Signal residuals during shell fighting in hermit crabs: can costly signals be used deceptively?

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Animals advertise aspects of individual quality in a range of situations including during agonistic contests over access to resources. The advertisement can be produced by different types of signal, which can be broadly classified into "conventional signals" and "costly signals." In both cases, the signals are thought to be honest such that any benefits to cheating are very limited due to prohibitive costs of advertising an inaccurately high level of quality. However, some individuals may benefit by low-level cheating in systems that are otherwise honest. Here, I test this possibility for a costly signal by analyzing residuals from relationships between a key parameter of signal magnitude and two measures of fighting ability from "shell fights" in hermit crabs. Contrary to the expectations for significant use of bluffing, individuals that performed at a greater magnitude than expected for their ability were more likely to win the encounter but used fewer repetitions than those that performed below the level expected for their ability. This indicates that the level of performance is primarily driven by the cost and that the functional significance of signal residuals in this case is that they provide information on several measures of fighting ability. Key words: contest, cost, deception, hermit crab, honesty, signal. [Behav Ecol 17:510–514 (2006)]

Animals use signals to advertise individual quality in a range of situations, including contests over resources. During agonistic encounters, opponents advertise their fighting ability or resource holding potential (RHP) by using "conventional signals" (Hurd, 1997) based on displaying an ornament or with "costly" (Maynard Smith and Harper, 1995) signals by performing an activity, as in hermit crabs (Briffa and Elwood, 2005), crickets (Hack, 1997), and fiddler crabs (Matsumasa and Murai, 2005) for example. For signals to be evolutionarily stable, most instances of signaling must be "honest" with performances that accurately reflect the sender's RHP. Zahavi (1977) argued that the honesty of biological signals could be guaranteed if the costs are correlated with the feature being advertised. On average, it should not be adaptive to produce a signal that indicates an inaccurately high level of quality because the costs of producing that signal would outweigh the potential benefits of an exaggerated advertisement. Although this "handicap principle" of honest signals is often discussed within the framework of sexually selected conventional signals (Hurd, 1997), signals that advertise other aspects of individual quality such as RHP may also be guaranteed by cost, and costly signals as well as conventional signals are expected to be honest (Grafen, 1990; Zahavi, 1977).

Although signals are expected to be honest on average, it is possible that low levels of "cheating" are stable within an otherwise honest population (Adams and Mesterton-Gibbons, 1995; Bond, 1989; Getty, 1997). Cheating is defined as benefiting from an exaggerated advertisement that results from producing an inaccurately high level of the signal. The presence of cheating may be detected by the analysis of residuals from a population-based relationship between a measure of RHP and a measure of signal magnitude (Hughes, 2000). Performances with positive residuals are greater than expected for the sender's RHP, whereas those with negative residuals are lower than expected (see figure 1 in Hughes, 2000). If individuals that exaggerate benefit from doing so, they should perform more repetitions of the signaling activity than those that do not exaggerate (Hughes, 2000). This exaggeration is only possible, however, if the signal residuals do not correlate with competitive ability. Deceptive use of the signal is not predicted in cases where either (1) signal residuals vary between outcomes or (2) individuals with lower than expected signal magnitude perform more or the same number of repetitions than those with positive residuals.

Hughes (2000) demonstrated "incomplete honesty" in the use of chelar displays in the snapping shrimp Alpheus heterochaelis, and similar results were reported in mantis shrimp Gonodactylus oerstedii (Adams and Caldwell, 1990) and fiddler crabs Uca annulipes. In the case of the latter two studies, it was suggested that cheating is possible due to a temporary disparity between the visual appearance of the chelipeds and their actual strength or weight.

Hermit crabs, Pagurus bernhardus, use "shell-rapping" signals to resolve contests over ownership of empty gastropod shells (Briffa and Elwood, 2000a; Briffa et al., 1998, 2003). An individual in a suboptimal shell (either because it is too small or of an unpreferred species) may attempt to evict another individual from its shell if that shell is of higher quality. Attackers initiate a fight by grabbing the defender's shell, and the defender withdraws tightly into its shell. The attacker then performs bouts of shell rapping where it repeatedly strikes the surface of its shell against that of the defender, using its abdominal muscles to provide the power. Shell rapping is performed in a series of bouts that are separated by pauses. After a series of bouts, the contest can end in one of two ways. The defender may make a decision to "give up" and release its grip of its shell, allowing the attacker to evict it by pulling it out through the aperture. Alternatively, the attacker may decide to give up without evicting the defender.

