1989 - 2014
25 YEARS
BEHAVIORAL ECOLOGY
Behavioral Ecology
The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2014), 25(4), 706–715. doi:10.1093/beheco/aru063

Editor's choice

Original Article

Dominant aggression as a deterrent signal in paper wasps

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Received 26 October 2013; revised 9 March 2014; accepted 13 March 2014; Advance Access publication 18 April 2014.

Low-level social aggression is a conspicuous feature of cooperative animal societies, but its precise function is usually unclear. One long-standing hypothesis is that aggressive displays by dominant individuals serve to reduce uncertainty about relative strength and deter subordinates from starting fights that they are unlikely to win. However, most formal theoretical models of this idea do not consider how the credibility of deterrent signals might change over time in social groups. We developed a simple model of dominant aggression as a deterrent signal, which takes into account how credibility changes over time and how selection should act on receiver memory. We then carried out an experimental test of the predictions of our model on a field population of the paper wasp, *Polistes dominulus*. The match between our theoretical and empirical results suggests that low-level social aggression can help to maintain the stability and productivity of cooperative associations in this species. Moreover, our work suggests that rates of aggression in animal societies and the robustness of social memories are likely to be intimately related.

Key words: **conflict, cooperation, cooperative breeding, fighting, social evolution, social memory.**

INTRODUCTION

Social aggression, defined as low-level aggression between the members of stable social groups (Cant et al. 2006b), is a widespread and conspicuous feature of animal societies. Dominant individuals often spend considerable time and energy harrying, shoving, mounting, biting, or chasing their subordinates (Reeve and Nonacs 1997; Cant et al. 2006b; Wong and Balshine 2010; Huchard and Cowlishaw 2011; Santema and Clutton-Brock 2012), whereas subordinate individuals are sometimes aggressive to dominants, a behavior labeled as "dominance testing" (Reeve and Ratnieks 1993). In a few species, aggression appears to be the means by which dominant individuals induce helpers to work harder (e.g., cooperative cichlids: Bergmüller and Taborsky 2005; naked mole rats: Reeve 1992). In most cases, however, social aggression appears to be linked to conflict over social rank or reproduction. Dominant individuals usually direct aggression toward their closest reproductive competitors in the group (e.g., paper wasps: Reeve 1991; Reeve and Nonacs 1997; Cant et al. 2006b; social fish: Ang and Manica 2010; Wong and Balshine 2010; ants: Hölldobler and Carlin 1989; Monnin and Peeters 1999; Monnin et al. 2002; and numerous cooperative birds and mammals: Walters and Seyfarth 1987; Zahavi 1990; Mason and Mendoza 1993; Clutton-Brock et al. 1998; Cant 2000; Creel 2005; Sapolsky 2005; Young et al. 2006). New dominants who have just inherited or usurped a higher rank are often more aggressive than established dominants as they seek to reinforce their newly acquired status (Chandrashekara and Gadagkar 1992; Premnath et al. 1996; Monnin and Peeters 1999; Cant et al. 2006b; Lamba et al. 2007; Wong and Balshine 2010). Low-level aggressive acts sometimes escalate into all-out fights over rank, which result in the death, eviction, or subordination of the loser (see Cant and Johnstone 2000 and references therein).

A long-standing hypothesis in the ethological literature is that aggressive dominance displays serve as a signal that reinforces asymmetries in resource-holding potential (RHP; which is defined by Parker 1974, as a measure of "absolute fighting ability") and resolves conflict over rank without recourse to out-and-out fighting (Schjelderup-Ebbe 1922, 1935; Hinde 1979; Maynard Smith and Harper 2003). The underlying assumption is that aggression by dominant individuals is an honest signal of strength or quality that deters subordinates from starting fights that they are unlikely to win. Insightful game theoretical models of this idea suggest that aggression can function as an honest signal of RHP if aggressive displays are themselves costly to produce, or if the act of aggression increases the risk of escalated contests (Maynard Smith and Parker 1976; Enquist 1985; Adams and Mesterton-Gibbons 1995;

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Maynard Smith and Harper 2003; Szamado 2008). Subordinates can then use the occurrence or intensity of dominance displays to avoid challenging the status quo when it is not in their fitness interests to do so (Maynard Smith and Harper 2003; Szamado 2011).

These models of aggression as a deterrent signal typically solve for evolutionarily stable values of mean signal intensity as a function of relative strength or resource value. Much less attention has focused on the timing and dynamics of deterrent signals and subordinate challenges, and several basic questions remain unanswered. Why should dominant individuals initiate aggressive interactions rather than wait for subordinates to challenge? How often should dominants be aggressive to their subordinate, and how often should subordinates test or challenge their dominant? Why does the frequency and intensity of aggression vary so much within and between species?

To address these questions, a good way forward is to make an explicit assumption about the function of aggression and derive testable predictions. Here, we adopt this approach to investigate the causes of variation in the rate and timing of aggression by dominant individuals toward their subordinates. We proceed on the explicit hypothesis that aggression by dominant individuals serves as a signal of strength or fighting ability that deters subordinates from challenging the status quo. We reason that where signaler strength or quality fluctuates, for example, due to stochastic variation in food intake, disease, stress, health, injury (e.g., Williams et al. 2008), growth (Wong et al. 2008), or senescence (Clutton-Brock and Sheldon 2010), the reliability of a dominant's signal as an indicator of current strength will decline with time since the signal was given, and subordinates should give less credence to signals in the (relatively) distant past compared with more recent signals. Dominants will therefore need to repeatedly signal to maintain a credible deterrent threat of escalated fighting. A corollary is that we should expect selection acting on subordinate memory to favor an optimal "rate of forgetting" of the information conveyed by dominance displays, with a faster rate of forgetting where strength is more stochastically variable over time.

