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How Often Do Animals Lie about Their Intentions? An Experimental Test

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abstract: During conflicts, animals may perform displays that convey information about their future antagonistic behavior. Although theory once predicted that such signals of "intent" would be utterly susceptible to dishonesty, empirical studies have established that animals sometimes do signal their intentions. It remains unclear, however, what level of honesty exists within such signals. Here I report interactive-model experiments designed to expose instances of falsified intent and to reveal how frequently signalers within an invertebrate population lie about their impending hostile actions. Hermit crabs (*Pagurus bernhardus*) were given the opportunity to aggressively threaten an approaching model, and their subsequent behavior was then examined after the model fled from them or probed them to the point of imminent collision. Discrepancies between an individual's advertised intention and what it actually did next were infrequent. If the model fled, nearly all crabs remained in place, regardless of whether they had initially threatened. If the model probed, crabs that threatened reliably stood their ground, thus backing up their threat, whereas those that did not threaten tended to back down and retreat. Much of what has been regarded as "lying about intent" in prior nonexperimental studies may actually represent uncontrolled noise, especially recipient-response dynamics.

Keywords: truthful signaling, honesty, bluffing, intervening contingencies, cues.

Introduction

Unlike most communication signals, whose messages are delineated on the basis of the context that occurs during signal production, signals of intent convey messages about contexts that have not yet occurred at the time the signal is produced. Many threat displays, for example, appear to transmit information about whether a signaler will aggress subsequent to its performance of the threat (Maynard Smith 1982*b*; Bradbury and Vehrencamp 1998). Such signals present an important dilemma for theorists interested in the stability of honest signaling: individuals could readily lie about their intentions, for instance, by signaling they were prepared to attack when in actuality they were not, and, as a consequence of such lying, some individuals could gain an advantage over their rivals during conflicts (Johnstone 1998; Maynard Smith and Harper 2003). Moreover, since many signals of intent involve only minor postural alterations, having evolved from what ethologists term "intention movements" (Hinde 1981), these signals possess few or no production costs to prevent them from being used deceitfully. Theoretical analyses therefore suggested early on (Maynard Smith 1974, 1979, 1982*a*) that signals of intent would be especially prone to dishonesty: these signals effectively permitted individuals to say one thing in the present but then do another in a forthcoming context.

In the decades since these early predictions of evolutionary game theory, observational studies of natural interactions have established that signals of intent are far from being completely corrupt: full-blown dishonesty would require that no relationship whatsoever exist between displays and subsequent behavior (Moynihan 1982), and data from invertebrates, fish, birds, and primates have shown instead that at least some information is in fact conveyed on intent across a broad array of animal species (e.g., Hazlett and Bossert 1965; Nelson 1984; Enquist et al. 1985; Waas 1991*b*; Adamo and Hanlon 1996; Laidre 2005). However, at present it is still unclear just how pervasive dishonesty is within signals of intent (Searcy and Nowicki 2005). Observational studies have reported relatively weak and imperfect relationships between signals and specific subsequent actions. But this imprecision need not be due to dishonesty (cf. Caryl 1979); it might instead be attributable to "noise." Noise can be generated by any variables that intervene between the instant of signal production and the eventual manifestation of the signaler's next act. For example, the recipient's response to a signal—fleeing—might preclude the need for the signaler to attack (van Rhijn 1980). As a consequence, threats might only occasionally predict follow-up aggression, even if dishon-

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esty is completely absent. Other important intervening variables exist in addition to how the recipient responds, such as the distance between signalers and recipients during their interaction (Paton 1986), the time interval between signal production and measurement of the signaler's next act (Searcy et al. 2006; Laidre and Vehrencamp 2008), and the possibility that signalers behave differently with different recipients, some of which they may already be familiar with (van Rhijn and Vodegel 1980; Silk et al. 2000). Given the difficulty of simultaneously controlling all of these potentially confounding variables when analyzing sequences of natural interaction (Hurd and Enquist 2001), another more powerful method exists for disentangling dishonesty from noise. This is an experimental approach, in which the interactions themselves are simulated using a model recipient.

