Victory displays: a game-theoretic analysis

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Two rationales have been proposed verbally for the function of victory displays, which are performed by the winners of contests but not by the losers. The “advertising” rationale is that victory displays are attempts to communicate victory to other members of a social group that do not pay attention to contests or cannot otherwise identify the winner. The “browbeating” rationale is that victory displays are attempts to decrease the probability that the loser of a contest will initiate a future contest with the same individual. We formally explore the logic of these rationales with game-theoretic models. The models show that both rationales are logically sound; however, all other things being equal, the intensity of victory displays will be highest through advertising in groups where the reproductive advantage of dominance is low and highest through browbeating in groups where the reproductive advantage of dominance is high. Key words: bystander effects, game theory, signaling, victory displays. [Behav Ecol 17:597–605 (2006)]

Although victory displays, ranging from sporting laps of honor to military parades, are well known in human societies, a variety of other animals are believed to exhibit post-conflict signaling; for a comprehensive review, see Bower (2005). For example, Graf and Bitz (2004) simulated intrusions into the territories of the African bird, the tropical bou-bou (Laniarius aethiopicus), and found that the majority of pairs that remained on their territories sang a characteristic duet after the encounter had ended; it was not sung by pairs that retreated. Similarly, “triumph ceremonies” have long been reported in a number of species of waterfowl (Heinroth 1910; Wachtmeister 2001). In the greylag goose (Anser anser), for instance, males voca-lize loudly after a successful attack on another individual in the flock and engage in pressed cackles on returning to their family group (Lorenz 1966). Additional examples include male green tree frogs, Rana clamitans, that have been reported to splash the water when pursuing their opponents after wrestling bouts (Wells 1978) and male New Zealand tree wetas, Hemideina crassidens (Orthoptera), that were the last to stridulate after winning aggressive encounters (Field and Rind 1992). Also, chemical signals communicating dominance, such as those observed in crayfish species (Zulandt Schnider et al. 1999; Bergman, Kozlowski, et al. 2005), tend to be produced more frequently by winners than losers (Breithaupt and Eger 2002; Bergman, Martin, and Moore 2005) and may therefore conceivably play a role in communicating victory.

Bower (2005) defines a victory display as a display performed by the winner of a contest but not by the loser. He offers in essence 2 possible explanations of their function: that they are an attempt to advertise victory to other members of a social group that do not pay attention to contests or cannot otherwise identify the winner and thus alter their behavior (“function within the network”) or that they are an attempt to decrease the probability that the loser of a contest will initiate a new contest (“function within the dyad”). We explore these rationales by building models. The first is called Model A (for advertising) and the second is Model B (for browbeating).

In either case, for tractability, we assume that a population is subdivided into triads, the smallest groups in which it is possible to compare the network and dyad rationales. For simplicity and because we want to study victory displays in their purest form, in isolation from other effects, we assume no variation in strength. It is therefore consistent to assume that a fight—if there is one—lasts for a fixed amount of time, with each contestant paying the same fixed cost. By contrast, postcontest costs differ if winner and loser because a winner displays whereas a loser does not. There is also a basic benefit that accrues to each individual for belonging to the group, regardless of its status within it; but because this term is constant for every outcome, it has no strategic effect, and so we can proceed as though it were 0.

Within any animal group, benefits beyond the basic level are determined by relative status. If there were always a linear dominance hierarchy, then rank would be a sufficient measure of status. But linear dominance hierarchies need not form: inconclusive contests are quite common (Jennings et al. 2005). Consider, for example, a triad of animals A, B, and C in which A defeats and dominates B and B defeats and dominates C; however, A does not dominate C and C does not dominate A because their contest was inconclusive. We cannot say that they share rank because there is no linear hierarchy. On the other hand, few would disagree that A has the highest status within this group and that C has the least, just as if there were a linear hierarchy with A on top and C on the bottom; but whereas the status of B may be about the same as if there were such a hierarchy, that of A is lower and that of C is higher. In essence, therefore, status is determined by a combination of dominance and what we shall refer to as “nonsubordination.” A contest outcome is one of dominance if one individual subordinates to the other, whereas the second does not, and a contest outcome is one of nonsubordination if either each “defers”—concedes dominance—to the other (as is possible only in Model A) or else neither defers to the other (as is possible only in Model B).

To capture the idea that dominance contributes more to fitness than nonsubordination, which in turn contributes more than being dominated, for each individual, let fitness increase (beyond the basic level) by \( \alpha \) for every individual it dominates and by \( \beta x \) for every individual that it fails to dominate that also fails to dominate it. The cumulative benefit to an individual is then \( \alpha \) times the associated number of dominances, \( \#D \), plus \( \beta x \) times the associated number of
nonsubordinations, #NS. For example, in the trial described in the preceding paragraph, the benefits accruing to A, B, and C would be \((1 + b)xz, xz, and bxz\), respectively, whereas in a linear hierarchy, they would be \(2xz, xz, and 0\). Thus, \(b\), a dimensionless parameter satisfying \(0 \leq b < 1\), is an inverse measure of the reproductive advantage of dominance, which is greatest when \(b = 0\) and least when \(b = 1\). It will be convenient to scale costs with respect to \(x\) as well. Accordingly, let \(c(x)\) be the cost of a contest and let \(c(s)x\) be the cost of displaying with intensity \(s\). Then the associated (relative) payoff is

\[ \alpha \cdot \#D + b\alpha \cdot \#NS - c(x)\alpha \cdot \#C = c(s)\alpha \cdot \#W, \]

where \#C is the number of contests and \#W is the number of wins.

