Current Biology *20*, 1637–1640, September 28, 2010 ©2010 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2010.07.042

Report

Social Punishment of Dishonest Signalers Caused by Mismatch between Signal and Behavior

Elizabeth A. Tibbetts[1,*] and Amanda Izzo[1]
[1]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA

Summary

Many animals use conventional signals of fighting ability to mediate aggressive conflict. Given the apparent benefits of signaling inaccurately high fighting ability, there is extensive interest in why animals communicate their abilities honestly [1]. One hypothesis is that inaccurate signalers receive social punishment that disfavors inaccuracy. Although the idea that social punishment can prevent dishonesty is appealing, questions about the evolutionary stability of this hypothesis remain [2]. For example, how do individuals know a rival is cheating? We independently manipulated a signal of fighting ability and agonistic behavior in *Polistes dominulus* wasps to test the behavioral mechanisms underlying social punishment. Remarkably, a mismatch between signal and behavior caused social punishment. Individuals with experimentally altered signals received more aggression from rivals. Individuals with experimentally altered behavior were less able to establish dominance relationships. In contrast, control individuals and those with experimentally altered signal and behavior suffered neither cost. They received little aggression and established stable dominance relationships. Therefore, individuals use information about the match between signal and behavior to assess the accuracy of rival signals. A mismatch produces costly social interactions. This simple behavioral mechanism provides a clear cost to signal inaccuracy that may maintain honest communication over evolutionary time.

Results

Polistes dominulus wasps have a conventional signal of agonistic ability that is used during aggressive contests among nest-founding queens. The amount of disruption or "brokenness" of *P. dominulus* facial patterns provides information about its bearer's agonistic ability (Figure 1). Dominant wasps have more broken facial patterns than subordinate wasps [3–5], and wasps use facial pattern brokenness to quickly assess the agonistic abilities of strangers before interacting [6]. Much previous work on the mechanisms that maintain signal accuracy has focused on costs associated with signal production [2]. However, many signals, including *P. dominulus* facial patterns, lack clear costs associated with signal production [7, 8]. Instead, social punishment may maintain signal accuracy over evolutionary time [3].

Social punishment of inaccurate signalers sounds like a straightforward method of preventing dishonest communication, but theoretical and empirical work has left numerous questions unanswered [8]. For example, how do receivers assess inaccuracy? Why are receivers aggressive to rivals with inaccurate signals? Here we address these questions by testing whether incongruence between signaled fighting ability and true fighting ability is the behavioral mechanism that mediates social punishment. This incongruence hypothesis provides a simple solution to key questions about social costs [9, 10].

We test whether incongruence between signal and agonistic ability produces social punishment by independently altering the signal and behavior of wasp queens. Facial patterns that signal fighting ability were altered using paint so that individuals received one of two treatments: either markings were altered so individuals signaled higher fighting ability than the original markings (signal alteration) or original markings were painted without altering their appearance (paint control). Agonistic behavior was altered using the juvenile hormone (JH) analog methoprene and the methods described in [11]. Individuals received either methoprene (behavior alteration) or acetone (hormone control). A complete factorial design was used such that queens received one of four treatments: (1) signal and hormone control, (2) signal alteration and hormone control, (3) signal control and behavioral alteration, or (4) signal and behavior alteration. After treatment, individuals were paired with an unmanipulated rival they had not previously encountered and interactions were observed for 2 hr. Eighty-one trials were performed, with approximately 20 pairs in each treatment group.

The results of this experiment demonstrate that incongruence between signal and behavior results in social punishment. Individuals with facial patterns that signaled inaccurately high agonistic ability (treatment 2) received more aggression from conspecifics than individuals from other treatment groups (Figure 2; $F_{3,77} = 3.8$, $p = 0.013$; LSD post hoc analysis on signal alteration versus control, $p = 0.015$; signal alteration versus signal and behavior alteration, $p = 0.035$; signal alteration versus behavioral alteration, $p = 0.002$). Aggression did not differ between the other treatment groups (all $p > 0.5$). Therefore, individuals that signal that they are stronger than their true behavioral dominance suffer social costs.

Individuals with facial patterns signaling inaccurately high fighting ability (treatment 2) also had difficulty establishing stable dominance hierarchies. Dominance ranks are typically stable after an individual submits to their rival [12], but signal inaccuracy interfered with rank stability (see Table S1 available online; $\chi 2_3 = 9.5$, $p = 0.015$). Individuals with experimentally increased advertised quality were more likely to be involved in trials with dominance switches than individuals from other treatment groups (standardized residual [st. resid.] = 2.2).

