Resource value and the context dependence of receiver behaviour

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Many animals use signals of fighting ability to minimize the costs of competition. Theory predicts that signals must be costly to remain reliable indicators of their bearer's abilities, but many signals of fighting ability lack obvious developmental costs. Instead, receivers are thought to maintain signal accuracy by behaving aggressively towards individuals with inaccurate signals (i.e. social costs). Models predict that the evolutionary stability of social cost signals depends on receivers trusting signals in certain contexts and testing signal accuracy in other contexts. Here, I use the signals of agonistic ability in *Polistes dominulus* wasps to provide the first experimental evidence that receiver responses to social cost signals are context dependent. During contests over low-value resources, wasps trust signals; they avoid patches of food guarded by rivals with elaborate signals. As the value of the resource increases, wasps become more likely to test signal accuracy. In fact, receivers challenge guards regardless of their signal phenotype when the resource is sufficiently valuable. Context-dependent receiver responses are likely to be an important behavioural mechanism underlying the evolution of social costs, as context-dependent responses allow receivers to minimize the costs of conflict while also ensuring signal accuracy.

Keywords: badge of status; sparrow; game theory; deception; honesty; conventional signal

1. INTRODUCTION

Aggressive competition over limited resources is costly. As a result, many animals minimize the costs of conflict by using signals to assess rivals (Maynard-Smith & Harper 2003; Searcy & Nowicki 2005). Signalling systems will remain evolutionarily stable only if the signals are honest indicators of their bearer's abilities. As a result, there has been extensive interest in the factors that maintain signal accuracy (Hill 1991; Andersson 1994). After all, deception seems intuitively advantageous. If a weak animal could successfully convince others that it were strong, it could acquire a better territory, more mates and higher status. Theory suggests that signals remain honest because signalling a high level of quality is relatively more costly for low-quality individuals (Zahavi 1975; Grafen 1990; Getty 2006), and classic work has shown that many signals have honesty-ensuring costs associated with signal production (Hill 1991; Andersson 1994; Johnstone 1995).

Although many signals have costs associated with their production, production costs are unlikely to be the only mechanism that maintains signal accuracy. Many organisms have signals that lack clear production costs (e.g. lizards, reviewed in Whiting *et al.* 2003; insects, Tibbetts & Dale 2004; bird plumage, Mennill *et al.* 2003, Pryke & Andersson 2003a, Qvarnström 1997 reviewed Senar 2006; bird song, reviewed Gil & Gahr 2002). In particular, many signals of fighting ability have no clear cost of signal production and appear largely 'arbitrary' in that they have no logical *a priori* connection with their bearer's fighting ability. This type of signal has been termed a conventional signal (or badge of status; Guilford & Dawkins 1995). The accuracy of conventional signals is thought to be maintained via social costs. That

is, inaccurate signallers receive more aggression from opponents than accurate signallers (Rohwer 1975). Increased aggression towards inaccurate signallers may arise from the receiver's selfish interest in evaluating the sender's true fighting ability when there is a mismatch between status badge elaboration and behaviour (Rohwer & Rohwer 1978).

Despite significant theoretical and empirical works on social costs, important questions remain unanswered (Martin & Forsman 1999; Parker & Ligon 2002; Tibbetts & Dale 2004; Senar 2006). For example, the evolution of agonistic signals with social costs is based on two ideas that initially appear contradictory. Signals of agonistic ability are expected to reduce the cost of aggressive conflict by allowing opponents to avoid costly fights that have predictable outcomes (Senar 2006). Therefore, receivers must frequently trust the accuracy of signals. However, if individuals always assume their opponent's signal is accurate, the system is open to cheating and signals will not remain accurate over evolutionary time. Signals with social costs will remain evolutionarily stable only if receivers aggressively 'test' the sender's true behavioural status (Rohwer 1977). Both requirements are met if receiver responses are context dependent. For example, receivers may test signal accuracy during contests over valuable resources, but accept the signal without aggressive testing when the value of the contested resource is low (Maynard-Smith *et al.* 1988). Although this idea was proposed almost 20 years ago, it has not been previously tested.

