

## EFFECTS OF BODY TEMPERATURE ON THE PREDATORY BEHAVIOUR OF THE LIZARD *PSAMMODROMUS ALGIRUS* HUNTING WINGED AND WINGLESS PREY

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The thermal dependence of predation success in the Mediterranean lacertid lizard *Psammodromus algirus* was studied using two types of prey (winged and wingless flies) that differed in their ability to escape predation at all  $T_b$ s (body temperatures) tested (25-27°C, 29-32°C, and 34-37°C). Both number of failures and handling time decreased significantly at higher  $T_b$ s, and capture success was much higher for wingless flies; in fact, low  $T_b$ s were associated with a significant increase in capture success only in the case of winged flies. At low  $T_b$ s, winged flies could be efficiently seized by lizards only if pursued from a short distance. The attack distance was therefore larger for the less mobile (and less detectable) wingless flies at low  $T_b$ s, which suggests a trade-off between attack distance and capture success under conditions of impaired locomotor performance. Results of this study show that the escape abilities of prey are crucial to evaluate the effects of temperature on the performance of reptiles as predators.

### INTRODUCTION

The body temperature ( $T_b$ ) of reptiles affects their behaviour by influencing biochemical and physiological mechanisms (Dawson, 1975), but the ecological and evolutionary implications of such thermal dependence are best revealed at the level of organismal performance (Huey & Stevenson, 1979; Huey, 1982, 1991). The increased efficiency of muscular contraction and neuromuscular coordination at higher temperatures (Putnam & Bennett, 1982; Marsh & Bennett, 1985), for instance, leads to higher sprint speeds (Bennett, 1980) that improve the ability to capture prey and the ability to escape predation (Christian & Tracy, 1981; Avery, Bedford & Newcombe, 1982; Van Damme, Bauwens & Verheyen, 1991). These abilities, in turn, directly affect Darwinian fitness (Huey, 1991). It is therefore not surprising that diurnal lizards use behavioural means to achieve relatively high and constant body temperatures (Cowles & Bogert, 1944), even if such thermoregulatory behaviour entails costs in time, energy or predation risk (Huey, 1974; Huey & Slatkin, 1976).

Within this context, one central aspect of the thermal biology of lizards that has received relatively little attention is the thermal dependence of predation success (though see Greenwald, 1974; Avery *et al.*, 1982; Avery & Mynott, 1990; Van Damme *et al.*, 1991). Most of the work on this subject has been carried out using experimental (and often clumsy) prey whose behaviour bears little resemblance with the predator avoidance tactics of arthropods under more natural field conditions (Edmunds, 1974; Curio, 1976; Endler, 1986). Without using fast-fleeing prey, it is difficult to

evaluate the role of predatory efficiency as a selective force leading the evolution of behavioural thermoregulation in reptiles (Avery *et al.*, 1982). The experiments reported here were designed to analyse to what extent the escape abilities of prey influence the thermal dependence of predation success in a Mediterranean diurnal basker. For this purpose, I employed two types of prey (winged and wingless flies) and offered them to lizards whose  $T_b$  had been previously fixed. The particular issues addressed were: (1) Do the escape abilities of prey influence the effects of lizard  $T_b$  on predation success?; (2) What aspects of the feeding system (e.g. handling time or attack distance) have larger sensitivities to  $T_b$  and/or prey fleeing abilities?; and (3) Considering the data available about  $T_b$ s of active lizards, how good are the performance levels of lizard predation expected under field conditions?

### METHODS

The predator of choice was *Psammodromus algirus*, a medium-sized lacertid lizard (adult snout-vent length: 60-85 mm; mass: 6-14 g) that actively searches for a variety of arthropod prey (Díaz & Carrascal, 1990, 1993) and most frequently inhabits broad-leaved (both deciduous and evergreen) forests with a well developed undergrowth of shrubs (Díaz & Carrascal, 1991). It is a shuttling heliotherm (Díaz, 1991) whose microhabitat selection is strongly related to thermoregulatory behaviour (Díaz, 1992).