We develop a simple graphical model of this problem and test some predictions of the model through a field experiment on the paper wasp *Polistes dominulus* (sometimes referred to by its alternative name *Polistes dominula*). In a previous model of aggression in dominance hierarchies (Cant et al 2006b), we assumed that the rate at which dominants display to subordinates should increase with the net fitness benefits to subordinates of supplanting the dominant. Here, we augment this basic cost/benefit approach by focusing in more detail on the cognitive mechanism by which subordinates make decisions. In particular, our model explores how uncertainty about dominant strength (as perceived by a challenger) should affect the optimal rate and timing of aggressive displays by dominants.

THE MODEL

Consider a hierarchy consisting of a dominant individual and a single subordinate. For simplicity, we assume that the 2 are unrelated in the graphical model, although we explore the effect of relatedness in the formal model in the Appendix. The subordinate faces a decision of whether to accept its position or enter into an escalated contest to win dominant status, with its attendant fitness benefits. We assume that the subordinate is of strength t, and the dominant is of strength s. The distribution of dominant strengths in the population is denoted $f(s)$. For given fitness costs of fighting and fitness benefits of winning, and a given subordinate strength t, there will be a threshold dominant strength $s^*(t)$ above which challenging is unprofitable and below which challenging is profitable for the subordinate. This threshold $s^*(t)$ will be greater for stronger subordinates and for higher net fitness benefits of challenging (e.g., where the rank 1 position is more valuable). In Figure 1a, we illustrate this threshold $s^*(t)$ relative to the distribution of dominant strengths in the population.

In the absence of any other information, the subordinate does best to base its decision on whether to challenge on the assumption that the strength of the dominant is drawn randomly from the distribution $f(s)$. However, if the subordinate has access to signals or cues that convey information about underlying strength, the subordinate should base its decisions on the assumption that the dominant is drawn from a narrower distribution $b(s)$, which we call the "belief function" $b(s)$ of the subordinate.

Now let the dominant individual engage in a costly aggressive display that reveals its true strength to be $\hat{s}$. Note the dominant might also be provoked into displaying by the subordinate, but for simplicity, we assume in this model that the subordinate is a passive receiver of signals only. Furthermore, unlike the threat signaling models of Adams and Mesterton-Gibbons (1995), in this model, we do not allow for bluffing by dominants. The honesty of dominant threat signals can be ensured if the primary cost of displays is punishment for dishonesty (Lachmann et al. 2001) or an increased probability of provoking an escalated fight (Szamado 2008).

The effect of the dominant's signal is to collapse the variance of the subordinate's belief function to zero or close to zero. If $\hat{s}$ lies above the threshold for challenging $s^*(t)$, the aggressive signal serves to deter a challenge from the subordinate (Figure 1b). Conversely, if $\hat{s}$ lies below the threshold $s^*(t)$, signaling serves to attract a challenge from a subordinate who may otherwise have remained peaceable. Deterrent signaling can thus stabilize or destabilize hierarchies, depending on the dominant's strength relative to the subordinate's threshold for challenging, which in turn depends on the subordinate's own strength and the costs and benefits of challenging.

What should happen to the subordinate's belief function over time (denoted T)? If strength is constant and subject to no stochastic influences at all, then a strong dominant would need to display once and once only to deter the subordinate forever (i.e., $b(s) = \hat{s}$ for $T = 0, 1, 2 \ldots \infty$). However, whenever strength fluctuates over time due to intrinsic or extrinsic stochastic factors, then it would be maladaptive for the subordinate to believe that dominant strength is $\hat{s}$ forever. Rather, a subordinate behaving optimally should allow their belief function to spread over time. This optimal spreading need not be symmetrical: where stronger individuals are of higher quality, have more resources, and are protected from harmful extrinsic insults, strong individuals are likely to get stronger rather than weaker over time, and the belief function $b(s)$ should spread asymmetrically over time with negative skew. Where there are physiological upper limits on strength, or strength reliably declines over time, $b(s)$ should spread with positive skew. In Figure 1c,d, we illustrate a putative optimal rate of the spread of the belief function over time, in which $b(s)$ reverts progressively to the population distribution of strengths $f(s)$, and hence the probability that a given challenge will be profitable increases over time.

If this spread in the belief function is not checked, enough of the distribution $b(s)$ may fall below the threshold $s^*(t)$ to make challenging profitable for the subordinate. To maintain the deterrent effect of an aggressive signal, a dominant will need to update its signal regularly to deter the subordinate from challenging. In effect, the dominant "buys time" by engaging in a costly display that collapses

