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Individual Variation in Social Aggression and the Probability of Inheritance: Theory and a Field Test

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ABSTRACT: Recent theory suggests that much of the wide variation in individual behavior that exists within cooperative animal societies can be explained by variation in the future direct component of fitness, or the probability of inheritance. Here we develop two models to explore the effect of variation in future fitness on social aggression. The models predict that rates of aggression will be highest toward the front of the queue to inherit and will be higher in larger, more productive groups. A third prediction is that, in seasonal animals, aggression will increase as the time available to inherit the breeding position runs out. We tested these predictions using a model social species, the paper wasp *Polistes dominulus*. We found that rates of both aggressive "displays" (aimed at individuals of lower rank) and aggressive "tests" (aimed at individuals of higher rank) decreased down the hierarchy, as predicted by our models. The only other significant factor affecting aggression rates was date, with more aggression observed later in the season, also as predicted. Variation in future fitness due to inheritance rank is the hidden factor accounting for much of the variation in aggressiveness among apparently equivalent individuals in this species.

Keywords: eusociality, queuing, dominance, cooperative breeding, inheritance, helping.

Individual variation in social behavior is one of the most striking features of cooperative animal societies. Kin selection theory suggests that this variation should ultimately be attributable to variation in either relatedness or the cost/

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benefit ratio of a given social act. Traditionally, most studies have focused on the predicted effect of relatedness on individual variation in behavior such as helping or social aggression. In many cases, however, animals either do not or cannot respond facultatively to within-group variation in relatedness (Queller et al. 1990; du Plessis 1993; Dunn et al. 1995; Kempenaers and Sheldon 1996; DeHeer and Ross 1997; Keller 1997; Strassmann et al. 1997; Clutton-Brock et al. 2000; Clutton-Brock 2002; Gilley 2003). The inability of relatedness to account for much within-group behavioral variation has focused attention on differences in cost as a potential explanation for individual differences in behavior (Heinsohn and Cockburn 1994; Boland et al. 1997; Clutton-Brock et al. 1998, 2000; Heinsohn and Legge 1999; Cant and Field 2001). From a life-history perspective, costs are measured in terms of decrements to expected future fitness. Expected future fitness (and hence the potential cost of a particular act) may vary between individuals because of differences in intrinsic quality or state, but often behavior varies widely even between apparently equivalent individuals of the same age, body size, sex, or dominance class (Wright 1997; Clutton-Brock et al. 2000, 2001; Cant and Field 2001; Gadagkar 2001; Cant 2003), suggesting that variation in individual attributes is neither the only nor sometimes even the most important cause of individual differences in behavior. What, then, is the cause of this variation?

In previous articles (Cant and Field 2001, 2005), we have argued that the missing factor underlying individual behavioral differences in the societies of vertebrates and primitively social insects is social structure or, more specifically, inheritance rank. In many societies, group members form a dominance or inheritance hierarchy in which low-ranking individuals can attain breeding status by outliving or supplanting those ahead of them in the queue (Strassmann and Meyer 1983; Wiley and Rabenold 1984; Hughes and Strassmann 1988a; Stacey and Koenig 1990; Field et al. 1999; Monnin and Peeters 1999; Monnin and Ratnieks 1999; Buston 2003, 2004; Monnin et al. 2003). Inheritance ranks can be settled by contests in which individuals of superior size, strength, or fighting ability assert

dominance over weaker individuals (Pardi 1948; Turillazzi and Pardi 1977; Queller and Strassmann 1989; Heinze 1990; Clarke and Faulkes 1997, 2001) or by some convention such as age, maternal rank, or order of arrival (Field et al. 1999; Engh et al. 2000; Seppä et al. 2002). In either case, the presence of an inheritance hierarchy erects systematic differences in the amount of future fitness that different group members stand to lose through engaging in risky behavior (Cant and Johnstone 2000; Kokko et al. 2001; Cant and Field 2001, 2005; Shreeves and Field 2002; Cant and English, forthcoming). For example, low-ranked *Polistes dominulus* cofoundresses, who have little expectation of direct fitness in the future, will work harder to rear the offspring of a dominant than will high-ranked individuals, who have a good chance of inheriting breeding status themselves (Cant and Field 2001). Since there are no other measurable traits that correlate with individual helping effort in this species, the step differences between ranks in the probability of inheritance apparently exert a stronger influence on helping effort than individual differences in quality or state (Cant and Field 2001, 2005).

Here we investigate the importance of inheritance rank for a second conspicuous feature of cooperative animal societies, social aggression. Certain group members inflict or receive many more acts of aggression than others. In some cases, these acts (which include bites, shoves, mounts, and charges) appear to regulate cooperative activity in the group by activating lazy workers, for example, or punishing defectors (Reeve and Gamboa 1987; Reeve 1992; Mulder and Langmore 1993; Clutton-Brock and Parker 1995; Balshine-Earn et al. 1998; Nonacs et al. 2004; Bergmüller et al. 2005; Flack et al. 2005), but a large proportion of aggressive "dominance" interactions seem to be related to maintaining or challenging social status (Reeve 1991; Reeve and Sherman 1991; Reeve and Ratnieks 1993; Cant and Johnstone 2000). Relatively mild interactions may sometimes escalate into more costly fights in which the winner establishes dominance over, evicts, or even kills the loser (e.g., social insects: Waloff 1957; Gamboa et al. 1978; Pollock and Rissing 1985; Heinze and Buschinger 1987; Balas and Adams 1996; vertebrates: Vehrencamp et al. 1986; Pusey and Packer 1987; Zahavi 1990; Davies 1992; Clutton-Brock et al. 1998). This means that members of an inheritance hierarchy may sometimes be able to "queue jump" by attacking those of higher rank rather than waiting peacefully for those in front to die. The amount that a subordinate of given rank stands to gain from attempting to queue jump in this way will depend on its probability of winning an escalated contest and the costs involved in fighting. It is not clear, however, whether the benefits of queue jumping should be higher or lower toward the front or the rear of the hierarchy. For example, a second-rank individual may have more to gain

from attacking and supplanting the individual ahead of it than does, say, a fifth-rank individual. But this same second-rank individual also stands a much better chance of inheriting without attacking and so may do better to refrain from potentially risky challenges. A model would help to clarify the relationship between rank and the payoff of challenging.

Our aims are to determine the conditions for which attempting to queue jump is more profitable than waiting peacefully in line and to explore how the payoffs of challenging those of higher rank vary down the hierarchy. We proceed on the hypothesis that low-level aggressive acts are used by higher-ranked individuals to assert dominance over or deter challenges from subordinates ("deterrent displays") and by lower-ranked individuals to test the strength or motivation of those ahead of them in the hierarchy before initiating a challenge ("dominance tests"). By making explicit our assumptions about the function of aggression in this way, we can model predicted patterns of behavior and test these predictions against nature.

The article is divided into two sections. In the first section, we develop two simple models to explore how the payoffs of engaging in costly dominance interactions should vary with rank and group size. We then go on to describe an experimental test of the assumptions and predictions of the models, using a model social species, the paper wasp *P. dominulus*.

