Optimization of Predator Avoidance by Salamanders Using Chemical Cues: Diet and Diel Effects

Dale M. Madison, John C. Maerz & James H. McDarby


Abstract

The allocation of time and energy to predator defense is a fundamental problem for animals. Predator avoidance may decrease the risk of injury or mortality, but it may also compromise foraging or reproduction, so potential prey should decide whether to avoid a predator based on predation risk. We show that red-backed salamanders (Plethodon cinereus) discriminate between substrates chemically conditioned by garter snakes (Thamnophis sirtalis) that were fed red-backed salamanders, earthworms, or nothing. At night, individuals avoided only the conspecific treatment, and this response was independent of any individual differences between snakes. During the day when garter snakes are much more active, all treatments were avoided. This avoidance appeared to be influenced by a diel rhythm of responsiveness rather than ambient lighting. Avoidance of prey alarm substances released during predation does not explain all these results, nor can simple avoidance of predator scent. A more complex mechanism is proposed that incorporates predator recognition, predator diet discrimination, and risk assessment. These data suggest that terrestrial salamanders may use chemoreception to identify garter snakes and their diets in order to optimize predator avoidance.

Introduction

The interactions between predator and prey are important to all areas of ecology (Lima & Dill 1990). Predators drive the evolution of prey defenses that emphasize either avoidance mechanisms, which reduce the likelihood of detection by a predator, or antipredator mechanisms, which reduce predator success after
detection has occurred (Sih 1985; Brodie et al. 1991b). Avoiding detection by depressing activity or seeking shelter may prevent immediate injury or death, but avoidance can reduce foraging and alter growth (e.g. Sih 1980; Petranka 1989; Wellborn et al. 1996; Werner & Anholt 1996; Devito et al. 1998). Consequently, potential prey should assess predation risk and balance (optimize) energy allocation between activities that promote immediate survival from predation and those that promote maintenance, growth, and reproduction (Petranka 1989; Skelly 1992; Horat & Semlitsch 1994; Anholt & Werner 1995; Skelly 1995).

Risk assessment by potential prey may entail diverse variables having to do with the predator, the prey, and the environmental context (e.g. Lima & Dill 1990; Brodie et al. 1991a; Lima 1998a,b). Concerning assessment of the predator, some prey species practice vigilance and inspection and adjust their wariness to attributes of predators, but the assessment of, and response to, individual differences in threat between conspecific predators has been generally neglected in ecological studies (Lima & Dill 1990). Knowledge of what an approaching predator has recently eaten could be valuable to a potential prey. Even generalist predators, especially when well-fed, may selectively search for particular prey (Fuchs & Burghardt 1971; Arnold 1978; Burghardt 1990), bypassing other prey in the process (Dukas & Clark 1995; Nams 1997), and a prey could save the cost of unnecessary action by avoiding only those predators searching for their species. While visual and acoustic information severely limits how much a prey can decipher about the immediate diet history (and hence prey specialization) of a nearby predator, scent from consumed prey emanating from the body and waste products of the predator can provide this information (e.g. Brown et al. 1995; Laurila et al. 1997; Smith 1997; Petranka & Hayes 1998).

In studies showing avoidance behavior in response to predator odor (Burghardt 1990; Weldon 1990; Elliot et al. 1993; Cupp 1994), it is often unclear whether the prey is responding to predator-specific chemicals (‘direct’ cues) or to products from recently consumed prey (‘indirect cues’; see Petranka & Hayes 1998). Little evidence exists that direct chemical cues may allow prey to assess qualitative differences in threat from conspecific predators, for example the likelihood of a predator detecting, attacking, and subduing prey. However, alarm substances released by an attacked prey may chemically label the predator as a higher risk and subsequently elicit avoidance of just that individual or its feces (e.g. Smith 1992; Mathis & Smith 1993; Wilson & Lefcort 1993; Brown et al. 1995; Chivers et al. 1996; Petranka & Hayes 1998). Social pheromones of a prey could conceivably label a predator, but this potential function has not been described.