**MODEL A: ADVERTISING**

We assume that all possible orders of interaction are equally likely. Let strategy \(s\) mean that an \(s\)-strategist displays with intensity \(s\). Let \(p(s)\) be the probability that a display of intensity \(s\) is observed by the noncontestant. We assume that

\[ c(0) = 0, \]

\[ c'(s) > 0, \quad p'(s) > 0, \]

and

\[ c''(s) \geq 0, \quad p''(s) < 0, \]

where a prime denotes differentiation with respect to argument; in essence, doubling the intensity of display would at least double its cost but less than double its effectiveness. There is a biological rationale for \(c''(s) > 0\); in keeping with many physiological processes involving reagents in short supply, we assume that small increases in the magnitude of low-strength signals are metabolically cheap, whereas further increases in the magnitude of high-strength signals are expensive. Conversely, with \(p''(s) > 0\), we require \(p''(s) > 0\) to ensure that \(p(s)\) does not exceed 1. Both of the focal individual’s opponents play the population strategy \(u\). Thus, a triad consists of a focal \(s\)-strategist and a pair of \(s\)-strategists.

We assume that observing the winner of a contest means indirectly observing the loser. Let the probability that an (indirectly) observed loser subsequently loses against the observer increase from \(1/2\) to \((1 + l)/2\), where \(0 \leq l \leq 1\): there is a potential “loser effect” (Dugatkin 1997; Hsu and Wolf 1999; Rutte et al. 2006) of sorts, but it kicks in only if the loser has been observed by its next opponent. Our rationale for allowing \(l > 0\) is that an individual has greater self-esteem and confidence when taking on an individual that it has observed to lose, which remains consistent with our assumption of equal fighting strengths. Let \(\lambda\) denote the probability that an animal defers to an opponent when it has observed that the opponent won against its previous opponent, where \(0 \leq \lambda \leq 1\). Then the probability that an observed winner subsequently wins against the observer increases from 1/2 to \(1 + (1 - \lambda) \cdot \frac{l}{2}\); there is a “winner effect” of sorts, but it kicks in only if the winner has been observed by its next opponent.

For greater generality, we allow the probability of deference \((\lambda)\) to an observed winner to vary with an individual’s own prior experience by using subscripts 0, 1, and 2 to denote, respectively, an untested individual, a prior loser, and a prior winner. That is, we denote the probability that an untested individual’s first opponent for a given order of interaction, and the other individual is O2.

### Table 1

<table>
<thead>
<tr>
<th>Case</th>
<th>Winners</th>
<th>Probability</th>
<th>Payoff</th>
</tr>
</thead>
<tbody>
<tr>
<td>(k)</td>
<td></td>
<td>(a_0(u, v))</td>
<td>(P_i(u))</td>
</tr>
<tr>
<td>1</td>
<td>F</td>
<td>F</td>
<td>(1/2p_F(u))</td>
</tr>
<tr>
<td>2</td>
<td>F</td>
<td>F</td>
<td>(1 - \lambda_0p_F(u))</td>
</tr>
<tr>
<td>3</td>
<td>F</td>
<td>O2</td>
<td>(1/2p_{O2}(u))</td>
</tr>
<tr>
<td>4</td>
<td>O1</td>
<td>F</td>
<td>(1 - \lambda_{O1}p_F(v))</td>
</tr>
<tr>
<td>5</td>
<td>O1</td>
<td>O2</td>
<td>(1 + \lambda_{O1}p_{O2}(v))</td>
</tr>
<tr>
<td>6</td>
<td>F</td>
<td>(O1)</td>
<td>F</td>
</tr>
<tr>
<td>7</td>
<td>F</td>
<td>(O1)</td>
<td>F</td>
</tr>
<tr>
<td>8</td>
<td>F</td>
<td>(O2)</td>
<td>F</td>
</tr>
<tr>
<td>9</td>
<td>F</td>
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<td>F/02</td>
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<tr>
<td>10</td>
<td>F</td>
<td>(O2)</td>
<td>O2</td>
</tr>
<tr>
<td>11</td>
<td>F</td>
<td>(O2)</td>
<td>O2</td>
</tr>
<tr>
<td>12</td>
<td>O1</td>
<td>(O1)</td>
<td>F</td>
</tr>
<tr>
<td>13</td>
<td>O1</td>
<td>(O1)</td>
<td>O2</td>
</tr>
<tr>
<td>14</td>
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<tr>
<td>15</td>
<td>O1</td>
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<td>18</td>
<td>O1</td>
<td>(O1)</td>
<td>O2</td>
</tr>
<tr>
<td>19</td>
<td>O1</td>
<td>(O1)</td>
<td>F/02</td>
</tr>
</tbody>
</table>

Parentheses indicate a contest in which the focal individual is not involved. A bold letter indicates that the individual’s opponent deferred after observing it win an earlier contest. Note that O1 and O2 do not label specific individuals: O1 is whichever individual happens to be the focal individual’s first opponent for a given order of interaction, and the other individual is O2.
individual, a prior loser, or a prior winner defers to an observed winner by \( \lambda_2, \lambda_3, \) or \( \lambda_2, \) respectively, where we assume that

\[
0 \leq \lambda_2 \leq \lambda_0 \leq \lambda_1 \leq 1.
\]

(5)

We also allow for a prior loser to defer to an observed loser with probability \( \lambda_3. \) However, we assume that neither an untested animal nor a prior winner ever defers to an observed loser.

