

Spontaneous Immobility of the Japanese Lacertid Lizard, *Takydromus tachydromoides*

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Abstract: Frequencies of movement, as an index of propensity for immobility, of *Takydromus tachydromoides* were measured in the encounters with a potential predator *Elaphe quadrivirgata* (Session A) or a sympatric non-predator *Eumeces laticutatus* (Session B), or in the absence of other animals (Session C). Frequency of movement in Session A was significantly lower than in Sessions B and C. In Session B, *T. tachydromoides* moved significantly less frequently during the first 10 min than during the latter 10 min. The lizards previously exposed to *E. quadrivirgata* reduced their movements in the subsequent Session B with significantly high frequency when compared with animals without such experience. It is suggested that immobility of *T. tachydromoides* is an adaptive antipredator behavior to avoid detection by a visually orienting predator.

Key words: Immobility; *Takydromus tachydromoides*; Antipredator behavior; *Elaphe quadrivirgata*; Lacertidae

Lizards employ a variety of morphological and behavioral antipredator mechanisms. Greene (1988) summarized reptilian antipredator mechanisms and listed 60 phenotypic categories, including concealing coloration, immobility, locomotor escape, and tail display. It is certain that almost all lizard species possess more than one defensive tactic and several lizards respond with different antipredator behavior according to the environmental and/or situational contexts which they confront (e.g., Hennig, 1979; Thoen et al., 1986; Greene, 1988).

"Spontaneous immobility" (or freezing) can be distinguished from "tonic immobility" (or animal hypnosis), a behavioral response to restraint in which the animal appears to be unresponsive to stimulation (after Herzog, 1984; Greene, 1988), yet different definitions of these two wordings are seen in some papers (e.g., Brodie et al., 1974). Immobility, often coupled with cryptic coloration, is considered to be the initial antipredator response that increases the probability that the prey will escape detection by visually orienting predators (e.g., Heatwole, 1968; Brodie et al., 1974; Gregory, 1979). On the other hand, tonic immobility is usually the final behavioral stage which is elicited after external restraint (see Arduino and Gould, 1984). Although there are several studies on tonic im-

mobility of iguanids and gekkonids in which the animal was held so that movement was impossible and restrained until tonic immobility resulted (e.g., Gallup, 1973; Hennig, 1979; Herzog, 1984), few quantitative studies have demonstrated immobility of lizards voluntarily exhibited in the presence of a predator.

Takydromus tachydromoides, a slender, fast-moving lacertid lizard possessing a long autotomous tail (Fukada and Ishihara, 1967), has a brownish body coloration which makes this animal very inconspicuous in grassy areas where it usually lives. In staged predatory encounters, this lizard exhibits several antipredator behaviors according to situational contexts (Mori, 1990). As in other animals, the initial response of *T. tachydromoides* seems to be immobility to avoid detection by a predator. In this paper, I demonstrate that the spontaneous immobility of *T. tachydromoides* is elicited by the presence of a predator. As a result, this behavior is interpreted as one of the antipredator tactics of this lizard.

MATERIALS AND METHODS

The subjects were 19 adult *Takydromus tachydromoides* (7 males and 12 females; snout-vent length, 46-61 mm) collected from Osaka (N=2) and Kyoto (N=10) Prefectures, and Kuchinoshima (N=4) and Takeshima (N=3) Islands in Kagoshima Prefecture, Japan.

Lizards from the latter three groups included the same individuals used in another experiment (Mori, 1990). There were no obvious behavioral differences observed between the four groups. All lizards were housed individually in clear plastic cages (315 × 170 × 235 mm) with a water bowl and a shelter, and were maintained under a natural photoperiod for two to four months before the experiments. The room temperature varied between 17 and 31°C. They were fed mealworms two or three times per week. Water was available ad libitum.

The testing arena (650 × 400 × 250 mm) was made of white polypropylene corrugated board except for a transparent plastic ceiling, and contained a cardboard floor marked with 2 cm grids. The arena was divided into two chambers (large: 510 × 400 × 250 mm, and small: 140 × 400 × 250 mm) by a plastic insert which could be removed from the arena by sliding it out through a slit at the front wall. After each trial, the arena was washed with water and the cardboard floor was replaced.

Trials consisted of three sessions. *T. tachydromoides* was introduced into the large chamber and a Japanese striped snake, *Elaphe quadrivirgata* (a well known natural predator of *T. tachydromoides*: Mori and Moriguchi, 1988: Session A), or *Eumeces latiscutatus* (a sympatric scincid lizard but not a possible predator of *T. tachydromoides*: Session B, control for the presence of a non-predator animal) was introduced into the small chamber. In Session C, only *T. tachydromoides* was introduced into the arena in the absence of other animals (control for experimental milieu). Each *T. tachydromoides* was tested in all the three sessions in non-fixed order. Each session was initiated by the removal of the insert from the arena and lasted for 20 min at most (see below). A ten-minute interval was allowed between sessions. A total of 11 *E. quadrivirgata* were used for Session A (one to three trials per individual). Temperature was

maintained between 27.0–30.5°C during the experiment.

