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Copeia, Vol. 1999, No. 4 (Dec. 17, 1999), 1123-1126.

Stable URL:
http://links.jstor.org/sici?sici=0045-8511%2819991217%293%3A1999%3A4%3C1123%3AWSMTS%3E2.0.CO%3B2-M

Copeia is currently published by American Society of Ichthyologists and Herpetologists.

Copeia, 1999(4), pp. 1123–1126

When Salamanders Misrepresent Threat Signals

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Male red-backed salamanders (*Plethodon cinereus*) defend feeding territories in the forest and vary the intensity of defense depending on the quality of food contained in their territories. Territorial quality was manipulated in a laboratory experiment by providing some residents with termites (a higher profitability prey type based on rate of assimilation) and others with ants (lower profitability). Significantly more termite-fed than ant-fed residents threatened and bit intruders. Both types of residents used honest signals (threaten and subsequently bite) and conventional signals (threaten but no subsequent bite). However, termite-fed residents spent significantly more time in threat posture when no bites followed than did residents fed ants. Termite-fed residents did not show a significant difference in the amount of time spent in threat posture before biting relative to residents fed ants. The low energetic cost of threat displays may predispose residents to "lying" (threat not backed up by a bite), but honest signals must be maintained for the conventional signal strategy to be maintained evolutionarily. Intruders are not likely to be "fooled" about the defensive intents of residents unless threat and subsequent biting are sometimes linked.

ARE salamanders prone to give honest signals or replace these with conventional signals during territorial conflicts between individuals? Honest signals are thought to be reliable indicators of the signaler's resource-holding potential (RHP; Maynard Smith and Parker, 1976), whereas conventional signals are not necessarily reliable indicators of the signaler's RHP (Dawkins and Guilford, 1991). Zahavi (1987) and Grafen (1990) asserted that animal signals are "honest" because they correlate positively with the quality (e.g., RHP in the case of territorial contests) of the signaler. These signals accurately reflect the RHP of the signaler only when they are costly (i.e., individuals with higher quality territories will send more costly signals; Grafen, 1990; Maynard Smith, 1991). Dawkins and Guilford (1991), however, suggested that signaling systems are open to a considerable degree of low level cheating because of the cost incurred by the receiver that had not previously been considered by scientists designing models of honest signaling. Hence, what was previously considered an honest signal might or might not be a reliable indication of the RHP of the signaler. Signals that are not reliable indicators of RHP would be considered "conventional" signals by Dawkins and Guilford (1991). Thus, when the cost of fighting is high (e.g., being injured) and the cost of assessment is low (e.g., involving short time and energy in exchange for valuable knowledge about the opponent), honest signals may be replaced by conventional signals. The use of conventional signals by a resident (signaler) may enable an intruder (receiver) to assess the signaler's RHP while both individuals avoid damaging fights (Dawkins and Guilford, 1991). Therefore, Dawkins and Guilford (1991) proposed that conventional signals will be favored in place of honest signals.

The red-backed salamander (*Plethodon cinereus*: Plethodontidae) defends feeding (and perhaps courtship) territories under cover objects (rocks, logs) on forest floors of northeastern North America (Mathis, 1990, 1991). Although red-backed salamanders forage on a wide variety of invertebrate prey (Jaeger, 1972), prey availability is limited between rainfalls (Jaeger, 1980), and individuals maintain territories during such periods (Mathis, 1989). Residents defend territories by displaying one or two patterns of threat behavior: all trunk raised (ATR, a "look big" threat posture; Jaeger and Schwarz, 1991) and biting (Jaeger, 1981). These same behavior patterns are also displayed by territorial intruders (Jaeger and Schwarz, 1991; Gabor and Jaeger, 1995). The loser of a biting contest in this species may suffer tail autotomy or damage to the nasolabial grooves on the snout, which are used to detect odors (e.g., of prey and pheromones) on the substratum (Jaeger, 1981). We define a "conventional signal" as a threat posture assumed by the resident that is not subsequently followed by biting. An "honest signal" is a threat posture assumed by the resident that is subsequently followed by the resident biting the intruder.

In a laboratory experiment, we first tested the hypothesis that resident males of the red-backed salamander use honest signals that depend on the food quality of their territories, as suggested by Zahavi (1987) and Grafen (1990). Second,

we tested the hypothesis of Dawkins and Guilford (1991) that conventional signals may replace honest signals when the cost of fighting is high. Our rationale was that a rich feeding territory is more worthy of defense by *P. cinereus* than a poor quality territory (Gabor and Jaeger, 1995). However, neither type of territory is worth the cost to the resident of being bitten by an intruder. Thus, if honest signaling is used, we predicted that residents in poor quality territories should bite less frequently and spend less time in a threat posture before biting than residents in food-rich territories, because the former should avoid retaliatory bites from intruders. Residents in food-rich territories should risk retaliatory bites by spending more time in a threat posture before biting and biting more frequently, both of which encourage intruders to depart (Jaeger et al., 1982) or become submissive (Jaeger and Schwarz, 1991). If conventional signaling is used, then we predicted that residents in food-rich territories should spend more time in a threat posture with no subsequent biting (i.e., the threat signal would be a "lie") than residents in food-poor territories. Residents in food-rich territories should also spend more time in a threat posture without subsequently biting (conventional signal) than in a threat posture with a bite following (honest signal).