One reason that little is known about the dynamics of signal assessment is that most research on animal contests has focused on behaviour during the contests themselves. For example, numerous studies have tested how resource holding potential (RHP) and resource value influence

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Figure 1. (a–d) Portraits of four *P. dominulus* paper wasps illustrating some of the naturally occurring diversity in the size, shape and number of black facial spots. Wasps are arrayed from low advertised quality (0 spots, (a)) to high advertised quality (2 spots, (d)).

behaviour during aggressive contests and contest outcomes (Maynard-Smith & Parker 1976; Enquist 1985; Bridge *et al.* 2000). Testing receiver responses *before* contests is the only way to explore signal assessment behaviour. This study will decouple the signal from the signaller behaviour to isolate the effect of signal elaboration and resource value on the receiver's behaviour before contests.

Polistes dominulus paper wasps have a conventional signal of fighting ability (badge of status) that provides a good system to test the role of resource value in badge assessment (figure 1). First, there are no clear developmental costs that could account for badge accuracy. The black pigment that comprises the badge accounts for less than 1% of the total black pigment on a wasp, suggesting that the amount of pigment required to produce the signal is unlikely to be particularly costly. In addition, the developmental costs are unlikely to be important because the aspect of the badge that signals quality is 'brokenness' or waviness of the black pigment, not the amount of black. Two wasps with a similar amount of black on their clypeus may signal different levels of quality based on the distribution of that pigment (figure 1). Second, previous experimental work demonstrates that social costs are important in maintaining signal accuracy. Wasps with inaccurate badges suffer social costs, as they receive more aggression from rivals than those with accurate signals (Tibbetts & Dale 2004). Therefore, paper wasps are a good system to test the role of resource value in badge assessment.

Previous work on paper wasps indicates that receiver responses to badges vary, suggesting that wasps are particularly well suited to research on the context dependence of receiver responses. Wasps trust rival signals during brief contests, even if signals have been experimentally altered so that they do not reflect their bearer's true abilities (Tibbetts & Lindsay 2008). During prolonged interactions, receivers discern signal inaccuracy and behave aggressively towards individuals with inaccurate signals (Tibbetts & Dale 2004). Here, I test whether the value of the resource being contested influences whether wasps trust or test the accuracy of rival signals. In addition to clarifying the behavioural dynamics of social costs, these experimental results will provide a useful comparison with classic game theoretic work on behavioural dynamics during animal contests.

2. MATERIAL AND METHODS

I tested how advertised quality and resource value influence whether or not focal wasps challenged rivals. Rival assessment decisions were tested by placing focal individuals in a trial arena that contained one patch of food guarded by another

wasp. Focal wasps had the option of approaching the guard to gain access to the food or avoiding the guarded food patch. Food sharing among wasps occurs both on and off nests. Wasps aggregate at rich food sources and access to food is influenced by dominance rank (Tibbetts & Reeve 2000; Dapporto *et al.* 2005). Although competition over food is important for wasps, future research that examines advertised quality and resource value in diverse contexts will also be important, as badges may also be used in other contexts.

Choice trials were performed in a triangle-shaped arena (7 cm wide $\times$ 6 cm long). There was a covered antechamber at the narrow end of the arena. At the other end of the arena, I placed a cube of sugar with a freshly freeze-killed guard wasp positioned on top. Wasps eat nectar in the wild and are reared on rock sugar in the laboratory. Focal wasps were placed in the antechamber for 5 min before being released into the trial arena. Each trial lasted 20 min. I scored whether the focal wasp avoided the guarded food patch or approached the focal wasp and ate the sugar. Eating was straightforward to distinguish. Focal wasps usually sat next to the sugar, opened their mandibles and licked the sugar. In a few cases, the focal wasp sat on top of the sugar cube. Within wasps that ate the sugar, I measured how much time they spent eating and the time between exiting the antechamber and starting to eat (i.e. latency to eat).

All focal and guard wasps were nest-founding queens that were collected from the wild in early May and housed in individual deli-cups. Guards and focal wasps were collected from sites at least 4 km apart to ensure that they had never previously interacted. All wasps were from single-foundress nests and were medium sized (100–120 mg).