We now consider each order of interaction in turn. Let us first consider the payoff to a u-strategist when it participates in the first 2 of the triad’s 3 dyadic interactions. The focal individual wins its first contest with probability \( 1/2 \) and is observed to win its second opponent with probability \( p(u). \) If the focal individual wins and has been observed, with probability \( \lambda_0, \) the opponent defers, and with probability \( 1 - \lambda_0, \) the 2 individuals engage in a fight, which they are equally likely to win. Hence the u-strategist’s probability of winning twice through a pair of fights, allowing for the possibility that its first win may not be observed, is \( \frac{1}{4} \cdot p(u) \cdot (1 - \lambda_0) + \frac{1}{4} \cdot (1 - p(u)) \cdot \frac{1}{2} = \frac{1}{4}(1 - \lambda_0)p(u); \) see Table 1, Case 1. Its probability of winning twice through a pair of fights, allowing for the possibility that its first win may not be observed, is \( \frac{1}{4} \cdot p(u) \cdot \frac{1}{2} + \frac{1}{4} \cdot (1 - p(u)) \cdot \frac{1}{2} = \frac{1}{4}(1 - \lambda_0)p(u); \) see Table 1, Case 2. In either case, the focal individual becomes the alpha individual at the top of a linear dominance hierarchy with benefit \( 2z, \) but its costs differ because in the second case it avoids the fixed cost that would have been associated with the second fight. Similarly, the probability that the focal individual comes to rest at the bottom of a linear hierarchy is the probability that it loses twice in succession. The probability that it loses the first time is simply \( 1/2. \) It is now a prior loser, and because its first opponent was a u-strategist, it has been indirectly observed to lose by its second opponent through the first opponent’s victory display with probability \( p(v), \) in which case its probability of losing again is \( (1 + I)/2. \) So the probability of losing twice is \( \frac{1}{2} \cdot p(v) \cdot \frac{1}{2} + \frac{1}{2} \cdot (1 - p(v)) \cdot \frac{1}{2} = \frac{1}{4}(1 + lp(v)); \) see Table 1, Case 5. Proceeding likewise for the other 2 outcomes, we find that the reward to a u-strategist in a population of u-strategists, conditional on participation in the first 2 contests, is

\[
f_{u}(u,v) = \frac{1}{3}f_{u}(u,v) + \frac{1}{3}f_{v}(u,v) + \frac{1}{3}f_{v}(u,v)
\]

where \( f_{u}(u,v) \) is the probability of the event defined by Case \( k \) in Table 1 and \( f_{v}(u,v) \) is the corresponding payoff to the focal individual. We handle the other 2 possible orders of interaction similarly. Suppose, for example, that the focal individual \( F \) is involved in the first and the third of the 3 contests, that it wins the first, and that its (future) second opponent \( O_2 \) wins the second contest, as in Cases 8–12 of Table 1. This event is equivalent to a double loss by \( F \)’s first opponent \( O_1, \) and its probability is therefore \( \frac{1}{2}(1 + lp(u)), \) the only difference from Case 5 above being that the winner of the first contest is a u-strategist instead of a u-strategist. The third contest is now between 2 prior winners. F has observed \( O_2 \)’s victory with probability \( p(v), \) \( O_2 \) has observed \( F \)’s victory with probability \( p(u), \) and conditional thereon, each defers to the other with probability \( \lambda_2. \) Thus, the probability of nonsubordination in the third contest is \( \lambda_2^2p(u)p(v); \) see Table 1, Case 9. The focal individual escalates if it is not the case that it has seen \( O_2 \) win and has deferred, that is, with probability \( 1 - \lambda_2p(v); \) similarly, \( O_2 \) escalates with probability \( 1 - \lambda_2p(u). \) So an actual fight occurs with probability \( \{1 - \lambda_2p(u)\} \{1 - \lambda_2p(v) \} \) and is won with equal probability by \( F \) (Table 1, Case 10) or \( O_2 \) (Table 1, Case 12). The remaining possibility for the third contest is that the outcome is dominance: either \( F \) escalates with probability \( 1 - \lambda_2p(v) \) and \( O_2 \) defers with probability \( \lambda_2p(u) \) (Table 1, Case 8) or else \( O_2 \) escalates with probability \( 1 - \lambda_2p(u) \) and \( F \) defers with probability \( \lambda_2p(v) \) (Table 1, Case 11). Proceeding likewise for the other 2 possible orders of interaction, the reward \( f_{v}(u,v) \) to a u-strategist in a population of u-strategists, conditional on participation in the first and the last of the 3 contests, and the reward \( f_{u}(u,v) \) to a u-strategist in a population of u-strategists is

\[
f_{u}(u,v) = \sum_{k=0}^{19} \omega_k(u,v)p_k(u), \quad f_{v}(u,v) = \sum_{k=20}^{36} \omega_k(u,v)p_k(u),
\]