Although it involves direct contact between the two animals, shell-rapping functions as a "repeated signal" advertising the RHP of the attacker (Briffa and Elwood, 2000a,b,c; Briffa et al., 1998). It is an energetically demanding activity (Briffa...
and Elwood, 2001), and the pattern of change in vigor during the fight (Briffa and Elwood, 2000b; Briffa et al., 1998) shows that a crab must function as a signal, its stamina, a key correlate of RHP (Payne and Pagel, 1997). Physiological data show that the level of resistance offered by defenders is based on their perception of the attacker’s RHP (Briffa and Elwood, 2005). Different parameters of the pattern of signaling contribute to the defender’s decision to give up, but the critical feature is the duration of the pauses between the bouts. These are inversely proportional to the attacker’s stamina and thus advertise the attacker’s RHP (Briffa et al., 1998).

The aim of this study is to analyze signal residuals, where the signal is the inverse of pause duration (1/P) in order to determine whether shell rapping can be used deceptively. The relationship between signal magnitude and RHP will be examined for two different measures of RHP: (1) the relative difference in weight (RWD) between attacker and defender and (2) the postcontest lactic acid concentration in attackers, which have both previously been shown to vary with outcome and attacker performance (Briffa and Elwood, 2001; Briffa et al., 1998).

If there is no difference in signal residuals between outcomes and if attackers with positive residuals perform a greater number of bouts, then shell rapping may be used dishonestly. It is important to note that contest duration is determined by the decision of the loser to terminate the contest by giving up rather than by any decision made by the winner. Therefore, the difference in the number of bouts can only be meaningfully tested for in attackers that failed to evict the defender because these attackers decided their own number of performances, whereas in successful attackers the number was determined by the duration of resistance in the defender. By analyzing these signal residuals, it will be possible to determine whether they vary between outcomes and whether the number of performances in attackers that give up varies between attackers with positive and negative signal residuals.

METHODS

Data sets were pooled from four previous studies (Briffa and Elwood, 2000c, 2001, 2002; Briffa et al., 1998) in order to analyze signal residuals. These all involved staged encounters between pairs of crabs, but they drew crabs from two different size classes (small $= 0.16$–0.48 g and large $= 0.9$–2.7 g). Although the distribution of attacker weight was bimodal, the mean relative difference in weight between attacker and defender (RWD), calculated by RWD = 1–(weight of defender/weight of attacker), following Briffa et al. (1998), was not different between the groups (small: $0.316 \pm SE = 0.012$, large: $0.333 \pm SE = 0.01$, $t_{62} = 1.1$, ns) and could thus be used as a continuous measure of RHP. Crabs were collected from Ballywalter and Minsterown, Northern Ireland, and taken to the laboratory in Belfast. Fights were staged by removing the crabs from their shells, by cracking the shell in a bench vice, and then allocating the crabs to pairs comprising a large individual, the potential attacker, and a smaller individual, the potential defender. Only male crabs that were free from recent moult, missing appendages, and obvious parasites were used in the observations. Optimal shell sizes were calculated from regression lines relating crab weight to preferred shell weight, obtained during previous shell-choice experiments (Jackson and Elwood, 1989). In each case, the large crab was supplied with a new shell of the preferred species but only 50% of the preferred size, whereas the small crab was supplied with a shell 100% adequate in size for the corresponding large crab. Thus, by evicting the small crab, attackers could make a substantial gain in shell quality. After a settling period of not less than 16 h, the crabs were transferred to an arena consisting of a crystalizing dish filled with a 1-cm layer of sand and aerated seawater. Observations were conducted behind a one-way mirror such that the observer could not be seen by the crabs. During the fight, the pattern of shell rapping was recorded using a handheld computer configured as a time-event recorder using The Observer 3.0 behavioral software package (1993, Noldus IT bv, Wageningen, The Netherlands). Fights were recorded until they were terminated either by the attacker evicting the defender or the attacker giving up. In all four studies, crabs were only used once before being returned to the sea or sacrificed for lactate analysis.

