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Research article

Accidental altruism in insular pit-vipers (*Gloydius shedaoensis*, Viperidae)

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Abstract. Darwinian theory predicts that organisms will display traits that benefit themselves rather than other individuals; exceptions to this rule usually are explicable by kin selection. Our studies on an insular population of venomous snakes in north-eastern China reveal a different situation. Only one species of snake (*Gloydius shedaoensis*, Viperidae) occurs on the island of Shedao, and displays altruism between size (age) classes. First, small snakes frequently kill prey items larger than they can swallow themselves. This behaviour enhances rates of feeding of larger conspecifics, which scavenge the birds' carcasses. Second, large snakes kill raptorial birds (sparrowhawks *Accipiter nisus*) that pose little or no threat to themselves. This behaviour reduces predation risk for smaller snakes. These effects are presumably accidental consequences of the high venom toxicity of the pit-vipers, which enable them to kill inedible prey and non-threatening predators at little cost. Nonetheless, this 'accidental altruism' may have significant ecological consequences. For example, these behaviours may contribute to the remarkably high population densities of snakes on Shedao.

Key words: *Accipiter*, *Agkistrodon*, China, field experiments, predator, snake

Introduction

The concept of the 'selfish gene' is a cornerstone of modern evolutionary theory. Under simple models of Darwinian selection, we expect to see the evolution of traits that enhance the fitness (probability of survival and reproduction) of individual organisms that possess those traits (e.g., Williams, 1966; Dawkins, 1976). In particular, we do not expect to see organisms behaving in ways that confer a cost to themselves and a benefit to other individuals. Although there are exceptions to this general prediction (as in kin-selection and reciprocal altruism models: Hamilton, 1967; Trivers, 1972), most evolutionary biologists would not expect to see distantly related individuals within a population acting to enhance each other's fitness.

During field studies on an insular population of venomous snakes, we found that small individuals (juveniles) enhance the food supply for larger animals (adults) by killing prey items that are then abandoned and are later consumed by the larger snakes. We also found that the larger snakes kill predators that are little or no threat to themselves, but are known to prey upon smaller animals. At first sight, this system fulfils the criteria for altruism noted above: individuals enhance the fitness of others (by providing food or removing predators) at some cost to themselves (venom expenditure). Such a situation appears inconsistent with a simplistic 'selfish gene' scenario, and hence warrants closer examination.

Materials and methods

Study area and species

Shedao is a small (0.73 km^2) island in the Bohai Sea, 13 km off the coastline of the Liaodong Peninsula in north-eastern China (38°57′ N, 120°59′ E: Sun *et al.*, 1990, 2002; Li, 1995). Because of its geographic location, the island serves as a stepping-stone for migrating birds during spring and autumn each year. In turn, these birds serve as the primary food source for an endemic pit-viper (*Gloydius shedaoensis*), which capture their prey from ambush (Li, 1995; Sun *et al.*, 2001; Shine and Sun, 2002). The snakes have highly toxic venom (Zhao *et al.*, 1979); bitten birds die in <1 min (pers. obs.). Venom expenditure presumably involves some cost: the feeding season only lasts 2–3 weeks, and snakes milked of all their venom require 10–15 days to fully replenish their supply (Li, 1995).

The snakes attain extraordinarily high population densities on this island, with up to one snake per $meter^2$ in suitable habitat (Huang, 1989; Sun *et al.*, 2001, 2002). Both adult snakes (>50 cm snout-vent length [SVL]; typically 60–65 cm SVL) and juveniles (25–50 cm SVL) lie in wait for small birds in the same kinds of ambush sites (Li, 1995; Shine and Sun, 2002; Sun *et al.*, 2002). Adult pit-vipers on the island appear to have no natural predators, but juvenile snakes are sometimes killed by sparrowhawks (*Accipiter nisus*: Koba, 1938; Li, 1995; L. Sun, pers. obs.).