Materials and Methods

We collected adult males with intact tails on Hawksbill Mountain in Shenandoah National Park, Virginia, during September 1991 and kept them individually in petri dishes (14.5 × 1.5 cm with damp filter paper) at 15 C on a 12:12 h light:dark cycle. We randomly partitioned the collection into 28 future territorial residents and 28 future intruders. Each resident and intruder was tested twice, in random order. In both tests, each resident was allowed to establish a territory (by pheromonal marking: Jaeger et al., 1986) for five days in a chamber (31.5 × 17.0 × 1.4 cm) lined with moist (spring water) paper towels. Five days is sufficient time for red-backed salamanders to establish territories (Nunes and Jaeger, 1989). For one test, the resident was fed 12–14 termites, *Reticulitermes* (adjusted in number for the snout–vent length of the salamander: Gabor and Jaeger, 1995); for the other test, it was fed an equivalent mass of ants, 24–26 *Solenopsis molesta*. We considered termites to be a more profitable prey type than ants because termites pass through the digestive tract significantly faster and with significantly higher digestion efficiency than ants (for analyses of the relative profitabilities of the types of prey used in this experiment, see Gabor and Jaeger, 1995). Moreover, Gabor and Jaeger (1995) demonstrated that both residents and intruders showed more aggressive behavior when termites had been fed to the resident than when ants had been fed to the resident. These results suggest that territories containing termites are considered, by the salamander, to be of higher quality. In our experiment, future intruders were treated identically except that they were fed an equal mass of *Drosophila virilis* (16–18 flies per salamander). Thus, all animals to be tested were on a positive energy budget (Jaeger, 1980).

On day 6, we removed the remaining prey, placed an intruder under a habituation cup (5.5 × 1.0 cm) in the resident's chamber, and placed the resident under another cup (position of cups randomized). Residents and intruders were matched for size (< 2 mm difference in snout–vent lengths) to reduce size asymmetries between them (Maynard Smith and Parker, 1976), and each resident encountered a different intruder in the termite versus ant treatments.

After 15 min, we removed the habituation cups and recorded the interactions of each pair for 30 min. We focused on bites and a well-defined threat posture [ATR (Jaeger and Schwarz, 1991), in which the salamander extends its legs downward, raising its head and trunk off of the substratum]. Jaeger (1984) experimentally demonstrated that this "look big" posture by residents precedes bites significantly more frequently than do alternative postures. We divided the resulting data for residents into two categories: (1) time spent in ATR before biting (honest signal); and (2) time spent in ATR when no biting followed (conventional signal) for each territory type. If more than one bite occurred in a contest, we analyzed data pertaining only to the first bite. We eliminated data when an intruder responded to a resident's ATR with a submissive display (Jaeger, 1984), because such a display by the intruder might alter the resident's subsequent behavior (to bite or not to bite). In addition, we also examined the total number of times that each resident displayed ATR and bit the intruder in ant and termite treatments. We compared frequency data between termite and ant treatments using chi-square test ($\alpha = 0.05$) and temporal data using two-tailed Mann-Whitney *U*-test ($\alpha = 0.025$ due to Bonferroni's adjustment).

Results

Significantly more residents in territories previously containing termites performed ATR (24

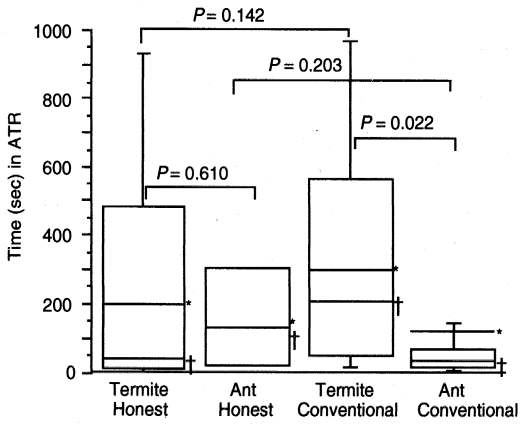

Fig. 1. The amount of time (sec) that territorial male residents of *Plethodon cinereus* spent in threat posture (ATR) when the resident was previously fed termites or ants and when the resident either followed ATR with a bite (honest signal) or did not follow it with a bite (conventional signal). The upper and lower horizontal lines of each box plot (Sokal and Rohlf, 1995) represent the first and third quartiles, the median is represented by †, and the mean is represented by *. The range is shown when it is not included in the box.

of 28) than those in territories previously containing ants (17 of 28): $\chi^2 = 4.46$, df = 1, $P < 0.05$. Significantly more residents in termite territories also bit intruders (13 of 28 = 46%) than those in ant territories (6 of 28 = 21%): $\chi^2 = 3.90$, df = 1, $P < 0.05$. Thus, territories with the more profitable prey type led to more threat and biting by residents against intruders.

