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Source: *The American Naturalist*, Vol. 155, No. 3 (March 2000), pp. 406-417

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: https://www.jstor.org/stable/10.1086/303328

VOL. 155, NO. 3 THE AMERICAN NATURALIST MARCH 2000

Power Struggles, Dominance Testing, and Reproductive Skew

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Submitted February 8, 1999; Accepted October 12, 1999

ABSTRACT: Models of reproductive skew are concerned with the partitioning of reproduction between dominant and subordinate members of a group. In an interesting extension of these models, Reeve and Ratnieks briefly considered whether it might benefit subordinates to engage in aggressive behavior to test the fighting ability of a dominant. Their analysis suggested that such testing should be more probable in groups that feature high skew and, hence, perhaps among closer relatives (because high relatedness favors high skew). Here we explore in more detail the possibility of dominance testing. Three models that differ in the outcome of fights over dominance are presented: in the first model, the loser of the challenge is killed; in the second model, the loser is evicted from the nest; and, in the third model, the loser becomes (or remains) subordinate. In each case we consider the independent effects of the parameters that determine skew (namely, relatedness, group productivity, and ecological constraints) on the predicted level of dominance testing. We then construct an amalgamated model to examine situations where fights may lead to any one of the three outcomes. Our analysis reveals that, in the majority of cases, higher relatedness will in fact lead to lower levels of aggression. Moreover, dominance testing need not be associated with high skew. Rather, the relationship between skew and dominance testing will depend on which factor (relatedness, group productivity, or level of ecological constraints) is principally responsible for variation in the distribution of reproduction.

Keywords: reproductive skew, dominance interactions, aggression, cooperative breeding, sociality.

Models of reproductive skew (Vehrencamp 1979, 1983; Reeve 1991; Reeve and Ratnieks 1993; Cant 1998; Reeve et al. 1998; Cant and Johnstone 1999; Johnstone and Cant 1999*a*, 1999*b*; Johnstone et al. 1999; Kokko and Johnstone 1999) represent an important development in understanding the evolution of apparently altruistic behavior. These models attempt to account for variation in the way reproduction is distributed among the members of an animal society or group, from high-skew societies, in which one or a few individuals monopolize reproduction, to low-skew societies, in which reproduction is shared more equitably.

Most models of skew are based on the idea that dominants benefit from the presence of subordinates and so are willing to concede a share of reproduction to them as an incentive to remain in the group (Vehrencamp 1979, 1983; Reeve 1991; Reeve and Ratnieks 1993; Reeve and Keller 1995; Johnstone et al. 1999; Kokko and Johnstone 1999). The size of these staying incentives is predicted to decrease (and reproductive skew to increase) according to three factors: first, the extent to which opportunities for independent breeding are constrained by ecological factors; second, the extent to which the presence of a subordinate increases the productivity of the group; and third, the relatedness between dominant and subordinate. Some studies of social insects, birds, and mammals are consistent with these predictions, although empirical testing of skew models remains at an early stage (reviewed by Keller and Reeve 1994; Reeve and Keller 1995; Bourke 1997; Emlen 1997; Reeve et al. 1998; but for alternative perspectives on skew, see also Cant 1998; Clutton-Brock 1998; Field et al. 1998; Cant and Johnstone 1999; Johnstone and Cant 1999*a*).

How should a subordinate respond to the skew imposed by the dominant? In an interesting extension to their skew model, Reeve and Ratnieks (1993) consider whether the subordinate in a two-member group will be rewarded for engaging in aggressive behavior to test the fighting ability of the dominant. They assume some probability that a test by the subordinate will reveal that the dominant is inferior in fighting ability, in which case the two individuals swap dominance roles. Dominance testing is assumed to carry a cost to colony efficiency, so that peaceful colonies are more productive than those in which dominance testing occurs. The main prediction of their model is that dominance testing is more likely to evolve where skew is high.

Since incentive models of skew predict high skew when

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Am. Nat. 2000. Vol. 155, pp. 406–417.

group members are closely related, the above finding led Keller and Reeve (1994, p. 100) to suggest that "exaggerated dominance behavior will often be characteristic of societies that are under severe ecological constraints and (counterintuitively!) that are composed of close relatives." (See also Reeve et al. 1998.) However, as Reeve and Ratnieks (1993) in fact point out, it is not clear from their model whether high relatedness per se should typically favor the evolution of aggressive dominance testing. They showed only that dominance testing will spread more easily in a high-skew, high-relatedness society than in a zero-skew, zero-relatedness society. Since factors other than relatedness, namely productivity and the level of ecological constraint, may act as the primary determinants of skew, the independent effect of relatedness has yet to be determined. Moreover, even the predicted relationship between skew and dominance testing is open to question because the same factors that determine skew may also directly influence the benefits of aggression.

Here we build on the two-player framework of Reeve (1991) and Reeve and Ratnieks (1993) to explore in more detail the predicted relationships between aggressive dominance testing and the factors that influence skew. We allow for three different possible outcomes of a successful challenge by the subordinate (death of the dominant, eviction of the dominant from the group, and a reversal of roles). We show that, in the majority of cases, a positive relationship between dominance testing and relatedness does not follow from the models; in fact, the opposite relationship is expected. Furthermore, the expected relationship between dominance testing and reproductive skew will depend on which factors are primarily responsible for variation in skew.

