動物学雜誌 ZOOLOGICAL MAGAZINE 91:239-244 (1982)

Predatory Behavior and Learning in the Lacertid Lizard, Takydromus tachydromoides, toward Unpalatable Prey Insects

YUTAKA JOHKI AND TOSHITAKA HIDAKA

Department of Zoology, Faculty of Science, Kyoto University, Sakyo, Kyoto 606 Japan

Received February 15, 1982 Revised version received April 15, 1982

ABSTRACT The prey recognition system in the predatory behavior of *T. tachydromoides* was analyzed experimentally using unpalatable *Pryeria* moths and edible mealworms. None of the *Pryeria* moths were either killed or eaten, while all the mealworms attacked were eaten. The learning of visual avoidance by *T. tachydromoides*, in which the lizard associates the unpalatability of *Pryeria* moth with its appearance and avoids it, seemed to exist, but its process appeared to be very slow. In the course of predatory behavior, the lizard first recognized the prey visually, but then checked it strictly through chemical cues. This suggested that not only visual but also other sensory cues such as olfactory and gustatory stimuli derived from the prey were necessary for the efficient avoidance learning in this lizard. (*Zool. Mag. 91: 239-244, 1982*)

Lizards are largely insectivorous and are supposed to be the main diurnal predators of insects as well as birds. It is known that many species among them can recognize and learn the coloration of their prey (Swiezawska, 1949; Sexton, 1960, 1964; Benes, 1969; Boyden, 1976). Color discrimination and learning in lizards were recently reviewed by Burghardt (1977). Nevertheless, studies on the color recognition and learning in lizards, in particular with reference to the meaning and the evolution of coloration in the prey insects, are still lagging behind compared with those in birds.

In our previous study (Johki and Hidaka, 1979) using the lacertid lizard, *Takydromus tachydromoides* Schlegel as the predator and the unpalatable larvae of the moth, *Pryeria sinica* Moore (Lepidoptera, Zygaenidae), as the prey, it was concluded that not only visual cues but also other factors such as olfactory and gustatory cues played an important role in the process of recognition and choice of prey insects in this lizard. In the present paper, we carried out feeding experiments using the same lizard species as the predator, in order to compare the results of our previous study and to make an attempt to generalize the process of predatory behavior in this lizard. Adults of the same species, *P. sinica*, were used as experimental food for the following two reasons. First, it is evident that this moth is an unpalatable prey for lizards from our preliminary observations, and second, they are different types of prey (moths *us* caterpillars), although belonging to the same species.

Materials

Takydromus tachydromoides is a common, terrestrial lacertid lizard in Japan and is an important predator of many insects and spiders (Jackson and Telford, 1975). Eleven adults of *T. tachydromoides* at least one-year of age were captured in the Ginkaku-ji area of Kyoto in May, 1977, and were reared for about four months until the experiment started. Only three kinds of foods, mealworms (larvae of *Tenebrio molitor*), armyworms (larvae of *Leucania separata*) and cricket nymphs, were fed to the lizards as ordinary foods. Food was given daily in a set time span (0:00 - 3:00P.M.).

About one week before the start of the experiment, lizards were isolated individually in lidless plastic cages (16 cm \times 30 cm and 23 cm deep), with pebble floors. Each cage was equipped with a shelter and a Petri dish containing water, and was sprayed with water once a day to prevent dryness.

The experimental prey, adult *Pryeria* sinica, belongs to the family Zygaenidae (Lepidoptera), all species of which are dayflying and whose larvae have relatively conspicuous color patterns. In several species of Zygaenidae such as *Zygaena* spp., both adults and larvae secrete poisonous substances which are supposed to play a protective role (Jones *et al.*, 1962; Bullini *et al.*, 1969; Rothschild, 1971). Adults of *P. sinica* can be seen once a year, from late October to middle November in Kyoto. They are somewhat bee-like, with yellow and black body hairs and transparent wings (Fig. 1). When disturbed, they emit a peculiar smell with the characteristic behavior of abdomen elevation.

