cells and consequently will have the greatest expected relatedness to the numerically predominant somatic cells (table 1), possibly accounting for their status as virtual dominants.

The authors thank L. Fletcher, A. Grafen, S. Emlen, J. Jeon, R. Johnstone, S. Little, J. Shellman, E. Tibbetts and two anonymous reviewers for valuable discussions and comments on the ideas in this paper. H.K.R. was supported by a US NSF-sponsored Presidential Early Career Award for Scientists and Engineers.

REFERENCES

- Bourke, A. F. G. 1997 Sociality and kin selection in insects. In *Behavioural ecology: an evolutionary approach*, 4th edn (ed. J. R. Krebs & N. B. Davies), pp. 203–227. Oxford University Press.
- Crozier, R. H. & Pamilo, P. 1996 *Evolution of social insect colonies: sex allocation and kin selection*. Oxford Series in Ecology and Evolution. Oxford University Press.
- Dantzig, G. B. 1998 *Linear programming and extensions*. Princeton University Press.
- Dunbar, R. I. M. 1988 *Primate social systems*. Ithaca, NY: Cornell University Press.
- Gilbert, S. F. 1991 *Developmental biology*. Sunderland, MA: Sinauer.
- Hastings, M. D., Queller, D. C., Eischen, F. & Strassmann, J. E. 1998 Kin selection, relatedness, and worker control of reproduction in a large-colony epiponine wasp, *Brachygastra mellifica*. *Behav. Ecol.* **9**, 573–581.
- Jeanne, R. L. 1991 The swarm-founding polistinae. In *The social biology of wasps* (ed. K. Ross & R. Matthews), pp. 191–231. Ithaca, NY: Cornell University Press.
- Johnstone, R. A. 2000 Models of reproductive skew: a review and synthesis. *Ethology* **106**, 5–26.
- Johnstone, R. A., Woodroffe, R., Cant, M. A. & Wright, J. 1999 Reproductive skew in multi-member groups. *Am. Nat.* **153**, 315–331.
- Michener, C. D. 1974 *The social behavior of the bees*. Cambridge, MA: Harvard University Press.
- Queller, D. C., Peters, J. M., Solis, C. & Strassmann, J. E. 1997 Control of reproduction in social insect colonies: individual and collective relatedness preferences in the paper wasp, *Polistes annularis*. *Behav. Ecol. Sociobiol.* **40**, 3–16.
- Ratnieks, F. L. W. 1988 Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *Am. Nat.* **132**, 217–236.
- Ratnieks, F. L. W. & Visscher, P. K. 1989 Worker policing in the honeybee. *Nature* **342**, 796–797.
- Reeve, H. K. 1998 Game theory, reproductive skew, and nepotism. In *Game theory and animal behavior* (ed. L. Dugatkin & H. K. Reeve), pp. 118–145. Oxford University Press.
- Reeve, H. K. & Emlen, S. T. 2000 Reproductive skew and group size: an N-person staying incentive model. *Behav. Ecol.* **11**, 640–647.
- Reeve, H. K. & Keller, L. 2001 Tests of reproductive-skew models in social insects. *A. Rev. Entomol.* **46**, 347–385.
- Reeve, H. K. & Ratnieks, F. L. W. 1993 Queen–queen conflict in polygynous societies: mutual tolerance and reproductive skew. In *Queen number and sociality in insects* (ed. L. Keller), pp. 45–85. Oxford University Press.
- Reeve, H. K., Emlen, S. T. & Keller, L. 1998 Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behav. Ecol.* **9**, 267–278.
- Shellman-Reeve, J. S. 1997 The spectrum of eusociality in termites. In *The evolution of social behavior in insects and arachnids* (ed. J. Choe & B. Crespi), pp. 52–93. Cambridge University Press.
- Vehrencamp, S. L. 1983 A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* **32**, 667–682.
- Wilson, E. O. 1971 *The insect societies*. Cambridge, MA: Harvard University Press.