Determining the Evolutionarily Stable Level of Skew

We start by deriving Reeve and Ratnieks's (1993) expression for the "staying incentive," that is, the minimum proportion of direct reproduction necessary to induce a subordinate to remain in association with a dominant. Let x denote the expected reproductive success of a subordinate that attempts to disperse and to breed independently relative to the expected success of an established breeder (in the absence of helpers, where $0 < x < 1$); lower values of x indicate more severe ecological constraints. Let k be the ratio of total productivity of a two-member group relative to an established single breeder (assumed to be >1). Finally, let r be the coefficient of relatedness between a potential subordinate and the dominant.

Stable associations occur when subordinates favor staying over dispersing and dominants are selected to accept them. Reeve and Ratnieks (1993) make use of Hamilton's rule (Hamilton 1964; Grafen 1984) to decide which of two alternative actions will be favored by natural selection. Consider two players, an actor (A) and a recipient (B). In general, the actor will favor strategy i over strategy j if

$$(A_i - A_j) + r(B_i - B_j) > 0, \qquad (1)$$

where r is the relevant coefficient of relatedness, A_i (or A_j) is the direct fitness associated with strategy i (or j), and B_i (or B_j) is the recipient's direct fitness when strategy i (or j) is performed.

From the above expression, Reeve and Ratnieks (1993) show that the condition for which a subordinate will remain with the dominant with no direct reproduction is given by $(x - 0) + r(1 - k) < 0$, that is, when $x < r(k - 1)$. If this condition is not met, the subordinate will require a fraction p of direct reproduction to make staying more profitable than dispersing. Substituting into (1), converting to an equality, and solving for p yields Reeve and Ratnieks's (1993) expression for the staying incentive p_s:

$$p_s = \frac{x - r(k - 1)}{k(1 - r)}. \qquad (2)$$

The last step is to ask whether, in fact, the dominant will be selected to offer the staying incentive or whether she would do better to allow the subordinate to disperse. Again applying expression (1), one finds that the dominant should yield the staying incentive when $x < k - 1$. If, in contrast, $x > k - 1$, then the dominant will not offer the staying incentive, and the subordinate will disperse.

Three Simple Models of Dominance Testing

Given the expression for the staying incentive p_s, we can ask what the subordinate stands to gain (in terms of inclusive fitness) by supplanting the dominant. A challenge should occur if and only if this inclusive-fitness reward is >0 (and the greater the reward, the more effort we can expect to be invested in aggressive behavior). We consider three outcome-models for fights over dominance: first, the "fatal fight" model, in which the two individuals enter into a lethal fight for control of the nest; second, the "loser disperses" model, in which the winner of the contest evicts the loser from the nest; and third, the "role reversal" model, in which the two individuals fight over who will be dominant and who will be subordinate. In each case we define f to be the probability that the subordinate is successful in its challenge, where $0 < f < 1$. (In many cases, however, f might be expected to be <0.5, since subordinates will often be of lower fighting ability than dominants. Note also that in this article we deal only with those cases where an association is initially stable, i.e., where $x < k - 1$.)

The three models we present are based on patterns seen in both social vertebrates and invertebrates. In social birds and mammals, fights over dominance can result in the eviction of losers, as in, for example, cooperatively breeding birds (e.g., the Arabian babbler *Turdoides squamiceps*, Zahavi 1990; the Tasmanian native hen *Tribonyx mortieri*, Maynard Smith and Ridpath 1972) and many primates (e.g., the gray langur *Presbytis entellus*, the vervet monkey *Cercopithecus aethiops*, and the gelada baboon *Theropithecus gelada*; see Pusey and Packer 1987 for a review). Such fights can also result in the reversal of dominance roles, as in, for example, dunnocks (*Prunella modularis*; Davies 1992), groove-billed anis (*Crotophaga sulcirostris*; Vehrencamp et al. 1986), suricates (*Suricata suricatta*; T. H. Clutton-Brock, personal communication), and many primates (reviewed by Walters and Seyfarth 1987). In contrast, fatal fights between group members over dominance are usually rare in vertebrates but have been observed in some primate species (Walters and Seyfarth 1987; M. Hasegawa, personal communication).

In social wasps, fatal fights for dominance do occur (e.g., *Polistes metricus*; Gamboa et al. 1978), but in most cases individuals disappear without it being known whether they have been killed by a rival, evicted, or died for other reasons (e.g., *Polistes bellicosus*, Field et al. 1998; *Liostenogaster flavolineata*, J. Field, personal communication). Reversal in reproductive dominance has been inferred from microsatellite analysis of parentage in *Polistes annularis* (Peters et al. 1995) and *P. bellicosus* (Field et al. 1998). In ants, overt aggression between queens is rare (Heinze 1993), but in some pleometrotic species, cofoundresses engage in aggressive, deadly battles after worker eclosion, until only one queen remains (e.g., *Lasius niger*, Waloff 1957; *Messor pergandei*, Pollock and Rissing 1985). In some functionally monogynous species, a stable dominance hierarchy is maintained by aggressive interactions among potential queens (e.g., the *Leptothorax muscorum* complex; Heinze and Buschinger 1987), but little is known about the frequency of role reversal (see Heinze 1993 for a review of queen-queen aggression).