Only three prior studies have carried out simulated experiments on intent by using model recipients. Recently, Searcy and colleagues (Searcy et al. 2006; Ballentine et al. 2008) used interactive playback in combination with a stationary taxidermic mount to simulate territorial intrusion in song sparrows and swamp sparrows, examining the reliability of song in predicting attack. The lack of realistic movement by the model in these experiments may have limited the strength of signal reliability, and, at least in the first study, substantial variation existed in birds' singing and subsequent behavioral strategies, with most parameters of song being poor predictors of aggression. A second study that experimentally measured intent did incorporate model movements (Waas 1991*a*, 2006). In this study playback was used to elicit threat calls in little blue penguins, and a stuffed model was then moved toward signalers to determine the extent to which their initial calls predicted aggression. The choice of call indeed revealed how likely penguins were to peck the model, suggesting that, in general, penguins were honest about their intentions. However, because penguins were tested within the confines of their burrow—whose only entrance or exit was blocked by the intruding model—they were effectively "cornered." As such there was no opportunity for a focal penguin to back out of fighting and run away subsequent to an otherwise intense threat call. Such postdisplay flight is important because it can be a useful operational indicator of lying (cf. Caldwell 1986).

This study attempts to build on Waas's and Searcy and colleagues' pioneering experiments, developing a methodology that might be used to estimate how often animals lie about their intentions. The underlying logic is that it should be possible to unveil instances of lying by engaging animals in simulated interactions that specifically inspect for mismatches between their advertised aggressive intention and their actual subsequent behavior. Lying about intent was broadly defined by Maynard Smith (1982*a*, p. 3) as follows: "If, in some species, signal *a* is usually followed by action *A*, then an animal which signals *a* but does not perform *A* can be said to be lying." This general definition can be tailored more specifically to aggressive threat displays, whose meaning is thought to implicate forthcoming hostility and antagonistic opposition (Bradbury and Vehrencamp 1998). With such displays, a signaler's intent could be tested by putting the signaler in a situation where it is compelled to back up its threat (by holding its ground) but where it still has the option of backing down. If simulated interactions are used, an operational definition of lying and truthfulness could then be applied as follows. Live signalers could be confronted (effectively have their threat "called") by a model recipient: the model would probe the signaler, escalating to the point of imminent physical contact shortly after the signaler made its choice of whether to display. Evidence for truthfulness would then entail a signaler (1) threatening and then subsequently either attacking or standing its ground after its threat was called (fig. 1, *endpoint b*) or (2) refraining from threatening, thereby making no attempt at exaggerating its aggressive intentions in the first place. Conversely, evidence for lying would entail a signaler threatening and then subsequently retreating after its threat was called (fig. 1, *endpoint a*). Applying this framework to natural animal signaling systems can enable a more fine-grained measure of the extent to which dishonesty exists in signals of intent. Notably, if such simulated experiments show that signalers consistently back up their threats when challenged—by standing their ground and therefore remaining committed to subsequent conflict—it would underscore the importance of experimentally controlling recipient-response dynamics if researchers are to obtain accurate estimates of signal reliability.

Hermit crabs (*Pagurus bernhardus*) provide a useful system to apply this basic paradigm and also to control for some of the factors that may have partially confounded prior studies of intent. First, data on natural interactions in *P. bernhardus* have shown that its threat displays—which involve raising the cheliped weaponry outward toward an adversary (see fig. 2)—advertise a displayer's intended next move (Hazlett and Bossert 1965) and frequently escalate to physical clashes (Laidre 2007). Moreover, in experiments in which crabs' personal risk was heightened, making it costly to escalate a conflict, individuals refrained from threatening (Laidre 2007). There is thus an a priori basis for assuming that the message conveyed by *P. bernhardus*'s displays is one of pending aggression and future hostile opposition. Second, unlike other systems (e.g., Waas 1991*b*), *P. bernhardus* does not possess a complex ladder of intermediary displays leading up to physical attack: its displays directly preface aggression, and so the