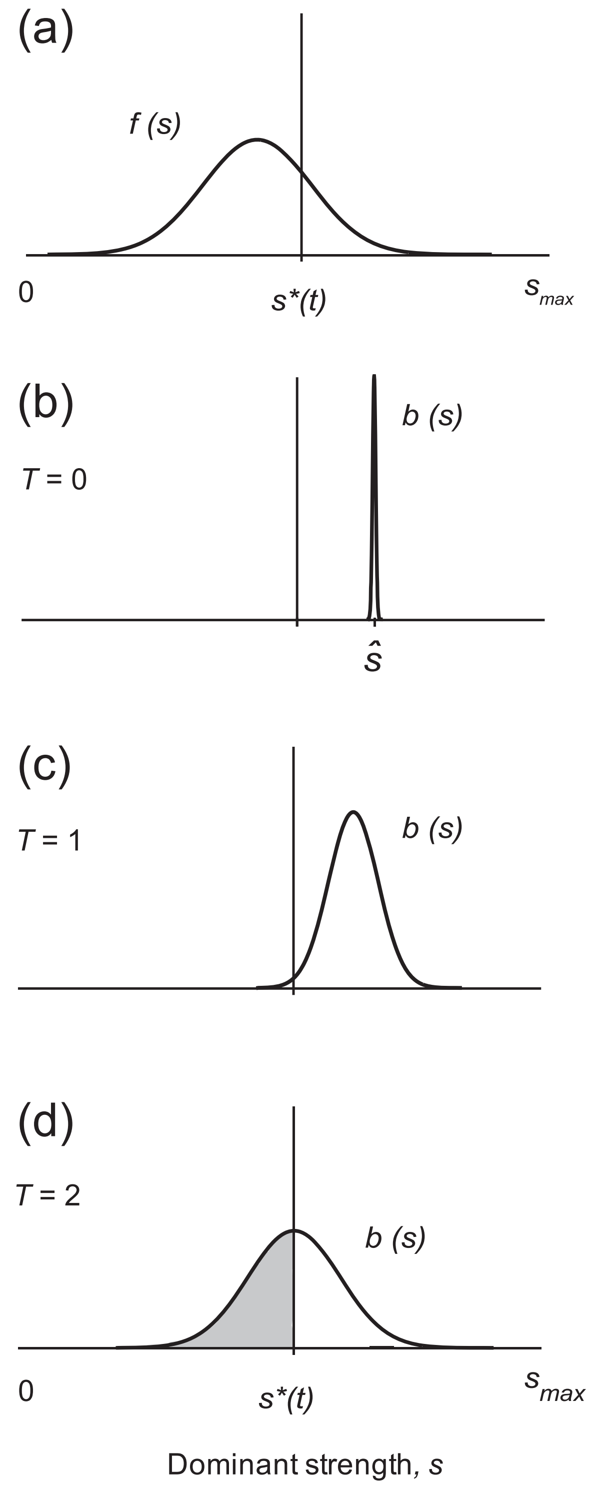

Figure 1
A graphical model of deterrent signaling. (a) Distribution of dominant strengths in the population $f(s)$ and the threshold dominant strength $s^*(t)$ below which challenging would be profitable for the subordinate, if she had access to this information; (b) the subordinate's "belief function" ($b(s)$) given that, at time $T = 0$, the dominant gives an honest signal that reveals that she is of true strength $\hat{s}$. Because $\hat{s} > s^*(t)$, this signal deters the subordinate from challenging; (c) and (d): if strength varies stochastically over time, the subordinate's belief function is expected to spread over time. In the example shown, we assume that the belief function reverts toward the distribution of dominant strengths in the population $f(s)$ as time progresses.

the subordinate's belief function to $\hat{s}$. Selection acting on subordinate social memory can explain why dominant individuals could gain from initiating aggressive interactions to keep their signal updated.

On the basis of the above arguments (and the formal arguments in the Appendix), we make the following predictions about the pattern and frequency of aggression: 1) dominants will display more frequently to stronger subordinates (because the threshold for challenging $s^*(t)$ will be higher for stronger subordinates); 2) dominants will display more frequently in more valuable or productive groups (because this will increase the payoff of challenging, and hence increases the threshold $s^*(t)$); and 3) denying dominants the opportunity to update their signal will increase the probability that subordinates challenge for dominance because in this case, a larger fraction of the subordinate's function will fall below the threshold $s^*(t)$. Predictions 1 and 2 are identical to the predictions of a model based on static costs and benefits of challenging versus accepting subordinate status (Cant et al. 2006b). We tested these 2 predictions by inducing fights over dominance rank experimentally using a method we have employed in previous studies (Cant et al. 2006a). Prediction 3 is specific to the model presented above in which we incorporate a time dimension and make assumptions about how selection acts on receiver memory. To test this latter prediction, we used a design in which we manipulated the opportunity for social interaction between dominant individuals and subordinate challengers, prior to inducing a fight.

METHODS

At our study population in southern Spain (Conil de la Frontera, Cadiz, 36°15′N, 06°10′W), foundresses form groups in early spring and build nests on hedges of *Opuntia* cactus. All our observations and experiments were conducted in March–April 2011 during the founding phase of the nesting cycle, before the emergence of workers (Cant et al. 2006a, 2006b).

Within each cofoundress group, there is a strict dominance hierarchy in which the dominant or rank 1 foundress lays most of the eggs and lower ranked "subordinates" (i.e., wasps at ranks 2 to N) do most of the foraging (Reeve 1991). Rank 2 subordinates can inherit the nest by outliving the dominant (Cant and Field 2001) or by successfully challenging for the position at the top of the hierarchy (Reeve 1991; Cant and Field 2001; Cant et al. 2006a; Leadbeater et al. 2010). Low-level social aggression is common in this population, occurring almost exclusively between individuals of immediate adjacent rank in the queue to inherit dominant status and with increasing intensity toward the top of the hierarchy (Cant et al. 2006b). Group size is very strongly correlated with cell number and productivity and so can be used as an index of the reproductive value of the contested dominant position (Cant et al. 2006b). Five types of aggressive behavior were classed as instances of low-level social aggression: "lunges," a quick darting movement culminating in physical contact; "grapples," whereby the dominant grasps another and pushes it, forcing it backward; "mounts," whereby the dominant climbs onto the body of another, who adopts a still, crouched position; "chases," where the dominant chases the recipient round the nest; and "bites," where the dominant chews the legs or other body parts of the recipient (Pfennig et al. 1983; Reeve and Nonacs 1992; Nonacs et al. 2004; Cant et al. 2006b).

We tested predictions 1 and 2 by videoing aggressive interactions and then provoking escalated contests over dominant status by temporarily removing dominant wasps. From previous work (Cant et al. 2006a; Leadbeater et al. 2010), we know that removing the dominant for 5–10 days, allowing the rank 2 wasp to inherit, and then returning the original dominant foundress results in an escalated fight for control of the nest in about 50% of cases (Cant et al. 2006a). The returning dominant foundress is always prepared to fight if the rank 2 does not immediately submit, and the original dominant is almost always successful in winning back her position (Cant et al. 2006a; Leadbeater et al. 2010). Hence, the decision to fight or not, and how long to fight before submitting, is made by the rank 2. We tested whether the aggression rate of dominant individuals toward rank 2 individuals prior to their removal predicted the probability that rank 2s would fight the returning dominant and the duration of these fights. We also tested whether the aggression rate of rank 2s after they were promoted to rank 1 was correlated with the rate of aggression they received from the dominant prior to the removal. The outcome of these tests allowed us to evaluate the predicted effect of fighting ability, which is otherwise difficult to measure because body size is not a good predictor of aggression or success in escalated contests in this population (Cant et al. 2006a, 2006b). Finally, we tested prediction 3 by allowing a subset of dominants to return to the nest for 4–16 h midway through the removal period, before removing them again. The design of the experiment is illustrated in Figure 2.