Facial patterns were used to test the role of advertised quality during choices. The aspect of *P. dominulus* facial patterns that signals agonistic ability is the amount of disruption or brokenness of the black facial coloration. The number of facial spots provides a straightforward proxy for brokenness, with 0 spots indicating low quality and 2 spots indicating high quality (Tibbetts & Lindsay 2008; figure 1). All wasps initially had a single clypeal spot indicating an average level of quality. Each guard's facial pattern was experimentally altered with Testors enamel paint before the trials. Guards were randomly assigned to a painting treatment. Half of the guard faces were altered so that they had no clypeal spots and signalled a low level of quality. The other half of the guards was altered so they had two clypeal spots and signalled a high level of quality. By choosing similar guards and randomly assigning the experimental treatment, I ensured that the only consistent difference between the guards was the number of facial spots. A total of 13 different guards were used across the 178 trials. Individual guard ID was initially included as a random effect in statistical analyses, but explained a negligible amount of

variance in trial outcome. This is important because it means that there was not individual-specific variation among guards that influenced focal wasp choices.

The value of the food resource was experimentally altered by restricting the focal wasp's food access prior to the trial. Three levels of food limitation were used: unrestricted food access before the trial; no food for 1 day before the trial; and no food for 3 days before the trial. As described above, I also used two different types of opponents: 0 facial spots and 2 facial spots. In total, each focal wasp was used in six trials: (i) unrestricted food with 0-spot guard, (ii) unrestricted food with 2-spot guard, (iii) 1-day starvation with 0-spot guard, (iv) 1-day starvation with 2-spot guard, (v) 3-day starvation with 0-spot guard, and (vi) 3-day starvation with 2-spot guard. I randomized the order of the treatments such that one-sixth of the focal wasps started with treatment (i), one-sixth started with treatment (ii), etc. As a result, there was no consistent order bias across treatments. Thirty wasps were used in the trials. Each wasp experienced six treatments, except one individual that died after four treatments. In sum, 178 different trials were performed.

(a) Statistical analysis

A mixed-effects logistic regression model was fitted using STATA (v. 10.0) to test the factors that influence whether or not focal wasps ate the sugar. The fixed effects included in the model were: trial order (from first trial to sixth trial performed by the focal wasp); starvation level (no starvation, 1 day without food and 3 days without food); guard facial pattern (0 spots or 2 spots); and the interaction between starvation level and guard facial pattern. The model also included crossed random effects of focal individual identity and guard identity. Guard identity explained a negligible amount of variance, so I simplified the model to include only the focal wasp random effect. Within wasps that ate the sugar, I tested how these same fixed and random effects influenced (i) latency to eat and (ii) the amount of time focal wasps spent eating. Mixed-effects REML regression models using STATA were used for the analyses with continuous outcomes.

3. RESULTS

The overall model significantly predicted whether or not focal wasps challenged the guard to eat the sugar (Wald $\chi^2=17.40$, $p=0.008$, log likelihood = -109.4). There was a significant interaction between treatment (hunger) and guard facial patterns ($z=-2.39$, $p=0.017$), suggesting that opponent effects were not consistent across treatment conditions. I confirmed that there was a significant interaction between treatments and guards using a Wald interaction test (figure 2; Wald $\chi^2=6.04$, $p<0.05$). The significant interaction term indicates that the effect of hunger level was context dependent rather than being consistent across guard facial patterns. Focal wasps approached 0-spot guards regardless of their hunger level; there was no significant change in probability of eating across hunger levels when focal wasps experienced a 0-spot guard (no starve versus 1 day $z=-0.62$, $p=0.54$; no starve versus 3 days $z=-0.85$, $p=0.395$). However, there was a significant change in eating across hunger levels when focal wasps experienced 2-spot guards (no starve versus 1 day $z=0.41$, $p=0.68$; no starve versus 3 days $z=2.52$, $p=0.012$). Focal wasps were much more likely to approach 2-spot guards after 3 days of starvation