Aggression in a Queue: Two Simple Models

Consider a group of size n with a single breeder at rank 1 and $n - 1$ nonbreeders at ranks 2 to n. All individuals are symmetrically related by coefficient r. We assume that individuals have equal expected life spans, so that in the absence of aggression, an individual at rank i can expect to inherit the rank-1 position with probability $1/i$ (Field et al. 1999; Cant and Field 2001, 2005; Shreeves and Field 2002). The direct fitness payoff to an individual that becomes the breeder may vary with group size and is given by the function $g(n)$ (abbreviated to g_n). We make the assumption of a single breeder at rank 1 for simplicity, but the predictions derived here would also apply to nonbreeders at ranks $b + 1$ to n in a strict queue in which the top b ranks reproduce. This is because the payoff of becoming the lowest-ranked breeder (at rank b) is independent of the degree of skew among the b breeders, and we can treat this payoff in the same manner as we treat the payoff of reaching the rank-1 position in the current model (Cant and English, forthcoming).

Rather than accepting an inheritance probability of $1/i$, a nonbreeder at rank i may try to queue jump by fighting the individual immediately above it in the queue. We develop two models that differ in the outcomes of such

fights. In the first model, the two individuals fight over which will be dominant and which subordinate; in the second model, the two individuals fight to the death. The cost of fighting in the former, "role reversal" model is reduced productivity on inheriting breeding status; in the latter, "fatal-fight" model, it is the mortality risk of engaging in a potentially fatal escalated contest. In reality, fights may lead to more than one potential outcome. We could, if we wished, construct an amalgamated model in which fights led to the subordination of the loser in a fraction q of cases and the death of the loser in the other fraction $(1 - q)$ of cases (Cant and Johnstone 2000). By keeping the two models separate, however, we can explore whether the nature of cost (namely, reduced reproductive capacity in model 1 vs. mortality risk in model 2) makes a difference to the expected patterns of aggression.

We assume throughout that the effort expended on testing by the subordinate and displaying by the dominant will depend on the payoff associated with entering into an all-out challenge. Where subordinates have little to lose and much to gain from challenging for dominant status, we expect them engage in greater levels of dominance testing (see also Cant and Johnstone 2000). These are also the circumstances for which a dominant has the most to lose in a fight over rank, so we would also expect the level of aggressive display to increase with the challenger's payoff. Thus, we focus on the payoff differential between challenging and not challenging as an index of the value of aggression rather than modeling the process of fighting itself (e.g., Enquist and Leimar 1983, 1990).

Let f denote the relative fighting ability of the subordinate member of the dyad, that is, the probability that the individual at rank i wins an escalated contest with the individual at rank $i - 1$. We initially assume that f does not vary with rank; that is, all individuals are of same strength relative to the individual above or below them in the hierarchy. Thus, a value of $f = 0.5$ implies that all individuals in the queue are of equal strength, $f = 0.4$ that a higher-ranked member of a rank dyad has 20% greater chance of than winning than the lower-ranked individual, and so on. We will also briefly explore cases where f may itself be a function of rank.

Model 1: Role Reversal

We wish to determine the inclusive fitness payoff of attempting to queue jump when at rank i versus queuing peacefully at that rank. By Hamilton's Rule, the inclusive fitness payoff to an actor A of adopting strategy I versus an alternative strategy J toward a recipient B can be written

$$W = (A_I - A_J) + r(B_I - B_J), \tag{1}$$

where r is the coefficient of relatedness between the actor and recipient, A_I and A_J are the direct fitness payoffs to the actor of adopting strategies I and J, respectively, and B_I and B_J are the corresponding direct fitness payoffs to the recipient (Hamilton 1964; Grafen 1984; Parker 1989). Thus, we can write the inclusive fitness payoff of challenging for a role reversal when at rank i versus remaining peacefully in the queue as follows:

$$
\begin{aligned}
W_I(i, f) &= \left\{ \left[\frac{f(g_n - c)}{i - 1} + \frac{(1 - f)(g_n - c)}{i} \right] - \frac{g_n}{i} \right\} \\
&\quad + r \left\{ \left[\frac{f(g_n - c)}{i} + \frac{(1 - f)(g_n - c)}{i - 1} \right] - \frac{g_n}{i - 1} \right\} \\
&= \frac{fg_n(1 - r) + c[1 - f(1 - r) - i(1 + r)]}{i(i - 1)}, \tag{2}
\end{aligned}
$$

where g_n is the productivity payoff associated with a group of size n and c is the personal cost of challenging.

How will the challenger's payoff (and hence levels of dominance behavior) change with rank? Treating rank as a continuous variable, we can differentiate equation (2) with respect to i to give

$$
\begin{aligned}
\frac{\partial W_I(i, f)}{\partial i} &= (fg_n[(r - 1)(2i - 1)] \\
&\quad + c\{1 + f[2i - 1 + r(1 - 2i)]\} \\
&\quad + i[i(1 + r) - 2])/[i^2(i - 1)^2].
\end{aligned}
$$

$$\tag{3}$$

The above expression can be positive or negative, depending on the values of f, r, and i. For challenges to be favored at all, however, we know that W_I must be greater than 0. Since W_I is an increasing function of subordinate strength f, there will be some critical value of f (which we denote $\hat{f}(i)$) for which the net payoff of challenging when at rank i is 0 and above which challenges are profitable. Setting expression (2) equal to 0 and solving for f yields the following expression for the critical strength:

$$\hat{f}(i) = \frac{c[i(1 + r) - 1]}{g_n(1 - r) - c(1 - r)}.$$

Substituting in place of f in equation (3) and simplifying, we have

$$\frac{\partial W_I(i, \hat{f}(i))}{\partial i} = \frac{c(1 + r)}{i - i^2}, \tag{4}$$

which is always negative. Thus, at the critical strength $\hat{f}(i)$, the challenger's payoff is a decreasing function of rank i. Moreover, we show in the appendix in the online edition of the *American Naturalist* that what holds for a subordinate of critical strength also holds for all stronger subordinates, that is, that $\partial W_1/\partial i$ is negative for all $f > \hat{f}(i)$. We conclude from the role reversal model that where challenges are profitable, the challenger's payoff (and, by extension, the effort expended on both dominance testing and dominance displays) will decrease down the hierarchy. Figure 1*A* illustrates how the challenger's payoff declines with rank for two values of the subordinate strength parameter f.

Model 2: Fatal Fight

Here we assume that escalated contests lead to the death of the loser. In this case, the inclusive fitness payoff to an individual at rank i of entering into a potentially fatal fight versus remaining peacefully in the queue is

$$
W_2(i, f) = \left\{ \left[\frac{fg_{n-1}}{i-1} + (1-f)(0) \right] - \frac{g_n}{i} \right\}
$$
$$
+ r \left\{ \left[f(0) + \frac{(1-f)g_{n-1}}{i-1} \right] - \frac{g_n}{i-1} \right\}
$$
$$
= \frac{ig_{n-1}[f + r(1-f)] - g_n[i(1 + r - 1)]}{i(i-1)}, \quad (5)
$$

where g_n and g_{n-1} are the productivities of groups of size n and $n-1$, respectively.