The combined data sets yielded a total of 364 fights for analysis of which the attacker gave up without evicting the defender in 82 cases. A subsample of 105 fights came from studies where postfight lactic acid was assayed in attackers and, of these, the attacker failed to evict the defender in 38 cases. The data were analyzed using Statview 3.0. Statistical tests were two tailed in all cases. Lactate concentration was performed using a standard enzymatic technique described elsewhere (Briffa and Elwood, 2005). Because postfight lactate is negatively correlated with RHP, the inverse, $1/[lactate]$, was used as the measure of ability.

RESULTS

Relationships between RHP and signal magnitude

Regression analyses were used to determine the relationships between each measure of RHP (independent variable) and 1/P (dependent variable). In both cases, there was a highly significant positive relationship (RWD: $F_{3,358} = 22.99, p < .0001$, $1/[lactate]$: $F_{1,105} = 13.24, p < .0005$) (Figure 1a,b) but a low $R^2$ (RWD: $R^2 = .06$, $1/[lactate]$: $R^2 = .12$) indicating high variance about each relationship.

Differences in signal residuals between outcomes

Unpaired $t$ tests were used to determine whether there was a difference in the two sets of residuals between winners (attackers that evicted the defender) and losers (attackers that gave up without effecting an eviction). In both cases, the residuals of losers were significantly lower than those of winners (RWD versus 1/P: $t_{89} = 7.44, p < .0001$, $1/[lactate]$ versus 1/P: $t_{82} = 3.83, p < .0002$) (Figure 2a,b). A series of one-group $t$ tests showed that all four mean residuals were significantly different from zero, indicating that winner residuals were significantly positive (RWD versus 1/P: mean = +0.003, $t_{278} = 3.35, p < .001$, $1/[lactate]$ versus 1/P: mean = +0.004, $t_{66} = 2.14, p < .05$) and that there was a highly significantly negative direction to loser residuals (RWD versus 1/P: mean = −0.1, $t_{80} = −8.3, p < .0001$, $1/[lactate]$ versus 1/P: mean = −0.007, $t_{56} = −6.15, p < .0001$).

Difference in number of bouts between attackers with positive and negative residuals

The number of bouts performed by attackers with positive and negative residuals, from fights where the attacker failed to evict the defender, was compared with unpaired $t$ tests. Attackers that left shorter pauses than expected for their RWD ($n = 12$) performed fewer bouts than those that left longer pauses than expected ($n = 80$) ($t_{89} = 3.89, p < .0002$) (Figure 3a), whereas there was no difference between the number of bouts performed by attackers with positive ($n = 8$) and negative ($n = 30$) residuals from the relationship between $1/[lactate]$ and the total number of bouts ($t_{55} = 0.89, p = .4$, power = 0.13) (Figure 3b).
DISCUSSION

Use of repeated signals during aggressive interactions is a widespread feature of animal contests. Male red deer, Cervus elephas, for example, perform bouts of vocalizations during contests over access to females (Clutton-Brock and Albon, 1979), as do anurans (e.g., Ryan, 1988) and birds (e.g., Ballintijn and ten Cate, 1999; ten Cate et al., 2002). In all these cases, it has been suggested that the signaling activity is energetically demanding and, therefore, costly to perform. The aim of the present study was to determine whether such costly signals could be used deceptively. In the shell fights I analyzed, signal magnitude (1/P) increased significantly with both measures of RHP (RWD and 1/[lactate]), but in each case, there was a large amount of variation around the relationship (Figure 1). Nevertheless, it appears that deception, by performing an inaccurately high level of the shell-rapping signal, is not a feature of these contests.

Although successful attackers on average performed significantly better than would be expected according to either measure of RHP (Figure 2), attackers that gave up performed significantly worse than expected. Furthermore, the negative deviation from the expected signal magnitude in this group was far greater than the positive deviation seen in successful attackers (Figure 2). Thus, it appears that it is only possible for successful attackers to achieve small increases in signal magnitude. By contrast, the performance of those attackers that failed to effect an eviction fell far below that expected for their RHP. Thus, positive signal residuals are unlikely to exaggerate the perceived ability of the attacker because signal residuals correlate closely with the attacker’s competitive ability. Furthermore, if significant levels of cheating were a feature of this system, we would expect to see those unsuccessful attackers that performed with greater than expected vigor performing more bouts before giving up than those showing negative signal residuals (Hughes, 2000), but this was not the case (Figure 3).