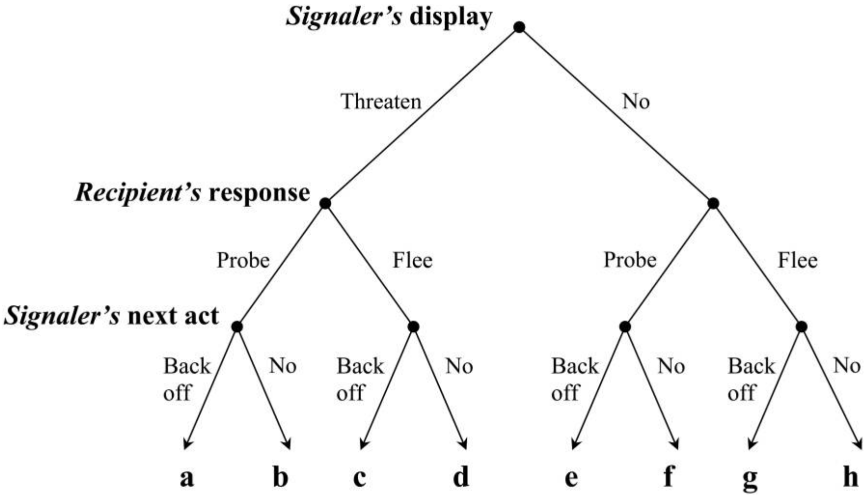

Figure 1: Schematic tree diagram of the dynamics of interaction between a signaler and a recipient. The sequence starts with the signaler either performing or not performing a threat, is followed by the recipient either probing or fleeing from the signaler, and ends with the signaler either backing down or standing its ground. The letters *a*–*h* denote the frequency with which particular sequences of the tree are traversed.

above operational definitions of truthfulness and lying are applicable. Third, *P. bernhardus* is known to respond to postured models as if they were live conspecifics (Hazlett 1968; Laidre 2007; Laidre and Elwood 2008), facilitating a simulated interaction approach. Finally, the opportunity for signalers to escape after a model probes them can readily be incorporated, as can three other design features suggested by Laidre and Vehrencamp (2008): the model can be postured in a threat pose, the model can be dynamically interactive (moving either toward or away from the signaler), and the demonstration of intent can be measured in the shortest possible time window (immediately after the model is moved).

The specific objectives of this study were fourfold. The first objective was to determine whether a signaler's subsequent behavior was strongly contingent on the response of the model (which either fled from or probed the signaler). Variation in recipient responses may be a major "noise" contributor that prevents a fine-grained measure of intent in natural interactions, though many prior studies have ignored this possibility in analyzing data. The second objective was to experimentally establish how often hermit crabs lied about their intentions (i.e., displayed as if they would behave aggressively, by threatening, but then retreated once they were probed). Assuming that at least some dishonesty coexists alongside honesty within the signaling system, the third objective was to determine whether liars were in any way distinct from the rest of the signaler population. Recent studies of lying in other animals (e.g., Hughes 2000) have suggested that smaller individuals may be differentially responsible for dishonesty. Yet it may also be possible that, at least in some cases, smaller individuals are not signaling dishonestly but are instead using cues to convey a different type of message (such as their intention to avert conflict rather than to aggress). Thus, the final objective of the study was to examine the possible importance of cues in modifying the meaning of signals of intent.

Methods

Field Collection and Crab Selection

Hermit crabs were collected weekly during July and August 2007 from tide pools off the coast of County Down, Northern Ireland, near the town of Ballywalter. The crabs were driven back to the laboratory, where all experiments were carried out, and after being used in the experiments, they were returned unharmed to the shore. Only crabs that were not molting, that had all appendages intact, and that were not otherwise injured were tested. These individuals were thus all physically capable of aggressing against a live conspecific or a model.

Model Construction

The model was constructed as follows. I first froze a naked crab (a medium-sized individual of 0.20 g), so that its body would be completely intact. The crab was then thawed under a lamp while I shaped its exoskeleton into the desired pose and placed its abdomen inside an appropriately sized shell. After the crab had dried for 1 h, I

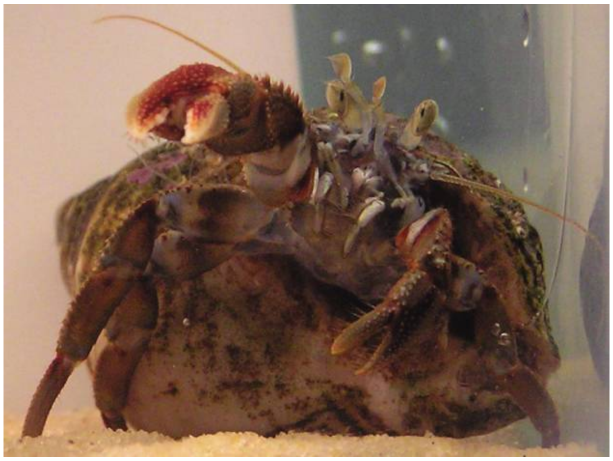

Figure 2: Hermit crab (*Pagurus bernhardus*) performing a cheliped threat display.

used clear waterproof glue (Loctite control gel) to bond its abdomen inside the shell and to hold its joints in a right cheliped extension threat pose. (Prior work conducted using models in nonthreat poses showed that such models failed to elicit threat in more than 100 live crabs.) A clear straw was then glued to the back of the model's shell, so that the model could be presented from a distance. Control presentations in which only the straw was presented failed to produce any consistent response other than no behavioral change at all; the model itself was the salient stimulus.