There was no significant difference in the amount of time spent in ATR before biting by residents in termite versus ant territories (Fig. 1 honest signal: $n_{termite} = 8$, $n_{ant} = 4$, $z = 0.510$). Residents fed termites spent significantly more time in ATR when no bites followed than residents fed ants (Fig. 1 conventional signal: $n_{termite} = 14$, $n_{ant} = 10$, $z = 2.284$). There was no significant difference in the amount of time spent in ATR before biting than before not biting by residents in termite territories (Fig. 1: $n_{honest} = 8$, $n_{conventional} = 14$, $z = 1.468$) or in ant territories (Fig. 1: $n_{honest} = 4$, $n_{conventional} = 10$, $z = 1.273$).

Discussion

The initial results of more residents performing ATR more frequently and biting more frequently in termite territories than in ant territories support the argument by Zahavi (1987) and Grafen (1990) that the threat signal will positively correlate with the RHP of the signaler and hence must be honest. However, when the data are broken down into time spent in a given signal, the data lend support toward the hypothesis of Dawkins and Guilford (1991) that not all signals are honest and that conventional signals may be favored in such cases. Although Jaeger (1984) demonstrated that ATR precedes bites more frequently than other postures, ATR was not consistently followed by a bite in our experiment. Hence, we infer that males of *P. cinereus* are not constrained to give honest signals (all trunk raised) about willingness to bite or not to bite during territorial defense.

Whether animal signaling systems are likely to be honest (Zahavi, 1987) or whether conventional signals may be used (Dawkins and Guilford, 1991) hinges to some extent on the cost of the signal to the sender relative to the receiver. Is all trunk raised a costly display (sensu Maynard Smith, 1994)? Certainly a salamander that lifts itself from the ground in all trunk raised exerts more energy than one that is in a resting posture (in which only the anterior trunk and head are raised; Jaeger, 1984). Yet movement costs only about 1.2×10^{-3} cal/min × g of salamander more than resting for *P. cinereus* (Jaeger and Barnard, 1981); if the resulting all trunk raised were to save just one dipteran prey from the intruder and the resident were to eat that prey item, the resident would assimilate about 2.57 cal/large fly (the size of *Drosophila virilis*) or 1.03 cal/small fly (the size of *D. melanogaster*) at 15 C (calculated from data in Jaeger and Barnard, 1981). Thus the cost of a threat signal is trivial compared to the possible reward of displacing an intruder from a feeding territory. The cost of losing a biting contest, though, would be considerable if the resident were to lose its tail or be bitten on the nasolabial grooves (Jaeger, 1981). Hence, the low cost of threat displays may predispose salamanders to lying (threat not backed up with a bite). This may explain why residents spent more time using a conventional signal (all trunk raised but no bite) in termite over ant territories. No other tactic is likely to have a higher payoff than conventional signals for the resident; that is, honest biters may save prey from intruders (high profit) but risk injury (high cost).

However, for the conventional signal strategy to be maintained evolutionarily, some threat signals would need to be honest. That is, this strategy should be successful only if the intruder is uncertain as to whether the threat posture (ATR) will or will not result in a bite. In territories where the resident was fed termites, residents maintained this uncertainty by using conventional signals in 63% (14 of 22; see results in Fig. 1) of the contests and biting the rest of

the time. In territories where the resident was fed ants, threatening without biting (71%; 10 of 14, see Fig. 1) was also more frequent than threatening with biting (29%; 4 of 14). We hypothesize, then, that territorial salamanders play a mixed ESS game (Maynard Smith, 1982) with intruders that favors both honest and conventional use of threat signals. Conventional signals may have a high payoff when they fool the intruder, but intruders are not likely to be fooled unless threat and subsequent biting are sometimes linked. The complex signaling tactics of territorial *P. cinereus* (see also neighbor recognition in Jaeger, 1981) appear to be consequences of the utility of deceiving intruders, the worth of the resource being defended, and the cost of a damaging fight to both the intruder and resident.

Future research, in light of these results, could examine whether neighbor recognition influences a salamander's signaling strategy. Dawkins and Guilford (1991) pointed out that conventional signals are most likely to be found in situations in which the full costs of honest signaling are avoided such as when animals recognize each other as individuals. Individuals of *P. cinereus* that are territorial neighbors are less likely to attack each other than are unfamiliar residents (dear enemy recognition; Jaeger, 1981). In such cases, these signalers can avoid the costs both of frequent fights and of constantly sending signals by remembering how each individual performed previously. Receivers too could avoid costly fights by receiving less costly conventional signals and remembering the fighting ability of a previously encountered individual.

Acknowledgments

We thank S. Wise for providing comments on this manuscript and authorities at Shenandoah National Park for the permit to collect salamanders. The research was supported by National Geographic Society grant 5721-96 and National Science Foundation grant DEB-9314081 to RGJ, and a Louisiana Board of Regents Doctoral Fellowship [grant LEQSF (1993-98)-GF-20, through RGJ] and National Science Foundation Postdoctoral Research Fellowship grant DBI-9750278 to CRG.

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