We have been examining evidence of avoidance optimization by the red-backed salamander, *Plethodon cinereus* (PC), toward the eastern garter snake, *Thamnophis s. sirtalis* (TS). The former is a small, inconspicuous inhabitant of most wood lots throughout the northeastern USA and often has a biomass equaling that of all mammals and doubling that of all bird species (Burton & Likens 1975). The garter snake is one of the most common predators in the USA (Rossman et al. 1996). The salamander forages on invertebrate prey in the leaf litter (e.g. Jameson 1944; Burton 1976; Jaeger et al. 1995; Wyman 1998); the garter snake

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feeds on salamanders (including PC; Hamilton 1951; Carpenter 1952; Moreno 1989), earthworms, insects, anurans, fish, birds, and small mammals (Mushinsky 1987; Rossman et al. 1996).


Our research has demonstrated that PC detects and avoids microhabitats scented with chemical traces of TS (Madison et al. 1999; McDarby et al. 1999). Because garter snakes form chemical search images and selectively hunt for preferred prey (Fuchs & Burghardt 1971; Arnold 1978; Burghardt 1990), we tested whether PC would avoid only the odors of garter snakes fed PC. We used different garter snakes in the different diet treatments, so we conducted a diet reversal experiment to control for the possible effects due to individual differences in snake chemistry unrelated to diet. We then tested whether PC would be more likely to avoid chemical traces of snakes during the day when food resources are less available and garter snakes are more competent predators (Drummond 1985; Ford & Burghardt 1993; Heinen 1995). Finally, we tested whether a diel response rhythm or ambient light conditions would influence avoidance behavior independent of snake diet.

**Methods**

We conducted four experiments using 370 adult PC (snout/vent length > 40 mm) and five adult male TS (snout/vent length > 36 cm) collected in woodlands near Binghamton, New York between May and Nov. 1995–1998. The species were housed in separate rooms under similar photoperiods. The salamanders were kept in individual Petri dishes (150 mm diameter × 15 mm high) lined with moistened filter paper, and were fed cricket nymphs every 5 d. The snakes were kept in separate 38-l aquaria with a water dish, an outside heating element, and a paper towel, and were fed a maintenance diet of local earthworms (Lumbricus sp.) and goldfish weekly. The snake diets tested were equal weights of PC, earthworms,
or nothing. In preparation for the diet tests, the garter snakes were maintained on their test diets for at least 2 wk prior to collecting substrate samples.

To collect snake substrate samples, the different aquaria were first scrubbed with Sparkleem detergent, rinsed thoroughly with distilled water, and then allowed to accumulate new odors for 10 d. A test sample consisted of a 200 ml distilled water rinse of the snake’s aquarium after the snake’s had been gently removed (without inducing release of cloacal scent; Oldak 1976). The samples were prepared just before experimental use. The snakes were given their diets in their aquaria just before and 7 d after washing, so samples were collected 3 d after the last feeding. Feeding consisted of placing a Petri dish (150 mm diameter × 15 mm high) with the diet (a cooled earthworm, salamander, or nothing) in the snake’s aquarium until the prey had been consumed, usually within 15 min. Cooling the prey slowed movement and resulted in the prey being consumed prior to crawling out of the feeding dish. This technique resulted in little or no direct contact of the prey with the aquarium. The salamanders tested were given a choice between a blank substrate with rinse from an unoccupied aquarium and a substrate with rinse from the aquarium of a snake on one of the three diets.

To prepare for a test, a semicircle of filter paper (75 mm radius) was immersed in a test solution, drained, and carefully placed on a randomly determined side of a covered 150 × 15 mm Petri dish. Another semicircle immersed in the blank solution was placed opposite the test sample with a 3 mm space between both semicircles to prevent cross contamination. Separate disposable surgical gloves were worn when handling the different solutions. Each test was conducted between 13.00 and 17.00h under fluorescent ceiling lights or 1–5 h after sunset using two 40 W red incandescent lights, unless stated otherwise.