When behavioral dominance alone was increased (treatment 3), individuals suffered a different type of social cost: they were less able to establish dominance (Table S2; $\chi 2_3 = 9.2$, $p = 0.026$). Dominance competition ends with one individual submitting to their rival by crouching and lowering their antennae [12]. Submission was less likely to occur in trials containing individuals with experimentally increased behavioral dominance (st. resid. = −1.7). Instead, trials were more likely to end with dominance rank unestablished (st. resid. = 1.9).

*Correspondence: tibbetts@umich.edu

Figure 1. Signal of Fighting Ability in Paper Wasps

Portraits of five *Polistes dominulus* wasps arrayed from individuals signaling low agonistic ability (left) to those signaling high agonistic ability (right).

Therefore, individuals that behave in a dominant manner but have low advertised quality also experience social costs.

Discussion

Overall, incongruence between signal and behavior results in social punishment. When individuals had facial patterns that signaled inaccurately high agonistic ability, they received more aggression from conspecifics (Figure 2) and had difficulty establishing stable dominance hierarchies. When behavioral dominance alone was increased such that individuals had facial patterns that signaled inaccurately low agonistic ability, individuals were less able to form dominance relationships and more likely to spend the entire trial competing over dominance rank without behavioral submission. Interestingly, individuals with experimentally increased signal and behavioral dominance suffered neither cost. They received a similar amount of aggression as controls and were able to establish stable dominance relationships. Therefore, receivers perceive the match between signal and behavior during competition. Any incongruence between behavior and signal interfered with stable behavioral interactions and produced costly social interactions.

Although the idea that incongruence between signal and behavior produces social punishment was one of the original hypotheses for the evolutionary stability of signals of fighting ability, it has received little recent attention. Rohwer [10] and Jarvi et al. [13] performed experiments that supported the incongruence hypothesis, but their experimental methods were later criticized. This study avoided the difficulties associated with previous tests. First, individuals were experimentally altered prior to meeting rivals to ensure that familiarity did not interfere with the results. Second, fighting ability was increased in a biologically realistic manner. This experiment was performed during the early nest-founding stage, a time when JH titers are associated with dominance (unpublished data) and experimentally increasing JH causes an increase in dominance rank [11, 12]. Further, there is a relationship between JH titers and signal elaboration among unmanipulated queens. Individuals with facial patterns signaling high agonistic ability have higher JH titers than individuals with facial patterns signaling low agonistic ability (unpublished data). The results of this experiment suggest that the relationship between JH titer and signal elaboration is essential for the communication system to function. Experimentally altering the relationship between hormone and signal elaboration creates a mismatch between behavior and signal that interferes with stable dominance relationships and produces substantial social costs.

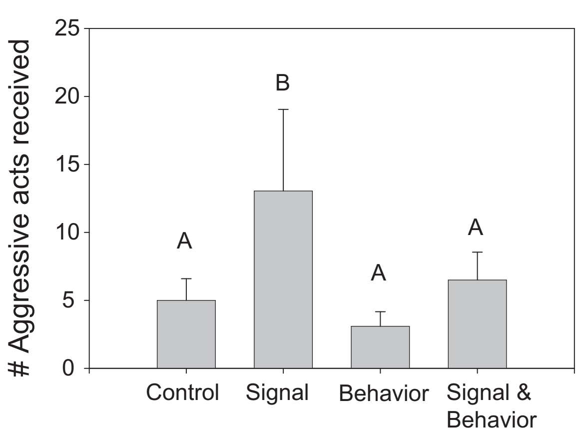

Figure 2. Aggressive Cost of Dishonest Signals

Mean (+) standard error aggressive acts received by individuals that experienced the following treatments: control, increased agonistic signal alone, increased agonistic behavior alone, and increased agonistic signal and behavior. Different letters denote statistically significant differences ($p < 0.05$).

The idea that increased aggression toward individuals with inaccurately high quality signals can maintain signal accuracy has been a source of some controversy. The aggression must be costly enough to "punish" the inaccurate signaler and disfavor the evolution of signal inaccuracy. At the same time, the aggression must benefit the aggressor, because altruistic punishment, or aggression that provides no benefit to the aggressor, is not favored by selection [14].

The incongruence hypothesis clarifies how aggressive punishment can favor the aggressor. This hypothesis proposes that aggression toward inaccurate signalers is a byproduct of the receiver's self-interest in assessing the signaler's true ability [9]. When an individual encounters a rival who signals that they are strong but behaves like they are weak, continued aggressive competition will allow the receiver to assess the rival's true agonistic ability. This will benefit the receiver by allowing it to attain higher dominance status than if it trusted the inaccurate signal. At the same time, it will be costly for the inaccurate signaler. Although this behavioral mechanism provides a logical explanation for aggressive punishment, it is difficult to measure the precise cognitive processes that occur during aggressive punishment. Nevertheless, our results suggest that simple self-interest can produce behavior that functions as social punishment and maintains signal accuracy over evolutionary time.