(7)

respectively, where the terms of the first summation are defined by Table 1 and those of the second by Table 2. Now, because all possible orders of interaction are equally likely, the (unconditional) reward to a u-strategist in a population of u-strategists is

\[
f(u,v) = \frac{1}{3}f_{u}(u,v) + \frac{1}{3}f_{v}(u,v) + \frac{1}{3}f_{v}(u,v)
\]

\[
= (1 - c(u)\{1 - \frac{1}{24}f(p)\{p(u) - p(v)\}
\]

\[
+ \lambda_0(3p(v) - 2p(u) - lp(v)^2))
\]

\[
+ \frac{1}{24}(1 - c(u))\{1 - lp(v)) \}
\]

\[
\times \lambda_1\{2 - lp(u) - \lambda_2p(v)p(u) - \{1 - lp(v)\}p(v)\}
\]

\[
+ \frac{1}{12}(\lambda_2^2p(u)p(v) + 2 + l\{p(u) + p(v)\})
\]

\[
+ 2\lambda_2^2\{1 + \lambda_0p(v)\}) (b - c_0)
\]

\[
+ \frac{1}{24}(2 + l\{p(u) + p(v)\})
\]

\[
\times \{(1 - c(u))\{p(u) - p(v)\} + 2(p(u) + p(v))\}
\]

\[
+ \frac{1}{24}(1 - c(u))\lambda_0^2(1 - lp(v))p(v)^2
\]

\[
- \lambda_2^2(2 + l\{p(u) + p(v)\})p(u)p(v)
\]

\[
+ \frac{1}{12}(3 - lp(v))p(v)
\]

\[
- \lambda_0(1 - lp(v))p(v)^2 + 2p(u)c_0
\]

\[
+ \frac{1}{12}\lambda_1\{2 - lp(u)\}p(u)
\]

\[
- \lambda_0(p(u) + lp(v)^2)p(v) + p(v)c_0
\]

\[
- \frac{1}{12}\lambda_2^2\{1 - c(u) - 4\lambda_0\} (1 + \lambda_0p(v)) - 2c_0
\]

(8)

after simplification.

The above expression leads to very cumbersome analysis that largely negates the benefits of analytical modeling. For clarity of exposition, therefore, we concentrate our analysis on the case where Equation 5 is satisfied with

\[
\lambda_0 = \lambda_1 = \lambda_2 = \lambda, \quad \lambda_3 = 0
\]

(i.e., the probability of deferring to a prior winner is independent of the prior experience of the observer and prior losers do not defer to observed losers) and discuss the effects of departures.
from these assumptions without presenting the cumbersome details of the corresponding analysis. Thus, Equation 8 reduces to

\[
f(u, v) = \frac{1}{3}f_{12}(u, v) + \frac{1}{3}f_{13}(u, v) + \frac{1}{3}f_{23}(u, v)
\]

\[
= (1 - c(u))\left\{1 + \frac{1}{24}(p(u) - p(v))\right\}
\times (2\lambda(3 - p(v)) - (\ell^2 + \lambda^2)p(v))
\]

\[
- \frac{1}{24}p(v)(1 - c(u))[2p(u) - (\ell^2 + \lambda^2)p(u)]
\]

\[
+ (6 - \lambda)p(u)p(v)
\]

\[
+ (6 - \lambda)p(v)p(v)\}a_0 - 2a_0
\]

\[
(10)
\]

A strategy \(v\) is an evolutionarily stable strategy (ESS) in the sense of Maynard Smith (1982) if it is uniquely the only reply to itself. From Appendix, the game defined by Equation 10 has a unique positive ESS if

\[
\frac{c(s)}{p(s)} < \left\{2\lambda(3 - p(0))(1 - \ell p(0)) + 2(\ell^2 + \lambda^2)p(0)\right\}
\]

\[
- 3\lambda p(0)(1 + \ell p(0))\}a_0 - \ell^2 p(0) + (4b - 3 + 2\ell p(0))
\times (3b - 1)\lambda^2 p(0)\right\}/2(12 - \lambda^2 p(0)[1 + \ell p(0)])
\]

\[
(11)
\]

and otherwise the ESS is 0; that is, at the ESS, a winner displays if Equation 11 is satisfied and otherwise does not display. For the sake of definiteness, we satisfy Equations 2–4 with

\[
c(s) = \gamma \theta a_0
\]

and

\[
p(s) = \varepsilon + (1 - \varepsilon)/(1 - e^{-6}),
\]

where \(\theta > 0\) has the dimensions of Intensity \(^{-1}\), so that \(\gamma (> 0)\) is a dimensionless measure of the marginal cost of displaying; here \(0 \leq \varepsilon \leq 1\). Then Equation 11 reduces to