In the analysis based on postfight lactate, there was no difference in the number of bouts, whereas in the case of residuals derived from RWD, the opposite pattern is seen with attackers that leave shorter than expected pauses performing fewer bouts than those with negative residuals (Figure 3). It has been previously noted that variation in the pattern of rapping during the fight can both escalate and de-escalate, depending on the outcome (Briffa et al., 1998), and this pattern of variation in signal magnitude fits some of the predictions of an energetic war of attrition model of repeated signals (E-WOA) where the signals are assumed to advertise stamina (Payne and Pagel, 1997). Of the attackers that give up, those that perform at a level higher than expected for the weight difference between the two roles (RWD) do not persist for as
As noted above, in addition to agonistic encounters, costly signals are used in other situations such as courtship, for example, abdominal drumming in wolf spiders (Kotiaho et al., 1998) and displays in frigate birds (Dearborn et al., 2005). If the relations between signal residuals, contest outcomes, and the number of repetitions are similar to those seen in the present analysis, it is unlikely that such signals are easy to bluff or that individuals that signal at a higher than expected rate gain any benefits from doing so. Even in the case of conventional signals, the costs associated with bluffing appear to be prohibitive. In sparrows, for example, experimental elevation of rank results in high costs in terms of increased risk of injury (Moller, 1988). Perhaps then, the incomplete honesty described during contests in mantis shrimp (Adams and Caldwell, 1990) and fiddler crabs (Backwell et al., 2000) is most likely in cases where there is a temporary disparity in relations between the visual appearance of an appendage used in displays and true fighting ability. Previous studies on signal honesty have focussed on conventional signals (e.g., Moller, 1988) rather than signals given by performance of a demanding activity, but the present data show that any benefits to exaggerating the shell-rapping signal must be extremely limited. Indeed, individuals that signal with a greater than expected magnitude also give up sooner than expected (Figure 3).

There are several interpretations of the handicap principle (Grafen, 1990), and costly signals may act as “strategic choice handicaps” where the cost varies between individuals and encounters and senders “choose” the cost they are prepared to pay. Previous studies suggest that shell rapping could work in this way as attackers that give up have high lactic acid levels (Briffa and Elwood, 2001), such that the lactate accumulation represents the “cost” they are prepared to pay. An alternative explanation, however, is that high lactate causes a giving up decision because it prevents effective rapping (Briffa and Elwood, 2005). In order to test this, it would be necessary to monitor energy use, for example, by respirometry, during the contest rather than measuring accumulated costs at the end of the contest. Further questions arise from the problem of multiple factors that may contribute to signal magnitude and from the possibility that several signal components may contribute to the overall signal. In costly signals, where the magnitude is given by the rate of performance of an activity, the situation is clearly more complex than in the case of conventional signals given by display of an ornament or weapon.

Shell rapping, however, is evidently an energetically demanding activity (Briffa and Elwood, 2001, 2002, 2004, 2005), and pause duration has consistently been shown to be the critical feature that determines attacker success but it increases during the encounter. The high metabolic costs have been shown to limit the agonistic ability of attackers (Briffa and Elwood, 2005) and may make physical eviction of a resisting defender more difficult. Thus, attackers could potentially benefit from exaggerating their RHP, but the present analysis suggests that the signal is unlikely to be used in this way. Analysis of residuals from other examples of costly signals used during fights can potentially reveal whether an absence of significant exaggeration is a typical feature of such systems.

I thank Jon M. Russ and two anonymous referees for comments on an earlier version of the manuscript.

REFERENCES


Figure 3
The effect of direction of residuals from the relationships between (a) RWD and 1/P and (b) postfight lactate and 1/P on the total number of bouts performed by unsuccessful attackers (no eviction) before deciding to give up. Different symbols above means denote a significant difference.


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