For testing, each salamander in a trial was transferred to the middle of a randomly chosen and positioned Petri dish in an experimental array of 20–40 dishes on a table. Brown paper collars 15 mm high were placed around each dish to visually isolate each salamander. Observations were then conducted through small holes in a curtain suspended 0.3 m from the table. The observer had no knowledge of the type or location of the treatment rinse in the dishes during a trial. The salamanders were observed sequentially for 3 s each, with the process repeated every 3 min for 60 min, giving 21 observations for each salamander. The side of the dish occupied by each salamander at each observation was based on where the midpoint of the trunk was located, the logic being that once the salamander had proceeded this far across a divide, the substrate was more likely to have been assayed and a decision made whether to continue movement in that direction. Each individual was only used in one trial, and adults of both sexes were used as gender has no apparent differential effect (McDarby et al. 1999).

A salamander was considered to have avoided a substrate if 10 or fewer positions (out of 21 possible) occurred on that substrate during the 60 min trial. The avoidance response resulting from our protocol was a clean, highly repeatable response, with the salamanders moving frequently and usually making an avoidance decision within the first 20 min of a trial and then moving only occasionally and usually staying in the chosen semicircular area for the remainder of the hour.
(Madison et al. 1999). The latter inactivity tended to produce extreme preference scores (e.g. 20 vs. 1, 2 vs. 19, etc.) regardless of whether the scent trace or the blank (water) side was ‘preferred’ (McDarby 1997). The bimodal character of the resulting response violates an important assumption of parametric statistical procedures (normal distribution), and so we routinely used the nonparametric chi-square goodness-of-fit test on nominal avoidance scores to test for significant departures from random expectation within one-way designs. No responses to any treatment differed between trials (the Fisher exact test was used because of the small expected frequencies), so the results for each treatment were pooled across trials. A chi-square goodness-of-fit test was then used to compare the binary frequency data, and a chi-square $2 \times 2$ contingency test was used to compare results across treatments (Siegel & Castellan 1988).

In the first of four experiments, we tested whether PC would avoid only the substrates from TS that had been fed PC. In one evening, we gave 90 PC a choice between a blank substrate and a test substrate with scent from a snake that had been fed either PC, earthworms, or nothing. Three replicate trials were conducted during the evening, with 10 PC tested per diet treatment per trial, giving a sample size of 30 per treatment. Within a trial, the location of each sample comparison (scented substrate vs. blank) was randomized within each group of three treatment comparisons by a stratified randomization procedure. Slight fecal deposits occurred in the aquaria where TS had been fed earthworm and PC, which remained mostly insoluble at the bottom of the rinse water bowls and was not transferred to the filter paper semicircles. Rinses collected at 20.00h were used in all three trials.

For the second experiment, we tested whether scent from the different source snakes, independent of diet, might influence PC behavior. We conducted two diet trials using normal protocol on different evenings 24 d apart, with the diets of the test snakes reversed between trials. For the first night trial, snakes 4 and 5 had been fed PC or nothing, respectively. Forty salamanders were tested, 20 salamanders per snake treatment comparison. For the 24 d prior to the second night trial, the diets of the two snakes were reversed, and then 40 PC were tested to rinses from these snakes, 20 per snake treatment.

In the third experiment, we tested whether time in the diel cycle might influence avoidance behavior. We conducted four trials, 30 PC each, with two trials in the early afternoon and two during the evening of the same day. The protocol was identical to the first experiment, except we: 1. omitted the earthworm diet treatment; 2. collected sample rinses prior to the daytime trials at 13.00h; and 3. used the same rinses for both day and night trials.