\[
\gamma \frac{1}{1 - \varepsilon} < \left\{2\lambda(3 - \ell k(1 - \ell k) + 2(\ell^2 + \lambda^2)\varepsilon\right\}
\]

\[
- 3\lambda(1 + \ell k)a_0 - \ell^2 \varepsilon + (2b(2 + 3\ell k)
\]

\[
- 3 - 2\ell k)\lambda^2 \varepsilon\}^2(12 - \lambda^2 p(0)[1 + \ell p(0)])
\]

\[
(14)
\]

which cannot be satisfied in the limit as \(\varepsilon \rightarrow 1\) and is most readily satisfied in the limit as \(\varepsilon \rightarrow 0\); there is therefore always a critical value of the baseline probability of observing victors, \(\varepsilon\), above which winners do not display. Note also that Equation 14 cannot be satisfied in the limit as \(\lambda \rightarrow 0\) but that its right-hand side increases with \(\lambda\); thus, conditions are the more favorable to a nonzero ESS, the greater the probability of deference to an observed winner. The resultant ESS is plotted in Figure 1a,b for \(a_0 = 0.1, \ell = 0.5, \gamma = 0.005\), and various values of \(b\) and \(\lambda\).

One could argue, however, that—at least among animals with sufficient cognitive ability—victory displays should be facultative: in a triadic interaction, there is no need to advertise after a second victory or after a first victory in the final contest because there is no other individual that can be influenced by the display. Our model is readily adapted to deal with this possibility, which has no effect on \(p_0(u, v)\) but removes a display cost \(c(u)\) from \(P_0(u)\) in 16 of the 36 cases in Tables 1 and 2, namely, Cases 1, 2, 4, 6–8, 10, 13, 15, 20–22, 24–26, 28, and 30. With Equation 10 thus modified, the analysis proceeds.
as before. As one would expect, we find that reducing the costs increases the intensity of display at the ESS, see Figure 1c,d.

We now consider the effect of departures from Equation 9. Increasing the value of any probability of deference to a prior winner, regardless of whether it is \(k_0\) (for an untested individual), \(k_1\) (for a prior loser), or \(k_2\) (for a prior winner), will always increase the intensity of signaling at the ESS. In particular, the effect of increasing \(k_1\) or \(k_2\)—subject to Equation 5—is illustrated by Figure 2. Moreover, increasing \(k_3\) from 0, that is, allowing prior losers to defer to one another, increases the intensity of display at the ESS for obligate signalers but has no effect at all on the ESS for facultative signalers because they would not display after the final contest. (Mathematically, a term in Equation 8 has no effect on the ESS unless it depends on \(u\). The only such term that appears by virtue of allowing nonzero \(k_3\) is the last. But this term is contributed by Cases 13, 25, and 26 of Tables 1 and 2 and therefore removes itself when we modify Equation 8 to allow for facultative display.)

Figure 2 also illustrates the effect of increasing the loser effect \(\ell\) it lowers the intensity of signaling at the ESS. Intuitively, with a loser effect, victory displays are not only good for winners but also bad for losers, and because animals may find themselves in either role at the ESS, the intensity of signaling should be lower.

In the absence of a loser effect (\(\ell = 0\)), the probabilities of deference to a winner and of observing a display enter the reward (Equation 8) only in terms of the probability \(k, p(s)\) that an individual observes a display of intensity \(s\) and subsequently defers to the signaler; here \(\lambda_i\) is constant, and \(p(s)\) increases with \(s\) (at a decreasing rate, which being a probability requires). An alternative interpretation of victory displays is that there is a constant probability of being observed, but the probability of deference increases with the intensity of display (again, of necessity, at a decreasing rate); that is, \(p\) is constant and \(\lambda_i(s)\) increases. Because the product of \(\lambda_i\) with \(p\) is the only combination that enters the reward, however, the effect of this reinterpretation in the case where \(k_i\) is independent of \(i\) (and \(\ell = 0\)) is merely to reproduce the same analysis, as illustrated by the dotted curve in Figure 2a.

In sum, the qualitative results of our analysis are robust in the following sense. For any values of the positive parameters \(c_0, \gamma, l, b, \lambda_0, \lambda_1, \lambda_2,\) and \(\lambda_3\) (the last 6 of which cannot exceed 1), there is a unique ESS at which animals display when \(\varepsilon\) lies below a critical value but otherwise do not display. This critical value is 0 if \(\gamma\) is too large but otherwise positive; it decreases with respect to \(\gamma\) or \(l\), increases with respect to any of the other 6 parameters, and is higher for facultative than for obligate signalers (except that it is independent of \(\lambda_3\) for facultative signalers). For subcritical values of \(\varepsilon\), the intensity of signaling at the ESS decreases with respect to \(\gamma\) or \(l\), increases with respect to any of the other 6 parameters, and is higher for facultative than for obligate signalers (with the same exception as before). Moreover, it largely does not matter whether the effect of signaling is interpreted as increasing the probability of being seen or of being deferred to.
Figure 2
Typical ESS for Model A (advertising). Intensity (scaled with respect to the parameter 1/θ to make it dimensionless) is plotted as a function of the baseline probability of observing victors, ε, for various values of the loser effect l and the probability of deference to a winner by a loser (λ1) or by a winner (λ2). Values of the other parameters (all dimensionless) are λ3 = 0.5 for the probability of deference to a winner by an untested individual, λ3 = 0 for the probability of deference to a loser by another loser, n0 = 0.1 for the fixed cost of a contest, b = 0.5 for the dominancy advantage, and γ = 0.05 for the marginal cost of displaying.