Identifying dominance ranks

We marked wasps and determined group membership by visiting nests early in the morning (ca. 0700 h), when it was too cold for the wasps to fly. Each wasp was measured and marked with small spots of colored enamel paint on the thorax following the methods employed in previous studies (Cant and Field 2001; Cant et al. 2006a, 2006b; Leadbeater et al. 2010; Leadbeater et al. 2011). Wasps were then released back to their nest and repeated censuses were conducted on sunny days to identify the dominant wasp on each nest (mean number of censuses = 22, range: 8–53 censuses, *N* = 24 nests; mean ± standard error [SE] time between censuses = 65 ± 5.1 min). Following previous studies (Cant and Field 2001; Cant et al. 2006b), we classed the dominant individual as the wasp that was present on the nest for more than 70% of daytime censuses (mean time on nest of dominants ± SE = 91.5 ± 1.77%, *N* = 24). On nests where there was more than 1 individual that met this criterion, we continued censusing until at least 3 censuses separated the dominant and the next most present individual (Leadbeater et al. 2010). These methods identified a single dominant on 18 out of 24 nests. For the remaining 6 nests, a video recording of behavior was observed (mean length of video: 2 h) to score the number of aggressive interactions between the most present wasps. We then classified the dominant wasp as the individual who initiated the most aggressive acts (Bridge and Field 2007). Group size (for use as an explanatory term in statistical analyses) was taken as the number of individuals observed more than once during censusing (median group size = 7; range: 2–11, *N* = 24). Shade temperature was recorded using Tinytag Transit 2 data loggers (Alana Ecology Ltd, Totnes, UK, www.nhbs.com) every 15 min throughout the experimental period.

Once the dominant wasp had been identified, we collected her in a tube and stored her in a refrigerator at 5 °C. The nest was then repeatedly censused for 3–5 days (mean = 10.5 ± 1.2 censuses) to identify which individual inherited the dominant position (i.e., which was the rank 2 wasp). As in previous studies (Cant et al. 2006a, 2006b), a single foundress increased her time on the nest following the removal of the dominant and was classed as the rank 2. For these newly promoted rank 2 wasps, the mean time on the nest was 82.43% (± 5.51%, *N* = 24) after promotion to rank 1, compared with 64.05% (± 4.60%, *N* = 24) when at rank 2. The rank 2 was confirmed from videos of the dominant's return because she is the first to engage with the returning rank 1 (Leadbeater et al. 2010).

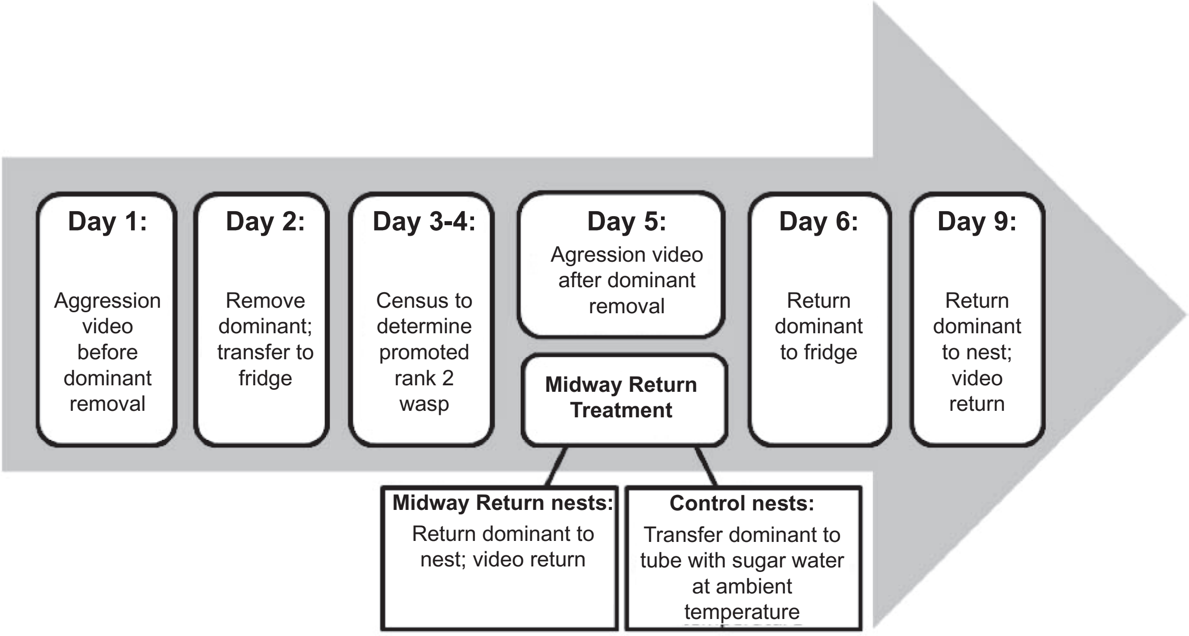

Figure 2
Schematic showing timing of video recordings, removal of dominant wasps, and returns.

Measuring aggression

Prior to the removal of the dominant, we videoed each nest for 3 h on a warm day (shade temperature range: 18–28 °C) between 1145 and 1745 h. Behavior was scored from a randomly selected 90-min segment of the videos. We recorded the number of aggressive interactions initiated by the dominant toward other group members and to the rank 2 specifically (as identified later following dominant removal). Aggressive interactions were classed as lunges, grapples, mounts, chases, and bites and given equal weight. The number of wasps present on the nest was counted every 5 min, and all departures and arrivals were recorded so that we could calculate the number of minutes that the dominant and the rank 2 were together on the nest. As in Cant et al. (2006b), we calculated a "dyadic aggression rate" for the dominant as the number of aggressive acts initiated per minute, for the period that the pair were both present on the nest. The "per capita aggression rate" from the dominant was also calculated as the total number of aggressive interactions initiated by the dominant per minute, per capita, with the per capita term calculated from the mean number of wasps present in 5-min scans in the recording period (mean ± SE number of wasps present during videoing = 3.91 ± 0.24, $N = 22$).