For the last experiment, we tested for a lighting effect by repeating expt 3 but using red light for all day and night tests instead of using fluorescent light during the day and red light at night. During the day, salamanders were given a 10 min habituation period under red light before observations began. Eighty salamanders were exposed to rinses from either an unfed TS (snake 4) or a PC-fed TS (snake 5) paired against distilled water, 20 salamanders per treatment, both day and night.
Results

Expt 1. Differential Substrate Avoidance Based on TS Diet

Salamanders significantly avoided the substrates from snakes on a PC diet, but did not avoid the substrates from snakes fed earthworms or nothing (Table 1). The differences were significant between the PC and earthworm diet trials (27 and 3 vs. 17 and 13; \( \chi^2 = 8.52, p < 0.01 \)) and between the PC and unfed treatments (27 and 3 vs. 16 and 14; \( \chi^2 = 9.93, p < 0.01 \)), but not between the earthworm and unfed diet treatments (17 and 13 vs. 16 and 14; \( \chi^2 = 0.07, p > 0.70 \)).

Expt 2. Diet Reversals to Control for Individual Differences in TS

The response elicited by substrates conditioned by individual TS was reversible based on snake diet (Fig. 1), and so at night PC first ignored the aquarium rinse of an unfed TS and then later avoided the rinse of the same TS if the TS had been fed PC. The opposite result occurred if the TS was first fed PC and then was later unfed.

Expt 3. Diel Rhythm Effect

As in expt 1, the salamanders at night avoided only the rinses of snakes on a PC diet, but during the day, snake substrates were avoided regardless of snake diet (Table 2). No significant diel change in avoidance occurred for PC-fed TS substrates (\( \chi^2 = 1.00, p > 0.30 \)), but there was a significant decrease in avoidance at night.

Table 1: The response of *Plethodon cinereus* during evening trials to chemical traces from *Thamnophis sirtalis* that had been fed *P. cinereus* (snake 1), earthworms (snake 2), or nothing (snake 3) for at least 2 wk preceding the trial. Shown are the numbers of salamanders in each repeated trial that preferred blank vs. snake substrates.

<table>
<thead>
<tr>
<th>T. sirtalis diet (snake ID)</th>
<th>Trial</th>
<th>Blank</th>
<th>Snake</th>
<th>( \chi^2 )</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. cinereus</em> (1)</td>
<td>1</td>
<td>9</td>
<td>1</td>
<td>19.2</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>9</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>9</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Earthworm</em> (2)</td>
<td>1</td>
<td>6</td>
<td>4</td>
<td>0.5</td>
<td>&gt; 0.500</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>5</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>6</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>17</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nothing</em> (3)</td>
<td>1</td>
<td>4</td>
<td>6</td>
<td></td>
<td>&gt; 0.700</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>4</td>
<td>6</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>8</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>16</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig. 1: The percentage of salamanders tested during two night trials 24 d apart that preferred substrates containing just distilled water (open bars) or a distilled water rinse from aquaria containing snakes (solid bars) that had been fed red-backed salamanders (S) or nothing (N). The identification of snakes 4 and 5 appear in parentheses. Sample size was 20 salamanders in each comparison. Significance level 0.05 (*).

Table 2: The response of Plethodon cinereus, day and night, to chemical traces from Thamnophis sirtalis that had been fed P. cinereus (snake 1) or nothing (snake 3) for at least 2 wk preceding the trial. Shown are the numbers of salamanders in each trial that preferred blank vs. snake substrates.

<table>
<thead>
<tr>
<th>T. sirtalis diet (snake ID)</th>
<th>Day No. preferring substrate</th>
<th></th>
<th>Night No. preferring substrate</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trial Blank Snake χ²</td>
<td>Trial Blank Snake</td>
<td></td>
<td>Total Blank Snake</td>
</tr>
<tr>
<td>P. cinereus (1)</td>
<td>1 8 2</td>
<td>4 9 1</td>
<td></td>
<td>23 7</td>
</tr>
<tr>
<td>2 7 3</td>
<td>5 9 1</td>
<td>6 8 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 8 2</td>
<td>Total 23 7</td>
<td>8.5*</td>
<td>Total 26 4</td>
<td>16.1**</td>
</tr>
</tbody>
</table>

Nothing (3)

