FORAGING MODE OF THE SAND LIZARD, *Lacerta agilis*, AT THE BEGINNING OF ITS YEARLY ACTIVITY PERIOD

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Submitted December 27, 2000.

At the beginning of its yearly activity period *Lacerta agilis* behaves as an ambush foraging lizard. Proportion of attacks on prey discovered while lizards are moving (PAM), movement per minute (MPM) and percent of time spent moving (PTM) are low. A correlation was found between MPM and PTM. There are no significant differences between PTM and MPM among sexes or age categories. Prey search locomotion is rarely used and is discontinuous when it occurs. Pause duration has a positive correlation with movement length. Lizards counterbalance long movements with longer pauses in order to increase the probability of prey detection and capture. Contrary to other ambush foraging lizards, *Lacerta agilis* frequently tongue flicks, probably in order to detect and identify prey animals.

Key words: *Lacerta agilis*, Lacertidae, foraging mode, ambush foraging, tongue flicks, Romania.

INTRODUCTION

Over 30 years ago, Pianka (1966) described two modes of foraging: ambush foraging and active foraging. Ambush predators are traditionally considered sedentary, waiting for mobile prey and attacking when the prey passes into the perceptual field; active foraging species spend much of their time moving actively while searching for prey (Huey and Pianka, 1981).

Foraging mode in lizards has a central role in the understanding of ecological and life history characteristics such as prey types and predators (Huey and Pianka, 1981), energy utilisation (Anderson and Krasnov, 1988), reproduction (Vitt, 1990; Colli et al., 1997), relative clutch mass (Vitt and Congdon, 1978; Vitt and Price, 1982), locomotor capacity (Huey et al., 1984), predator escape modes (Vitt, 1983), learning ability (Day et al., 1999), and chemosensory behaviour (Cooper, 1994, 1995, 1997).

Perry (1999), based on precise quantitative information and a phylogenetic autocorrelative test of 83 species in 12 families of lizards, pointed out that there was a family level conservation of the foraging modes of lizards. The family Lacertidae displays the widest spectrum of foraging modes; both foraging modes may even be exploited even within the same genus (Pianka, 1993). In spite of the fact that ambush species such as *Pedioplanis lineoocellata*, *Meroles suborbitalis* (Pianka et al., 1979), and *Acanthodactylus scutellatus* (Perry et al., 1990) exist within the family, the Lecertidae is generally considered to consist chiefly of active foragers. This is because even sit-and-wait lacertids spend a much higher proportion of time moving than do iguanian lizards that use the same foraging mode (Cooper, 1994). Intrafamilial and intaragenic variation in foraging mode is also known in the Gekkonidae (Werner et al., 1997) and Scincidae (Cooper and Whiting, 2000).

This paper presents several aspects of the foraging behaviour of the sand lizard, *Lacerta agilis*, at the beginning of its yearly activity period. Specifically, I investigated:

1) Whether *Lacerta agilis* actively searches for food as do most other lacertids or is sedentary and waits for mobile prey;

2) Whether there is a difference in foraging mode of *Lacerta agilis* between sexes or age categories; and

3) Whether *Lacerta agilis* tongue flicks to detect prey items.

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MATERIAL AND METHODS

Study Animals

Lacerta agilis is a medium sized (up to 90 mm snout-vent length and 220 mm total length, 20 g) oviparous, insectivorous heliothermic lizard that is widely spread over Europe from England in the west to Russia in the east and from Sweden in the north to France in the south.

Study Site

Sf. Gheorghe is situated in the geographic centre of Romania in the north-eastern part of Brasov depression. The relief is represented by hilly wooded area and plain meadows. The climate is characterised by 7.6°C average annual temperature, with relatively hot summers (18°C) and cold winters (–4.7°C). Annual rainfall averages about 549 (400 – 600) mm per year with the driest month (February) averaging approximately 22.4 mm and the wettest month (July) averaging approximately 84.4 mm. When the study was conducted the average daily temperature was 13.4°C the maximum (25.9°C) was reached in the afternoon of 30th of April, the minimum (–1.6°C) in the night of 3rd of May. The relative humidity of the air was 65.5% ranging between 22 and 100%. Only a low quantity of rainfall was measured (15 mm).