All trials were recorded with a video tape monitor (National NV-8480, VHS type) and a color video camera (National VZ-C70). Propensity for immobility was evaluated by quantifying the frequencies of movement by videotape analyses. The bottom of the arena was divided into eight equal sections, and the number of times the lizard changed sections was counted (i. e., amount of movement). The frequency of movement (FM) was calculated for each session as (amount of movement) / (observed duration). In all B and C sessions, duration of observation was 20 min. It is likely that the actual snake attack affected the behavior of *T. tachydromoides*, especially in the frequency of movement. Thus, in Session A, observation was terminated when the snake first attacked or pursued the lizard. Escape movements of *T. tachydromoides* after the attack of the snake were not included in the amount of movement. Consequently, the observation period varied from 0.33 to 20 min (\bar{x} = 8.3 min) in Session A.

Statistical significance was tested by Mann-Whitney's U-tests or Wilcoxon signed-ranks tests (between two samples) and Friedman two-way ANOVA (among three samples) followed by multiple comparisons (Siegel and Castellan, 1988).

RESULTS

Two *T. tachydromoides* never moved for 20 min in Session A in which the snake also remained motionless. Other 11 lizards remained motionless until the snake closely approached, and then, the lizards escaped by running, which was followed by the attack of the snake. On the other hand, only one individual remained immobile throughout in both Sessions B and C.

The type of session affected FM of *T. tachydromoides* significantly ($X^2 = 19.6$, $dF = 2$, $p < 0.001$). The FM was significantly lower in

TABLE 1. Amount of movement (AM), duration of observation (OD) and frequency of movement (FM = AM/OD) of *Takydromus tachydromoides* in encounters with *Elaphe quadrivirgata* (Session A) or *Eumeces latiscutatus* (Session B) and in the absence of other animals (Session C). The FM is also calculated for the first and latter 10 min separately, for Sessions B and C.

Session	N	AM		OD (min)		FM		FM			
		\bar{x}	Range	\bar{x}	Range	\bar{x}	Range	First 10 min		Latter 10 min	
								\bar{x}	Range	\bar{x}	Range
A	19	4.6	0–48	8.3	0.3–20	0.59	0–6.8				
B	19	42.8	0–96	20	—	2.14	0–4.8	1.61	0–4.8	2.68	0–5.5
C	19	54.5	0–128	20	—	2.72	0–6.4	2.83	0–6.8	2.62	0–6.6

Session A ($\bar{x}=0.59$) than in Sessions B and C ($\bar{x}=2.14$ and 2.72 , respectively; $p<0.05$; Table 1). There was no significant difference in FM between Sessions B and C ($p>0.05$).

Because duration of observation in Sessions B and C (20 min) was much longer than in Session A ($\bar{x}=8.3$ min), it is possible that the higher FM in the former two sessions may reflect the effect of acclimation of *T. tachydromoides* to the arena rather than the reducing effect of the presence of a predator in Session A. Therefore, Sessions B and C were partitioned into 2 10-min blocks, and a Wilcoxon signed ranks test was conducted in Sessions B and C separately. The FM for the first 10 min in Session B ($\bar{x}=1.61$) was significantly lower than that for the latter 10 min ($\bar{x}=2.68$; $z=-3.00$, $p<0.01$). There was no significant difference in FM between the first and latter 10 min in Session C ($z=-0.57$, $p>0.05$).

Comparison of FM among the three sessions was made again, but this time only the first 10 min data were used as for Sessions B and C because the time effect was significant in Session B (see above). The type of session significantly affected the FM ($\chi^2=19.7$, $dF=2$, $p<0.001$). The FM in Session A ($\bar{x}=0.59$) was significantly lower than in either Session B or C ($\bar{x}=1.61$ and 2.83 , respectively; $p<0.05$). There was no significant difference in FM between Sessions B and C ($p>0.05$).

Another factor that may affect FM is the order of sessions. The lizard that had encountered a snake seemed to immobilize more frequently in the subsequent sessions, especially in Session B. Order effects were analyzed with Mann-Whitney's U-test for Session B. *T. tachydromoides*, both in the first and the latter 10 min, moved less frequently in the presence of *Eumeces latiscutatus* after being exposed to a snake than not ($U=14$ for the first and 15 for the latter, $P<0.05$ for each; Table 2).

Finally, FM among the three sessions was

TABLE 2. Frequency of movement (FM) of *Takydromus tachydromoides* in the encounters with *Eumeces latiscutatus* for the first and the latter 10 min of the observation period. *T. tachydromoides* was exposed to a snake (Session A) prior to Session B (A-B) or not (B-A).