Differentiating equation (5) with respect to i to yields

$$
\frac{\partial W_2(i, f)}{\partial i} = \frac{i^2 g_{n-1}[f(r-1) - r] + g_n[1 - 2i + i^2(1+r)]}{i^2(i-1)^2},
$$
$$(6)$$

which again may be positive or negative, depending on the specific parameter values. We know from the appendix, however, that where challenging is profitable, the sign of $\partial W_2/\partial i$ is the same as the sign of $\partial W_2/\partial i$ evaluated at the critical strength $\hat{f}(i)$; so we need only find the sign of $\partial W_2/\partial i$ at this critical strength to establish the expected relationship between the challenger's payoff and rank. Setting expression (5) equal to 0 and solving for f yields

$$
\hat{f}(i) = \frac{irg_{n-1} - g_n[i(1 + r) - 1]}{i(1 - r)}. \quad (7)
$$

Substituting back into equation (6) and simplifying yields
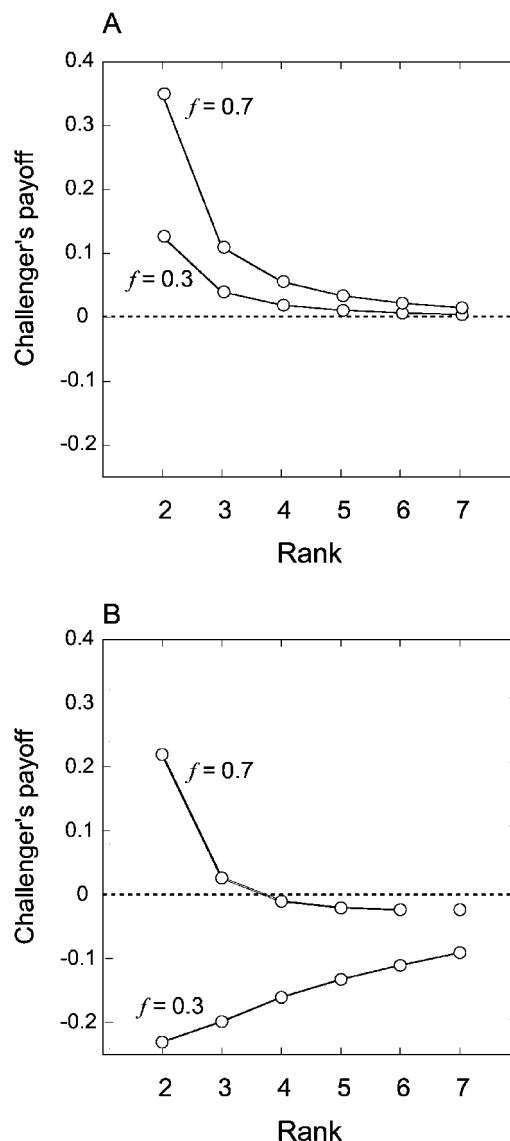
Figure 1: Challenger's payoff versus inheritance rank for two values of the relative subordinate strength parameter f for (*A*) model 1 (role reversal) and (*B*) model 2 (fatal fight). In model 1, challenging is profitable for all ranks for both values of f. In model 2, challenging is profitable only where subordinates are strong ($f = 0.7$) and of high rank (ranks 2 and 3). Where challenging is profitable (i.e., $W > 0$), the challenger's payoff decreases down the hierarchy in both models. Other parameter values: $r = 0.25$, $g_n = g_{n-1} = 1$, $c = 0.08$.

$$
\frac{\partial W_2(i, \hat{f}(i))}{\partial i} = \frac{g_n}{i^2 - i^3}, \quad (8)
$$

which is always negative. Thus, $\partial W_2/\partial i$ is also negative for all $f > \hat{f}(i)$. We conclude from the fatal-fight model that where challenges are profitable, the payoff associated with

challenging will decrease down the hierarchy. This pattern is illustrated in figure 1*B*.

We have assumed up to this point that *f* does not vary with rank. If, however, the highest rank is taken by unusually large or strong members of the population, we might expect the disparity in fighting ability to be greatest between the highest-ranked individuals. To model this possibility, we allow *f* to increase down the hierarchy, from a low value for $i = 2$ (implying a much stronger rank-1 individual compared to the rank-2 individual) to a value of approaching 0.5 for $i = n$ (implying that the two individuals at the bottom of the hierarchy are of equal strength). Figure 2 shows how the challenger's payoff in model 1 varies with rank under these conditions (the challenger's payoff in model 2 for the same parameter values is uniformly negative and is not shown). The figure shows that a sufficiently large increase in *f* between ranks can counteract the decline in the challenger's payoff with rank (e.g., cf. ranks 2 and 3), but in general, the predicted decrease in payoff down the queue is rather robust to changes in our assumptions about the distribution of strengths within the queue.

Effect of Group Size

What is the expected relationship between group size and the level of aggression between ranks in the two models described above? This depends on how breeder produc-

tivity varies with group size. It is clear from expressions (2) and (5) that both W_1 and W_2 are increasing functions of g_n, so, holding group size constant, we expect more productive groups to show elevated levels of aggression at all ranks. Where the fitness of a breeder is an increasing function of group size, we expect the level of aggression between individuals of a particular rank dyad to be higher in larger groups, at least where initial and inherited group sizes are correlated. (Conversely, where breeder fitness decreases with increasing group size, the opposite pattern will hold.) This prediction is illustrated in figure 3, which shows the results of model 1 when breeder productivity *g* is an increasing linear function of group size. Qualitatively similar results can be obtained using model 2, although, again, in this model the challenger's payoff is typically negative unless *f* is assumed to be very high ($\gg$0.5; see fig. 1*B*).

Time Constraints

Our models assume constant mortality rates, with no upper bound on potential life span and no constraint on the length of time that an individual may potentially wait to inherit. For seasonal animals, such as temperate *Polistes* wasps, however, there is only a limited time available to reach the top breeding position. To explore the effect of such time constraints on aggression, we focus on the challenger's payoff in a two-member group, but the qualitative
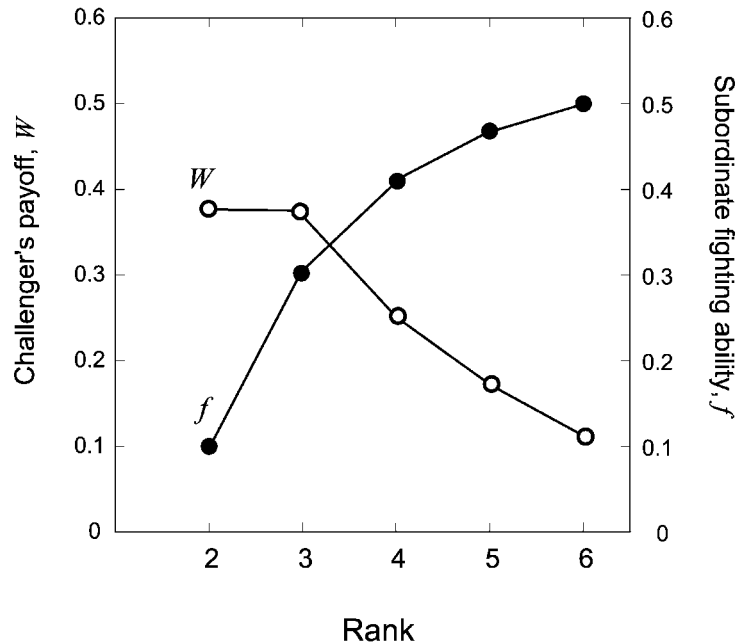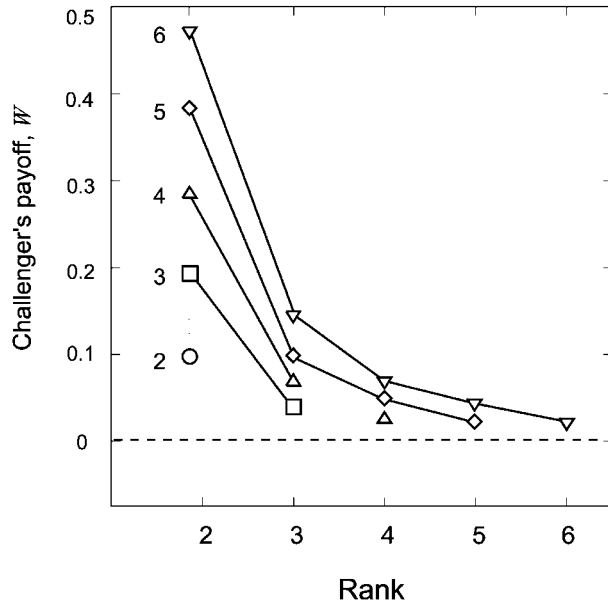

Figure 2: Challenger's payoff in model 1 versus rank when relative fighting ability of the subordinate increases down the queue.