Animals used in the experiments reported here were nine adult lizards (mean [ $\pm$ SD] snout vent length of 74.3 $\pm$ 5.02 mm, and mean [ $\pm$ SD] body mass of 9.9 $\pm$ 2.26 g) collected in an open forest of *Quercus*

*pyrenaica* oaks at the northern slope of the Sierra de la Morcuera (40°35'N, 3°53'W, province of Madrid, Central Spain). Upon arrival at the laboratory, lizards were housed in leaf-litter filled terraria (100 x 50 x 30 cm) with a 60-W bulb providing heat for 8 hr per day and allowing lizards to maintain temperatures within previously reported field activity ranges (20–38°C; Carrascal & Díaz, 1989; Díaz, 1992). Food (mealworms, blowflies and wasp larvae) and water were supplied *ad libitum*.

The experiments on predatory behaviour were carried out in a 90 x 50 x 40 cm wooden cage with a transparent wall allowing direct observation of lizards, and whose floor had been ruled with a 10 x 10 cm grid to facilitate recording attack distances. A few dead branches were used to provide environmental complexity. Illumination was natural daylight complemented with an additional bulb inside the cage. I took advantage of natural fluctuations in temperature, together with the effects of varying the power of the bulb used (40, 60, or 100 W) and its distance from the substrate (15–30 cm), to manipulate the thermal environment in such a way that the operative temperatures monitored using copper models (Bakken & Gates, 1975; Bakken, 1992) fell within one of three distinct temperature ranges, hereafter referred to as low (25–27°C), moderate (29–32°C), and high (34–37°C). Models were copper cylinders with a small hole allowing insertion of the sensing tip of an electronic digital thermometer (precision of  $\pm 0.1^\circ\text{C}$ ) that were placed under the bulb to mimic the location of “basking” lizards. Model verification was obtained by comparing equilibration temperatures of models against those taken from anesthetized *P. algirus* under varying conditions of radiant heating. In addition, cloacal temperatures measured after each trial (see below) confirmed the accuracy of operative temperature copper thermometers (mean  $T_b \pm \text{SD}$  in  $^\circ\text{C}$ ,  $n$ , range; low temperature:  $26.1 \pm 0.47$ , 17, 25.4–27.0; moderate:  $31.0 \pm 0.97$ , 17, 29.4–32.5; high:  $35.9 \pm 0.79$ , 20, 34.4–37.2). These ranges were realistic considering available data about body temperatures in the field (Carrascal & Díaz, 1989; Díaz, 1992) and preferred body temperatures, that is, temperatures lizards would attempt to achieve in the absence of physical and biotic restrictions (Licht, Dawson, Schoemaker & Main, 1966); in *P. algirus*, mean selected  $T_b$  is about 35.2°C (unpublished data).

Experimental prey were commercially supplied blowflies (*Calliphora* sp.) with an average body length of 10.4 mm and an average head width of 3.1 mm. All flies were offered to the lizards within two days after their emergence from pupae, thus eliminating differences in escape ability that could have been acquired in previous encounters with predators. Flies were kept in refrigerated chambers at 4°C until the moment they were taken out, in groups of four, for lizard feeding. Immediately after extraction, two randomly chosen

flies had their wings removed by cutting their base. The dichotomy between these two types of prey seemed an appropriate one under the experimental conditions employed, because even winged flies could eventually be captured (after several trials, if necessary) due to the limited distance they could fly in the feeding enclosures. In addition, defence against predators is assumed to be a basic function of insect flight, and dipterans, that are among the more efficient insect fliers, make a small but evenly distributed contribution to the diets of more than 90 species of desert lizards (Pianka, 1986). This probably reflects the fact that rapid movements not only favour predator avoidance, but also elicit the attack response of visually-guided predators such as insectivorous amphibians and reptiles (Freed, 1988; Díaz & Carrascal, 1993). In addition, dipterans have been shown to make a major contribution to the diet of at least some populations of *P. algirus* (Carretero & Llorente, 1993).

The four prey (two winged and two wingless flies) were subsequently introduced into a matchbox that was allowed to warm up for a few minutes under a 60-W bulb. At the same time, an individual lizard was placed in the experimental cage and given 5 min to habituate to the feeding environment and have its  $T_b$  equilibrated within the range selected (low, moderate, or high); the lizards were allowed to sit under the bulb and warm up before the experiment was started. The sequence of temperatures for each individual was deliberately non-systematic to prevent within-subject order effects. Following this interval, the matchbox containing the flies was simultaneously opened and thrown into the experimental cage, as far from the predator as possible. An obvious problem of this experimental protocol, but one which is impossible to solve in a study involving ectotherms, is that fly temperatures in the terrarium cannot be controlled, so that results could reflect in part the physiology of the flies, not just of the lizards. Anyway, results (see below) showed that temperature effects on the escape behaviour of flies did not compensate for the reduced predation success of lizards at low temperatures.