MODEL B: BROWBEATING
The nub of our second model is to observe a distinction between losing and subordination. According to the browbeating rationale, a victory display is an attempt to decrease the probability that the loser of a contest will initiate a new contest with the same individual. As long as there is a chance that the loser will challenge the winner to another fight in the future, the winner has won a battle for dominancy but not the war. If, on the other hand, the victory ensures that the loser will never challenge, then victory is tantamount to dominance. Thus, an equivalent statement of the browbeating rationale is that a victory display is an attempt to ensure that victory equals dominancy.

Some things are the same as in Model A: Advertising. Each contest lasts for a fixed amount of time, with each contestant paying the same fixed cost; strategy s means that an v-strategist displays with intensity s; and c(s) is the cost of a victory display with intensity s. But now let q(u) be the probability that a display of intensity s by a winner elicits submission on the part of the loser; thus, an v-strategist wins with probability 1/2 but wins and dominates only with the smaller probability, 1/2q(s). Because (we assume) nothing is signaled or observed outside each dyad, the order of interaction is irrelevant: because both of the focal individual’s opponents play the population strategy v, a triad consists of a u-strategist and a pair of v-strategists, with 2 contests between a u-strategist and a v-strategist and 1 between a pair of v-strategists. For the first type of contest, the probability that the u-strategist comes to dominate the v-strategist is 1/2q(u), the probability that the u-strategist is dominated by the v-strategist is 1/2q(v), the probability that a winning u-strategist fails to browbeat a losing v-strategist into submission is 1/2{1 − q(u)}, and the probability that a winning v-strategist fails to browbeat a losing u-strategist into submission is 1/2{1 − q(v)}. For a contest between 2 v-strategists, the corresponding probabilities have replaced u. We assume that Equations 2–4 continue to hold but with q in place of p; that is,

\[ c(0) = 0, \quad c'(s) > 0, \quad c''(s) \geq 0, \quad q'(s) > 0, \quad q''(s) < 0. \]  

(15)

The various possible configurations are readily distinguished as indicated in Table 3. Suppose, for example, that the focal u-strategist wins twice but fails to dominate either opponent. Then, from Equation 1, its payoff is \[ a \cdot 0 + b \cdot 2 - n_0 \cdot 2 - c(u) \cdot 2 = 2(b - 2c(u) - 2n_0) \cdot x. \]

The associated probability is \( \frac{1}{2} \{1 - q(u)\} \); see Table 3, Line 3. Or suppose that the focal u-strategist wins only once but succeeds in dominating that opponent, whereas it avoids being dominated by the other opponent. Then, from Equation 1, its payoff is \[ a \cdot 1 + b \cdot 1 - c(u) \cdot 2 - c(s) \cdot x \cdot 1 = \{1 + b - c(u) - 2n_0\} \cdot x \] it pays the cost of display only once because it wins only once. There are 2 ways in which this payoff can arise. If the u-strategist dominates its first opponent and is undominated by its second, then the associated probability is \( \frac{1}{2}q(u) \cdot \frac{1}{2} \{1 - q(v)\} \) and if the u-strategist dominates its second opponent and is undominated by its first, then the same associated probability arises as \( \frac{1}{2} \{1 - q(v)\} \cdot \frac{1}{2}q(u) \). Adding, the probability associated with payoff \( \{1 + b - c(u) - 2n_0\} \) is \( \frac{1}{2}q(u) \{1 - q(u)\} \); see Table 3, Line 4. The other 8 cases are similar. The upshot is that the reward to a u-strategist in a population of v-strategists is

\[ f(u, v) = \sum_{b=1}^{10} \rho_b(u, v)Q_b(u) = \{q(u) + b(2 - q(u) - q(v)) - c(u) - 2n_0\} \cdot x. \]  

(16)

Now the ESS is

\[ v = \begin{cases} 0 & \text{if } \epsilon'(0) \geq (1 - b)\alpha q'(0) \\ v_b & \text{if } \epsilon'(0) < (1 - b)\alpha q'(0) \end{cases} \]  

(17)

where \( v_b \) is uniquely defined by

\[ (1 - b)\alpha q'(v) = \epsilon'. \]  

(18)

(Appendix). For example, with costs the same as in Model A: Advertising but

\[ q(s) = \delta + (1 - \delta)(1 - e^{-0t}), \]  

(19)

we have \( v_b = \frac{1}{\epsilon} \ln \left(\frac{(1 - b)(1 - \delta)}{\epsilon} \right) \). There is now a critical value of \( \delta \), the baseline probability of submission (i.e., the probability that a victor elicits permanent submission from a loser in the absence of a display), above which winners do not display; on rearranging Equation 17, we find that the ESS is given by
Table 3