Figure 3: Challenger's payoff versus rank for different group sizes. Results were calculated assuming that breeder productivity increases linearly with group size (specifically, $g(n) = n/2$) and that initial and inherited group sizes are the same. Numbers to the left of symbols denote group size. Other parameter values: $r = 0.25$, $c = 0.1$, $f = 0.5$.

prediction holds for groups of larger size (see appendix). We assume that there is a finite time period T available to inherit, after which subordinates have no chance of successfully reproducing. Individuals that are dominant at time T obtain a constant productivity g_n. This simple model probably applies well to paper wasps, since many of the original cofoundresses disappear after worker emergence, and data suggest that individuals that have not inherited by this time are unlikely to do so thereafter (Hughes and Strassmann 1988*b*; M. A. Cant and J. Field, unpublished data). For other seasonal species, however, where T marks the end of the breeding season rather than the founding period, one would expect productivity g to decline to 0 as the time taken to inherit approaches T, rather than dropping from a constant value to 0 at this threshold. In the appendix, we present a model that incorporates this decline in productivity over time and yields qualitatively identical results.

Let both members of the group suffer constant instantaneous mortality rate m. The probability that the rank-2 individual inherits by time T is the probability that the rank-2 individual is alive at time T multiplied by the probability that the rank-1 individual is dead by time T, or $e^{-mT}(1 - e^{-mT})$. The challenger's payoff for the rank-2 individual in models 1 and 2 can be written

$$W_1(T, 2, f) = \{f(g_n - c)e^{-mT} + (1 - f)(g_n - c) \\ \times [e^{-mT}(1 - e^{-mT})] - g_n[e^{-mT}(1 - e^{-mT})]\} \\ + r\{f(g_n - c)[e^{-mT}(1 - e^{-mT})] \\ + (1 - f)(g_n - c)e^{-mT} - ge^{-mT}\}$$

and

$$W_2(T, 2, f) = g_{n-1}fe^{-mT} - g_n[e^{-mT}(1 - e^{-mT})] \\ + r[g_{n-1}(1 - f)e^{-mT} - g_n e^{-mT}].$$

Differentiating these two expressions with respect to the time available to inherit, T, we obtain

$$\frac{\partial W_1}{\partial T} = me^{-2mT} \\ \times \{2fg_n(r - 1) + c[e^{mT}(1 + r) + 2f(1 - r) - 2]\} \quad (9)$$

and

$$\frac{\partial W_2}{\partial T} = me^{-2mT}[g_n e^{mT}(1 + r) - g_{n-1}e^{mT}(f + r) - 2)]. \quad (10)$$

In the two-player models, the critical strengths below which the challenger's payoff is 0 are given by

$$\hat{f}_1(T) = \frac{c[e^{mT}(1 + r) - 1]}{(g - c)(1 - r)}$$

for model 1 and

$$\hat{f}_2(T) = \frac{g_n(1 - e^{-mT} + r) - rg_{n-1}}{g_{n-1}}$$

for model 2. Substituting into equations (9) and (10), respectively, and simplifying, we obtain

$$\left. \frac{\partial W_1}{\partial T} \right|_{f = \hat{f}_1} = -cm(1 + r)e^{-mT}$$

and

$$\left. \frac{\partial W_2}{\partial T} \right|_{f = \hat{f}_2} = -g_n me^{-2mT},$$

both of which are clearly negative. Thus, at the critical strength for challenges to be profitable, the challenger's payoff increases as the time available to inherit decreases. Moreover, we show in the appendix that this relationship also holds for all $f > \hat{f}$. The conclusion is that the challenger's payoff and predicted levels of aggression will be higher where there is less time available to inherit. This prediction is illustrated in figure 4, which shows the challenger's payoff in model 1 as a function of time for three different values of average life span (the reciprocal of instantaneous mortality rate m).

In summary, our models make three predictions. First, the payoff associated with entering a fight over dominance increases as one approaches the front of the queue. We would thus expect that the effort expended on dominance-testing behaviors and the aggressive displays used to deter challenges will decrease down the hierarchy. Second, where larger groups are more productive, the aggression levels between a particular dyad of adjacent ranks are predicted to increase with increasing group size. Finally, where there is a limited time available for breeding, we expect levels of aggression at all ranks to increase as the breeding season progresses.

Aggression and Inheritance Rank in Paper Wasps

We carried out an experimental test of the predictions described above, using cofoundress associations of the paper wasp *Polistes dominulus* in southern Spain (Conil de la Frontera, Cadiz). Paper wasps fit the assumptions of our queuing model reasonably well. At our study site, nests are founded each spring by groups of one to 10 cofoundresses, usually relatives (Cant and Field 2001; Shreeves et al. 2003). The foundresses form a dominance hierarchy in which the top-ranking female lays most of the eggs while lower-ranking subordinates provide most of the help (Turillazzi and Pardi 1977; Reeve 1991; Queller et al. 2000; Cant and Field 2001). Cofoundresses are of similar age and so are likely to have similar life expectancies (before taking into account differences due to variation in helping effort), and lower-ranked individuals can inherit the position of breeder if they outlive those ahead of them in the queue. At our study site, we estimated that 30% of dominants on multiple-foundress nests disappeared during the founding period, thereby allowing the rank-2 subordinate to inherit dominant status before worker emergence (Cant and Field 2001). Opportunities for inheritance may also exist later in the season, when reproductives are
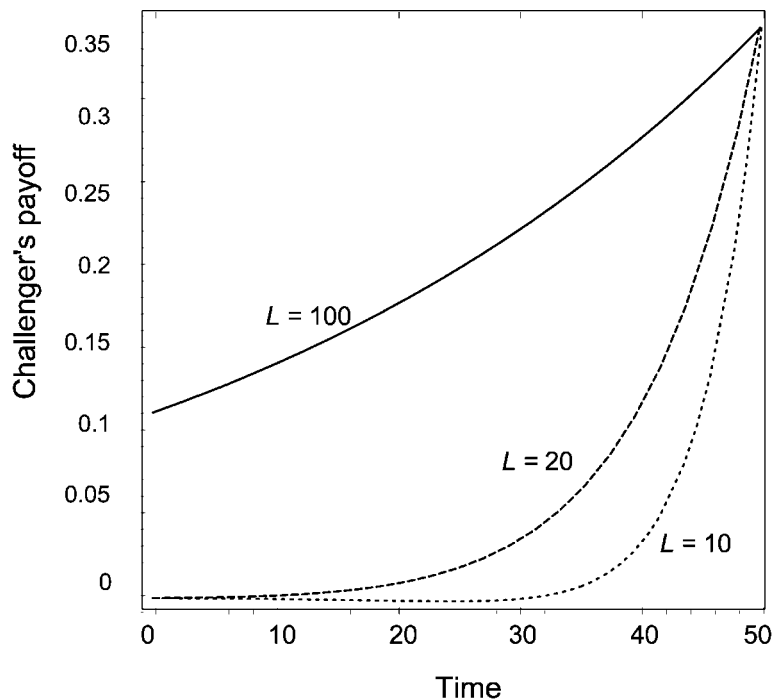
Figure 4: Challenger's payoff in model 1 versus time when there is a strict limit to the time available to inherit. In this example, the breeding season ends at $T = 50$. The three curves correspond to three values of average expected life span L ($= 1/m$). The challenger's payoff in model 2 also increases over time.

produced, but many of the original foundresses disappear after worker emergence, and individuals that are dominant at the time of worker emergence often remain so for a long period thereafter (M. A. Cant and J. Field, personal observations). This means that subordinates may have only a limited time in which to inherit if they are to attain breeding status by the time reproductives are produced. Group productivity (number of cells) increases linearly with group size ($n = 66$ nests, $r = 0.94$, $P < .0001$; Cant and Field 2001), and foundresses apparently do not discriminate between degrees of relatedness among nestmates (Queller et al. 1990; Keller 1997; Strassmann et al. 1997).