Model 1: Fatal Fight

We start by considering whether a subordinate (Beta) will be rewarded for attempting to kill the dominant (Alpha) and become a lone breeder (this situation is identical to that modeled by Reeve and Ratnieks [1993]). If we retain the notation used in Reeve and Ratnieks's model and use expression (1), we can obtain the following expression for W_1, the inclusive-fitness reward to Beta for challenging:

$$W_1 = (f - kp_s) + r[(1 - f) - k(1 - p_s)]. \tag{3a}$$

Substituting $p_s = x - r(k - 1)/k(1 - r)$ into (3a) yields, after simplification,

$$W_1 = f(1 - r) - x. \tag{3b}$$

When $x < r(k - 1)$, the subordinate will stay without any direct reproduction (i.e., $p_s = 0$), and expression (3b) no longer holds. Instead, we need a separate expression for Beta's reward from challenging when $p_s = 0$. This reward, which we denote W_1^0, is obtained by substituting $p_s = 0$ into (3a) to give

$$W_1^0 = f(1 - r) + r(1 - k). \tag{3c}$$

Model 2: Loser Disperses

Suppose that the loser of a fight is evicted from the group, then the reward to a subordinate for challenging the dominant is given by

$$\begin{aligned} W_2 = {} & \{[f + (1 - f)x] - kp_s\} \\ & + r\{[fx + (1 - f)] - k(1 - p_s)\}, \end{aligned} \tag{4a}$$

which simplifies to

$$W_2 = f[1 - x + r(x - 1)] \tag{4b}$$

for $p_s > 0$. Again considering the case where $p_s = 0$, which occurs when $x < r(k - 1)$, we have

$$W_2^0 = f[1 - x + r(x - 1)] + r(1 - k) + x. \tag{4c}$$

Model 3: Role Reversal

Suppose a successful challenge by Beta results in the reversal of dominance roles between the two individuals; if the challenge is unsuccessful, Beta remains in the position of subordinate. This is the situation considered by Reeve and Ratnieks (1993) in their treatment of dominance testing. Following Reeve and Ratnieks, we can define f, in this case, as the probability that a dominance test reveals that Alpha is now inferior in fighting ability to Beta, in which case the two players swap dominance roles. Dominance testing is assumed to carry a cost to colony productivity, such that associations in which testing occurs have productivity k_T, where $k_T < k$. We label as "peaceful" those associations in which no dominance testing occurs, while associations that feature dominance testing are called "fractious." The staying incentive in a fractious association is then given by $p_{sT} = [x - r(k_T - 1)]/[k_T(1 - r)]$.

From expression (1) above, we see that the inclusive-fitness reward to a subordinate who tests the dominant, W_3, is given by

$$W_3 = \{[fk_T(1 - p_{sT}) + (1 - f)k_Tp_{sT}] - kp_s\} + r\{[fk_Tp_{sT} + (1 - f)(1 - p_{sT})k_T] - k(1 - p_s)\}. \quad (5a)$$

The analysis of Beta's reward in model 3 is slightly more complicated because staying incentives may be 0 in one or both types of association. For example, consider the case where $r(k_T - 1) < x < r(k - 1)$. In these circumstances, subordinates will stay in a peaceful association with 0 reproduction, since $x < r(k - 1)$, but if they choose to test the dominant, thereby reducing productivity, whichever individual remains or becomes subordinate after the test will require some fraction of direct reproduction in order to make staying worthwhile, since $x > r(k_T - 1)$. We require separate expressions for three possible cases: case 1, where staying incentives are required in both types of association (i.e., $p_s > 0$, $p_{sT} > 0$); case 2, where no staying incentives are required in either type of association (i.e., $p_s = p_{sT} = 0$); and case 3, where a staying incentive is required in a fractious association but not in a peaceful one (i.e., $p_s = 0$, $p_{sT} > 0$). Note that our assumption that $k > k_T$ means that $p_s \leq p_{sT}$, so we need not consider the case where $p_{sT} = 0$, $p_s > 0$.

Case 1. Where staying incentives are required for both peaceful and fractious associations to be stable (i.e., $p_s > 0$ and $p_{sT} > 0$), we can (as above) substitute our expressions for p_s and p_{sT} into (5a) to yield, after simplification,

$$W_3 = f(k_T - 2r + k_Tr - 2x). \quad (5b)$$

Case 2. Here the challenger's reward is denoted by W_3^{00}. Substituting $p_s = p_{sT} = 0$ into (5a) gives the following expression:

$$W_3^{00} = fk_T(1 - r) + r(k_T - k). \quad (5c)$$

Case 3. Where $p_s = 0$ and $p_{sT} > 0$, we find that the fitness reward associated with testing is given by

$$W_3^{0+} = f(k_T - 2r + k_Tr - 2x) + r(1 - k) + x. \quad (5d)$$

Results

Below we summarize the results of the three models presented above. We first give the conditions under which dominance testing is favored in each model and then go on to summarize the influence of the key parameters (relatedness, group productivity, and ecological constraint) on the likelihood of aggression occurring (or the level of effort that subordinates should invest in such behavior).