Adult *Pryeria sinica* used in this study were obtained in the laboratory about two months earlier than in nature by rearing the pupae under short-day conditions (Ishii *et al.* in prep.).

Experimental Procedure

The experiment was conducted as previously described (Johki and Hidaka, 1979) but mealworms were chosen as the palatable control insects this time. One experimental



Fig. 1. Adult male Pryeria sinica exhibiting the "abdomen-elevation" behavior.

 $\mathbf{240}$

prey, adult P. sinica was given once a day to each lizard by dropping it within 10 cm of the lizard's snout, and the response of the lizards was observed. Each lizard was allowed two minutes to respond to the prey, because this duration of time was shown in the course of our observations so far to be sufficient for the lizard's response to occur. The step at which the lizard interrupted predatory behavior was recorded. Immediately after a two-minute trial, the control prey, a mealworm, was given. When the control prey was not eaten, the data was discarded, assuming that the lizard was reluctant to eat all kinds of prey for some reason. The experiment was carried out for 15 days.

As described in our previous paper (Johki and Hidaka, 1979), the predatory behavior of lizards was divided into seven successive steps. They 1) watch (visually perceive) (W), 2) approach (A), 3) smell by tongue (Sm), 4) touch by tongue (T), 5) snap (Sn), 6) kill (K), and 7) eat (E) the prey.

The process of avoidance learning of the lizards toward unpalatable prey based on visual, olfactory and gustatory senses was analyzed in the following way. When disturbance by an experimenter or any other accidental agent was unlikely, interruptions at "watching" (W) or "approaching"

(A) could be regarded as occurring by some visual suppression, interruptions at "smelling" (Sm) as by olfactory and those at "touching" (T), "snapping" (Sn) or "killing" (K) as by gustatory. If the lizards learn to avoid the unpalatable prey by sight alone as the experiment proceeds, then the frequency of interruptions at the visual steps (W and A) in the predatory behavior will increase. This will lead to a daily decrease of Sm, which is considered to be the transition from the visual to the olfactory step. The ratio of Sm/W will then decrease daily. A daily decrease in the ratio of T/W will likewise show the progress of visual + olfactory avoidance learning, and a daily decrease in the ratio of Sn/W will show the process of establishment of avoidance learning through the overall sensory information.

Results

Response of lizards to Pryeria moths

The results of the experiment are presented in Table 1 (for each day) and in Table 2 (for each lizard). The incidence of seven successive step responses described in the Experimental Procedure (total of eleven lizards tested) to *Pryeria* moths and mealworms (control) is shown in Fig. 2 as the percentage to "watching (W)". All controls attacked were eaten by all eleven lizards, while none of the *Pryeria* moths were

Table 1. Response of Takydromus tachydro-
moides to Pryeria moths (for each day).
The number of each seven successive
step responses counted are shown.
W: watching, A: approaching, Sm:
smelling by tongue, T: touching by
tongue, Sn: snapping, K: killing, E:
eating.

Day	W	Α	Sm	Т	Sn	к	Е
1	8	7	7	7	1	0	0
2	11	10	10	8	3	0	0
3	10	5	5	3	1	0	0
4	10	7	5	5	2	0	0
5	10	10	8	7	5	0	0
6	8	8	8	5	4	0	0
7	11	9	6	5	4	0	0
8	5	4	3	2	1	0	0
9	6	5	3	1	1	0	0
10	5	1	0	0	0	0	0
11	5	5	2	0	0	0	0
12	7	4	3	2	0	0	0
13	7	5	3	1	0	0	0
14	8	5	3	2	0	0	0
15	6	4	2	2	0	0	0
Total	117	89	68	50	22	0	0
(%)	(100)	(76)	(58)	(43)	(19)	(0)	(0)

either killed or eaten. The frequency of response at each step from "W" to "K" decreased almost linearly.