Our fieldwork consisted of two stages. First we recorded aggressive interactions in intact groups, and then we carried out repeated removals to identify the order in which group members inherited the rank of dominant breeder. This is possible in our study species because the rank-1 individual almost never leaves the nest, so replacement dominants can easily be identified from census data (Cant and Field 2001; Shreeves et al. 2003). We also carried out a comparison of the aggression rates of a subset of individuals before and after they were promoted in rank, to test our assumption that rank determines aggression level rather than vice versa.

Methods

Marking and Recording of Behavior

Nests were located throughout March 2003 on hedges of *Opuntia* cactus in a 100×200-m area of fallow pasture. After finding a nest, we returned early in the morning (ca. 0700 hours), when it was too cold for the wasps to fly, and captured all group members by brushing them off the nest into a kitchen sieve. Each foundress was measured for wing length and individually marked with a unique color combination of enamel paint spots applied to the thorax (e.g., Field et al. 1999, 2000; Cant and Field 2001). Repeat visits were made early in the morning for a further 4–5 days to capture any remaining unmarked individuals or new joiners. Starting on 25 March, we carried out repeated censuses (three to five censuses per day, intercensus interval 45 min–1 h) on sunny afternoons (when foraging is most frequent) to determine the identity of the rank-1 individual (average number of censuses = 15, range: 8–25). Following previous studies (Cant and Field 2001), we classed as dominant those wasps that were present on the nest for more than 66% of daytime censuses (mean time on nest of dominants $\pm$ SE = 94% $\pm$ 1.9%). This criterion identified a single dominant in 25 out of 29 nests. In the remaining four nests, two wasps were present for more than 66% of the time, and we labeled as dominant the individual that was on the nest the most (see also Cant

and Field 2001). Observations of egg laying, ovarian dissections, and preliminary genetic analyses indicate that our dominance criterion based on time on the nest is an excellent predictor of reproductive dominance in this species (M. A. Cant and J. Field, unpublished data).

After identifying the rank-1 foundress, we videotaped each nest continuously for 3 h on a warm day (shade temperature range 19.5°–27.0°C) between 1100 and 1700 hours. The first video recording was made on 18 April, the last on 15 May. All nests were videotaped in the founding phase before the emergence of workers.

Identifying Inheritance Ranks

The morning after each nest had been videotaped, we removed the rank-1 individual previously identified from daytime censuses. Starting the next day, we conducted repeated daytime censuses for 3 days or more (average of 14 censuses) and identified new dominants as the wasps (one per nest) that increased their time on the nest above the 66% criterion described above. In most cases, the new dominant was easy to identify because typically only one wasp per nest showed a marked increase in time on the nest after the removal of the original dominant (mean time on nest for replacement dominants is 92% $\pm$ 3.7% vs. 50% $\pm$ 4.0% for the same individuals when at rank 2). For six nests, however, two wasps were present for more than 66% of censuses, so we again ranked the dominant as the individual that was present the most. The replacement dominant was then removed, and the nests were again censused repeatedly for 3–5 days until the next individual to inherit rank 1 could be identified using the criteria above. The process was repeated until the rank-5 individual had been identified or until only two wasps remained on the nest and therefore no further removals were necessary to identify ranks.

In addition, just before the second removal (i.e., 3–5 days after the removal of the original dominant), we videotaped a subset of 12 nests for a second time. This enabled us to compare the behavior of the same individuals before and after they were promoted to the rank-1 position. Our aim here was to test the assumption of our models that rank determines aggression level rather than aggression level determining rank. If the direction of causality is, as we assume, from rank to aggression level, we would expect the same individuals to be more aggressive after they were promoted in rank.

Measurement of Behavior and Statistical Analysis

We analyzed an average of 160 min (range 90–180 min) of videotape from each of the 29 nests for which data on inheritance ranks were available. For each nest, we built

up a dominance matrix in which we recorded the identity of the initiator and the recipient of each act of aggression. Three types of act were recognized as aggressive: "darts," whereby an individual suddenly leapt across the nest toward another group member but did not necessarily make contact; "lunges," which were similar to darts but culminated in physical contact; and "grapples," whereby one wasp grasped and physically pushed another backward, usually forcing it around to the rear of the nest. The three categories include most of the behaviors categorized as "aggressive" in previous studies of *Polistes* (Gamboa et al. 1990; Reeve and Nonacs 1992, 1997; Nonacs et al. 2004), with the exception of mounting behavior, which was misscored in the video analyses and is not included here. It should also be noted that the aggressive function of dart behavior has recently been questioned by Sumana and Starks (2004), working on postemergent colonies of *Polistes fuscatus*, mainly because they found no correlation between the rate at which an individual received darts and other dominance behaviors. In our study, this correlation was very strong ($\chi_1^2 = 10.38$, $P < .001$), so we followed previous studies in classing darts as aggressive (Gamboa et al. 1986; Reeve and Gamboa 1987; Reeve and Nonacs 1992, 1997; Tibbets and Reeve 2000; Nonacs et al. 2004). We scored aggressive acts as independent only if no other aggression had occurred during the previous 2 s between the two individuals involved; sometimes two individuals rapidly exchanged multiple aggressive acts for a second or more, but we scored these as a single act attributed to the initiator of the exchange. Data on the three classes of aggressive act were given equal weights and summed before analysis.

We noted the identity and timing of all arrivals and departures from the nest. As in a previous study (Cant and Field 2001), the proportion of time spent off the nest varied widely between group members. To control for this variation, we calculated total aggression rates as the number of aggressive acts per minute that an individual was on the nest. The term "total aggression rate" is used to distinguish this measure from the "dyadic aggression rate," which refers only to those acts of aggression exchanged with an individual of adjacent rank. Since higher-ranked individuals spent more time on the nest, high-ranking dyads were together for longer periods than low-ranking dyads and therefore had more opportunity to interact in the 3-h period for which the nest was videotaped. We therefore calculated the number of minutes that individuals of adjacent rank were together on the nest. Dyadic aggression rates were then calculated as (number of aggressive acts to other individual)/(number of minutes together on the nest). As a shorthand, we labeled acts of aggression directed toward an immediate subordinate as

dominance "displays" and acts of aggression directed toward an immediate superior as dominance "tests."