Model B payoff to a focal u-strategist from all possible configurations

<table>
<thead>
<tr>
<th>Case</th>
<th>Configuration</th>
<th>Probability</th>
<th>Payoff</th>
</tr>
</thead>
<tbody>
<tr>
<td>k</td>
<td>#W</td>
<td>#D</td>
<td>#NS</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>1</td>
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</tr>
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<td>1</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>

#W: Number of wins by focal u-strategist; #D, number of animals dominated by u-strategist; and #NS, number of animals to which u-strategist is not subordinate.

\[
\theta_v = \begin{cases} 
\ln \left( \frac{(1-\delta)(1-\delta)}{\gamma} \right) & \text{if } \delta < 1 - \frac{\gamma}{1-\gamma} \\
0 & \text{if } \delta \geq 1 - \frac{\gamma}{1-\gamma} 
\end{cases} \quad (20)
\]

It is plotted in Figure 3 for \( \gamma = 0.05 \) (as in Figure 1) and various values of \( b \).

Note that \( p \) and \( q \) are equivalent mathematical functions: the only difference between \( p(u) \) defined by Equation 13 and \( q(u) \) defined by Equation 19 is that in the first case we denote the baseline probability of achieving the desired effect by \( p(0) = \varepsilon \), whereas in the second case we denote the same probability by \( q(0) = \delta \). We use different symbols for baseline probability because the desired effects (attention to remote victors and submission to current opponents, respectively) are different.

**DISCUSSION**

We have used formal game-theoretic models to quantitatively explore the validity of 2 rationales for the function of victory displays, both proposed by Bower (2005). The advertising rationale (Model A: Advertising) is that victory displays are an attempt to communicate victory to other members of a social group that cannot, or do not, pay attention to contests. The browbeating rationale (Model B: Browbeating) is that victory displays are an attempt to decrease the probability that the loser of a contest will initiate a future contest with the same individual. We have shown that both rationales are logically feasible. In either case, victory displays are evolutionarily stable if the desired effect (attention to a remote victor or submission to a current opponent) has a significantly lower probability of arising in the absence of a display.

To focus on factors favoring the evolution of victory displays, we have ignored the question of why such displays should be respected, either by observers in Model A: Advertising or by losers in Model B: Browbeating. A likely answer is that respecting displays avoids the costs of potentially protracted disputes. Even arbitrary cues such as prior victory displays may be used to settle contests quickly when information about relative strength is absent or imperfect; the corresponding behavioral rule is widely known as a convention and yields a smaller benefit to some contestants than could have been obtained through fighting. For example, Mesterton-Gibbons and Adams (2003) showed that the probability of a conspicuous landmark being accepted as a conventional solution to a problem of territorial division is remarkably high when variance in strength is sufficiently low and this accords with intuition: information about relative strength is most worth having when variance is high. Here we have assumed that the variance in fighting ability is zero but not that this information is available to the contestants. Zero variance in actual fighting ability does not rule out differences in perceptions of fighting ability based on observations of winning or losing, the only cues on which our assumptions allow such perceptions to be based.

Our first model predicts that the advertising display of a winner to a social group becomes important only when it is hard for the audience to determine the winner (thus as the baseline probability of observing victors, \( \varepsilon \), approaches 1, the ESS becomes 0). The presumed victory displays by tropical boubous were typically sung from higher perches than were used for other duets, which led Grafe and Bitz (2004) to
suggest that the signal was directed to other pairs outside their own territories, rather than to the intruder per se. Similarly, Bower (2000) reports that winning song sparrow (Melospiza melodia) males typically sang from higher perches after contests. That higher perches are utilized in signaling suggests that it is not always easy for bystanders to observe the winner, and this may be particularly common in environments where individuals are partly concealed, such as rainforest canopy.

The possibility has been increasingly recognized that bystanders might gain in a strategic way by observing the details and outcome of conflicts between others (McGregor and Peake 2000; Peake 2005). For instance, Earley and Dugatkin (2002) investigated the dynamics of aggressive interactions in the green swordtail (Xiphophorus helleri) and found that “eavesdropping” significantly reduced the bystander’s propensity to initiate aggression, escalate, and win against an earlier observed winner. Johnstone (2001) investigated the evolutionary success of an eavesdropping strategy that plays haw when facing an opponent that lost the previous round and plays dove when facing an opponent that won (see Maynard Smith 1982, for the classic hawk–dove game). He showed that eavesdroppers can spread under a range of conditions and, paradoxically, that the frequency at which both opponents play hawk is higher in the new equilibrium than in the traditional hawk–dove game. Although our postconflict signaling model also allows for a probability of deference after observing a winner, it is rather different in that we allow all individuals to make use of information obtained as a bystander and evaluate an ESS based on continuous variation in signaling intensity rather than the success of discrete strategies.