The evolution of signals with social costs is based on two ideas that initially appear contradictory. Signals of fighting ability minimize the costs of conflict by allowing individuals to assess the abilities of rivals prior to engaging in aggressive competition [2]. However, if individuals make contest decisions based on their rival's signal alone, the communication system would be open to cheating. Therefore, as the results of this study demonstrate, individuals must also test whether a rival's signal matches its true fighting ability. What is the benefit of having a signal if receivers must also test a rival's true abilities?

One explanation for the apparently contradictory requirements of social cost signals is that receiver behavior depends on social context. For example, during short-term interactions over low-value resources, wasps make decisions based on a rival's signal, regardless of whether or not the signal accurately reflects its bearer's true agonistic ability [6]. However, during longer-term interactions or contests over valuable resources, receivers challenge rivals and test signal accuracy [3, 15]. If challenged, individuals with inaccurate signals suffer costly social interactions (this study, [3]).

Context-dependent responses to signals occur in other taxa and may be one of the reasons that social costs have been controversial. For example, individuals with experimentally altered signals may rise in status without experiencing a social challenge [16, 17] or they may experience a social challenge and fail to rise in status [3, 13]. The variation in receiver response across contexts can easily create confusion, especially if a taxon is only tested in one experimental context. Therefore, careful experimental design is important for understanding the function and evolutionary stability of signals with social costs.

Overall, the mechanisms that mediate social costs have been a source of some controversy, with particular questions about whether social costs provide a stable cost of ornamentation [8]. This study demonstrates that signal incongruence is an important behavioral mechanism that mediates social punishment. Receivers test rival signals during certain social interactions. Any incongruence between signal and behavior causes increased social conflict, thereby disfavoring signals that do not reflect their bearer's true ability. These results provide a simple behavioral mechanism whereby social punishment can maintain the accuracy of signals over evolutionary time.

Experimental Procedures

Nest-founding queens were collected from sites around Ann Arbor, MI, soon after they emerged from diapause. The early founding period is a time of intense conflict because foundresses compete with many rivals before starting a nest. When multiple individuals nest together, the dominant queen is the primary reproductive [18]. Cooperating cofoundresses may be related but are often unrelated [19].

After collection, individuals were paired with a similarly sized rival (<0.005 g difference). The size difference between rivals was small (1% ± 3% average weight) and did not vary across treatment groups ($F_{3,77}$ = 0.74, p = 0.53). Further, original facial patterns did not vary across treatment groups (sender, $F_{3,77}$ = 1.0, p = 0.39; receiver, $F_{3,77}$ = 1.5, p = 0.22). One wasp in each pair remained unmanipulated and served as the signal receiver, whereas the other individual was treated by altering its behavior and/or signal. Rivals were collected from sites at least 5 km apart and were housed separately to ensure they did not interact prior to the behavioral trials.

Behavioral Alteration

The JH analog methoprene was used to experimentally alter behavioral dominance. Methoprene is commonly used as a JH analog because it has a longer biological half-life than JH, 14–24 hr versus 1.5 hr. Previous work has shown that methoprene increases dominance in hymenoptera [20], including *P. dominulus* [11, 12]. Individuals were treated with 5 μg of methoprene in 1 ul acetone three times a week for 2 weeks, for a total of six hormone treatments. Controls were treated with 1 ul acetone alone using the same treatment schedule. Tibbetts and Izzo [11] used the same method to treat *P. dominulus* foundresses, finding that the JH-treated individual dominated her rival in 70% of the trials. Hormone treatment of adult foundresses increases behavioral dominance without influencing signal elaboration [11].

Signal Alteration

The facial pattern of the treated wasp received one of two treatments: either markings were altered with paint so they signaled a higher level of agonistic ability than the original markings (signal alteration) or original markings were painted without altering their appearance (paint control). Painting control and signal alteration individuals received a similar amount of the same type of paint in the same area of the face. However, the appearance of the experimental group was altered so that the facial patterns signaled that they were within the top quarter of the population, whereas the appearance of the painting control remained the same. This experimental design explicitly tests how a wasp's appearance influences receiver behavior.