Statistics were carried out using the Genstat 6.0 package. We used a $\log(Y+1)$ transformation on aggression data to improve the fit of the residuals to assumptions of normality. Data on proportion of time on nest were arcsine transformed before a GLMM analysis. Data were then analyzed using a general linear mixed model (GLMM) with normal errors ("REML" in Genstat 6.0). We fitted rank, group size, date, relative body size, temperature, nest size (number of cells), and number of pupae as fixed effects. Nest identity was fitted as a random effect in all models. Fixed-effect terms were dropped from the full model by backward elimination until further removals led to a significant ($P < .05$) decrease in the explanatory power of the model, as assessed from a Wald statistic that is asymptotically distributed as χ^2 (Genstat 6.0). The significance of each term was tested in the presence of the main effects only, by adding each term individually to this minimally adequate model. Relevant two-way interactions were also tested (in the presence of the main effects) but were not included in the results unless significant. All tests were two-tailed.

Results

Data on both aggressive behavior and inheritance ranks were available for 29 nests comprising a total of 113 individuals. The proportion of time that individuals were present on the nest varied with both rank and group size, with lower-ranked individuals present less frequently, and individuals of a given rank spent less time off the nest in larger groups (GLMM with nest as random effect: effect of rank $\chi_1^2 = 30.75$, $P < .001$; effect of group size $\chi_1^2 = 5.99$, $P < .014$). Thus, the results derived from this 3-h continuous observation period closely match those of a previous study (Cant and Field 2001), in which time off the nest was calculated from repeated censuses over an 8-day period.

Aggression rates (mean number of aggressive acts per minute on the nest) varied widely between individuals (mean $\pm$ SE = 0.043 $\pm$ 0.006, range: 0–0.39). In the GLMM analysis of total rates of aggression toward other group members, only rank and date caused a significant increase in deviance when dropped from the minimum adequate model (table 1, top half). Individuals of high rank were more aggressive to other group members than those of low rank, and individuals were more aggressive later in the season (fig. 5). Temperature, group size, the number of cells in the nest, and the number of pupae had no significant effects on rates of aggression toward other individuals. To counter possible problems with pseudoreplication, we also tested the effect of group size on ag-

Table 1: General linear mixed model of factors affecting total aggression rates

Model terms	χ^2	df	P
Aggression toward other group members:			
Rank	14.01	1	<.001
Date	9.84	1	.002
Number of pupae	2.51	1	.11
Temperature	1.58	1	.21
Group size	.58	1	.45
Wing length	.09	1	.77
Developmental stage	.95	3	.81
Nest size (cells)	.02	1	.89
Aggression received from other group members:			
Date	10.80	1	.001
Developmental stage	1.40	3	.24
Temperature	.68	1	.41
Group size	.46	1	.50
Number of pupae	.33	1	.57
Nest size (cells)	.18	1	.67
Wing length	.07	1	.78
Rank	.06	1	.81

gression for each rank separately but found no significant effect for any rank (all $P > .05$).

Only date had a significant effect on the rate at which an individual received aggression, with more aggression being received later in the season. Other variables (rank, temperature, group size, number of cells, number of pupae) had no significant effect (table 1, bottom half). Group size had no significant effect on rates of aggression received when each rank was tested separately (all $P > .05$). The rank-1 individual received significantly less aggression than those at lower rank (mean acts received per min on nest: for rank 1, 0.03 ± 0.009; for other ranks, 0.052 ± 0.008; $\chi_1^2 = 4.32$, $P = .04$; fig. 5).

Dyadic Aggression: A Test of the Models

The great majority of aggressive interactions (both as actor and as recipient) were between individuals of adjacent rank, in accordance with the assumptions of our model. The mean $\pm$ SE aggression rate toward individuals one rank below was 0.033 ± 0.006, which was almost twice the rate of aggression toward all other individuals in the group combined (0.019 ± 0.004; $\chi_1^2 = 4.63$, $P = .03$) and four times the per capita rate of aggression toward these other individuals (0.008 ± 0.002; $\chi_1^2 = 16.8$, $P < .001$). Similarly, the rate of aggression toward individuals one rank above was twice the per capita rate of aggression toward individuals at other ranks (aggression rate toward individuals one rank above $= 0.018 \pm 0.005$; $\chi_1^2 = 3.47$;
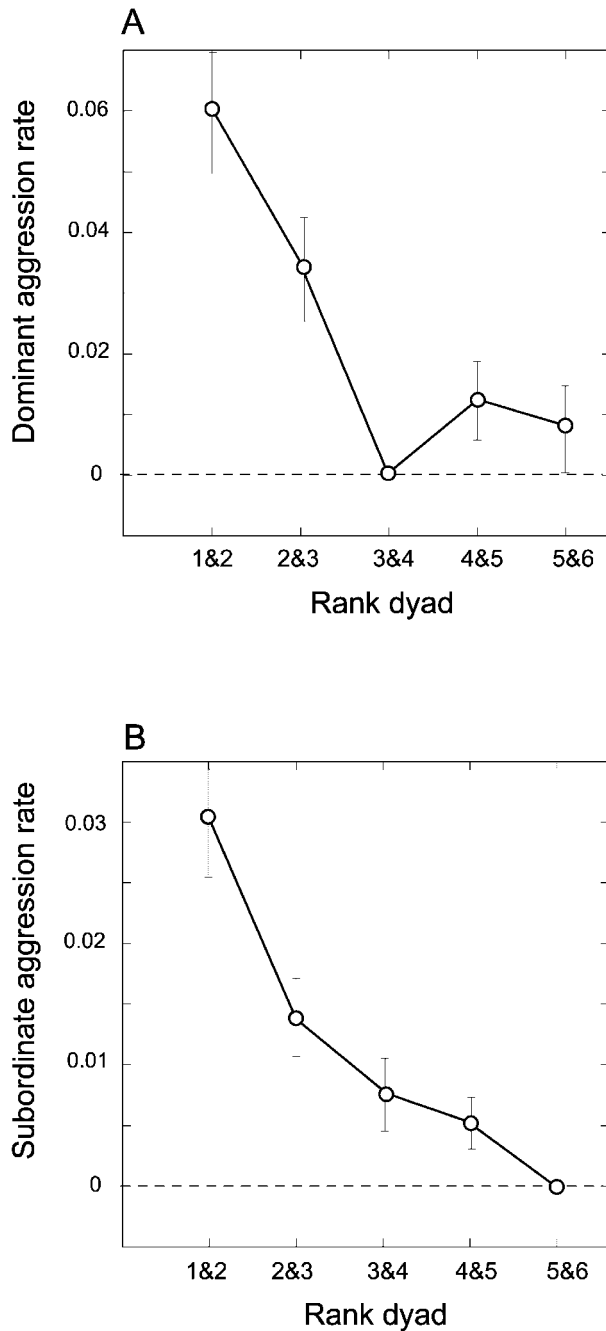
$P = .06$). The bias in the direction of aggression toward individuals of adjacent rank, calculated as (rate toward those of adjacent rank)/(rate toward those at other ranks), did not itself vary with rank ($\chi_1^2 = 2.27$, not significant).