This study took place in meadows near Sf. Gheorghe from April 20 through May 7, 2000. The habitat is on a 10 – 20° slope with southern exposure 80% covered by herbs and grasses with an average height of 15 – 30 cm as well as by *Crataegus monogyna*, *Rosa canina*, *Juniperus communis* bushes and small *Fagus sylvatica* (15 – 50 cm) trees. The study site is surrounded in the east, west and south by *Fagus sylvatica* forest while in the north, at the base of the slope, it is bordered by a brook, two artificial lakes, and a road.

Sampling Methods

To examine foraging activity, the habitat was visited daily. Observations on foraging were restricted to sunny days at times when the lizards were active. Lizards were detected by walking slowly through the habitat while scanning the area for activity. When a lizard was detected, the observer remained motionless and waited until convinced that normal activity of the lizard had not been disturbed. The observation of each individual for 10 consecutive minutes was attempted but it was not always possible because lizards sometimes went out of sight. Eleven sand lizards were observed for the full 600 sec and the average observation period of the 25 individuals (10 adult males, 5 adult females, and 10 juveniles) was 442.84 sec. Observations of less than 3 min were disregarded as were those in which lizards had been disturbed by the observer. Care was taken to avoid the observation of the same individual more than once. Sex, age category (juvenile or adult), and observation time of each individual were recorded. Time spent moving and perching, tongue-flicking behaviour and feeding attempts (successful and unsuccessful) were noted. In addition feeding attempts were scored as having been initiated after an active search or as a result of an ambush. Tongue flicks were considered associated with movement if they appeared within 1 second after movement cessation. Tongue flicking behaviour was observed only in adults as comparative data are available only for this age class. Postural adjustments, head, limb or tail movements were not recorded. Movements made in order to take up new ambushing positions were recorded, as were searching movements.

Data Analysis

From the raw data three indices of the foraging activity were calculated: the number of movements per minute (MPM), percentage of time spent moving (PTM) (Pianka et al., 1979) and the percentage of attacks on prey discovered while lizards were moving compared to total attacks (PAM) (Cooper et al., 1999).

Owning to the non normal distribution of MPM and PTM the significance level of differences between sexes and age categories were tested by the nonparametric Kruskal–Wallis one-way analysis of variance (Précsényi, 1995). Relationship between MPM and PTM, and pause and movement duration were examined using Spearman rank correlation. Mann–Whitney *U*-test was performed to examine differences between the duration of the movement made by the lizard when shifting to other perching site and the duration of active prey search movement made between two pauses.

RESULTS AND DISCUSSION

Based on the statistical measure of MPM and PTM the sand lizard is an ambush predator, both having very low values (MPM = 0.215 ± 0.25; PTM = 1.59 ± 2.41). The third index, PAM also indicates ambush foraging (PAM = 0.00) as all of the prey capture events ($n = 4$) occurred during perching. These values, low as in other ambush foraging lizards

(Table 1), suggest that *L. agilis* is sedentary and waits for mobile prey.

For lacertids the two indices, MPM and PTM, give the same verdict. For *L. agilis* there is a significant positive correlation between MPM and PTM ($r_s = 0.957$, $p < 0.001$) (Fig. 1). A correlation was found between the two indices for four species of Israeli lacertids lizards (Perry et al., 1990).

The average values of MPM and PTM differ within sexes or age categories (Table 2) but the difference is not significant (MPM: $H = 2.179$, $df = 2$, $p > 0.05$; PTM: $H = 1.709$, $df = 2$, $p > 0.05$). Among lizards there are usually sexual differences in the foraging mode, with males being more active than females (Perry, 1996, quoted by Werner et al., 1997). During mid-April through mid-May there are significant differences in the foraging mode of the two sexes of *Cnemidophorus tigris* (Anderson, 1993, 1994). The lizards' foraging mode can vary within species according to sex, age, place, time, and food availability (Ananjeva and Tesellarius, 1986). There may be differences in the foraging mode of the sand lizard throughout the whole year. The weight of the food, and the number and diversity of invertebrates consumed by Romanian sand lizards increase from April to June, when a maximum is reached. This is followed by slight decreases in July and August, and reaches a minimum in October (Valenciuc et al., 1988).