Experimental Setup and Model Presentations

Crabs were introduced in groups of 30 into a plastic arena (45 cm × 75 cm, 8 cm high) that was roughly the size of a small tide pool in the field and filled with approximately 20 L of seawater. Immediately following their introduction, crabs were observed while they explored the arena for 15 min, after which time they began to settle into specific spots usually several centimeters apart from one another. In natural interactions, both in the field and in the laboratory, hermit crabs will aggressively maintain individual distances (Hazlett 1975). As a consequence, when one crab invades another's personal space, it can precipitate a threat from the approached crab that may then lead to actual aggression. The interactive-model experiments were meant to simulate this type of interaction, with the model functioning as the invader.

The model presentations worked as follows. After finding a crab that was stationary and neither interacting with nor being approached by other crabs, I zoomed my video camera in on it and began recording. By videoing all trials, I could focus solely on controlling the model's movements and then later code the live crab's behavior from the recordings, which were made with a Sony digital video camera (Handycam model DCR-HC26). Before being introduced into the arena, the model was randomly allocated to either a "prober" or a "fleer" condition. In both conditions the model was introduced 10 cm from the focal crab and was then moved toward the crab at a normal approach rate (1 cm/s). After the model arrived at a distance 2 cm from the anterior of the focal crab—which in natural encounters is the threshold that precipitates aggressive interactions—the model was kept stationary for 2 s. This gave the live crab an opportunity to threaten the model by presenting or extending its cheliped. Following the 2-s pause and regardless of whether the crab threatened, the model was then moved either 1 cm forward (the prober condition) or 1 cm backward (the fleer condition). The model was then left in place for another 2 s, giving the live crab the opportunity to exhibit immediate subsequent behavior (fig. 1 provides a schematic of this interaction sequence; an example video clip can be found in video 1, available in the online edition of the *American Naturalist*).

To check for any potential bias (in which the movement of the model was faster or slower if live crabs exhibited certain behaviors), I quantified the times of all model presentations and compared these in relation to each of the different behaviors exhibited by live crabs. I did not find any significant differences in the model presentation times across different live crab behaviors. For example, there was no difference in the time of the model's initial 8-cm approach between threateners versus nonthreateners (threat-

Video 1: Still photograph from a video (available in the online edition of the *American Naturalist*) depicting a live crab displaying at and then attacking a probing model.

eners: 8.9 ± 0.2 s; nonthreateners: 8.9 ± 0.2 s; $t = 0.15$, df = 202, $P = .88$). For crabs that were subsequently probed, there was no difference in the time of the model's 1-cm probe between individuals that (*a*) threatened versus did not threaten (threateners: 1.1 ± 0.1 s; nonthreateners: 1.1 ± 0.1 s; $t = 0.54$, df = 98, $P = .59$), (*b*) attacked versus did not attack (attackers: 1.1 ± 0.1 s; nonattackers: 1.1 ± 0.1 s; $t = 0.52$, df = 98, $P = .61$), or (*c*) retreated versus did not retreat (retreaters: 1.1 ± 0.1 s; nonretreaters: 1.1 ± 0.1 s; $t = 0.87$, df = 98, $P = .39$). There was therefore no evidence that any bias existed in the model presentations.

Each live crab was tested individually against the same model; after interacting with the model, the tested crab was then removed from the arena and was placed in an individually labeled dish for future weighing and sexing. Between trials the model was thoroughly washed to eliminate any potential chemical cues from prior interactions (see Briffa and Williams 2006). All individuals within a given group of 30 were tested. The timing and distance-based features of the simulated interactions paralleled those observed in natural interactions. In a few cases, focal crabs avoided the model before it had reached the specified 2-cm approach criteria; these crabs were removed from the arena and were not considered in the analyses. In total, 204 crabs were successfully tested and included in the analyses.

Measurement of Intent and Statistical Analyses

Signaling of intent consists of essentially a three-step process involving the initial signal produced by the signaler, the response of the recipient, and, finally, the signaler's subsequent action (Hurd and Enquist 2001). In the present experiments, a hermit crab signaler either threatened or did not, the model then either fled or probed, and the signaler then exhibited one of three alternative forms of subsequent behavior: "attack" (defined as initiating physical contact, typically a pinch or a strike), "stand one's ground" (defined as remaining in place but not attacking), or "retreat" (defined as moving away or withdrawing into one's shell). Intent can be measured as the pairing between a signaler's initial signal and the subsequent behavior it performs.