Conditions under Which Testing Is Favored

We expect subordinates to engage in dominance testing when the reward to challenging the dominant is >0. The conditions for which this is the case in each of the three models are as follows (we remind readers that W_i denotes the fitness reward for challenging in model i when incentives are given and that W_i^0 denotes the fitness reward when incentives are not given):

Model 1: Fatal Fight

$$W_1 > 0 \text{ for } f > \frac{x}{1 - r}. \quad (6a)$$

$$W_1^0 > 0 \text{ for } f > \frac{r(k - 1)}{1 - r}. \quad (6b)$$

Model 2: Loser Disperses

$$W_2 > 0 \text{ for } f > 0. \quad (7a)$$

$$W_2^0 > 0 \text{ for } f > \frac{r(k - 1) - x}{r(1 - x) + x - 1}. \quad (7b)$$

Model 3: Role Reversal

$$W_3 > 0 \text{ for } f > 0. \tag{8a}$$

$$W_3^{00} > 0 \text{ for } f > \frac{r(k - k_T)}{k_T(1 - r)}. \tag{8b}$$

$$W_3^{0+} > 0 \text{ for } f > \frac{r(k - 1) - x}{k_T(1 + r) - 2(r + x)}. \tag{8c}$$

Not surprisingly, therefore, all three models predict that subordinates are more likely to engage in dominance testing the greater their fighting ability. Challenging the dominant will always be favored in the loser disperses and role reversal models when the staying incentive is >0 (i.e., $x > r[k - 1]$), since conditions (7a) and (8a) always hold. Consequently, it will always benefit unrelated subordinates to try to evict the dominant or to challenge for a role reversal, since, when $r = 0$, $x > r(k - 1)$ and the staying incentive is >0. Note that in the case of model 2, associations in which staying incentives are offered will ultimately prove unstable since Beta will challenge until either she or Alpha is evicted.

Next, we analyze the relationship between the factors that combine to determine the stable level of skew (namely relatedness, productivity, and the level of ecological constraints) and the benefits of aggressive dominance testing (which is expected to determine the level of observed aggression). The independent effect of each factor can be found by examining the partial derivatives of our expressions for the challenger's reward with respect to r, k, and x. Each factor is considered in turn.

Influence of Relatedness

What is the expected relationship between relatedness and dominance testing? The partial derivatives of (3b) and (3c), (4b) and (4c), and (5b)–(5d) with respect to r are given by

Model 1

$$\frac{\partial W_1}{\partial r} = -f \tag{9a}$$

$$\frac{\partial W_1^0}{\partial r} = 1 - k - f \tag{9b}$$

Model 2

$$\frac{\partial W_2}{\partial r} = f(x - 1) \tag{10a}$$

$$\frac{\partial W_2^0}{\partial r} = f(x - 1) \tag{10b}$$

Model 3

$$\frac{\partial W_3}{\partial r} = f(k_T - 2) \tag{11a}$$

$$\frac{\partial W_3^{00}}{\partial r} = k_T(1 - f) - k \tag{11b}$$

$$\frac{\partial W_3^{0+}}{\partial r} = f(k_T - 2) - k + 1 \tag{11c}$$

Since derivatives (9a) and (9b) and (10a) and (10b) are always negative, models 1 and 2 predict a negative relationship between relatedness and dominance testing. From expression (11a), we see that model 3 predicts a negative relationship for $k_T < 2$ and a positive relationship for $k_T > 2$ in the case where staying incentives are required in fractious associations; that is, $r < x/(k_T - 1)$. Regardless of whether fractious associations require incentives or not, where peaceful associations are stable without staying incentives, the relationship between relatedness and dominance testing is uniformly negative (expressions [11b], [11c]; see fig. 1).

Influence of Group Productivity

The partial derivatives of the challenger's reward in models 1 and 2 (with and without staying incentives) with respect to k are given by

$$\frac{\partial W_1}{\partial k} = \frac{\partial W_2}{\partial k} = 0 \text{ and } \frac{\partial W_1^0}{\partial k} = \frac{\partial W_2^0}{\partial k} = -r$$

and those of the role reversal model by

$$\frac{\partial W_3}{\partial k} = 0 \text{ and } \frac{\partial W_3^{00}}{\partial k} = \frac{\partial W_3^{0+}}{\partial k} = -r,$$

while the partial derivatives of model 3 with respect to the productivity of a fractious association, k_T, are

$$\frac{\partial W_3}{\partial k_T} = \frac{\partial W_3^{0+}}{\partial k_T} = f(1 + r) \text{ and } \frac{\partial W_3^{00}}{\partial k_T} = f + r(1 - f).$$