Three to 5 days after the initial removal of the dominant wasp, each nest was videoed again (Figure 2) for a continuous 2-h period on a warm day (shade temperature range: 16–26 °C) between 1100 and 1715 h. We analyzed an average of 86 min (range: 71–90 min) of these second videos per nest to score the number of aggressive interactions initiated by the promoted rank 2 wasp toward other individuals. We measured the per capita aggression rate of the promoted rank 2 wasp using the same method as for the dominant wasp in the first round of videos (mean ± SE number of wasps present during videoing = 3.49 ± 0.28, $N = 22$).

Removing the dominant to induce escalated contests

The morning after the first round of videos we removed the rank 1 wasp and transferred her to a clear tube with a perforated cap. The tube was then stored in a refrigerator at 5 °C for a period of 3–5 days. This temperature is several degrees above the minimum overnight temperature at the site in early spring (minimum March–April temperature in Conil 0 °C; www.meoweather.com), and wasps in the fridge became immobile in the same way as overwintering wasps and those on the nest at night. Of the 24 removed dominants, we matched pairs of wasps for group size and then randomly assigned 1 wasp from each pair to "Treatment" (T) and "Control" (C) groups. Both Treatment and Control wasps were removed from the fridge after 3–5 days and allowed to warm to ambient temperature. Treatment wasps were released approximately 1 m from their nest on a warm afternoon (between 1345 and 1545) after 3–5 days (depending on the weather) and allowed to reestablish their position. The nest was videoed to record the return of the dominant (median time from release to return = 15 min 33 s, range: 21 s–39 min 07 s, $N = 12$) and the duration of any subsequent aggressive activity. At either 1800 (3 nests) or 0700 the next morning (9 nests), we recaptured the rank 1 and placed her back in the fridge. Foundresses are usually inactive between 1800 and 0800, so we estimate that the rank 1 and rank 2 had 2–4 h to interact behaviorally before we collected the rank 1 wasp. Control wasps were given a drop of 50% sugar water and kept in their tube at ambient temperature for the same period before being transferred to a new tube and returned to the fridge. Thus, T dominants had the opportunity to update their signals, whereas C dominants did not.

After a further 3–8 days (depending on weather conditions), all rank 1 wasps in storage were released back to the nest between 1130 and 1615 h on a warm sunny afternoon (shade temperature range: 17–27.5 °C) (Figure 2). Nests were again videoed to record the return of the dominant (median time from release to return = 24 min, range: <1 to 82 min) and any subsequent aggressive activity.

Each time a rank 1 wasp was released back to the nest we videoed her return and recorded the occurrence and duration of escalated contests with the rank 2. Following Cant et al. (2006a) and Leadbeater et al. (2010), a contest was defined for the purposes of analysis as "escalated" if the interaction lasted longer than 4 s. In practice, escalated contests over rank are conspicuous and easily distinguishable from low-level social aggression: The contestants engage in prolonged and intense grappling, which sometimes progresses to a "falling fight" whereby the 2 wasps lock hold of one another and fall from the nest in an attempt to deliver a fatal sting (Cant et al. 2006a; Leadbeater et al. 2010 See the Supplementary video at http://www.beheco.oxfordjournals.org/ for a typical escalated fight between a returning dominant and a rank 2 wasp). The contest was deemed to have ended once an individual was observed to submit to the other by lowering her antennae and allowing the winner to mount and antennate her. The duration of escalated contests was timed from the videos using a stopwatch.

Statistical analyses

Statistical analyses were performed using R Version 3.0.2 (R Development Core Team 2010). In analyses concerning the probability of an escalated contest ($N = 24$), generalized linear mixed models (GLMMs) were fitted using lmer in the lme4 R package, assuming a binomial error structure and a logit link function to account for the binary nature of the response variable (escalated vs. non escalated). We fitted the date of the final release back to the nest as a random effect, and treatment (T or C), the total number of days that the rank 1 was away from the nest, median group size, and the rank 1's dyadic aggression rate to the rank 2 (prior to removal) as explanatory terms.

To analyze the relationship between aggression received by the rank 2 and her own aggression rate following promotion to rank 1, we used a GLMM with the date of the video recording fitted as a random effect. The rank 2's aggression rate was modeled as a count of aggressive acts initiated by the rank 2 using a log link function and Poisson errors, with the $\log_e$ of "wasp minutes" as an offset, equivalent to "exposure" in Poisson regression models (Scott Long 1997; Crawley 2007). The offset "wasp minutes" was calculated as [number of minutes the rank 2 was observed with other foundresses present] multiplied by [mean number of other wasps present during the video]. We fitted the original rank 1's dyadic rate of aggression to the rank 2, the number of days the dominant wasp was away up to the date of midway treatment, and median group size (as a continuous variable) as explanatory terms. In each analysis, the maximal model was fitted and least significant terms were dropped sequentially until further removal resulted in a significant change in residual variance ($P < 0.05$), as determined from χ^2 values. This process was continued until the minimum adequate model (that containing only significant variables) was achieved. Model plots of minimum adequate models were produced to ensure models met the assumptions of normality of errors and homogeneity of variance across values of the explanatory variables. For presentational