I first confirmed that threatening and not threatening conveyed different messages, the former indicative of aggression and the latter not. I then examined whether subsequent behaviors (attacking, standing one's ground, and retreating) were contingent on recipient response. I used χ^2 tests to compare the differences in threateners' and nonthreateners' subsequent behavior when the model fled versus when it probed. All statistical tests were two tailed.

Hermit crab cheliped threat displays have sometimes been divided into two categories, cheliped "extensions" and "presentations," despite the fact that these signals grade into each other. In this study, no differences were detected in what cheliped extension and presentation predicted about crabs' future behavior (attacking and staying vs. retreating) in the overall sample ($\chi^2 = 0.79$, df = 1, $P = .37$), in the sample in which the model probed ($\chi^2 = 1.69$, df = 1, $P = .19$), or in the sample in which the model fled ($\chi^2 = 0.40$, df = 1, $P = .53$). In the results, therefore, these displays are grouped together as "threats."

Verification of intent was possible only in crabs that were probed because these were the individuals that were effectively forced to "show their cards" and demonstrate whether they were really telling the truth about their future aggressive actions. Therefore, when only individuals that were probed are considered, liars were defined as those that threatened and then subsequently retreated, whereas honest individuals were defined as those that threatened and then subsequently attacked or stood their ground. Other individuals that were probed but that did not initially threaten were defined as honest because they made no attempt to exaggerate their likelihood of attacking—and it is such exaggeration that is the mode of dishonesty predicted by theory (Maynard Smith 1982*a*). The level of dishonesty was thus calculated as the number of liars out of all crabs that were probed (i.e., fig. 1, $a/[a + b + e + f]$).

During video analyses, I also looked for possible cues that might co-occur with threats during signal production, potentially altering their meaning. For instance, threats performed while the signaler is backing up slightly might be "defensive" threats rather than "offensive" threats (Wilson 1975), conveying information on retreat rather than attack likelihood. Given such cues, I reexamined the level of dishonesty to see whether the calculated level could be even lower.

Results

Initial and Subsequent Behavior

Less than half of all crabs (41.7% of $N = 204$) threatened; the rest of the crabs kept their chelipeds tucked beneath their ventral region in the normal resting posture. There was no significant difference in weight between threateners and nonthreateners (weight of threateners: 0.238 ± 0.016 g; weight of nonthreateners: 0.268 ± 0.017 g; $t = 1.26$, df = 202, $P = .21$). Moreover, individuals of superior weight (relative to the model) were not more likely to threaten than those of inferior weight: of the $N = 96$ individuals that weighed less than the model, 51.0% threatened, whereas of the $N = 108$ individuals that weighed

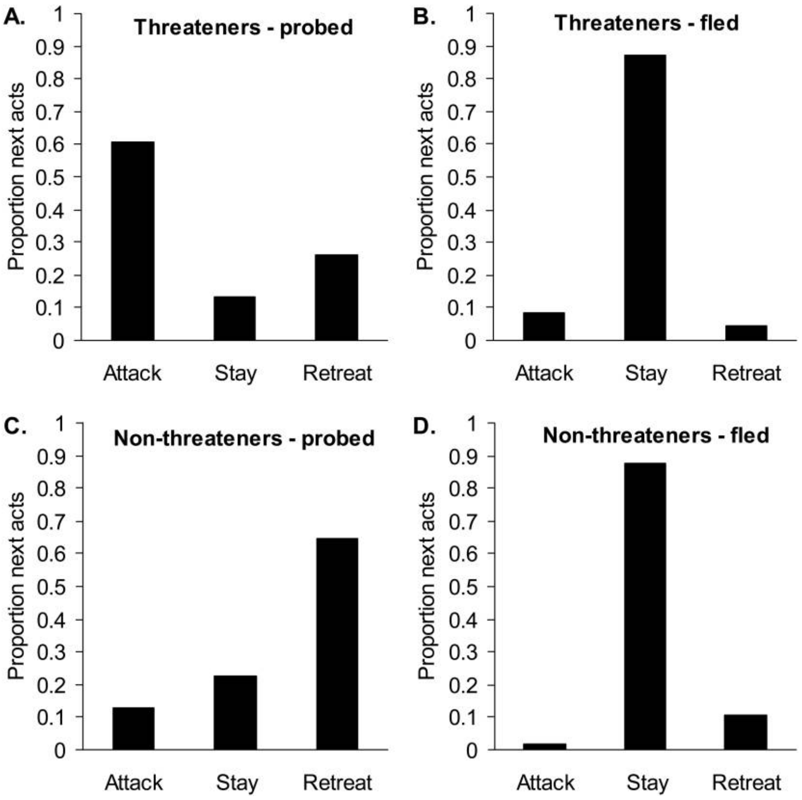

Figure 3: Proportion of crabs whose subsequent behavior involved attacking, standing their ground, or retreating from a model if (*A*) they displayed and the model then probed them ($N = 38$), (*B*) they displayed and the model then fled from them ($N = 47$), (*C*) they did not display and the model then probed them ($N = 62$), and (*D*) they did not display and the model then fled from them ($N = 57$).