The rate at which higher-ranking individuals were aggressive to their immediate subordinates decreased down the hierarchy (fig. 6A). In the GLMM model, only rank and date had significant effects on this aggressive display rate (table 2, top half), with display rate decreasing down the hierarchy and increasing through the founding period. Similarly, the rate at which lower-ranking individuals tested their immediate superiors decreased down the hierarchy (fig. 6B). Again, the GLMM analysis for this case indicated that rank and date had significant effects but that the other terms in the model were nonsignificant (table 2, bottom half). The increase in dyadic aggression through the founding period is illustrated in figure 7, which shows the rate of tests and displays combined against day of the year. Group size had no significant effect on either display rate or test rate for all individuals or when tested for each rank separately (all $P > .05$). Thus, we found good support for the prediction of models 1 and 2 that rates of aggression (both testing and displaying) will decrease down the hierarchy and increase through the founding period. There was no support, however, for the predicted effect of group size.
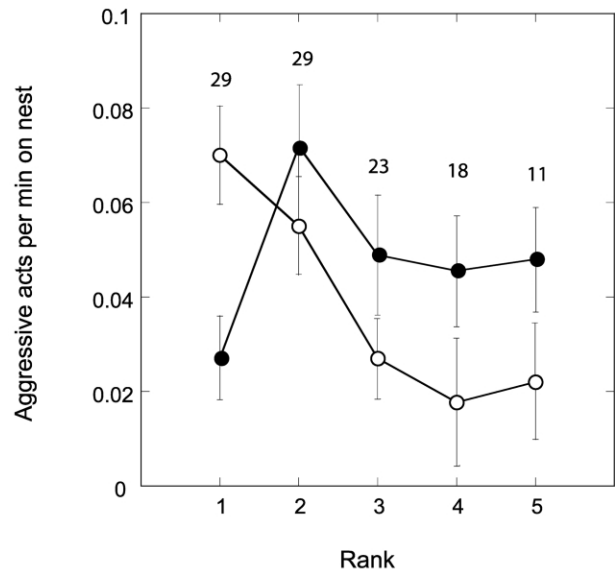
Figure 5: Rates at which aggressive acts were performed (*open circles*) and received (*filled circles*) versus inheritance rank. Error bars represent $\pm$ SE. Numbers above error bars indicate the number of individuals at each rank.

Figure 6: Dyadic aggression rates of individuals at adjacent ranks. Dyadic aggression rate was calculated as number of aggressive acts performed toward the other member of the dyad per minute that both individuals were present on the nest. *A*, Aggression rate of relative dominants toward their immediate subordinates; *B*, aggression rate of relative subordinates toward their immediate superiors. Since group size had no significant effect on dyadic aggression, points shown represent means ± SE for all group sizes combined.

Aggression before and after Inheritance

For a subset of 12 nests, we were able to compare the dyadic aggression levels of individuals at ranks 2 and 3 before and after the first removal, that is, before and after they were promoted to ranks 1 and 2, respectively. The display rate of the original rank-2 individual increased significantly after it had inherited the rank-1 position ($\chi^2_1 = 11.62$, $P < .001$; fig. 8). Indeed, the aggressive display rates of these replacement rank-1 individuals exceeded the display rates of rank-1 individuals on unmanipulated nests before removals ($\chi^2_1 = 5.38$, $P = .02$; fig. 8). The rate at which the original rank-3 individuals tested their immediate superiors was marginally higher after promotion but not significantly so ($\chi^2_1 = 0.62$, not significant; fig. 8), and there was no difference between the testing rates of these rank-3 individuals that had been newly promoted to rank 2 and those at rank 2 on unmanipulated nests before experiment ($\chi^2_1 = 0.02$, not significant; fig. 6). There is thus evidence that aggression rates are causally influenced by rank rather than vice versa. However, the very high rates of aggression observed after promotion to the dominant position, over and above the normal levels for rank-1 individuals, suggest that such elevated aggression serves to establish dominant status on a recently disturbed nest.

Discussion

Our models suggest that fights over dominance are more profitable in terms of inclusive fitness toward the front of

Table 2: General linear mixed model of factors affecting dyadic aggression rates

| Model terms	χ^2	df	P
Aggression toward immediate subordinate ("displaying"):			
Rank	13.57	1	<.001
Date	9.94	1	<.001
Number of pupae	2.78	1	.09
Relative size	2.47	1	.12
Developmental stage	3.2	3	.36
Group size	.24	1	.63
Temperature	.01	1	.92
Nest size (cells)	.00	1	.97
Aggression toward immediate superior ("testing"):			
Rank	5.34	1	.02
Date	4.55	1	.03
Number of pupae	2.22	1	.13
Developmental stage	3.78	3	.29
Temperature	1.13	1	.29
Nest size (cells)	.96	1	.33
Group size	.42	1	.52
Relative size	.24	1	.62
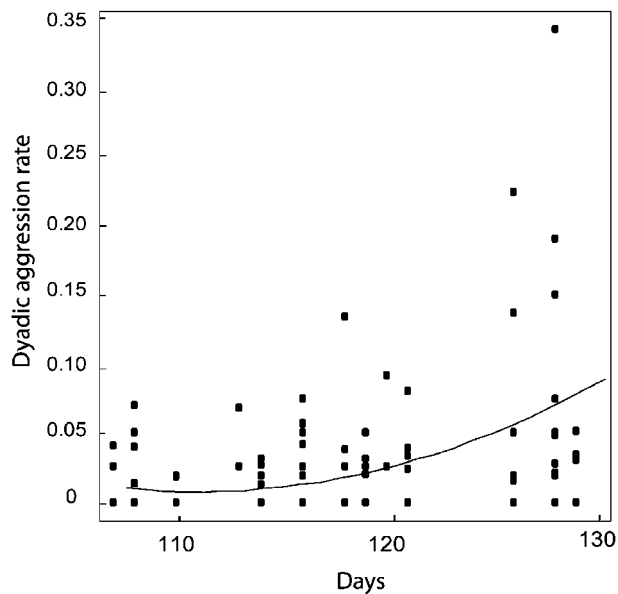
Figure 7: Dyadic aggression rate versus day of the year on which nests were videotaped. The quadratic regression is shown ($Y = 2.31 - 0.041X + 0.0002X^2$; $R^2 = 0.14$, $P = .002$).

a social queue. Accordingly, we expect individuals of high rank to invest more than those of low rank in both deterrent displays toward their subordinates and dominance tests toward their superiors. The results of our experiment on *Polistes dominulus* offered strong support to this prediction. Cofoundresses of high rank engaged in more aggressive behavior than those of low rank. The great majority of this aggression was directed at individuals of adjacent rank, whether higher or lower in the hierarchy. Aggression rates toward subordinates increased radically after individuals were experimentally promoted to rank 1, suggesting that aggression depends on rank rather than vice versa and that particularly high levels of aggression are used by newly promoted dominants to establish their status. A similar pattern has been observed in the polistine wasp *Ropalidia marginata* (Chandrashekara and Gadagkar 1992; Gadagkar 2001) and the queenless ant *Dinoponera quadriceps* (Monnin and Peeters 1999). In both these species, the aggression level of the replacement dominant returned to typical levels after a few days, suggesting that very high levels of aggression function to stabilize dominant rank but are unnecessary once status is established.

These results suggest that individuals possess information about their own ranking and the rankings of others in the queue to inherit dominance and direct their aggressive behavior toward their closest rivals in terms of social status. Indeed, the position of an individual in the queuing system apparently exerts a stronger influence on

aggressive behavior than any other observable attribute of the individual. There was no relationship between body size and rates of display or testing or between body size and inheritance rank (Cant and Field 2001). Cofoundresses are of the same sex and of similar age and have similar expected life spans. Preliminary genetic data suggest no correlation between rank and relatedness (J. Field and M. A. Cant, unpublished data), and foundresses probably do not discriminate between degrees of relatedness among nestmates (Queller et al. 1990; Keller 1997; Strassmann et al. 1997). The social structure of the group, revealed by our removal experiment, is the hidden causal factor responsible for much of the individual variation in within-group aggression in this species.