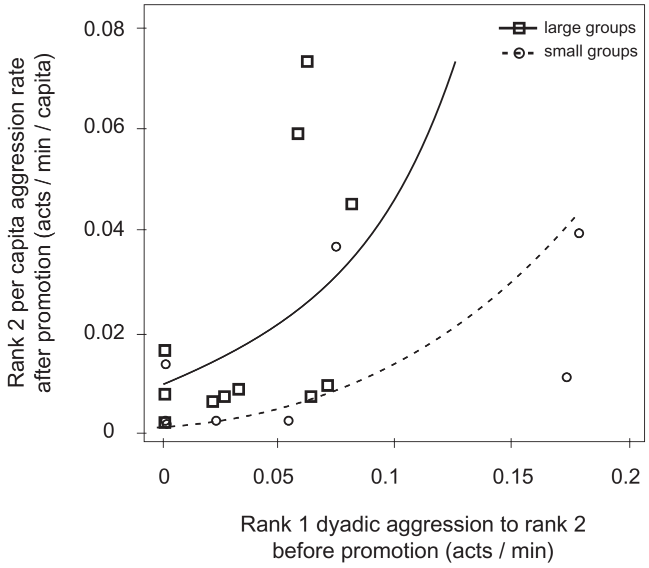

Figure 3
Patterns of aggression before and after the removal of the rank 1. Per capita aggression rate of rank 2s (acts per minute per capita) after they were promoted is plotted against the rate at which they received aggression from the rank 1 wasp ("dyadic aggression rate") before promotion. Lines show predicted means from a GLMM, split into large (>median) and small (<median) group size categories (*N* = 11 nests in each category).

purposes (Figure 3), we also split groups into large and small categories depending on whether they were larger or smaller than the median group size (7 individuals). Four groups of median group size were randomly assigned to small or large categories by flipping a coin. Qualitatively, identical results were obtained regardless of how these 4 groups were allocated between size categories. Five nests had zero rates of aggression before and after the dominant removal. To check whether multiple zero–zero points had undue leverage, we reran the analysis with a single randomly chosen zero–zero point and again obtained qualitatively identical results from this reduced sample.

RESULTS

Do dominants display more frequently to stronger subordinates?

The great majority of aggressive acts by dominant wasps were directed at the rank 2 wasp, that is, the wasp that subsequently inherited the nest. The mean ± SE rate of aggression from the rank 1 to the rank 2 wasp (i.e., the "dyadic aggression rate" of the dominant) was 0.0433 ± 0.011, which was almost 4 times the mean rate of aggression from the rank 1 toward other individuals on the nest (per capita aggression rate to other ranks: 0.0130 ± 0.003; paired *t*-test, $t_{23} = 2.71$, $P = 0.013$). Interestingly, rank 2 wasps that were subject to higher rates of dyadic aggression were subsequently more aggressive themselves when they inherited the rank 1 position (GLMM: $\chi^2_1 = 19.56$, $P < 0.0001$; Table 1; Figure 3). This result held when group size was treated as a categorical variable, greater or less than the median group size of 7 (GLMM: rank 2 dyadic aggression, $\chi^2_1 = 27.76$, $P < 0.0001$; Figure 3), and after removing 4 nests that had zero aggression values before and after promotion of the rank 2 (GLMM: dyadic aggression: $\chi^2_1 = 13.05$, $P < 0.001$). Rank 2s that received more aggression from the dominant were also more likely to fight her when she was returned to the nest at the end of the removal period (GLMM, $\chi^2_1 = 4.84$, $P = 0.028$; Table 2). Thus, dominants were more aggressive to 1) subordinates that themselves became more aggressive after promotion and 2) subordinates that were more likely to fight the returning dominant.

Table 1
GLMM of factors affecting the promoted rank 2's rate of aggression

Explanatory variable	χ^2	*P*
Dyadic rate of aggression, rank 1 to rank 2	19.56	<0.0001
Group size	3.38	0.066
Number of days dominant away	1.23	0.27

The date of the video of the rank 2's rate of aggression was included as a random effect in the model.

Table 2
GLMM of factors affecting the probability of an escalated contest occurring on the return of the original dominant at the end of the experimental period

Explanatory variable	χ^2	*P*
Treatment (midway return vs. control)	8.28	0.004
Dyadic rate of aggression, rank 1 to rank 2	4.84	0.028
Group size	1.39	0.24
Total number of days away	0.17	0.68

The date of the original dominant's final return to the nest was included as a random effect in the model.

Do dominants display more frequently in larger groups?

Rank 2 wasps in larger groups were more aggressive to their subordinates, per capita, after promotion to the dominant position, although the statistical effect of group size was borderline (GLMM: group size, $\chi^2_1 = 3.38$, $P = 0.066$; Table 1). However, we found no significant effect of group size on the dyadic or per capita rates of aggression of dominants prior to removal (dominant dyadic aggression: GLMM, $\chi^2_1 = 1.62$, $P = 0.20$; per capita aggression: GLMM, $\chi^2_1 = 0.92$, $P = 0.34$). Thus, we found some support for prediction 2 in recently disturbed hierarchies but not in established hierarchies. Contrary to a previous study on this population (Cant et al. 2006a), we found that the promoted rank 2 wasp was not more aggressive than the original dominant before her removal: Specifically, there was no significant difference in the total rate of aggression by the original dominant and the total rate of aggression by the promoted rank 2 wasp (paired *t*-test, $t_{21} = 0.702$, $P = 0.490$).

Does denying dominants the opportunity to update their signal increase the probability that subordinates challenge for dominance?