more than the model, only 32.4% threatened (one crab was exactly equal in weight to the model and was included in the latter category; $\chi^2 = 6.54$, df = 1, $P = .01$). Also, the number of individuals from each sex did not differ between threateners and nonthreateners (sex ratio of threateners: 0.55 male/female; sex ratio of nonthreateners: 0.86 male/female; $\chi^2 = 2.01$, df = 1, $P = .16$). Thus, no evidence existed to suggest that the act of threatening was specific to one or the other sex or that threatening was performed only by individuals with a certain absolute or relative level of resource-holding potential.

In contrast, there was strong evidence to suggest that the act of threatening conveyed information about crabs' intentions. In particular, crabs' initial signaling behavior (threatening vs. not) was not independent of their post-signaling behavior (attacking vs. staying vs. retreating): individuals that threatened were more likely to attack, whereas individuals that did not threaten were more likely to retreat ($\chi^2 = 27.0$, df = 2, $P < .0001$; fig. 3). Moreover, most of the attacks that occurred (75.0% of $N = 36$) were preceded by a threat, whereas most of the retreats that occurred (79.3% of $N = 58$) were preceded by the absence of a threat ($\chi^2 = 24.8$, df = 1, $P < .0001$).

Effect of Model's Response

Crabs' subsequent actions were strongly contingent on the model's response: threateners were more likely to attack if the model probed them rather than fled from them ($\chi^2 = 46.5$, df = 2, $P < .0001$; fig. 3*A*, 3*B*), whereas nonthreateners were more likely to retreat if the model probed them rather than fled from them ($\chi^2 = 50.7$, df = 2, $P < .0001$; fig. 3*C*, 3*D*). Most of the differences in crabs' subsequent actions between the prober and the fleer conditions were based on an increase in the number of individuals that stayed when the model fled: just under 90% of both threateners and nonthreateners remained in place if the model fled (fig. 3*B*, 3*D*). Interestingly, the ratio of attackers to retreaters remained similar when the model probed versus fled: among threateners, there were two

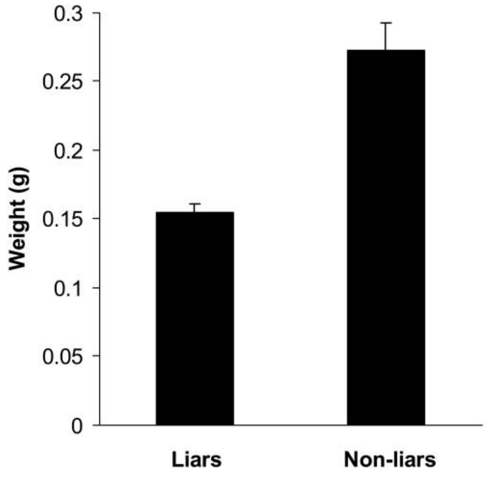

Figure 4: Weight of liars ($N = 10$) and nonliars ($N = 90$). Mean + SE is shown.

times as many attackers as retreaters in both the prober and the fleer conditions, and among nonthreateners, there were five times as many retreaters as attackers in both the prober and the fleer conditions.

Liars and Possible Message-Altering Cues

In spite of the strong overall reliability of threats, scope for dishonesty still existed. Ten out of the 100 crabs that were probed were operationally "liars" because these 10 individuals threatened but then retreated rather than attacking or standing their ground.

Liars were distinguishable from nonliars: they weighed significantly less and were more than 40% lighter in mass on average ($t = 2.03$, df = 98, $P = .0447$; fig. 4). The number of liars, however, may actually have been even lower than the calculated 10 individuals. This is because the threats that liars produced were sometimes given with a possible cue that appeared to alter the signal's meaning: instead of remaining stationary in bodily position, threateners sometimes backed up during the performance of their threat, moving one or more body lengths away right as the model reached the 2-cm approach criterion. This backing-up cue appeared to change the threat's message from an offensive to a defensive version: of threateners that were probed, those that paired their threat with a backing-up movement were more likely to subsequently retreat than to attack ($\chi^2 = 5.09$, df = 1, $P = .0241$; fig. 5). When the backing-up cue was taken into account, the number of liars was reduced to just three individuals, or to a 3% level of dishonesty.