Thus, models 1 and 2 predict no influence of group pro-

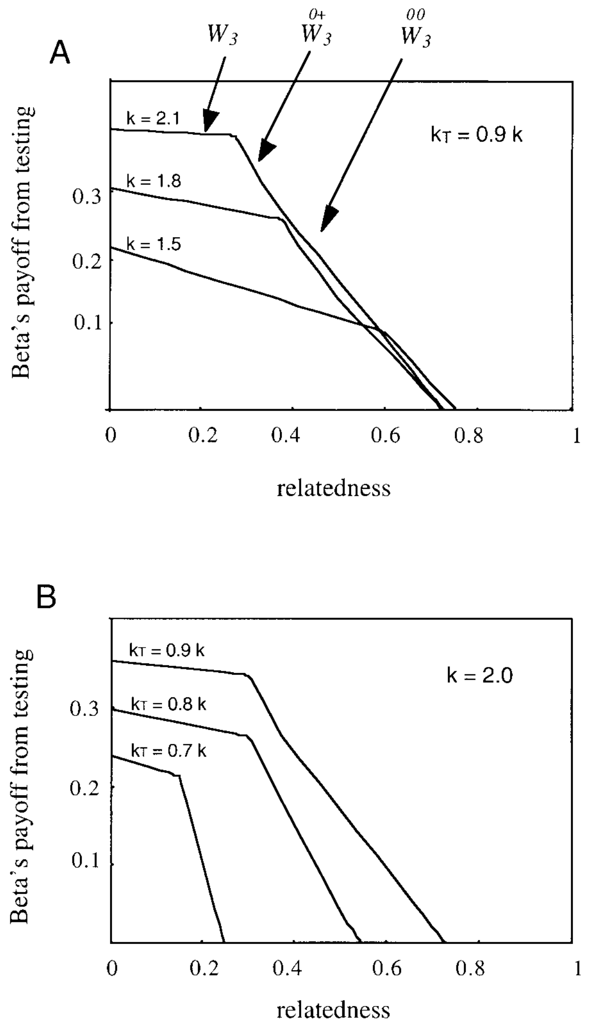

Figure 1: *A*, Subordinates reward (W_3) for challenging the dominant in model 3 as a function of relatedness (r) to the dominant for three levels of group productivity in the absence of testing (k) and where testing carries a 10% cost to this productivity (i.e., $k_T = 0.9k$, where k_T is the productivity of an association in which testing occurs, which we call a "fractious" association). As relatedness increases from 0 (in the region marked W_3 on the uppermost curve), the magnitude of the staying incentive required for group stability decreases. At the point where peaceful associations are stable with 0 staying incentive, the curves change slope abruptly (in the region marked W_3^{0+}). At higher relatedness still, both peaceful and fractious associations are stable with 0 staying incentive (in the region marked W_3^{00}. *B*, Reward for challenging the dominant as a function of relatedness for three levels of costliness of testing (10%, 20%, and 30%). In this example, the productivity of a peaceful association is twice that of a lone nester (i.e., $k = 2$). (Other parameter: $x = 0.3$.)

ductivity on dominance testing for the cases where reproduction is shared and a negative association between dominance testing and productivity for cases where the staying incentive is 0. This is because, where subordinates require a staying incentive, the fraction of reproduction offered is just enough to match the fitness the subordinate could expect by dispersing, so the amount to be gained from fighting (fitness as sole breeder minus fitness when receiving the staying incentive) is independent of group productivity. For $p_s = 0$, this is no longer the case: the subordinate's fitness in the association is larger than it could expect from dispersing, and, hence, it becomes less likely to attempt to kill or to eject the dominant (which would break up the partnership).

Model 3 predicts no relationship between the productivity of peaceful associations and testing for the case where staying incentives are offered, for a similar reason. However, there is a negative relationship between testing and productivity of peaceful associations when $p_s = 0$ because here Beta's fitness reward, if she remains in the association peaceably, increases with k. This model also predicts increased dominance testing as the productivity of fractious associations (k_T) increases because this effectively reduces the cost of testing.

Influence of Ecological Constraints

The expected fitness of a subordinate that disperses, x, is inversely proportional to the level of ecological constraints. The partial derivatives of the three models with respect to x are given by

$$\frac{\partial W_1}{\partial x} = -1, \tag{12a}$$

$$\frac{\partial W_1^0}{\partial x} = 0, \tag{12b}$$

$$\frac{\partial W_2}{\partial x} = f(r - 1), \tag{13a}$$

$$\frac{\partial W_2^0}{\partial x} = f(r - 1) + 1, \tag{13b}$$

$$\frac{\partial W_3}{\partial x} = -2f, \tag{14a}$$

$$\frac{\partial W_3^{00}}{\partial x} = 0, \tag{14b}$$

$$\frac{\partial W_3^{0+}}{\partial x} = 1 - 2f. \tag{14c}$$

Expressions (12a), (13a), and (14a) are all negative, which implies that the level of dominance testing should increase as ecological constraints become more severe (i.e., as x decreases) for the case where the subordinate is receiving some share of reproduction (see also Reeve and Ratnieks

1993). Where the subordinate receives 0 staying incentive, in contrast, increasingly severe constraints reduce the probability that the subordinate will try to evict the dominant (expression [13b]) but have no effect on the benefits of fighting the dominant to the death (expression [12b]). In the role reversal model, increasingly severe constraints have no effect when the subordinate will stay with 0 incentive in both peaceful and fractious associations (case 2; expression [13b]). If, however, testing reduces productivity to the extent that a staying incentive is required (i.e., case 3; expression [13c]), increasingly severe constraints can lead to a decrease in dominance testing (for $f < 0.5$).