In our second model, there is no audience effect, so a browbeating display to a losing intruder would be expected to arise even when visibility is naturally high. Not surprisingly, as the baseline probability of submission δ increases beyond a certain level, it does not pay to employ a browbeating signal at all as the effect will arise without a display. In both models, the lower the rate at which signaling costs increase with signal intensity, the higher the potential for a nonzero ESS. Thus, as one might expect, as signaling becomes cheaper there is more intense postvictory signaling at equilibrium.

However, there is an important difference in prediction between the 2 models we have presented. In the case of advertising, the intensity of display at the ESS increases with respect to the parameter b, an inverse measure of the reproductive advantage of dominating an opponent compared with simply not subordinating. By contrast, in the case of browbeating, the intensity of display at the ESS decreases with respect to b. This result is already implicit in Figures 1 and 3, but in Figure 4, we have made it explicit by plotting the 2 ESSs against one another. Therefore, all other things being equal, the intensity of advertising victory displays will be highest when there is little difference between dominating an opponent and not subordinating (a set of conditions likely to generate low reproductive skew). By contrast, the intensity of browbeating victory displays will be highest when there are greater rewards to dominating an opponent (a set of conditions that is likely to generate high reproductive skew). As Bower (2005) notes, it is not known how common postconflict displays are because they have not been systematically studied, so it is important not to read too much into the current taxonomic distribution of victory displays. However, it is interesting that 2 of the best candidates for advertising victory displays, the tropical boubou (Grafe and Bitz 2004) and song sparrow (Bower 2005), are socially monogamous species. Bower (2005) presents examples of postvictory stridulation in crickets and wetas as possible cases of what we have called a browbeating display. Many of these species exhibit resource defense polygyny (for example, Kelly 2005), with clear potential for high reproductive skew.

Models of necessity simplify, and ours are no exception. To compare and contrast between advertising and browbeating explanations, we have created separate models, but in reality, a victory display may be aimed both at the current opponent and at a wider audience. Moreover, the social benefits of victory displays may be realized in other ways, beyond reducing the costs (and maximizing the benefits) of future antagonistic interactions, such as in attracting and keeping mates. For analytical tractability, our social network comprises only collections of 3 individuals, and although we hope to have captured the essence of both advertising and browbeating using this approach, signaling intensities may well depend on group size. For example, if there is more than one bystander in the immediate social group, then the benefits of advertising intensely may be higher, particularly, if the majority of individuals in the audience face the winner in subsequent contests. Perhaps most importantly, as noted above, our models assume, rather than predict, that observers of victory signals are more likely to defer to these winners (Johnstone 2001). This approach may well be justified on the basis that a costly display honestly indicates a victor’s continued vigor and high quality (Zahavi A and Zahavi A 1997; Bower 2005). Future models might address the evolution of this phenomenon from a more fundamental level, for instance, by allowing variation in fighting strength.

As Bower (2005) argues, although many postconflict displays by winners seem too complex to be explained simply as the consequence of a surge in hormones, or simple emotional

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**Figure 4**

Comparison of advertising and browbeating ESSs. Intensity (scaled with respect to 1/0 to make it dimensionless) is plotted as a function of dominance advantage b. Values of the other parameters (all dimensionless) are 1 for the fixed cost of a contest, I = 0.9 for the loser effect (i.e., the probability that an observed loser again loses is 0.75), γ = 0.05 for the marginal cost of displaying, λ = 0.9 for the probability of deference, and ε = 0.1 = 5 for the baseline probability of the desired effect (attention to remote victor in Model A: submission to current opponent in Model B) in the absence of a display. See the remark at the end of Model B: Browbeating. For obligate signalers, the advertising ESS is shown dashed; for facultative signalers, it is shown dotted.
release, very little formal research has been conducted to document the behavior of winners after contests are over. We hope that, by quantitatively supporting the feasibility of victory displays using traditional game-theoretic models, we will prompt others to investigate this fascinating phenomenon.

APPENDIX

ESS conditions

Strategy $v$ is a strong, global ESS in the sense of Maynard Smith (1982) if

$$f(v, v) > f(u, v), \quad \text{for all } u \neq v. \quad (A1)$$

Because of Equation 15 and $b < 1$, $f$ defined by Equation 16 satisfies $\frac{\partial f}{\partial u} = -e^v(u) + (1 - b)aq^v(u) < 0$, for all $u \geq 0$; and similarly, because of Equations 3 and 4, $f$ defined by Equation 8 satisfies $\frac{\partial f}{\partial u} < 0$, for all $u \geq 0$ (but the resulting expression is far too cumbersome to be presented here). Hence in either case, $v = 0$ is the unique, strong global ESS whenever

$$\left.\frac{\partial f}{\partial u}\right|_{u=0} \leq 0, \quad (A2)$$

and $v = v^*$ is the unique, strong global ESS whenever

$$\left.\frac{\partial f}{\partial u}\right|_{u=0} > 0, \quad (A3)$$

where $v = v^*$ is the only root of the equation

$$\left.\frac{\partial f}{\partial u}\right|_{u=v} = 0. \quad (A4)$$

This research was supported by National Science Foundation award DMS-0421827 to M.M.G. and Natural Sciences and Engineering Research Council of Canada Discovery Grant to T.N.S. We are grateful to 2 anonymous reviewers for valuable and constructive comments.

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