Learning of lizards

Figures 3a, b, c show the daily change

Table 2. Response of *Takydromus tachydromoides* to *Pryeria* moths (same data as Table 1 but rearranged for each lizard).

Lizard No.	W	Α	Sm	Т	Sn	K	Е
1	12	9	9	8	5	0	0
7	6	4	4	3	1	0	0
9	8	5	4	4	2	0	0
11	7	5	3	2	0	0	0
13	12	10	7	6	5	0	0
15	15	8	5	4	3	0	0
17	11	8	6	5	3	0	0
18	15	14	11	7	2	0	0
19	8	4	3	2	0	0	0
21	13	12	7	4	0	0	0
22	10	10	9	5	1	0	0
Total	117	89	68	50	22	0	0

in the ratios of Sm/W, T/W and Sn/W, respectively. Sm/W was almost 100 % early in the experimental period, but it decreased as the experiment proceeded. Although T/W also had a tendency to decrease from 100 % in the process of the experiment, it fluctuated slightly and began to increase again at the end of the experimental period. Unlike these ratios, Sn/W was very low in the early period, gradually increased, reaching a peak on days 5-6, and then decreased again, stabilizing at 0 % in the last stage of the experiment.

Discussion

Analysis of the lizards' avoidance learning process toward their prey based on visual and chemical senses is the main subject of this study. Especially, the process of visual avoidance learning in such an insectivorous predator will be important in discussing the meaning of body color in insects.

As described in the Results, the daily

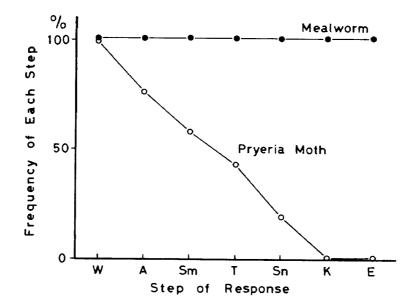


Fig. 2. Response curve of *Takydromus tachydromoides* to *Pryeria* moths and control mealworms based on Tables 1 and 2. The incidence of each step response (total of eleven lizards) is shown as the percentage to the number of "watching" steps.

$\mathbf{242}$

change in the Sm/W ratio can be regarded as showing the process of visual learning in lizards, the daily change in T/W as visual + olfactory learning and the daily change in Sn/W as overall learning. If these assumptions are correct, then the daily decline of Sm/W (Fig. 3a) will mean a reduced degree of facility in transition from the visual to the next (olfactory in this case) step in the predatory behavior. This probably represents

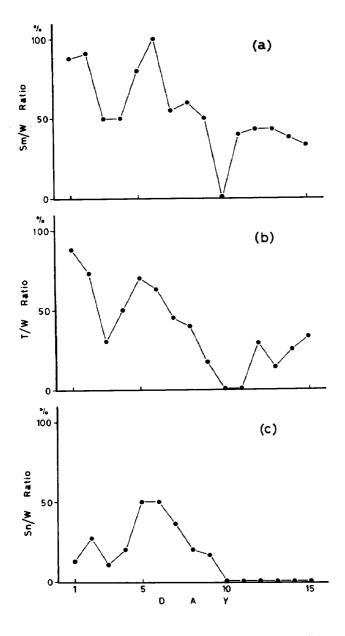


Fig. 3. Daily changes in the ratio, (a) Sm/W, (b) T/W and (c) Sn/W (based on Table 1).

the lizards' learning to associate the visual character of the prey with its unpalatability. It is thus suggested that the appearance of the *Pryeria* moth is functioning as a "warning signal", at least for *T. tachydromoides*. Here "warning signal" includes the conspicuous body color (warning coloration), bee-like shape, abdomen-elevation behavior which may be the threatening (Blest, 1964), and so on. The process of visual avoidance learning in *Takydromus*, however, seems to be very slow because a steady decrease in Sm/W started only from day 7 (Fig. 3a).

The T/W ratio also had a tendency to decline, but at the end of the experimental period it increased again (Fig. 3b). This may be due to vague olfactory avoidance learning.