A More General Model

Thus far we have examined the rewards of challenging separately for each of the three models. In effect this assumes that in any one scenario only a single outcome is possible. In many biological situations, however, fights over dominance may lead to one of a number of possible outcomes, and the benefits associated with challenging will depend on the relative likelihood of each outcome. We can address this possibility by amalgamating our three models into a single, more general model. We do not, however, provide a full analysis of the general model here; rather, we focus solely on the relationship between dominance testing and relatedness when fights may lead to any of the three outcomes described above.

Let q_1, q_2, and q_3 denote the probabilities that fights lead to the death, dispersal, or subordination of the loser, respectively (where $q_1 + q_2 + q_3 = 1$).

The fitness reward to a challenger (W_{all}) is then given by

$$W_{\text{all}} = q_1 W_1 + q_2 W_2 + q_3 W_3, \tag{15a}$$

where $p_s > 0$, or

$$W^0_{\text{all}} = q_1 W^0_1 + q_2 W^0_2 + q_3 W^{00}_3, \tag{15b}$$

where $p_s = p_{sT} = 0$. (For simplicity we do not consider case 3 of the role reversal model, i.e., where incentives are required in fractious associations but not in peaceful associations).

Substituting our expressions for the reward in models 1, 2, and 3 (i.e., [3b] and [3c], [4b] and [4c], and [5b] and [5c]) into (15a) and (15b) yields, after simplification,

$$\begin{aligned} W_{\text{all}} &= q_1 f(1 - r) - q_1 x + q_2 f(r - 1)(x - 1) \\ &\quad + q_3[k_T(r + 1) - 2(r + x)]; \\ W^0_{\text{all}} &= q_1 f(1 - r) - q_1 x + q_2 f(r - 1)(x - 1) \\ &\quad + q_3[k_T(r + 1) - 2(r + x)]. \end{aligned}$$

Differentiating with respect to r gives

$$\frac{\partial W_{\text{all}}}{\partial r} = q_3 f(k_T - 2) + q_2 f(x - 1) - q_1 f; \tag{16a}$$

$$\begin{aligned} \frac{\partial W^0_{\text{all}}}{\partial r} &= q_1(1 - f - k) + q_2[1 - f(1 - x) - k] \\ &\quad + q_3[k_T(1 - f) - k]. \end{aligned} \tag{16b}$$

What do these partial derivatives tell us about the relationship between dominance testing and relatedness in the general model? First, considering the case where the staying incentive is 0, we see that all three terms on the right-hand side of expression (16b) are negative. Thus, where $p_s = 0$ the general model predicts that dominance testing will decrease as relatedness increases. For the case where staying incentives are required for the association to be stable (i.e., $p_s > 0$), we see from expression (16a) that $\partial W_{\text{all}}/\partial r$ will be negative when $q_3 f(k_T - 2) < q_1 f - q_2 f(x - 1)$ or

$$k_T < 2 + \frac{q_1 + q_2(1 - x)}{q_3}.$$

Thus, where $p_s > 0$ we expect increased relatedness to lead to a decrease in dominance testing, except where q_3 is large relative to q_1 and q_2 and the productivity in a fractious association is somewhat >2. This condition is more restrictive than the equivalent condition in the role reversal model (refer to expression [11a]). To illustrate, if we set $x = 0.5$ and assume that the third outcome, the subordination of the loser, is twice as likely as either the death or dispersal of the loser (i.e., $q_1 = q_2 = 0.25$; $q_3 = 0.5$), then the relationship between dominance testing and relatedness is expected to be negative unless $k_T > 2.75$. For most biologically plausible situations, therefore, the general model confirms the prediction that dominance testing should be less pronounced among relatives, particularly if there is a chance that the loser of a fight may be killed or evicted.

Discussion

Our three models of dominance testing reveal that relatedness, group productivity, and level of ecological con-

Table 1: Independent effects of parameters which determine skew on level of aggressive dominance testing

	Increasing relatedness		Increasing group productivity		Increasing constraints on dispersal	
Model	Incentives	No incentives	Incentives	No incentives	Incentives	No incentives
Fatal fight	↓	↓	0	↓	↑	0
Loser disperses	↓	↓	0	↓	↑	↓
Role reversal	↓ ($k_T < 2$) ↑ ($k_T > 2$)	↓	0	↓	↑	0 or ↓

Note: Table shows predictions of three models that differ in the outcome of challenges (fatal fight, loser disperses, and role reversal). Up arrows indicate increased aggression. Down arrows indicate reduced aggression. Zeros indicate no effect; K_T denotes the productivity of an association in which testing occurs relative to the productivity of a lone breeder.

straint all have independent effects on the expected level of aggression. The direction of these effects depends not only on the consequences of dominance testing (i.e., on which model is chosen), but also on whether or not subordinates require a staying incentive. A full summary of the models' predictions is given in table 1.

Aggression and Relatedness

A central result of our analysis (apparent from table 1) is that relatedness will typically be negatively correlated with aggression. The only exception to this pattern occurs when dominance testing leads to role reversal (i.e., in model 3), when group productivity is very high ($k_T > 2$), and when (despite this high productivity) staying incentives are required for group stability.