Lizard behaviour was observed for the next five minutes or, alternatively, until all prey had been captured. A stop watch ( $\pm 0.1$  s precision) was used for measuring handling times, defined as the time elapsed between the first seizure of a prey by a lizard, and the first complete closure of the jaws after it had been swallowed. All observations were dictated to a tape recorder, so that the following variables could be noted when transcribing the tapes: (1) thermal regime (low, moderate or high temperature); (2) type of prey (winged or wingless) being attacked; (3) number of attacks, i.e. chases and jaw closures in an obvious attempt to catch a prey; (4) number of captures (ranging between one and four); (5) number of failures (attacks minus captures); and (6), when attack was successful (that is, when it led to prey capture), attack distance ( $\pm 1$

cm), defined as the distance between the lizard's snout and the location of the fly when the lizard started moving towards the prey before seizing it. In addition, the behaviour of both prey types (percentage of time immobile vs. percentage of time walking or flying) was monitored in a series of two minutes observations of randomly selected flies (10 winged and 10 wingless) that were released two at a time into the empty experimental cage.

After ending a trial, the lizard was taken out from the experimental cage and its  $T_b$  was immediately measured ( $\pm 0.1^\circ\text{C}$ ) with a Miller-Weber cloacal quick-reading mercury thermometer. All lizards were successfully tested (a trial was successful when it led to the capture and consumption of at least one prey) at each temperature range at least twice, always in different days. Individual data were averaged for each trial, and, in order to avoid pseudoreplication (Hurlbert, 1984), trial means were averaged over experimental subjects within temperature ranges. Mean ( $\pm$ SD) number of replicates per lizard was  $3.00 \pm 0.62$  at each temperature interval (range 2-4,  $n = 27$ ). Data on capture efficiency, handling times, and attack distances were analysed using repeated measures two-way (temperature by type of fly) analyses of variance, after having checked their conformity with the assumptions of ANOVA.

## RESULTS

Wingless flies spent significantly less time moving ( $t = 2.42$ ,  $n = 10$  for both series of data,  $P < 0.05$ ) than did winged flies (mean  $\pm$  SD:  $28 \pm 22\%$  vs.  $53 \pm 25\%$ , respectively). The body temperature of lizards influenced both capture efficiency and handling time (Figs. 1a & 1b), since warmer lizards had higher capture success (number of failures:  $F_{2,16} = 4.23$ ,  $P < 0.05$ ) and shorter handling times ( $F_{2,16} = 3.67$ ,  $P < 0.05$ ). The winged-wingless condition had no significant effect on handling time ( $F_{1,8} = 2.85$ ,  $P > 0.1$ ), but lizards were clearly more successful in capturing winged flies ( $F_{1,8} = 183.79$ ,  $P < 0.001$ ). No interaction was found between the effects of prey type and  $T_b$  on capture success or handling time ( $P > 0.1$  in both cases), though the effect of  $T_b$  on number of failures was significant for winged flies ( $F_{2,16} = 3.68$ ,  $P < 0.05$ ) but not for wingless ones ( $F_{2,16} = 2.64$ ,  $P > 0.1$ ). The attack distance, that was smaller for winged flies ( $F_{1,8} = 9.08$ ,  $P < 0.05$ ), varied significantly with  $T_b$  ( $F_{2,16} = 6.48$ ,  $P < 0.01$ ) because at low temperatures attack distances were much reduced for winged flies; there was a marginally significant interaction ( $F_{2,16} = 3.49$ ,  $P = 0.055$ ) between the effects of  $T_b$  and type of prey on attack distance (Fig. 1c).

The proportion of trials in which first capture was a winged fly (ranging between 0/2 and 4/4 for each experimental subject at each  $T_b$  range) tended to increase at higher  $T_b$ s (Fig. 2; repeated measures ANOVA model with linear contrast:  $F_{1,8} = 5.12$ ,  $P = 0.053$ ). At low  $T_b$ s, lizards captured wingless flies in first place

more frequently than expected by chance (equal proportions of 0.5 for each prey type:  $t_8 = 2.38$ ,  $P < 0.05$ ), whereas no significant deviations from random were found at moderate and high  $T_b$ s ( $t_8 = 1.06$  and  $t_8 = 0.78$ , respectively;  $P > 0.1$  in both cases).