The Sn/W ratio, an index to the overall learning of lizards, is low in the early stage of the experiment (Fig. 3c). This is probably due to a shyness of lizards toward the "novel" prey. In the case of avian predators, hesitation in attacking "novel" prey was pointed out by Coppinger (1969, 1970). If such a hesitation also existed in the lizard, then the following increase in Sn/W (Fig. 3c) will be interpreted as a decrease in shyness toward the *Pryeria* moth, and the following re-decline of Sn/W as caused by the unpleasant experience. After day 10, none of them attacked the *Pryeria* moths.

The patterns of the daily change in Sm/W and Sn/W are similar to those in our previous work (Johki and Hidaka, 1979). Although the present experiment was carried out in autumn while the previous one in late spring, an obvious qualitative difference was not detected. This fact coincides with Benes' (1969) report that in the whiptail lizard, *Cnemidophorus tigris*, the seasonal effect on feeding behavior was not qualitative but quantitative.

In our previous study, it was concluded that in the predatory behavior of the *Takydromus* lizard, the prey was first $\mathbf{244}$

recognized visually, but there followed a strict check through chemical cues. We confirm such characteristics again in this work.

Acknowledgment

This work was supported in part by a Grant-in-Aid for Special Project Research on Mechanisms of Animal Behavior from the Japanese Ministry of Education, Science and Culture.

References

- BENES, E. S. (1969) Behavioral evidence for color discrimination by the whiptail lizard, *Cnemidophorus tigris*. Copeia 1969: 707-722.
- BLEST, A. D. (1964) Protective display and sound production in some New World arctiid and ctenuchid moths. Zoologica N.Y. 49: 161-181.
- BOYDEN, T. C. (1976) Butterfly palatability and mimicry: Experiments with Ameiva lizards. Evolution 30: 73-81.
- BULLINI, L., V. SBORDONI AND P. RAGAZZINI (1969) Mimetismo mülleriano in popolazioni italiane de Zygaena ephialtes (L.) (Lepidoptera, Zygaenidae). Arch. Zool. Ital. 54: 181-214.
- BURGHADT, G. M. (1977) Learning process in reptiles. *Biology of the Reptilia*, ed. by C. GANS, Vol. 7 pp. 555-681.
- COPPINGER, R. P. (1969 and 1970) The effect of experience and novelty on avian feeding behavior with reference to

the evolution of warning coloration in butterflies. Part I. Behavior 35: 45-60 (1969). Part II. Amer. Nat. 104: 323-335 (1970).

- JACKSON, D. R. AND S. R. TELFORD, JR. (1975) Food habits and predatory role of the Japanese lacertid, *Takydromus tachydromoides*. Copeia 1975: 343-351.
- JOHKI, Y. AND T. HIDAKA (1979) Function of the "warning coloration" in larvae of a diurnal moth, *Pryeria sinica* MOORE (Lepidoptera, Zygaenidae). *Appl. Ent. Zool.* 14: 164-172.
- JONES, D. A., J. PARSONS AND M. ROTHSCILD (1962) Release of hydrocyanic acid from crashed tissues of all stages in the life-cyle of species of the Zygaenidae (Lepidoptera). Nature 193: 52-53.
- ROTHSCHILD, M. (1971) Speculation about mimicry with Henry Ford. Ecological Genetics and Evolution, ed. by R.
 CREED, Blackwell, Oxford, pp. 203-223.
- SEXTON, O. J. (1960) Experimental studies of artificial batesian mimics. *Behaviour* 15: 224-252.
- (1964) Differential predation by the lizard, Anolis carolinensis upon unicoloured and polycoloured insects after an interval of no contact. Anim. Behav. 12: 101-110.
- SWIEZAWSKA, K. (1949) Colour-discrimination of the sand lizard, Lacerta agilis.
 L. Bull. Int. Acad. Pol. Sci. Let. Ser. B, Sci. Nat. 11: 1-20.