Discussion

Theoretical views on animal communication have oscillated dramatically over the past several decades. Originally considered a harmonious and cooperative exchange of information (Cullen 1966; Smith 1977), signaling among animals was regarded more skeptically following the application of evolutionary game theory (Maynard Smith 1974, 1979). Game-theoretic analyses suggested that lying mutants could invade otherwise honest populations, eventually destabilizing the communication system: recipients would then no longer even bother attending to signals, and the signals themselves might ultimately fall into disuse (Andersson 1980; Maynard Smith 1982*b*). Proposals such as the "handicap principal," however, provided a possible solution to this problem of downward-spiraling corruption: honesty might prevail due to signaling costs, which nullified the incentives for cheating and which guaranteed that only reliable information was transmitted (Zahavi 1977; Grafen 1990). Yet recent mathematical models have shown that even when such costs exist, large-scale deception can nevertheless persist within signaling systems (e.g., Adams and Mesterton-Gibbons 1995; Számadó 2000; Rowell et al. 2006). Indeed, it is entirely possible that the relative occurrence of dishonesty may far outstrip that of honesty and such systems may still remain evolutionarily stable (Számadó 2000). Empirical studies are thus critical in that they can establish more precisely the actual levels of dishonesty found within natural populations.

In this study of intent, honesty was said to occur if a signaler stood its ground or attacked after its threat was called or if a signaler altogether refrained from threatening,

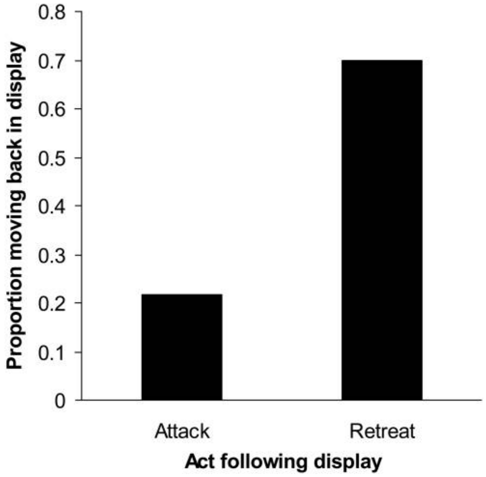

Figure 5: Proportion of crabs whose threat display was performed while they were moving backward and who, after being probed, then either attacked ($N = 23$) or retreated ($N = 10$).

thus making no attempt to exaggerate its aggressive intentions. The results showed that, given this basic definition (cf. Maynard Smith 1982*a*), lying occurred very rarely. Specifically, of all individuals that were probed, only 10% subsequently retreated after giving a threat.

Moreover, these few apparent "liars" may not all have actually been lying: these individuals tended to exhibit cues that could have altered the message conveyed by their signals. When these individuals backed up at the instant of threat performance, their threats may have taken on a defensive rather than an offensive meaning (Wilson 1975), predicting the signaler's intention to retreat if provoked further. Hence, some of the observed "dishonesty" could be explained on the basis of message-modifying cues that co-occurred with displays, winnowing down the level of lying to a mere 3%. Overall, therefore, signals of intent in hermit crabs appear to be very reliable predictors of subsequent behavior, despite the inherent conflict of interest between communicating rivals. Future studies employing an interactive-model technique with several models—each matched to the size of every live individual—could yield even stronger measures of reliability.

Recent estimates of the occurrence of dishonesty in signals of fighting ability have suggested that, in some instances, more than 40% of signals may be deceitful (Backwell et al. 2000; Wilson et al. 2007; see also Steger and Caldwell 1983; Adams and Caldwell 1990; Hughes 2000). Although these estimates are not directly comparable to signals of intent in hermit crabs (given the limited phylogenetic affinities), it is nevertheless notable that, in conflict circumstances, signals of intent can be as equally reliable as or even more reliable than some signals of fighting ability. Early theoretical conjectures (Maynard Smith 1974, 1979, 1982*a*, 1982*b*) were thus clearly mistaken in predicting that dishonesty would necessarily attain a higher level in signals of intent compared with signals of fighting ability. But what accounts for the relative infrequency with which hermit crabs lie about their future actions compared with how often some other crustaceans, such as fiddler crabs (Backwell et al. 2000) and crayfish (Wilson et al. 2007), lie about their fighting ability?