Order	N	FM			
		First 10 min		Latter 10 min	
		\bar{x}	Range	\bar{x}	Range
A-B	7	0.64	0-1.7	1.43	0-3.0
B-A	12	2.17	0.1-4.8	3.41	0.9-5.5

analyzed using the data from 12 trials where Session B was conducted prior to Session A. As for Sessions B and C only the first 10 min data were used. The FM was significantly affected by the type of sessions ($\chi^2=18.2$, $dF=2$, $p<0.001$). The FM in Session A ($\bar{x}=0.26$) was significantly lower than in Sessions B and C ($\bar{x}=2.17$ and 3.60 , respectively; $p<0.05$; Table 3). There was no significant difference in FM between Sessions B and C ($p>0.05$). As for the latter 10 min, there was no significant difference in FM between Sessions B and C ($\bar{x}=3.41$ and 3.58 respectively; $z=-0.67$, $p>0.05$).

DISCUSSION

Any behavioral antipredator adaptation should be accompanied by the ability of the prey to assess potential predation situations accurately. The primal stage of such situation assessments is to judge whether an animal that the prey confronts is dangerous (i.e., a predator) or not. It is clear that *T. tachydromoides* can discriminate predators from non-predators and reduces its own movement to avoid detection by the former. This behavior may be adaptive because in many species of predators including *Elaphe quadrivirgata*, prey movement is a critical factor in mediating attack (Herzog and Burghardt, 1974; Ota, 1986).

Ducey and Brodie (1983) reported that the

TABLE 3. Frequency of movement (FM) of *Takydromus tachydromoides* observed in Sessions A, B, and C. Only the data of the trials in which Session B was conducted prior to Session A are presented. The FM is also presented for the first and latter 10 min separately, for Sessions B and C. See Table 1 for explanations of sessions.

Session	N	FM		FM			
		\bar{x}	Range	First 10 min		Latter 10 min	
				\bar{x}	Range	\bar{x}	Range
A	12	0.26	0-2.4				
B	12	2.79	0.8-4.8	2.17	0.1-4.8	3.41	0.9-5.5
C	12	3.58	0.9-6.4	3.60	0-6.8	3.58	1.2-6.6

type of contact with the same predator (body or tongue) affects the response of salamanders. Although the sample size is very small, similar results were also obtained in *T. tachydromoides*: the lizard remained motionless when the snake made contact with its body (2 cases), whereas the lizards which had immobilized started running immediately after the snake made contact with the head (3 cases). When to shift from immobility to running escape may be crucial. If escape is employed too early, the lizard may attract predator's attention to itself if otherwise it could go unnoticed. Contact with the head of the snake increases the immediate strike threat as compared to nearness of a predator (body contact), so the running escape may be more advantageous in such situations. Therefore, encountering a predator, *T. tachydromoides* first immobilizes to avoid detection, but if the disadvantage of remaining motionless increases, it shifts its defensive behavior to the next stages, such as tail vibration or fleeing (Mori, 1990).

The presence of *Eumeces latiscutatus*, a non-predator, also affected the behavior of *T. tachydromoides* especially in the earlier stage of the encounter, but not so much as in the presence of snakes. Furthermore, *T. tachydromoides* reduced its activity much more in the presence of *E. latiscutatus* when it had been exposed to a snake in the preceding encounter: *T. tachydromoides* seems to be warier of another animal in such cases. This seems to reflect the effect of the earlier experience (Gregory, 1979) or the responses to the remnants of chemical substances of the snake in the arena. In either case, the enhanced immobility may be adaptive because both a recent encounter with a predator and the presence of predators' odor imply the high probability of the presence of a nearby predator (Thoen et al. 1986).

ACKNOWLEDGMENTS.—I wish to thank T. Hidaka for reviewing the manuscript and H. Ota for carefully reading an early draft of this paper. I also thank T. Hayashi, T. Hikida, H. Ota, and H. Takahashi for collecting animals. This research was partially supported by a Grant-in-Aid for Special Project Research on "Biological Aspects of Optimal Strategy and Social Structures" from the Japan Ministry of Education, Science and Culture.

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要 旨 ニホンカナヘビ *Takydromus tachydromoides* の不動行動

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ニホンカナヘビにおいて、不動行動をする傾向の指標として移動頻度を、その捕食者であるシマヘビ、非捕食者のニホントカゲと出会わせるとき（セッションA, B）、および、ニホンカナヘビだけにしたとき（セッションC）との間で比較した。セッションAにおける移動頻度はセッションB, Cにおけるそれよりも有意に低かった。セッションBにおいては、ニホンカ

ナヘビは前半の10分間の方が後半の10分間よりも動く頻度が有意に低かった。直前にシマヘビとのセッションを経験したニホンカナヘビは、経験しなかった個体よりも、それに続くセッションBにおいて移動頻度が有意に低かった。ニホンカナヘビの不動行動は、視覚によって獲物を見つけ出す捕食者に対する適応的な対捕食者行動であると考えられた。

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