Dominant and promoted rank 2 wasps engaged in an escalated contest following the return of the original dominant at the end of the experimental period on 11 out of 24 nests, and in 3 cases, the rank 2 won the fight. Rank 2 wasps that had had the opportunity to interact socially with the dominant midway through the removal period were less likely to fight the dominant when she was finally released back to the nest (GLMM, $\chi^2_1 = 8.28$, $P = 0.004$; Table 2; Figure 4), and those fights that did ensue were of shorter duration compared with fights on control nests (LMM using

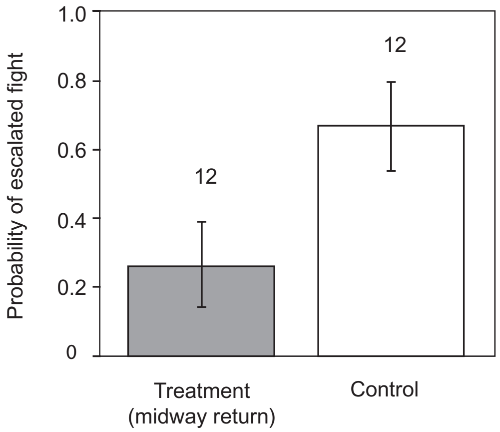

Figure 4
Results of the updating experiment. The columns show the probability of an escalated fight occurring at the end of the removal period on control nests versus treatment nests in which dominants interacted with the promoted rank 2 midway through the removal period. Columns show means ± SE; sample size equals 12 nests in each category.

log-transformed data, $L_1 = 5.45$, $P = 0.0196$), as predicted from our model. Although sample sizes were small, there was no relationship between the duration of contests midway through and at the end of the removal period (paired *t*-test, $t_3 = 1.17$, $P = 0.328$), suggesting that fights midway through the removal period did not lead to lasting injury or damage to either wasp.

DISCUSSION

Our study supports our hypothesis that aggression by dominant *P. dominulus* foundresses functions, in major part, as a deterrent signal. As in a previous study (Cant et al. 2006b), dominant females directed most of their aggression to the individual next in line to inherit the rank 1 position. Dominant females were more aggressive to subordinates that were subsequently more likely to fight them for the rank 1 position, as expected if it requires more aggression to deter a stronger subordinate from challenging. Finally, denying dominant and subordinate the opportunity to engage in aggression had a destabilizing effect on the hierarchy. Although overt aggression is often taken as a sign of unsettled or unstable social relationships (Cant and Johnstone 2000), our results suggest that aggressive dominance displays may in fact help to maintain the peace and stability of social hierarchies.

Allowing the original dominant to interact with the promoted rank 2 midway through the removal period reduced the probability of escalated fighting at the end of the removal period. This result fits with our hypothesis that, in the absence of any signals from the dominant, subordinates should grow increasingly uncertain about relative strength over time. It is important to recognize the limitation of our experimental design here and possible alternative explanations for this result. It may be, for example, that social interaction refreshes information about the dominant's identity rather than strength or simply signals to the subordinate that the dominant is still alive. Reintroducing the dominant might interfere with or reset a process of physiological change in subordinates that have recently inherited the dominant position, making them less inclined to later fight the returning dominant for control of the nest. These are plausible alternative hypotheses about the proximate mechanism that governs the decision to fight, but our qualitative arguments concerning changes in receiver belief or the need to update signals to deter subordinate challenges should still hold. For example, we could redraw Figure 1 with values of some trait related to identity scaled on the *x* axis (e.g., the degree of facial badge blackness or "brokenness," Tibbetts and Dale 2004; or cuticular hydrocarbon profile, Sledge et al. 2001) or augment our model with an assumption about the physiological process involved in becoming dominant. However, the fact that dominants are most aggressive to those subordinates that are most likely to challenge their position lends support to our assumption that aggression by dominants conveys information about strength or the net benefits of challenging for dominance, not merely identity.

Rank 2 wasps in larger, more productive groups were more aggressive after promotion, as expected if these wasps need to signal more intensely to establish their dominance on more valuable nests. However, in neither this study nor a previous one (Cant et al. 2006b) did we find an effect of group size on the aggression rates of established dominant females (i.e., prior to the dominant removal experiment), or on the probability of escalated fighting. Thus, the relationship between group size and aggression is not straightforward, and aggression may be used differently by established versus newly promoted dominants. In *P. dominulus*, the polistine wasp *Ropalidia marginata* (Chandrashekara and Gadagkar 1992; Lamba et al. 2007), the ponerine ant *Dinoponera quadriceps* (Monnin and Peeters 1999), and group-living fish *Neolamprologus pulcher* (Wong and Balshine 2010), newly promoted dominants are most aggressive in the first few days after promotion and less aggressive when their position is established. These results may indicate that the information content or meaning of aggressive signals has a cumulative component, so that after an initial phase of high aggression, a dominant is able to cement and maintain its social status at a lower signaling cost.

A particularly interesting result was the strong positive relationship between the aggression rates of the original dominant and the replacement dominant. Rank 2s that received high rates of aggression from the original rank 1 went on to exhibit high rates of aggression toward their subordinates after they were promoted. This pattern might conceivably arise if the aggression rate of dominants and subordinates are not causally linked but instead correlate with some feature of the nest or group. For example, the pattern may arise because some nests are intrinsically more valuable than others or because some dominant–subordinate pairs were more closely related than others. However, in a study of 72 nests, Leadbeater et al. (2010) found no difference in aggression rate or the probability of fighting in groups of relatives compared with groups that contained unrelated foundresses. Nor does nest size or stage of larval development (controlling for date in the season) influence aggression rates (Cant et al. 2006b). Thus, there are no obvious or readily detectable features of nests or individuals, which can explain why the aggression rates of rank 2s after promotion should correlate strongly with the rate at which they received aggression from the rank 1 before promotion. Two other possibilities are 1) that rank 1 and rank 2 individuals assort by strength or quality, so that strong challengers tend to be paired with strong dominants, and this is reflected in the rate at which they both display aggressively and 2) that rank 2 aggressive behavior is shaped by their experience of observing, or being subjected to, the aggressive behavior of their dominant. To test these hypotheses would require an experiment to tease out the causal effect of receiving aggression on future aggressive behavior. For example, aggression in a dominant individual might potentially be upregulated by treatment with hormones (e.g., juvenile hormone; Barth et al. 1975) or neurostimulants (e.g., cocaine; Barron et al. 2009).