A major factor contributing to these variable levels of dishonesty may be the frequency of aggressive probing. If individuals produce a signal that is unrepresentative of their underlying bodily state or their genuine intention, there is a chance that they may be physically tested by a recipient. And when such checks are frequent or injurious enough, then lying may be a perilous strategy (Enquist 1985; Markl 1985). In hermit crabs, potentially damaging physical contact occurs commonly after displays, more than 30% of the time after just one crab within a dyad threatens and more than 70% of the time after both crabs within a dyad threaten (Laidre 2007). Crabs that were unprepared to follow through with their advertised offensive intentions would thus risk being harmed relatively often. In contrast, in Wilson et al.'s (2007, p. 285) study of dishonest signals of strength in crayfish, direct physical contact reportedly occurred "only in a small proportion of interactions." In fiddler crabs as well, probing appears to be less frequent because a large portion of the recipient population consists of females who never physically challenge male signalers. Given this reduced chance of being probed, both crayfish and fiddler crabs may have greater opportunity to misrepresent their signals.

Probing, however, is generally thought to be a costly endeavor for recipients (Dawkins and Guilford 1991): by coming within striking range of an opponent, a recipient may risk being wounded in the process of executing a probe. Why then do hermit crabs engage in probing so frequently? One reason may be due to their peculiar natural history. Hermit crabs inhabit portable, externally derived shelters: the shells of gastropods (Hazlett 1981). A well-outfitted recipient, embedded in its shell, therefore possesses the equivalent of a protective suit of armor as it confronts a signaling conspecific. A signaler, in contrast, even if likewise possessing a shell, must extend itself far out of this protective encasing to perform a display, which can make it more vulnerable to attack and injury (Laidre 2007). For a signaler that had no intention of aggressing, it is therefore likely that the expected cost of being attacked by a probing recipient would outweigh the value of the resource that was being disputed (in this study, personal space). This high cost-to-benefit ratio may explain why the strategy of threatening was employed by a minority of crabs: in circumstances where the value of the resource is low relative to the potentially costly consequences of signaling, attempts at lying would be unprofitable and thus should be rare (Maynard Smith and Harper 2003; Stenseth and Sætre 2004).

Given the low incidence of dishonesty within signals of intent in hermit crabs, are signals of intent in other animals as reliable? Too few controlled experiments have been conducted to date to answer this question definitively. However, it remains possible that signals of intent are generally more reliable than data from natural observation have so far suggested. This is for at least two reasons. First, cues have rarely been explicitly examined in prior studies of intent (Caryl 1982; for an exception see Waas 1991*a*, which presents display categories such as "distance reducing" and "stationary"). If cues are commonly produced alongside other species' signals of intent, then taking them into account could enable more accurate measures of intent, even outside of an experimental context. In this study, for instance, it was the lightweight individuals in the population who made use of the backing-up cue while threatening. Although initially classified as "liars" (because their threats predicted retreat), these smaller individuals would presumably be inclined to avert rather than incite conflict: their reduced size would make the cost of being retaliated against even more severe. Thus, by combining a threat signal with slight backward movement, individuals may effectively convey an alternative—but still honest—intention: their readiness to retreat. Another possibility, however, is that backing up while threatening is a form of "bet hedging" in which smaller individuals attempt to reduce the risk of retaliation during deception. Further research examining the extent to which recipients actually pick up on the backing-up cue might help distinguish these possibilities.

In addition to variables that co-occur with signals, variables that intervene between a signaler's display and its next act may likewise deflate the reliability of signals of intent. These critical noise-generating variables have generally not been taken into account in prior analyses (see "Introduction"). Caryl (1979, p. 142), for example, set an unfortunate trend that has persisted in many later studies in which researchers assume that "between the moment when [a signaler] makes a display and the moment when it attacks, flees, or stays, the world stands still." Such an assumption neglects potentially important intervening variables, one of which (recipient response) was explicitly examined in this study. By having the model either flee or probe following a signaler's initial act, it was possible to determine the influence of this response on what the signaler did next. When the model fled, threateners almost never attacked, and their subsequent behavior was nearly indistinguishable from that of nonthreateners. These results suggest that failure to control for recipient response (and possibly other intervening variables as well) may lead to a substantially weakened relationship between a signaler's initial and subsequent acts. As more experimental studies of intent accumulate, it might be found that in many additional species, signals of intent are more reliable than has previously been appreciated.

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