## DISCUSSION

Perhaps the most remarkable finding of this study is that the effects of body temperature on the predatory efficiency of lizards were more clear-cut for winged prey than for wingless ones (Fig. 1). A number of previous studies have shown that reptilian handling times increase as  $T_b$  decreases (Avery *et al.*, 1982; Avery & Mynott, 1990; Van Damme *et al.*, 1991). These increases are probably due to a reduction in neuromuscular coordination at tissue or lower levels (Putnam & Bennett, 1982; Marsh & Bennett, 1985) that would also affect sprint performance and hence ability to chase fast-moving prey (Huey & Stevenson, 1979; Huey, 1982).

The unsuccessful attempts to feed at low temperatures are similar to Greenwald's (1974) observations on strike efficiency in gopher snakes and to the results reported by Avery *et al.* (1982) and Van Damme *et al.* (1991) with *Lacerta vivipara*. These later authors, however, could not demonstrate a decrease in capture

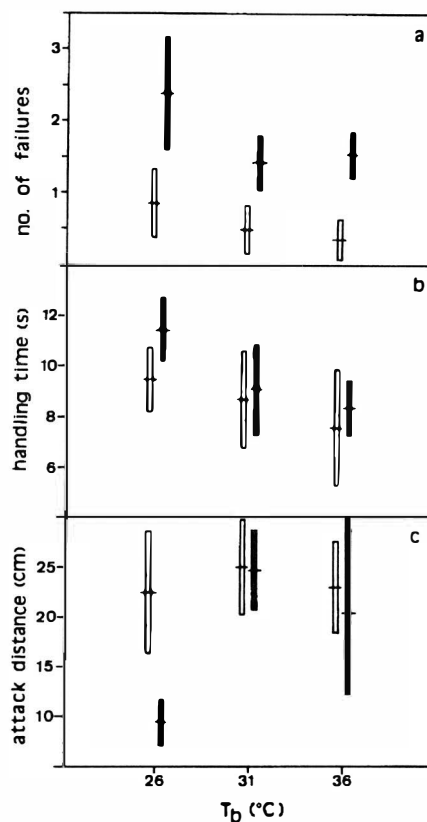


FIG. 1. Mean ( $\pm 2$ SE) number of (a) unsuccessful capture attempts, (b) handling time (in s), and (c) attack distance (in cm), according to body temperature and type of prey (winged vs. wingless flies). Solid and white bars represent winged and wingless prey, respectively.  $n = 9$  data (means of two to four replicates per individual lizard) for each prey type -  $T_b$  combination.

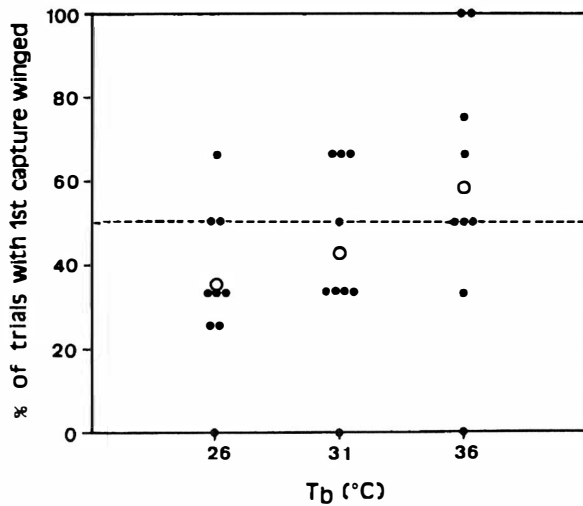


FIG. 2. Proportion of trials in which first successful capture was a winged fly for each of the nine lizards tested at each temperature range. The dashed line indicates the null hypothesis of equal number of first captures for both prey types, and the circles show the mean values at each temperature range.

success at low  $T_b$ , probably because they employed crickets with their hind legs removed to prevent escape from the terrarium. Results of the present study show that the escape abilities of prey are crucial to evaluate the effects of temperature on the performance of reptiles as predators.