This finding runs counter to the predictions of a recent model of conflict developed by Reeve and Keller (1997). Their analysis reveals that the scope for conflict in a group, that is, the difference between the maximum amount of reproduction that a subordinate can obtain (without triggering eviction by the dominant) and the minimum that it must receive (to make staying worthwhile), increases with relatedness. Consequently, they suggest that within-group aggression should be more intense among closer kin. We argue, however, that their prediction fails to take into account the impact of relatedness on the benefits to be gained by depriving a competitor of reproduction. Although the scope for conflict may be greater when dominant and subordinate are close kin, the actual inclusive-fitness reward to the subordinate for defeating the dominant is likely to be lower. To take an extreme example, the scope for conflict will be greatest when $r = 1$ (see Reeve and Keller 1997), yet under these circumstances both dominant and subordinate should be neutral as to the division of reproduction. Consequently, there can be no gain to dominance testing, only a cost in terms of group productivity.

In line with the above argument (and with the results of this model), other analyses, which explicitly calculate the benefits of subordinate behavior, such as those of Reeve and Nonacs (1997) and Reeve et al. (1998), also suggest that optimal investment in selfish behavior (which may manifest itself as aggression) should decrease with relatedness (although this is not explicitly stated in the former article, we show that it is the case in the appendix). We conclude, therefore, that because subordinates have more to gain by challenging unrelated dominants, aggressive testing is more likely in associations of nonkin.

Aggression and Reproductive Skew

Because all three fundamental parameters of the model (relatedness, group productivity, and ecological constraint) influence both the expected level of skew and the profitability of dominance testing, the relationship between reproductive skew and aggression depends on how these contrasting effects interact. For example, consider the effects of relatedness and the level of ecological constraints (for the case of nonzero incentives). Increasing relatedness favors high skew and reduced testing, whereas increasingly severe constraints favor high skew and increased testing. Thus, predictions about the relationship between skew and dominance testing depend on which factor is deemed to be principally responsible for variation in skew. Where the costs of dispersal vary among groups (or species) that are of genetically similar composition, we predict a positive relationship between skew and dominance testing. In contrast, if groups (or species) vary in relatedness but are subject to similar levels of ecological constraint, we predict a negative association between skew and dominance testing. We therefore disagree with Reeve and Ratnieks's (1993) simple prediction, often cited, that higher skew will lead to increased aggressive dominance testing (Reeve and Ratnieks 1993; Keller and Reeve 1994; Bourke and Franks 1995; Bourke 1997). Furthermore, the level of ecological constraints and within-colony relatedness may themselves be positively correlated (Bourke 1997), in which case their contrasting effects will tend to cancel out any consistent relationship between skew and dominance testing.

Empirical Evidence

Empirical evidence concerning the relationship between dominance testing and the factors that influence skew is scarce. Most attempts to examine this relationship contrast populations, species, or groups of species that exhibit "syndromes" associated with different levels of skew (Keller and Reeve 1994; Reeve et al. 1998) and so are unable to control for the effects of the other factors that help to determine skew. For example, Jamieson (1997) compared two populations of pukeko that exhibited high and low skew. In the high-skew population, group members were closely related, ecological constraints were severe, and levels of within-group aggression were high; in the low-skew population, in contrast, relatedness was low, ecological constraints were weak, and dominance behavior was less pronounced. Reeve et al. (1998) suggest that the pattern of aggression fully accords with the predictions of concession theory, but, as we have shown, concession models actually predict a negative relationship between relatedness and dominance testing where $k_T < 2$, as in pukeko (Craig and Jamieson 1990). For our current purpose, however, the main problem with this example (and others given in Reeve et al. 1998) is that the independent effects of relatedness on dominance testing are confounded by differences in ecological constraints.

One way around the problem of confounding variables is to compare species among which ecological constraints vary but relatedness does not, or vice versa. An example is provided by Bourke and Heinze's (1994) study of skew, ecological constraints, and queen-queen aggression in nine species of leptothoracine ants. They found that increased aggression between queens was associated with high skew and severe constraints on dispersal. Reeve and Keller (1997) cite this result in support of their counterintuitive prediction that aggression should be more pronounced among relatives. However, Bourke and Heinze (1994) were unable to examine the pattern of queen-queen relatedness in their study, and, as they point out (Bourke and Heinze 1994), preliminary evidence suggests that queen-queen relatedness does not differ between the species that exhibited high and low skew. They propose, therefore, that it is differences in the costs of dispersal rather than in relatedness that are responsible for the observed patterns of skew (see also Bourke and Franks 1995, pp. 289–290). Our models support this latter view: if variation in skew across species was caused by variation in relatedness (rather than by ecological constraints), we would predict higher levels of dominance testing where skew was low.