At the beginning of its activity period, the sand lizard attacks 0.021 prey per minute. *Cnemidophorus tigris* spends about 87% of its time in foraging related

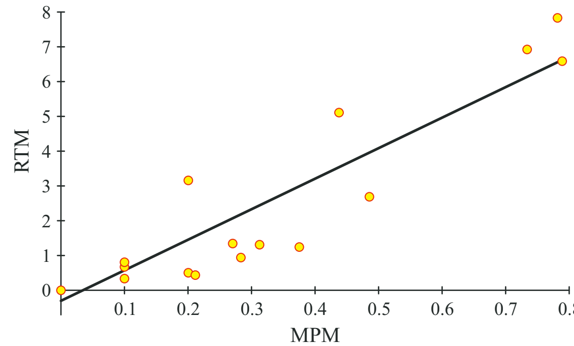

Fig. 1. Relationship between time spent moving (PTM) and the number of movements per minute (MPM).

TABLE 1. Lizards Foraging Mode Indices Obtained from Literature and from the Present Study

Family	Species	*n*	FM	MPM	PTM	Reference
Lacertidae	*Acanthodactylus boskianus*	7	A	2.01	28.8	Perry et al., 1990
	Acanthodactylus scutelltus	26	SW	1.01	7.7	Perry et al., 1990
	Lacerta laevis	16	A	1.61	30.5	Perry et al., 1990
	Lacerta agilis	25	SW	0.21	1.59	Present study
Gekkonidae	*Gekko japonicus*	12	SW	0.15	8.94	Werner et al., 1997
	Pachydactylus turneri	11	SW	0	0	Cooper et al., 1999
	Hemidactylus turcicus		SW	0.44	1.91	Perry, 1999
Chamaeleontidae	*Agama atra*	24	SW	0.27	0.01	Cooper et al., 1999
Cordylidae	*Platysaurus capensis*	22	SW	1.27	6.62	Cooper et al., 1997

Note. FM, foraging mode; MPM, movement per minute; PTM, percent of time spent moving; SW, sit-and-wait or ambush foraging; A, active foraging.

TABLE 2. Descriptive Statistics for Movement per Minute (MPM) and Percent of Time Spent Moving (PTM)

	Parameter	Mean	SD	SE	Min – Max	Range	CV
	MPM	0.21	0.25	0.05	0– 0.78	0.78	119.6
	PTM	1.59	2.41	0.48	0– 7.82	7.82	151.2
Males	MPM	0.2	0.26	0.08	0– 0.789	0.789	127.6
	PTM	1.26	2.05	0.64	0– 6.57	6.57	161.8
Females	MPM	0.07	0.11	0.05	0– 0.27	0.27	159.6
	PTM	0.4	0.6	0.27	0– 1.35	1.35	149.6
Juveniles	MPM	0.29	0.28	0.09	0– 0.78	0.78	97.7
	PTM	2.52	3.05	0.96	0– 7.82	7.82	120.9

Note. $n = 25$, 10 males, 5 females, 10 juveniles; SD, standard deviation; SE, standard error; CV, coefficient of variance.

movement (i.e., PTM = 87) and attacks 0.07 prey per minute (Anderson, 1993). *Kentropyx calcarata* spends 31.4% of its activity time moving and attacks 0.06 prey per minute; Mabuya nigropunctata moves 6.55% of its activity time and attacks 0.03 prey per minute (Vitt et al., 1997). The "extreme" ambush predator, *Corytophanus cristatus* feeds only on large arthropods, prey capture being infrequent (perhaps not even daily) (Andrews, 1979).