The physical condition and vulnerability to predation experienced by prey (e.g. wingless flies) may determine what defence tactics should be adopted (Endler, 1991), for instance whether to freeze or flee (Bauwens & Thoen, 1981). Alternatively, wingless flies could move less than winged ones as a consequence of recent injury. Whatever the reasons for fly behaviour, immobility is useful as an antipredator defence as long as predators rely on sensory modes that detect motion (Edmunds, 1974; Endler, 1986), and lizards (including *P. algirus*; personal observation) often do not detect objects outside their tongue-flicking reach unless such objects are moving. Nevertheless, this antipredator strategy did not seem to be very efficient in the case of wingless flies, as it could not compensate their reduced fleeing speed: wingless flies were in fact captured before winged flies at low  $T_b$ s (Fig. 2).

On the other hand, in a series of feeding trials with *P. algirus* similar to the ones reported here, and allowing for the effects of prey size, the attack distance was larger for moving prey than for immobile ones (Díaz & Carrascal, 1993). One should therefore expect attack distance to be larger in the case of the more mobile winged flies. However, no difference was found at moderate or high  $T_b$ s, and the reverse was true at low  $T_b$ s: the attack distance decreased only in the case of the more difficult and mobile prey, suggesting a trade-

off between attack distance and capture success under conditions of impaired locomotor performance. Though I did not compare distances for attacks that did and did not result in prey capture, lizards did in fact attempt to make long distance attacks on winged flies at low temperatures; these long distance attacks were at least partially responsible for the high number of failures on winged flies at low  $T_b$ s shown in Fig. 1. In lizards, sprint speed exhibits a high thermal dependence, with slower and clumsier movements at lower  $T_b$ s (Bennett, 1980; Hertz, Huey & Nevo, 1983; Avery & Bond, 1989; Van Damme, Bauwens, Castilla & Verheyen, 1989; Van Damme *et al.*, 1991). Reduced locomotor performance at low  $T_b$  would have enhanced the escape abilities of winged flies by increasing the time available for detecting lizards. This would have reduced the mean distance of successful attacks to winged prey at low temperatures, and would have increased the mean number of unsuccessful, long distance attacks to such prey.

To what extent can the results obtained in this study be used to predict performance by field-active lizards under more natural conditions? According to a sample of 302 field  $T_b$  readings in a nearby area (part of which have been reported elsewhere, see e.g. Carrascal & Díaz, 1989; Díaz, 1992), most active lizards had  $T_b$ s within the moderate and high ranges defined above (47.7% of the readings between 28.6 and 33.5 °C, and 33.1% higher than 33.5 °C, respectively). However, 19.2% of the  $T_b$  readings were at or below 28.5 °C, so that a relatively large number of active lizards would be expected to show a diminished efficiency when trying to capture flying prey. Although some of these low  $T_b$ s probably correspond to lizards within the period of morning warm-up, when reduced capture abilities might not be relevant, a high proportion of the winged prey (assuming similar thermal sensitivities for most winged insects) would have effectively avoided lizard predation in the field. In fact, casual observations of this and other lacertid species (e.g. wall lizards, *Podarcis*) suggest that attacks to diptera are likely to succeed only when launched from a very short distance.

One final speculation is that improved ability to capture fast-fleeing, winged prey is likely to evolve if such "difficult" prey become more common than "not-so-difficult" ones, which is the expected result of stronger selection for prey defences than for predator counter-defences (Dawkins & Krebs, 1979; Endler, 1991). This suggests that reduced ability to capture fast-fleeing prey at low  $T_b$  may have been a major selective force leading to the evolution of behavioural thermoregulation in reptiles (Avery *et al.*, 1982). Results of this study indicate that high  $T_b$ s (that were close to the value of mean preferred  $T_b$ ) not only improve predatory efficiency, but also widen the range of prey that is actually available for lizards, because only at high  $T_b$ s can lizards counterbalance the escape abilities of their more difficult and faster fleeing prey.

## ACKNOWLEDGEMENTS

My gratitude is due to L. M. Carrascal, M. Díaz, T. Santos, and two anonymous reviewers, for constructive criticisms on a previous draft, and to Bartolomé and Montse for providing plenty of mealworms. Luis Carrascal also contributed useful statistical advice.

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*Accepted: 24.3.94*