Methods

We visited the island from 2 to 17 May 2000 to conduct behavioural studies on the snakes. We collected 25 dying or freshly dead birds within our 2 ha study area with evidence of recent snakebite (blood oozing from puncture marks made by the fangs). The sample included five sparrowhawks, two quails and 18 passerine birds. Only three of these birds were small enough (<26 mm chest diameter) to be ingestible by at least some juvenile pit-vipers (based on sizes of 13 birds that we recorded inside juvenile snakes). Nine were too large (>45 mm; X5 sparrow-hawks, X1 Yellow-legged Button-quail *Turnix tanki;* X1 Rock Pigeon *Columba livia*; X1 Gray Nightjar *Caprimulgus indicus*; X1 Brown Shrike *Lanius cristatus*) for any snake to eat (based on diameters of 49 prey that we recorded inside adult snakes) and the remaining 13 were too large for juvenile pit-vipers to ingest, but small enough to be eaten by adult snakes (27–44 mm).

The heads and necks of most of these dead birds were coated in saliva, showing that snakes had tried (and failed) to ingest them. Abandoned birds are soon eaten by larger snakes; in one case, we watched a medium-sized snake (62 cm SVL) kill a large quail and attempt to swallow it for >60 min. The snake finally abandoned the attempt, and the quail was consumed by a larger snake (74 cm SVL) the following day. Five dead birds that we placed out were eaten by larger snakes in <24 h.

Response to potential prey

These data show that many birds are eaten by snakes other than the ones that killed them, and suggest also that this phenomenon is due to gape-limitation: that is, small snakes can kill large birds but cannot swallow them. However, we do not have direct evidence that very small snakes strike (and thus, kill) birds too large to swallow. To obtain such data, we approached snakes that we found in ambush positions in the field, and lowered a dead bird towards them attached to a 50-cm length of fishing line (3 kg test) on the end of a 1.9-m fibreglass fishing rod. The bird was dangled 5–10 cm in front of the snake's head, and moved about over the next 60 sec to simulate a live bird. The observer recorded whether or not the snake performed a defensive display (tail-twitch) and whether or not it struck at the 'target'. We offered juvenile snakes dead birds that were either small enough to be ingested (16 mm chest diameter: *Phylloscopus inornatus* and *P. proregulus*) or too large for ingestion (30 mm: *Parus major* and *Erithacus sibilans*).

Response to potential predators

Why are sparrowhawks killed by snakes, despite being too large for ingestion by any Shedao pit-viper? In particular, are these birds killed only by small snakes (to which they are a much greater potential threat) or by large snakes as well? We examined this question by dangling dead birds or feather-covered models in front of snakes that we found in ambush positions, in the same way as described above. The dead birds that we used were: (1) sparrowhawks (*Accipiter nisus*) 50–55 mm in chest diameter and weighing 93–98 g; and (2) a non-predatory bird of the same size (gray nightjar, *Caprimulugus indicus*) 55 mm in chest diameter and weighing 93 g. The other stimuli were small circular artificial models 30 mm in diameter (water-filled balloons inside lengths of stocking) and covered in either: (3) sparrowhawk feathers; or (4) feathers of a non-predatory species (great tit *Parus major*) that is often eaten by the snakes (unpubl. data). We attempted to maintain statistical independence by using each snake in only one trial; the order of presentation of stimuli was randomised.

Results

Response to potential prey

Many of the juvenile snakes that we tested were young-of-the-year (<30 cm SVL), for which even the 16-mm prey were too large to ingest. Nonetheless, the juvenile pit-vipers struck at and tried to consume not only ingestible-size prey items (13 of 14 trials with 16 mm prey), but also at prey that far exceeded the snake's swallowing capacity (16 of 18 trials with 30 mm prey).

Response to potential predators

Snakes offered the dead nightjar showed little overt reaction (in 20 trials, we saw three tail-twitches and one defensive strike; see Fig. 1). Snakes offered the passerine model sometimes tail-twitched (12 of 46 trials), but they struck in about 30% of trials, and behaved as seen in natural feeding strikes (pers. obs.). That is, the snakes (i) often held onto the model after seizing it; and (ii) either remained at their foraging sites after the trial, or moved slowly to the ground tongue-flicking vigorously (as is typical of post-strike prey-location behaviour in natural feeding events: pers. obs.). In strong contrast, 37 of 40 snakes presented with either the dead sparrowhawk or the sparrowhawk model recoiled vigorously from the stimulus, launched an immediate strike, and then dropped from their branch and coiled defensively beneath it, tail-vibrating vigorously for long periods (often >60 sec). They usually tail-twitched (36 of 40 trials) and never held onto the hawk or hawk-model after striking. Some snakes gaped their mouths widely prior to the strike, presumably as an additional threat display. Many of these snakes remained so highly aroused for several minutes more that we could not walk past them without eliciting repeated vigorous strikes – a behaviour that we never saw in other circumstances.