Finally, our study raises the broader question of how individual or trait recognition systems cope when phenotypes change stochastically or progressively over time. Laboratory studies of *Polistes fuscatus* aggression show that foundress paper wasps have the capacity to form social memories of individual identity that last over a week and use these memories to avoid repeat escalated fights in repeat encounters (Sheehan and Tibbetts 2008). Our results suggest that similar long-term memories exist in natural social hierarchies of *P. dominulus* (contrary to the findings of Sheehan and Tibbetts 2008 and Tibbetts and Sheehan 2013 working on laboratory colonies). However, our data suggest that there are limits to the robustness of these memories: Memories of strength (or identity) deteriorate over time. Because the neural and physiological processes required to maintain pristine memories are likely to be costly (Dukas 1999; Mery and Kawecki 2005), selection acting on receiver psychology should allow the forgetting of cues when these become unreliable as indicators of underlying state. Thus, receivers should forget cues more rapidly where phenotypes are stochastically more variable in time. McNamara and Houston (1987) make a similar argument about the influence of environmental stochasticity on optimal nonsocial memory.

Where phenotypes change in a predictable or progressive manner, receiver memory systems could conceivably cope by progressively adjusting the templates against which phenotypes are matched. In Figure 1, for example, the subordinate's belief function is plotted on the assumption that dominant strength reverts to the mean in the long term. If, by contrast, dominant individuals are likely to grow stronger over time because of superior access to food, or lower exposure to parasites, the subordinate's belief function would spread with negative (i.e., left) skew, and dominants would need to signal much less frequently than is the case in Figure 1. The testable predictions are that aggressive signaling will be most frequent where strength is variable and deteriorates with time. For paper wasps, geographic variation between populations (Tibbetts et al. 2011) in ecological stochasticity, parasitism, season length, or rates of senescence could be used to test these predictions.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

FUNDING

The study was funded by the Royal Society and the Natural Environment Research Council of the UK.

We are grateful to David Hodgson for statistical advice and to Luke Holman and 2 anonymous referees for comments on the manuscript.

APPENDIX

PAYOFFS OF CHALLENGING UNDER UNCERTAINTY

To derive the model in more formal terms, consider a dominant and a single subordinate who are related (symmetrically) by coefficient r. Let v be the value of the resource; and c_w and c_l be the cost of fighting to the winner or loser of fight, respectively (both assumed $< v$). The subordinate's probability of winning an escalated conflict with the dominant is denoted p. Challenging is profitable for the subordinate when the following inequality is satisfied:

$$p(v - c_w - rc_l) + (1 - p)(-c_l + rv - rc_w) > rv \tag{A1}$$

The left hand side of (A1) is the inclusive fitness payoff of challenging; the right hand side is the inclusive fitness payoff of accepting the status quo. For simplicity, assume that the stronger player always wins the fight, that is, $p = 0$ for $t < s$, and $p = 1$ for $t > s$. Thus, in this case, the critical dominant strength below which challenging is profitable ($s^*(t)$ in the graphical model) is equal to t. Qualitatively identical results are obtained if we instead assume that p is a smoothly increasing function of t (e.g., $p = zt/(zt + s)$, where z would allow for a rank-specific asymmetry in the probability of winning). We further assume that $t \neq s$ (so there are no ties), and we set the strength of the weakest member of the population to zero. If the subordinate has no information about the strength of the dominant, the probability of winning and losing are given by

$$p = \int_0^t f(s)\mathrm{d}s \tag{A2}$$

$$1 - p = \int_t^{s_{\max}} f(s)\mathrm{d}s \tag{A3}$$

where $f(s)$ is the distribution of dominant strengths in the population.

If the subordinate has some information about dominant strength, for example, because the dominant has recently given an honest signal, the decision to challenge will depend on the subordinate's belief function $b(s)$, which itself may vary with time elapsed since the last signal T. (e.g., panels b–d of Figure 1). Substituting $b(s)$ for $f(s)$ in (A2) and (A3), we can substitute into (A1), convert to an equality, and rearrange to obtain the following expression for the subordinate's inclusive fitness payoff of challenging:

$$W_{\text{sub}} = (v - c_w - rc_l)\int_0^t b(s)\mathrm{d}s + (-c_l + rv - rc_w)\int_t^{s_{\max}} b(s)\mathrm{d}s - rv$$

or (A4)

$$W_{\text{sub}} = (v - c_w - rc_l)B(t,T) + (-c_l + rv - rc_w)(B(s_{\max},T) - B(t,T)) - rv$$

where $B(s,T)$ is the cumulative distribution of $b(s)$ at time T, that is, the fraction of the distribution $b(s)$ that lies below the threshold for challenging ($s^*(t) = t$) at time T. In the graphical model, we assume that $B(t,T)$ (represented by the shaded area in Figure 1d) is an increasing function of T.

The subordinate will be selected to challenge where $W_{\text{sub}} > 0$. Rearranging (A4), taking $B(s_{\max},T) = 1$, and simplifying, we can write this condition as

$$B(t,T) > \frac{c_l + rc_w}{(1 - r)(c_l - c_w + v)} \tag{A5}$$

We can now readily derive the 3 predictions tested in the paper. Prediction 1 (that dominants will display more frequently to stronger subordinates) follows because of the assumption that $\partial B(t,T)/\partial T > 0$. Because $\partial B(t,T)/\partial t > 0$ by definition (because B is a cumulative probability distribution), increasing t reduces the time T, which needs to elapse before inequality (A5) is satisfied. Prediction 2 (that dominants will display more frequently in larger, more valuable groups) follows because increasing v reduces the right hand side of inequality (A5). Prediction 3 derives directly from the assumption that $\partial B(t,T)/\partial T > 0$, so condition (A5) is more likely to be satisfied the longer the period T since the subordinate last received a signal from the dominant.

Finally, the model predicts that increasing relatedness will reduce the frequency with which dominant individuals display because the right hand side of (A5) is an increasing function of r. Note that in our paper wasp system, around 25% of groups contain foundresses that are unrelated to the dominant wasp (Leadbeater et al. 2010). However, we did not expect relatedness to influence the outcome of our experiments because neither aggression (Leadbeater et al. 2010) nor the probability of an escalated contest in response to dominant removal (Cant et al. 2006a) vary with relatedness.

Handling editor: Alexei Maklakov

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