Figure 2. The proportion of focal wasps that challenged the guard for access to the food patch varied with the focal wasp's hunger level and the guard's facial pattern. Wasps were very likely to challenge guards with facial patterns that signalled low quality (0 spots) regardless their hunger level. By contrast, hunger strongly influenced focal wasp behaviour towards guards with facial patterns that signalled high quality (2 spots); hungry wasps were more likely to challenge 2-spot guards than satiated wasps. After 3 days without food, focal wasps challenged guards without regard to the guard's advertised quality; they were equally likely to challenge guards with facial patterns that signalled high or low quality. Filled circles, 0-spot guard; open circles, 2-spot guard.

than after no starvation (figure 2). The guard challenge model also took into account focal wasp ID and trial order. Guard ID was initially included as a random effect in the model. However, guard ID explained a negligible amount of variance, so the model was simplified to exclude it from the final analysis. Focal wasp ID explained some variance in the model, so it was included as a random effect in the final model. A likelihood ratio test demonstrated that focal wasp ID had a marginally significant influence on the probability of eating (LR test versus logistic regression: $\chi^2=2.37$, $p=0.06$), suggesting that individual focal wasp behaviour varied. Finally, treatment order was a significant predictor of whether or not the focal wasp ate ($z=2.03$, $p=0.043$, probability of eating: order 1 = 0.4, order 2 = 0.6, order 3 = 0.67, order 4 = 0.60, order 5 = 0.62, order 6 = 0.68). Although there appeared to be a slight increase in the probability of a focal wasp eating over the trials, trial order was randomized across treatments. Therefore, trial order did not influence the overall experimental outcome. In sum, the results of the eating model support the key experimental prediction. Focal wasps approached 0-spot guards regardless of hunger level, whereas focal wasps were more likely to approach 2-spot guards after experiencing 3 days of starvation.

Within the 106 trials in which wasps ate the sugar, the overall model significantly predicted the time from release until eating (Wald $\chi^2=14.24$, log restricted-likelihood = -318.4, $p=0.03$). The only individual predictor that was statistically significant was hunger level. There was a general decrease in latency to eat as hunger increased (table 1; 0 spot: no starve versus 1 day $z=-1.78$, $p=0.076$; 0 spot: no starve versus 3 days $z=-2.05$, $p=0.04$; 2 spots: no starve versus 1 day $z=-0.12$, $p=0.907$; 2 spots: no starve versus 3 days $z=-2.09$, $p=0.036$). Trial order, guard facial pattern and guard $\times$ treatment interaction were not significant predictors of latency to eat

Table 1. Wasps spent more time eating and had a shorter latency to eat after a prolonged period without food. However, time spent eating and latency to eat did not vary significantly with the guard's facial pattern (mean $\pm$ s.d.).

	latency to eat (min)		time spent eating (min)	
	0-spot guard	2-spot guard	0-spot guard	2-spot guard
unlimited food	7.0 $\pm$ 6.1	8.2 $\pm$ 6.0	1.8 $\pm$ 4.8	1.9 $\pm$ 4.2
1 day without food	4.1 $\pm$ 4.5	7.8 $\pm$ 5.1	5.6 $\pm$ 6.5	2.5 $\pm$ 2.9
3 days without food	3.3 $\pm$ 5.2	3.8 $\pm$ 5.4	11.1 $\pm$ 5.8	11.2 $\pm$ 6.7

(all $p > 0.1$). Although focal wasp ID was not a statistically significant predictor of overall variance in the model ($\chi^2 = 0.39$, $p = 0.2664$), I included focal wasp ID in the model as a random effect because it explained some variance. Guard ID explained negligible variance and was not included in the model as a random effect. Overall, the major predictor of latency to eat was hunger level. Wasps challenged the guard sooner as their hunger increased (table 1).