The models predict that individuals of high rank should invest more in challenging behavior, even when this involves potential mortality risks. This offers an interesting contrast to our previous models of helping effort, which predict that higher-ranked subordinates should invest less in potentially risky foraging behavior (Cant and Field 2001, 2005). The difference arises because in the aggression models, the benefits of a successful challenge increase exponentially as one approaches the front of the queue, whereas the productivity or mortality costs of fighting remain constant across ranks (at least in the basic models; but see fig. 2). In the helping model, by contrast, the benefit of a given unit of helping effort is constant across ranks, while
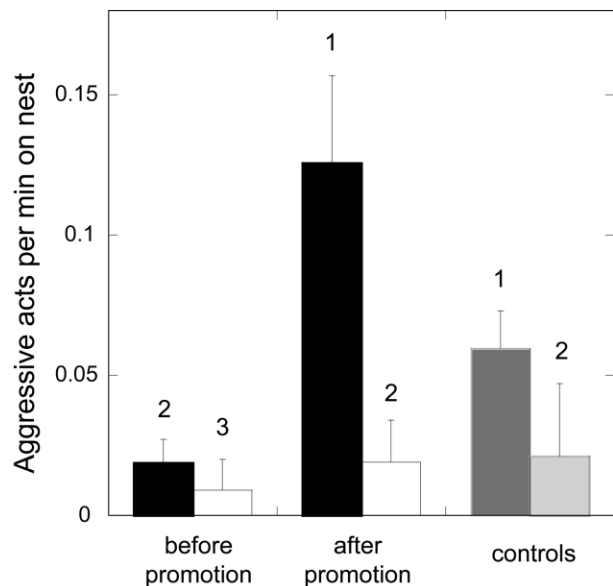

Figure 8: Dyadic aggression rates of individuals at ranks 2 and 3 before and after they were experimentally promoted to ranks 1 and 2, respectively. Numbers above each column indicate rank. Columns marked "controls" are the dyadic aggression rates of individuals at ranks 1 and 2 on unmanipulated nests. Error bars represent SE.

the fitness loss associated with dying in the queue increases exponentially as one ascends in rank. To solve for optimum levels of both types of behavior, we would need to make some assumption about the informational sequence by which decisions are made. If helping effort is decided before the decision of whether to challenge, we would expect the results of our aggression models to be reinforced, since the low helping effort associated with high ranks would tend to increase their value even further compared to lower ranks. Consequently, high-ranking wasps would be predicted to be both lazy and aggressive and low-ranking wasps to be both hard-working and peaceable.

The only variable other than rank that had a significant influence on rates of aggression was date, with more aggression observed later in the season. This is the result regardless of whether the costs of challenging are in terms of survival (model 2) or reduced future fecundity (model 1). Wasps possess potentially lethal weaponry in the form of a sting, and escalated contests in *Polistes* are known to be fatal in some cases (Gamboa 1978). It is therefore quite plausible that the primary cost of fighting in this species is the chance of death or serious injury. Tibbets and Reeve (2000) also found that rates of aggression increased through the founding period in *P. dominulus*, and a similar pattern has been observed in other *Polistes* species (Gamboa and Stump 1996; Reeve et al. 2000). Reeve and coworkers interpret this finding as supporting the transactional theory of reproductive skew, since skew increases through the founding phase, and in some circumstances high skew is expected to lead to elevated levels of overt conflict in the group (Reeve 2000; but see Cant and Johnstone 2000 for a clarification of this prediction). Our models provide an alternative explanation. We suggest that the rate of aggressive interactions (both displays and tests) increases through the founding period because the mortality risks and other costs associated with fighting become less of a concern as the time available to inherit starts to run out.

We predicted that group size would exert an effect on rates of aggression because larger cofoundress associations are more productive, increasing the value of challenging for a given rank. This was not supported by our data. Individuals of given rank were not more aggressive in larger groups, nor was aggression correlated with the size of the nest or the number of pupae, two variables that might be expected to be correlated with the value of the nest as a resource. In a related study, we found that newly promoted rank-2 individuals are more likely to engage in escalated contests to retain the dominant position in larger groups, which would again suggest that larger groups represent a greater "prize" to a potential challenger aiming to ascend in rank (M. A. Cant, S. English, H. K. Reeve, and J. Field, unpublished manuscript). It may be, however,

that other forces place a limit on aggression in large groups, such as an elevated probability of errors of recognition or information (Reeve 1989, 1991; Starks et al. 1998) or a stronger "bystander" or "eavesdropper" effect (Dugatkin 2001; Johnstone 2001). In addition, recent data on ovarian development suggest that larger groups contain a greater fraction of potential egg layers (Cant and English, forthcoming), so it is possible that the greater productivity of large groups is offset by increased competition from cobreeders, although we do not have genetic evidence for this. Whatever the reason, the conclusion from our data is that an individual's relative position in the queue has a more important influence on the costs and benefits of low-level aggressive behavior than our measures of the absolute value of the resource that may be inherited.

Our model offers an alternative perspective on social aggression to those of either transactional or tug-of-war models of reproductive skew (Reeve et al. 1998; Reeve 2000). These models start from the premise that aggression is used by dominants to suppress reproduction in subordinates and by subordinates to claim a share of reproduction from dominants. For example, the transactional model of Reeve and Keller (1997) shows that it will always pay a dominant individual to appease a potential challenger by offering it a share of reproduction. By contrast, the tug-of-war model assumes that the distribution of reproduction is the outcome of a scramble competition in which the dominant individual exerts a stronger "tug" (Reeve et al. 1998; Cant and Shen 2006). In either case, the contested resource is current reproduction, and future benefits of group membership are explicitly excluded. The contested resource in our models, by contrast, is social status and the future benefits this brings. It would be simple to adapt our framework to allow for variation in the current benefits of rank by assigning a fraction of reproduction to each rank. The challenger's payoff would then depend on both rank and the disparity in reproductive share between a rank dyad, with lower aggression expected where skew between ranks is low (M. A. Cant et al., unpublished manuscript). This approach would assume that aggression is a response to the degree of skew between two ranks (which is determined in some unspecified way first) rather than being the determinant of skew (as assumed by transactional and tug-of-war models). One way to test this would be to manipulate aggression levels (perhaps by handicapping one of the combatants) to see whether this changed the level of skew. Skew models are, in any case, unable to account for acts of aggression between nonbreeders. On the basis of ovarian dissections, many of the low-ranking individuals in our groups undoubtedly are nonbreeders (Cant and English, forthcoming), and aggression between nonbreeders is common in

other primitively eusocial societies (Monnin and Peeters 1999; Gadagkar 2001).

Where lifetime reproductive success depends crucially on rank, high rank will be the most keenly contested resource within the group. How, then, is rank decided? In many cases, dominant animals are physically stronger than their subordinates (i.e., $f < 0.5$ in our model). Sometimes, however, inheritance rank is determined by some convention such as age or order of arrival, and subordinates may be larger or stronger than their superiors (Strassmann et al. 1987; Field et al. 1999; Cant and Field 2001; Seppä et al. 2002). Our models help to explain how such conventions can be stable. Where time available for inheritance is long relative to expected life span and fights are costly, the payoff of challenging is often negative, so individuals may do best to wait peacefully to inherit even if they are stronger than those above them in the queue. By contrast, where fights are cheap and there is little time to inherit, we expect a higher frequency of escalated fighting within the queue and a closer correlation between rank and resource-holding potential. The lack of a consistent correlation between size and rank in some species of *Polistes* may thus be explained by the potentially lethal nature of escalated fights over dominance in these species (Strassmann et al. 1987; Reeve 1991) and by the relatively high probability of inheritance for subordinates (Queller et al. 2000; Cant and Field 2001).

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