After treatment, pairs were allowed to compete for dominance in 2 hr videotaped bouts. The average time to dominance establishment in control trials was 46 min. Later, videotapes were scored by an observer blind to treatment who scored aggression rates and dominance ranks. Dominance ranks were determined using mounting behavior. During a mount, the dominant wasp crawls on top of the subordinate wasp. The dominant individual typically drums her antennae on the subordinate, whereas the subordinate crouches and lowers her antennae [12]. If neither individual successfully mounted her opponent, the trial was scored as having no dominance established. Aggression levels were recorded by scoring the number of mounts, bites, and grapples.

Categorical data was analyzed using a chi-square analysis. Because some cells had an expected count of less than 5, p values were calculated using the exact test in SPSS v. 17. This analysis compares the observed distribution of data to expected values generated by 10,000 generation Monte Carlo simulations. Aggression data were log transformed to increase their normality and analyzed using an analysis of variance to test how experimental treatment influenced aggression received by treated wasps.

Supplemental Information

Supplemental Information includes two tables and can be found with this article online at doi:10.1016/j.cub.2010.07.042.

Acknowledgments

Thanks to Dustin Hennigar for videotape analysis.

Received: June 2, 2010
Revised: July 26, 2010
Accepted: July 28, 2010
Published online: August 19, 2010

References

1. Maynard-Smith, J., and Harper, D. (2003). Animal Signals (New York: Oxford University Press).
2. Searcy, W.A., and Nowicki, S. (2005). The Evolution of Animal Communication (Princeton, NJ: Princeton University Press).
3. Tibbetts, E.A., and Dale, J. (2004). A socially enforced signal of quality in a paper wasp. Nature *432*, 218–222.
4. Zanette, L., and Field, J. (2009). Cues, concessions and inheritance: Dominance hierarchies in the paper wasp *Polistes dominulus*. Behav. Ecol. *20*, 773–780.
5. Tibbetts, E.A., and Shorter, J.R. (2009). How do fighting ability and nest value influence usurpation contests in *Polistes* wasps? Behav. Ecol. Sociobiol. *63*, 1377–1385.
6. Tibbetts, E.A., and Lindsay, R. (2008). Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. Biol. Lett. *4*, 237–239.
7. Tibbetts, E.A. (2010). The condition dependence and heritability of signaling and nonsignaling color traits in paper wasps. Am. Nat. *175*, 495–503.

8. Senar, J.C. (2006). Color displays as intrasexual signals of aggression and dominance. In Bird Coloration Function and Evolution, Volume 2, G.E. Hill and K.J. McGraw, eds. (London: Harvard University Press), pp. 87–136.
9. Caryl, P.G. (1982). Telling the truth about intentions. J. Theor. Biol. *97*, 679–689.
10. Rohwer, S. (1977). Status signaling in Harris sparrows: Some experiments in deception. Behaviour *61*, 107–129.
11. Tibbetts, E.A., and Izzo, A.S. (2009). Endocrine mediated phenotypic plasticity: Condition-dependent effects of juvenile hormone on dominance and fertility of wasp queens. Horm. Behav. *56*, 527–531.
12. Roseler, P.F. (1991). Reproductive competition during colony establishment. In The Social Biology of Wasps, K.G. Ross and R.W. Matthews, eds. (London: Comstock Publishing Associates), pp. 309–335.
13. Jarvi, T., Walso, O., and Bakken, M. (1987). Status signaling by *Parus major*: An experiment in deception. Ethology *76*, 334–342.
14. Clutton-Brock, T.H., and Parker, G.A. (1995). Punishment in animal societies. Nature *373*, 209–216.
15. Tibbetts, E.A. (2008). Resource value and the context dependence of receiver behaviour. Proc. Biol. Sci. *275*, 2201–2206.
16. Pryke, S.R., and Andersson, S. (2003). Carotenoid-based status signalling in red-shouldered widowbirds (*Euplectes axillaris*): Epaulet size and redness affect captive and territorial competition. Behav. Ecol. Sociobiol. *53*, 393–401.
17. Senar, J.C., and Camerino, M. (1998). Status signalling and the ability to recognize dominants: An experiment with siskins (*Carduelis spinus*). Proc. R. Soc. Lond. B. Biol. Sci. *265*, 1515–1520.
18. Reeve, H.K. (1991). Polistes. In The Social Biology of Wasps, K.G. Ross and R.W. Matthews, eds. (London: Comstock Publishing Associates), pp. 99–148.
19. Queller, D.C., Zacchi, F., Cervo, R., Turillazzi, S., Henshaw, M.T., Santorelli, L.A., and Strassmann, J.E. (2000). Unrelated helpers in a social insect. Nature *405*, 784–787.
20. Robinson, G.E., and Vargo, E.L. (1997). Juvenile hormone in adult eusocial Hymenoptera: Gonadotropin and behavioral pacemaker. Arch. Insect Biochem. Physiol. *35*, 559–583.