Within the 106 trials in which wasps ate the sugar, the statistical model significantly predicted the amount of time spent eating (Wald $\chi^2 = 43.03$, log likelihood = -318.6 , $p < 0.0001$). The significance of the model can be attributed to a huge increase in time spent eating as hunger increased (table 1; 0 spot: no starve versus 1 day $z = 1.83$, $p = 0.067$; 0 spot: no starve versus 3 days $z = 4.92$, $p = 0.000$; 2 spots: no starve versus 1 day $z = 0.88$, $p = 0.379$; 2 spots: no starve versus 3 days $z = 4.24$, $p = 0.00$). Order, guard facial pattern and guard by treatment interaction were not significant predictors of time spent eating (all $p > 0.1$). Guard ID and focal wasp ID both explained some of the variance in time spent eating, so both were included as random effects in the model. A likelihood ratio test demonstrated that together, both random effects had a nearly significant influence on the probability of eating (LR test versus logistic regression: $\chi^2 = 5.55$, $p = 0.06$). Therefore, the major predictor of amount of time spent eating was hunger level. Wasps spent more time eating as their hunger increased (table 1).

4. DISCUSSION

Despite long-standing interest in the role of social costs in maintaining signal accuracy, there has been little empirical research on the behavioural mechanisms that mediate social costs. Here, I provide the first experimental evidence that receiver responses to badges are context dependent. Satiated wasps were more likely to approach a guarded food patch if the guard signalled a low level of quality (no black facial spots) than if the guard signalled a high level of quality (two black facial spots). However, after 3 days without food, wasps were equally likely to approach food patches guarded by opponents with high and low quality facial patterns (figure 2). Therefore, receiver responses to badges are context dependent. Individuals trust rival badges during contests over low-value resources, but challenge rivals regardless of badge phenotype when the resource is sufficiently valuable.

Evidence for context-dependent badge responses is particularly interesting because context-dependent responses are hypothesized to be the behavioural mechanism that reconciles the apparently contradictory requirements of the social cost hypothesis. The

evolutionary stability of badges is based on two principles that initially appear to be in conflict. First, receivers must use badges to make decisions about rivals. If receivers do not pay attention to badges, they are not useful signals (Maynard-Smith & Harper 2003; Searcy & Nowicki 2005). At the same time, badge accuracy is thought to be maintained via increased receiver aggression towards individuals with inaccurate signals (Rohwer 1977; Tibbetts & Dale 2004), so the accuracy of the signalling system would breakdown if receivers *always* trust the information conveyed by badges. Consequently, receivers must occasionally test whether badges accurately reflect their bearer's abilities. Both requirements are met if receivers trust badges in certain situations and aggressively test badges in other situations. This study provides experimental evidence that receiver trust is based on the value of the contested resource.

In addition to supporting a basic, previously untested prediction of badge models, these results help clarify why some previous badge research appears to be inconsistent. For example, some studies have shown that individuals with experimentally altered badges rise in status after badge alteration (Fugle & Rothstein 1987; Pryke & Andersson 2003b). In other studies, individuals with altered signals fail to rise in status (Jarvi *et al.* 1987; Møller 1987; Tibbetts & Dale 2004). Although the varying experimental outcomes have produced controversy about badges, they make sense if receiver responses are context dependent. Receiver responses may vary depending on whether or not receivers interact with senders, the length of their interactions and the value of the resource being contested (Maynard-Smith *et al.* 1988; Senar 2006). Therefore, variation in experimental outcomes can be viewed as an important mechanism to maintain signal accuracy rather than an experimental complication. Future research in a range of contexts is key to unifying badge research and developing a more cohesive understanding of the information provided by badges and the role of social costs in maintaining badge accuracy.

(a) *Badges and resource holding potential*

Previous research has defined badges in two different ways, either as signals of aggressive intent or RHP (Searcy & Nowicki 2005). The basis of aggressive intent models is that badges reflect strategies that are at an ESS. As a result, the models predict that there are no uncorrelated asymmetries associated with badge phenotype; that is, individuals with more elaborate badges are not 'better', they are just pursuing a different strategy. The alternative is that badges signal their bearer's fighting ability or RHP. Thus far, theoretical and empirical works are most consistent with badges signalling RHP. First, models predict that signals of RHP are more likely to be

evolutionarily stable than signals of aggressive intent (Johnstone & Norris 1993; Hurd 2006). Second, empirical data suggest that individuals with more elaborate badges are of higher quality than those with less elaborate badges. For example, birds with more elaborate badges tend to be older and larger than those with less elaborate badges (Rohwer 1975; Veiga 1993; Pärt & Qvarnstrom 1997; Nakagawa *et al.* 2007). Wasps with more elaborate badges tend to be larger (Tibbetts & Dale 2004; Tibbetts 2006) and in better physical condition (Tibbetts & Curtis 2007) than those with less elaborate badges. Therefore, badges probably function as signals of RHP.