Most of its time, *L. agilis* perches motionless, usually near bushes or other shelter, occasionally changing to a different perch site in the vicinity of the same shelter. Prey search locomotion is rarely exhibited. The active searching sand lizard moves in a discontinuous fashion alternating bursts of locomotion with short pauses (pause-travel locomotion or saltatory search) as observed at other lacertids (*Podarcis muralis*, *P. pityuensis*, *Lacerta viridis*, and *L. trilineata*) by Avery et al. (1987). Among sand lizards, pause duration has a positive correlation with the movement length ($r_s = 0.711$, $p < 0.05$). There can be a trade-off between the length of movement and the success of prey searching. Lizards counterbalance long movements with longer pauses in order to increase the probability of prey detection and capture. The pauses increase the probability that prey at any distance from snout will be eaten compared with a moving lizard (Avery, 1993). There is no significant difference ($z = -1.1704$, $p > 0.05$) between the duration of the movement made by the lizard when shifting to other perching site and the duration of active prey search movement made between two pauses (Table 3).

Ambush and active foraging lizards differ in sensory modality; ambushers using visual cues while active foragers visual or olfactory cues (Perry and Pianka, 1997).

Only 26% of adult *Lacerta agilis* flicked their tongue to the substrate, performing 29 tongue flicks in 7 cases at a frequency of 0.245 tongue flick per minute. All individuals performed more than one tongue flick in a rapid succession (4.14 ± 2.03). Six times tongue flicking occurred at the end of search movement, once preceding prey capture. Like sand lizards, phrynosomatid lizards restricted tongue flicking of substrates to the end of transitional movements (Cooper et al., 1994). Sand lizards performed considerably more tongue flicks per minute than did phrynosomatid lizards (Table 4). Phrynosomatid lizards are considered ambushers, whereas lacertids are considered active foragers (Cooper, 1994). Families of active foragers use their tongue to detect and identify prey, families of ambush foragers lack prey chemical discrimination (Cooper, 1994). Active foragers take advantage of the trail left by prey animals (Schwenk, 1994) when seeking out prey by moving widely through the environment. Foraging mode (Perry, 1999) and chemoreception (Schwenk, 1993) are strongly influenced by phylogeny and demonstrate a correlated evolution (Cooper, 1997). Families of ambush foragers have lost prey chemical discrimination (Cooper and van Wyk, 1994).

Cordylid lizards, members of Scleroglossa, as well as lacertid lizards, are ambush foragers (Cooper et al., 1997) and lack tongue mediated chemosensory behaviour (Cooper and van Wyk, 1994; Cooper and Steele, 1999). *Lacerta agilis*, also adopt ambush foraging but use tongue mediated chemosensory behaviour.

TABLE 3. Descriptive Statistics for Active Search Movement and Shift Movement Length (in seconds)

Parameter	*n*	Mean	SD	SE	Min – Max	Range	CV	Mode
Shift	21	3.85	3.11	0.68	1 – 12	11	80.9	2
Active search	11	4.9	2.07	0.62	2 – 8	6	42.9	5

Note. SD, standard deviation; SE, standard error; CV, coefficient of variance.

TABLE 4. Tongue Flicking Rate at Phrynosmatidae (P) and Lacertidae (L) lizards

Species	*n*	*t*, min	Em	Ot	Tf per min	PTF, %	Reference
Sceloporus jarrovi (P)	48	476.07	5	0	0.019	10	Cooper et al., 1994
Sceloporus vigatus (P)	42	415.9	10	1	0.067	24	Cooper et al., 1994
Urosaurus ornatus (P)	34	33.67	7	0	0.033	21	Cooper et al., 1994
Cophosaurus texanus (P)	6	56.62	1	0	0.018	16	Cooper et al., 1994
Lacerta agilis (L)	15	110.16	6	1	0.245	26	Present study

Note. *t*, observation time; Tongue flick appearance: Em, end of movement; Ot, other times; PTF, percent of tongue flicking lizards.

These contradictions between adaptation to ambush foraging and the presence of tongue mediated chemosensory sampling are only apparent because chemoreception in squamates reflect family level features and not adaptation to local conditions by different species (Schwenk, 1993). Tongue mediated chemosensory sampling is a common feature of lacertid lizards, which can be used to detect prey items (Cooper, 1990, 1991) as well as predators (Thoen et al., 1986).

Acknowledgements. I am grateful to Kovásznay Csengele for field assistance and for help preparing the manuscript. An anonymous reviewer gives helpful advice. This study was supported by "Iskola" Foundation.

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