Similarly, studies of single populations may be able to assess the independent effects of relatedness without the difficulty of confounding variables, provided that individuals in different groups face similar dispersal costs. In the most comprehensive test of skew theory to date, Field et al. (1998) measured relatedness, skew, and dominance testing in 24 cofoundress associations of the paper wasp *Polistes bellicosus.* They found that second-ranking females were less aggressive toward the dominant where skew was high (the opposite pattern to that predicted by Reeve and Ratnieks [1993]), but there was no effect of relatedness on the frequency of aggressive interactions initiated by the second-ranking female toward the dominant. It may be, however, that paper wasps are not an appropriate species with which to test our predictions concerning relatedness at an intraspecific level. At this level of analysis, the predictions of concession models regarding relatedness and aggression (or relatedness and skew, for that matter) will only hold for species in which individuals have the ability to discriminate degrees of relatedness among individuals or at least to respond to the average relatedness within their group. In wasps, there is considerable evidence to suggest that individuals do not discriminate variation in relatedness among nest mates in this way (see Gamboa et al. 1986; Queller et al. 1990; Keller 1997). It is also worth pointing out that Field et al. (1998) found no correlation between dominance testing and group productivity, in agreement with our predictions (although this kind of negative evidence does not constitute strong support for our models).

Future Modeling Possibilities

In this article we have focused on aggressive dominance testing by subordinates. We emphasize, however, that this is not the only form of antagonistic interaction that can occur. Dominants may, for instance, initiate aggression in order to block or punish reproductive attempts by subordinates (Reeve and Keller 1997); they may also employ exaggerated (and costly) threat signals to deter related subordinates from trying to fight them (R. A. Johnstone, unpublished manuscript). Indeed, in many leptothoracines and paper wasps, it is the alpha queens who initiate the majority of aggressive encounters with subordinates rather than the other way around (Heinze and Smith 1990; Bourke and Franks 1995). Ideally, therefore, tests of conflict models should not rely on crude measures of the overall frequency of antagonistic interactions but should attempt to discriminate between conflicts initiated by the dominant (instances of "policing") and those initiated by the subordinates (instances of "testing"; e.g., Heinze and Smith 1990; Reeve and Nonacs 1997; Field et al. 1998). The effects of relatedness, ecological constraint, and other relevant parameters may vary according to the type of aggression under consideration.

A further modeling possibility, relevant to analyses of both policing and testing, is the incorporation of temporal changes in the model parameters. For instance, when considering a matrifilial association, the likelihood of the juvenile subordinate surviving to breed independently if it should disperse is likely to increase as it grows older. At the same time, so too will its probability of defeating the dominant parent. It would thus be interesting to consider the age at which it would first be beneficial to challenge (or disperse) and the expected changes in the distribution of reproduction up to and (if neither individual dies or is evicted) after that point (see Day and Taylor 1998).

Acknowledgments

We thank A. Bourke, T. Clutton-Brock, N. Davies, M. Hasegawa, J. Herbers, H. Kokko, P. Nonacs, K. Reeve, R. Woodroffe, and three anonymous referees for useful comments and discussions. J. Field's comments on an early version of this article proved particularly helpful. M.A.C. was funded by the Biotechnology and Biological Sciences Research Council. R.A.J. was funded by a Royal Society University research fellowship.

APPENDIX

The Influence of Relatedness on Aggression in the Model of Reeve and Nonacs

Reeve and Nonacs (1997) consider the optimal level of aggression, a, of one individual (the actor) in association with another (the recipient), where both have a symmetrical genetic relatedness, r. The total productivity of the association is equal to

$$e(a)P_2 + [1 - e(a)]P_1, \tag{A1}$$

where $e(a)$ is a decreasing function of a (which ranges from 0 to 1) and $P_2 > P_1 > 0$ (the ratio P_2/P_1 will be referred to as v, the "value of the recipient"). The share of productivity obtained by the actor, denoted by $s(a)$, is an increasing function of a (which also ranges from 0 to 1).

From the above, we may deduce that the inclusive-fitness reward to an actor who adopts a level of aggression a is given by

$$\begin{aligned} I &= \{s(a) + r[1 - s(a)]\}\{e(a)P_2 + [1 - e(a)]P_1\} \\ &= [r + (1 - r)s(a)][e(a)(v - 1) + 1] \end{aligned} \tag{A2}$$

and that the optimal level of aggression, a^*, is that which satisfies $\partial I/\partial a = 0$ at $a = a^*$.

By the implicit function theorem, the partial derivative of a^* with respect to r satisfies

$$\frac{\partial a^*}{\partial r} = -\frac{\partial^2 I/\partial r \partial a}{\partial^2 I/\partial a^2} \text{ at } a = a^*. \tag{A3}$$

Now the denominator of the above expression is negative (since a^* maximizes I), so that the sign of $\partial a^*/\partial r$ is the same as that of the numerator. From (A2), the numerator is given by

$$\begin{aligned} \frac{\partial^2 I}{\partial r \partial a} &= (v - 1)\{[1 - s(a)]e'(a) \\ &\quad - e(a)s'(a)\} - s'(a) < 0. \end{aligned} \tag{A4}$$

Since this expression must be negative (given our assumptions that $0 \leq s(a) \leq 1$, $e'(a) < 0$, $v > 1$, and $s'(a) > 0$), we may conclude that the partial derivative of a^* with respect to r is also negative or, in other words, that the actor's optimal level of aggression decreases with actor/recipient relatedness.

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Associate Editor: Joan M. Herbers