A number of classical studies have explored the influence of RHP on behavioural dynamics during prolonged aggressive contests (Maynard-Smith & Parker 1976). Typically, the individual with higher RHP is more aggressive and persistent and more likely to win the contest than the individual with lower RHP. This general pattern is consistent with individuals using mutual assessment to establish relative RHP differences among rivals, but recent work suggests that animals may primarily make competitive decisions based on their own abilities (Taylor & Elwood 2003; Prenter *et al.* 2006). In fact, mutual assessment may be relatively uncommon, as it may be too costly or difficult to reliably assess opponent abilities in many taxa.

Badges provide an easily quantified measure of RHP, so mutual assessment of relative RHP is expected to be common in species with badges. This experiment used freshly killed guard wasps to remove the influence of signaller behaviour on the dynamics of pre-contest assessment and to test the effect of signal phenotype on receiver behaviour. The results show that individuals avoid rivals with more elaborate badges but are willing to challenge rivals with less elaborate badges during contests over low-value resources. Therefore, individuals use badges to make informed decisions about rival RHP without costly behavioural interactions.

(b) Resource value

Previous work has also examined the influence of resource value on aggressive contests. Models predict that individuals will be more persistent and more likely to escalate during contests over higher value resources (Enquist & Leimar 1987). Empirical work largely supports this prediction (Bridge *et al.* 2000; Cant *et al.* 2006). For example, hermit crabs (*Pagurus longicarpus*) have more intense fights over optimally sized shells than shells that are too small (Gherardi 2006).

This experiment tested behavioural dynamics before contests, finding that receivers become more likely to challenge opponents as the value of the resource increases. When the resource is sufficiently valuable, receivers apparently ignore the badge; they become just as likely to challenge opponents with high or low RHP. This experiment differs from previously published work on resource value because it tested how resource value influenced whether or not an individual chose to engage in an aggressive contest, while previous work has focused on behaviour during contests and/or the outcome of contests.

Although this experiment differs from previous studies on resource value in animal contests, the results have some similarities that may clarify the evolutionary origin of social costs. The apparent complexity of social costs makes

it intuitively difficult to understand how their evolutionary stability can be maintained via individual-level selection alone. However, social costs based on the incongruence hypothesis (Rohwer 1977) have only three main requirements: (i) receivers must challenge rivals regardless of signal phenotype in certain situations, (ii) receivers must be able to discern signal inaccuracy during a challenge, and (iii) receivers must be more aggressive to individuals when their badge does not reflect their true abilities. The first requirement could be fulfilled by a simple, self-interested decision rule like 'challenge rivals during contests over high-value resources'. The data demonstrate that wasps use this rule during rival assessment. Previous work on resource value and animal contests suggests that the tendency to be more aggressive during fights over valuable resources may also be common in species that lack badges (Enquist & Leimar 1987). The other two aspects of social costs would be satisfied if receivers are more aggressive to rivals when they perceive some incongruence between behaviour and signal. This aggressive testing could be a simple consequence of the receiver's selfish interest in assessing a rival's true abilities; yet, it could also be the cost that maintains signal accuracy. Therefore, social costs could originate from straightforward, self-interested decision rules. Of course, over evolutionary time, these simple behaviours may be shaped by selection to optimize social costs.

Overall, this study provides the first experimental evidence that receiver responses to status badges are based on the value of the contested resource. Receivers avoid rivals with elaborate badges during contests over low-value resources. However, receivers are less likely to trust badges during contests over high-value resources. These results clarify an important behavioural mechanism underlying the evolutionary stability of social costs. Therefore, aggressive receiver behaviour may play an important role in ensuring the accuracy of conventional signals of agonistic ability.

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