<table>
<thead>
<tr>
<th></th>
<th>Trial Blank Snake χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 10 0</td>
<td>4 4 6</td>
</tr>
<tr>
<td>2 6 4</td>
<td>5 4 6</td>
</tr>
<tr>
<td>3 7 3</td>
<td>6 6 4</td>
</tr>
<tr>
<td>Total 23 7</td>
<td>8.5*</td>
</tr>
</tbody>
</table>

*p < 0.01, **p < 0.001; ns, not significant.
toward unfed TS substrates ($\chi^2 = 5.71, p < 0.05$). A comparison of the night results of expts 1 and 3 shows that the 7h earlier collection of the sample rinses in expt 3 (13.00h vs. 20.00h for expt 1) had no measurable effect on the avoidance of substrates conditioned by PC-fed TS ($\chi^2 = 0.16, p > 0.50$) or unfed TS ($\chi^2 = 0.27, p > 0.50$).

**Expt 4. Diel Rhythm vs. Test Lighting Effect**

Salamanders tested under red light during the night showed the same results as in expts 1–3, with the soiled substrates from PC-fed TS eliciting avoidance (17 of 20 avoiding) but not the substrates from unfed TS (12 of 20 avoiding; Fig. 2). During the day, regardless of testing under red light, the substrates were avoided from both PC-fed TS (15 of 20 avoided) and unfed TS (16 of 20 avoided), similar to the results collected under fluorescent light in expt 3.

**Discussion**

The response of PC to chemical traces from TS night and day was consistent with the avoidance of snake odors by the same or other plethodontid species (Cupp 1994; Madison et al. 1999; McDarby et al. 1999). The results of Murray & Jenkins (1999) using the same test species generally corroborated our daytime results, but their observations of greater avoidance of substrates from PC-fed TS vs. earthworm-fed TS indicated a night-time response, as described previously (McDarby

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**Fig. 2**: The percentage of salamanders tested under red light during day and night trials that preferred substrates containing just distilled water (open bars) or a distilled water rinse from aquaria containing snakes (solid bars) that had been fed red-backed salamanders (S) or nothing (N). The identification of snakes 4 and 5 appear in parentheses. Sample size was 20 in each comparison. Significance levels 0.05 (*) or 0.01 (**).
Because Murray & Jenkins recorded observations 3 h before to 1 h after
dark (Murray, pers. commun.), some mixing of day and night responses would be
expected, and so their results may be consistent with ours.

It is difficult to explain our results without evoking threat assessment by PC.
The night avoidance of substrates from PC-fed TS, but not earthworm-fed TS,
could by itself be interpreted as a cancellation of a snake avoidance response by
an attraction to the scent of earthworms, which are a common prey of PC (Jameson
1944). But if cancellation occurs, why would the avoidance response not also be
cancelled during the day? PC forage continuously day and night (Burger 1935;
Jaeger 1978), and so the motivation to feed and an attraction to earthworm scent
should be similar. If the risk of snake predation was greater during the day, then
a predominance of avoidance would be expected based on risk-assessment theory.
Confounding effects of food odors would also no explain why PC avoided sub-
strates from unfed TS during the day, but not at night, which was repeated under
both fluorescent and red lighting. The only reasonable explanation seems to be
that PC detected the substrates from unfed snakes, avoided them during the day,
but ignored them at night.

An alternative to a flexible, risk-assessment hypothesis that would explain the
above variability in avoidance behavior is a fixed, diel shift in behavior from a
daytime avoidance of snake scent to a night-time avoidance of PC ‘alarm’ sub-
stances from attacked/depredated conspecific salamanders (e.g. Lutterschmidt et
al. 1994; Marvin & Hutchinson 1995; Chivers et al. 1996, 1997; Woody & Mathis
1997). While we have no evidence to reject the possibility of a taxon-specific
avoidance response during the day, we do not believe the alarm hypothesis applies
to the night-time avoidance behavior, despite the occurrence of an alarm substance
in P. dunni (Chivers et al. 1997). We have shown that PC do not avoid substrates
upon which PC have been injured and induced to autotomize their tails, and nearby
PC have even attempted to eat the wiggling tail (Madison, unpubl.). In addition,
substrates from injured or uninjured PC have equivalent effects in scent component
studies demonstrating that only when the rinses from TS and PC were combined
did these components offset (cancel) the avoidance response stimulated by the rinse
from PC-fed TS (McDarby 1997).