The statistical significance of these differences can be evaluated using log-likelihood ratio tests from a logistic regression with stimulus type as the independent variable. We analysed data for adult and juvenile pit-vipers sep-

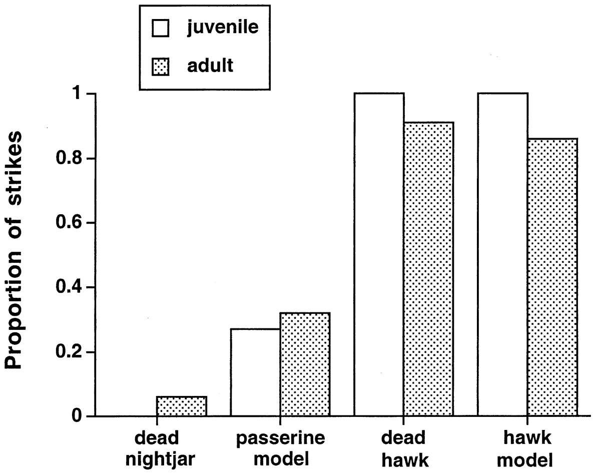

Figure 1. Responses of free-ranging pit-vipers to dead birds and to artificial models covered with feathers. The graphs show the proportions of trials in which snakes struck at four kinds of stimuli: a dead nightjar (a bird species that does not eat snakes); a model covered in passerine feathers; a dead sparrowhawk (a species that eats juvenile snakes); and a model covered in sparrowhawk feathers. Data are shown separately for adult (>50 cm SVL) and juvenile (<50 cm SVL) snakes. See text for statistical analysis and sample sizes.

arately, but found very similar patterns of response in each age class (Fig. 1). Stimulus type affected whether or not the snake displayed (adults, $\chi^2 = 32.33$, $df = 3, p < 0.0001$; juveniles, $\chi^2 = 23.01$, $df = 3, p < 0.0001$) and whether or not it struck at the 'target' (adults, $\chi^2 = 33.18$, $df = 3, p < 0.0001$; juveniles, $\chi^2 = 30.36$, $df = 3, p < 0.0001$). Almost every strike hit the 'target' (0 of 1 for nightjar trials, 18 of 18 for passerine models, 16 of 19 for sparrowhawks, 17 of 18 for sparrowhawk models).

We also recorded the latency to strike after the stimulus was first presented. Restricting analysis to trials in which the snake struck at the bird, the strike was launched more quickly against the sparrowhawk and sparrowhawk model than against the passerine model (Fig. 2). The single strike against the nightjar was launched much later, after 52 sec. ANOVA with stimulus type as the factor confirms the significance of this difference in latencies to strike (omitting the single nightjar record, $F_{2,51} = 4.24$, $p < 0.02$). Post-hoc tests (Tukey–Kramer) showed that the response to the passerine model differed from those to the two hawk stimuli ($p < 0.05$).

Discussion

The snakes' response to the sparrowhawk model was as strong as that to the sparrowhawk itself, suggesting that chemosensory cues play an important role

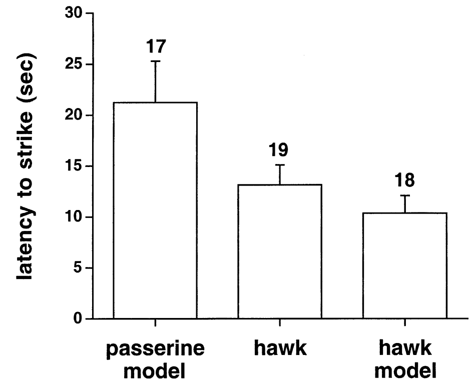

Figure 2. Latencies to strike after free-ranging pit-vipers were presented with stimuli of various kinds. The graphs show the mean latencies (±1 standard error) for trials in which snakes struck at three kinds of stimuli: a model covered in passerine feathers; a dead sparrowhawk; and a model covered in sparrowhawk feathers. See text for statistical analysis.

