Acta Herpetologica 1(2): 141-146, 2006

Escape behaviour in the Neotropical frog *Hylodes asper* (Anura: Leptodactylidae)

Claudio E.G. Patto [1], Marcio R. Pie [2]

[1]*Science Department, St Francis College, R. Belgica 399, São Paulo, SP, Brazil 01448-030.* E-mail: claudiop@stfrancis.com.br
[2] *Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brazil.* Corresponding author. E-mail: pie@ufpr.br

Abstract. Predation is an important selective pressure in natural populations, leading to the bewildering diversity of antipredation strategies found in nature. However, studies focusing on real-time assessment and management of risks by prey are underrepresented in the literature, particularly in the case of anurans. In this study we report on field observations of the escape behavior of the Neotropical frog *Hylodes asper* (Leptodactylidae). Escape distances varied according to the time of the day in both juveniles and adults. Moreover, there was a significant influence of age on the escape distance of an individual, with adults escaping at a greater distance than juveniles.

Keywords. *Hylodes asper*, escape behavior, Brazilian rainforest.

Predation is an important selective pressure in natural populations, what is reflected in adaptations such as crypsis, protective armor, and mimicry (Edmunds, 1974; Curio, 1976). But even cryptic animals must make day-to-day and even moment-to-moment decisions regarding when and where to be active (Lima and Dill, 1990; Rowe and Owings, 1990; Pie, 2005). Therefore, animals must be able not only to assess the risks associated with interacting with a predator, but also to make behavioral decisions in ways that minimize these risks (Rowe and Owings, 1990). However, studies focusing on real-time assessment and management of risks by prey are underrepresented in the literature (Lima and Dill, 1990; Kramer and Bonenfant, 1997; Kavaliers and Choleris, 2001; Welton et al., 2003). One possible way of addressing this question is to study the factors that influence the maximum distance a prey allows a predator to approach before fleeing, also called escape distance (ED) (Rand, 1964). In this study we report on field observations of the escape behavior of the Neotropical frog *Hylodes asper* (Leptodactylidae), assessing differences in the ED according to age and the time of the day.

This study was conducted in a small basin of mountain streams in the Brazilian Atlantic Rainforest. This microbasin comprises approximately 15 ha of forest drained by about 500 m of streams, varying in elevation from 500 to 600 m above sea level in Paranapiacaba, Municipality of Santo André, State of São Paulo, Brazil (23°28'S; 45°52'W). *Hylodes*

asper is a diurnal stream breeder frog (SUL = 20 to 50 mm) frequently found in this region, usually perched on river rocks and logs. Further details on this species and its habitat can be found in Heyer et al. (1990).

The protocol for measuring the ED is described as follows: a human observer walked cautiously and at constant speed towards the frog, up to a distance of 30 cm, when the observer attempted to capture it (in case it had not escaped before). The ED was then registered as the smallest distance between the observer and the frog at the moment of the escape. In case the animal did not escape or escaped after being touched the ED was registered as zero. The same observer conducted all the experiments. Although the use of a "fake realistic predator" would be ideal, the logistic constraints of getting to the field site would render that alternative impractical. In addition, very little is known about the biology of this species to be able to determine which type of predator would be most realistic. Finally, human observers have been successfully used as surrogate predators in a variety of studies (e.g. Cooper, 2003; Martin et al. 2004, 2005). We carried out these field experiments on two different days, a sunny day (n = 42) and an overcast day (n = 155 observations). Observations were conducted along a transect, which was not revisited during the experiments, assuring the independence of the observations.

The EDs varied significantly across the day, being larger during the morning hours, smaller near midday, and larger again during the afternoon (Fig. 1, Table 1). This variation was more pronounced during the sunny day, with four-fold variation in mean ED (Fig. 1A). This pattern was also present, but less pronounced, in the cloudy day (Fig. 1B). There was a significant interaction between time of day and weather (Table 1), showing that the daytime curve of escape distance varied with the cloudiness of the day. When age classes were analyzed separately, adults and juveniles differed in their mean ED along the day (Tables 2, 3). Adults escaped at a greater distance from the experimenter than juveniles. There was no significant interaction between ED for the different age classes and time of the day (Table 2), showing that daytime ED curves are similar for both age classes. It is important to note that the time of the day was used as a proxy to environmental variation such as temperature, humidity, and luminosity. We therefore cannot single out temperature as the source of variation, yet this limitation does not invalidate our results, particular with respect to the difference between juveniles and adults.

There is a very good visual match between the color pattern of *Hylodes asper* and the rocks from the creeks were it is commonly found (pers. obs.). Therefore, crypsis is presumably the first antipredator strategy employed by this frog species. Additionally, there is also a backup strategy, which is to flee, jumping from the perching rock into the water.

This strategy is efficient if the predator is able to overcome the initial crypsis strategy and detects a perching frog as a potential prey. However, if the frog flees every time it

Table 1. Two-way ANOVA comparing the mean escape distance along the daytime and according to the weather.