Because our results appear to support risk assessment by PC, it is important
to consider whether the underlying assumptions concerning PC biology are valid.
The risk-assessment model assumes that foraging during the early evening is impor-
tant for PC, especially following recent rains, and that PC should persist in foraging
unless there were significant threats to survival. Insect prey are especially abundant
on the forest litter at night (Jaeger 1978), and the higher humidity at night reduces
the risk of dehydration that is a major inhibitor of PC activity (Heatwole 1960,
1962; Sugalski & Claussen 1997). Evening is also a time when Thamnophis sp. are
only occasionally active (during warmer weather; Reichenbach & Dalrymple 1986),
and the risk of predation by TS would therefore be lower. Logically, then, salam-
anders should avoid only the most threatening predatory stimuli at night, specifically
the scent traces of snakes that have recently fed on PC.

During the day, TS is much more active and presumably more likely to be
opportunistic when selecting prey (Heckrotte 1962; Reichenbach & Dalrymple 1986; Gibbons & Semlitsch 1987). Although PC feed under cover throughout the day (Burger 1935; Jaeger 1978), wariness of PC to snake scent should be greatest then because snakes may complement chemoreception with visual cues during prey search (Drummond 1985; Ford & Burghardt 1993; Heinen 1995), and because dehydration risks increase during the day (Heatwole 1960, 1962; Madison & Shoop 1970; Jaeger 1978; Sugalski & Claussen 1997). The daytime cover used by PC probably reflects these risks, and certainly any sudden exposure to a predator breaking into or otherwise gaining access to a shelter should be responded to with aversion, whether by immediate fleeing or by seeking refuge after immobility (e.g. Brodie et al. 1974, 1991b). Thus, selective chemosensory avoidance behavior above the litter at night, and general avoidance of snake chemical traces in the interstices of the forest floor during the day, are reasonable expectations for PC in response to TS.

If PC always encountered TS soon after detecting the latter’s substrate trails, it is doubtful whether persistent activity would ever occur regardless of snake diet history, simply because the temporary resource loss during avoidance would be negligible relative to the cost of losing a tail or being killed. Knowing how long avoidance persists, what the decay rates are for the substrate trace in nature, whether traces can be detected at a distance, and when and how often TS use the same foraging routes day and night is important before the risk-assessment hypothesis can be examined much further. Garter snakes are known to follow conspecific scent trails (Heller & Halpern 1981; Ford 1986; Halpern 1992; Ford & Burghardt 1993; Mason 1993), but little is known about snake foraging strategies and the propagation and longevity of scent traces in natural habitats.

The combined, day/night results support that red-backed salamanders recognize garter snake scent and that the mechanism governing avoidance does not simply shut off when the predator is relatively inactive at night, as has been observed in aquatic snails (Turner 1994, 1996). Instead, the mechanism remains operational and limits avoidance to those individual snakes whose diets represent the greatest threat. The day results suggest that factors beyond diet, such as the arousal state or foraging efficiency of the predator, become important in the decision whether to avoid snake scent. What may be operating is a risk-sensitive mechanism that evaluates snake diet and the predator’s daily activity pattern in determining the relative costs and benefits of avoidance based on chemical residues from a predation event occurring at least 3 d earlier. In regard to the settings of the mechanism, geographical variation may occur at lower elevations and latitudes where warmer temperatures may modify TS activity and shift the set points for risk taking by PC through the diel period. To our knowledge the only comparable data occur for aquatic snails (Turner 1994, 1996) and certain fishes (review by Smith 1992, 1997). Our data suggest that at least some terrestrial amphibians may be more sensitive to the chemical essences and activity states of predators than previously recognized, and we have introduced a model system for more thorough inquiry into the subtleties of an important terrestrial, predator–prey association.
Acknowledgements

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