in hawk recognition. The virtual lack of reaction to the dead nightjar shows that stimulus size alone is not sufficient to initiate a strong defensive response. Most previous studies on determinants of antipredator behaviour in snakes have focused on visual rather than chemical stimuli (e.g., Scudder and Chizsar, 1977; Herzog *et al.*, 1989). However, the Shedao pit-vipers are not unique in their use of chemosensory information in this respect. Chemosensory cues from the integument of ophiophagous snakes initiate defensive responses in a variety of pit-viper taxa (Weldon and Burghardt, 1979; Weldon *et al.*, 1992). The scent of mammalian predators may similarly induce antipredator responses in rattlesnakes (Cowles and Phelan, 1958).

Our data show that small pit-vipers kill birds too large to ingest, and that larger pit-vipers kill hawks that pose little or no threat to themselves. The relatively slow rate of venom replenishment (Li, 1995) suggests that this venom expenditure comprises some cost, albeit perhaps a trivial one. Although the behaviours provide no benefit to the snakes involved, they do benefit other individuals in the snake population: larger snakes consume the birds killed by smaller conspecifics, and small snakes experience less threat from sparrowhawk predation. Thus, the system appears to fulfil the basic criteria for altruism.

Given the high densities of snakes on Shedao, and the fact that bitten birds can often fly many meters before dying, it seems extraordinarily unlikely that close relatives of the ‘altruist’ experience any disproportionate benefit from these behaviours. Thus, conventional explanations for altruism (such as kin selection and reciprocity) are untenable. Instead, the phenomenon appears to be a simple consequence of specific aspects of our study system:

(1) *The high venom toxicity of these snakes*: Because they are able to kill birds very easily and with little cost, they do so relatively indiscriminately. For example, the dramatic display evoked by sparrowhawks may enhance survival of juvenile snakes, but why is the same reaction shown by adult snakes (which are rarely if ever taken by hawks: Li, 1995)? This ontogenetic persistence may simply reflect little selection against the behaviour in older animals.

(2) *The difficulty of evaluating the size of potential prey items prior to striking*: A juvenile pit-viper may strike (and thus, kill) a bird much too large for it to ingest because the snake has very little time in which to evaluate prey size. The birds move from branch to branch with stops of <2 sec (pers. obs.). The bird's size may be difficult to judge from its silhouette, because outspread wings would massively affect the 'target' size. The costs of refraining from striking (a lost meal) may far outweigh the costs of striking too large a bird (wasted venom). Thus, we might expect pit-vipers of all body sizes to be optimistic, and strike at any prey item that is conceivably ingestible.

(3) *Opportunistic consumption of birds killed by other snakes*: Because bird numbers and snake densities are high on Shedao, snakes are much more likely to encounter recently killed birds than would be true in most other systems. Scavenging dead prey items has been reported in other snake taxa, including pit-vipers (Wharton, 1969; Bedford and Griffiths, 1995; Capula *et al.*, 1997).

Even though the readiness of Shedao pit-vipers to strike at 'incorrect' stimuli (oversize prey and non-dangerous predators, at least from their own perspective) is presumably due to the low costs of such behaviour rather than to some adaptive advantage, it may nonetheless have a significant impact on the fitness of other individuals – and thus, on the ecology of Shedao. Pit-vipers on this island attain much higher population densities than in any other system yet studied (1 snake/m^2: Li, 1995; Sun *et al.*, 2001). This high density is at least partly due to 'accidental altruism': small snakes provide food for larger conspecifics, and large snakes protect smaller animals by removing their only significant predators. A similar food-sharing phenomenon has been reported in another population of island reptiles (Auffenberg, 1981). Although the phenomenon does not fit easily into our current adaptationist framework, it may nonetheless be widespread. Charles Darwin (Darwin, 1887) suggested that such exceptions to the general rule warrant close scrutiny, because ultimately they may shed light on wider questions.

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