Variable	df	F	P
Time of day	6	8.739	< 0.001
Weather	1	3.246	0.073
Time of day x Weather	6	3.535	0.002

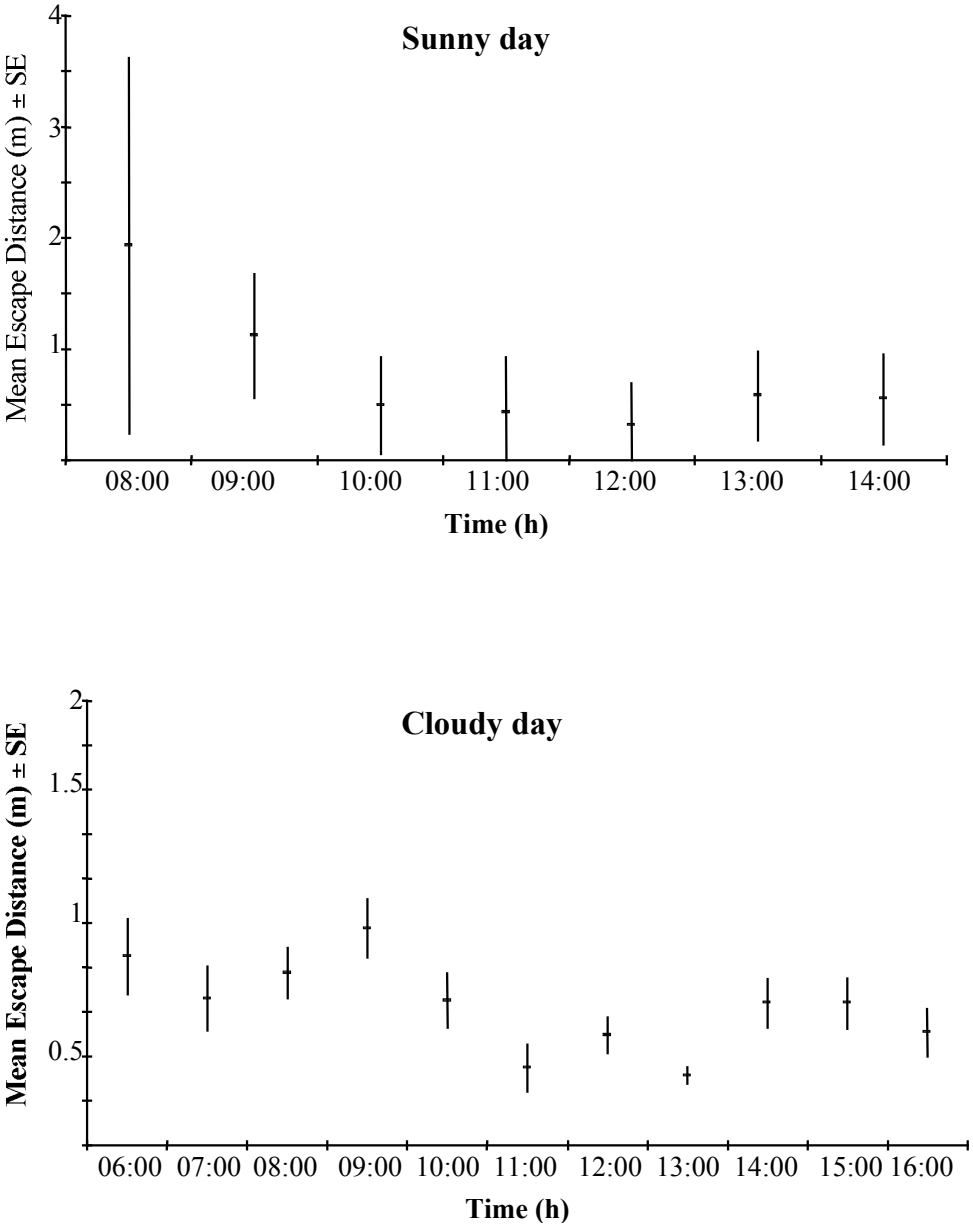

Fig. 1. Daily variation in escape distance (ED) in *Hylodes asper* along two different days (means ± SE).

detects a potential predator, besides the energetic costs of the escape itself and the interruption of other important activities like foraging and searching for mates, this response exposes the frog to the predator for a couple of seconds, and may actually increase the predation risk if it is taken at the wrong moment. The decision of when to shift from one

Table 2. Two-way ANOVA comparing the mean escape distance along the day and according to the observed age class.

Variable	df	F	P
Time of day	9	2.076	0.035
Age	1	7.365	0.007
Time of day × Age	9	1.159	0.320

Table 3. Variation in mean adult and juvenile ED along the day.

Hour	n	Adult		n	Juvenile	
		Mean (m)	SE		Mean (m)	SE
6-8	17	0.853	0.143	8	0.488	0.173
8-10	17	0.900	0.096	3	0.333	0.192
10-12	22	0.536	0.112	9	0.356	0.119
12-14	21	0.371	0.063	16	0.381	0.095
14-16	24	0.667	0.068	5	0.500	0.224
16-18	7	0.643	0.146	6	0.350	0.143

strategy to the other is critical, and factors like the physiological state of the frog must be very important (Whiting 2002). The motor performance of ectotherms such as frogs declines with temperature (Heckrotte, 1967; Bennet, 1980; Lillywhite, 1987). Hence, at lower temperatures, frogs would tend to have slower escape responses, and therefore a higher probability of capture. In this case, frogs would be expected to be more cautious by fleeing sooner. The variation in ED of *H. asper* throughout the day and according to the weather detected in the present study is consistent with these predictions. Many studies have demonstrated the influence of temperature on the defensive behavior of a variety of ectotherm vertebrates. Prior & Weatherhead (1994), studying the rattlesnake *Sistrurus c. catenatus*, showed that warmer snakes were more likely to rattle and/or flee than cooler snakes. Snakes are also more aggressive when tested at a lower temperature (Arnold and Bennet, 1984; Scheffelin and de Queiroz, 1991), also striking with higher velocity, greater accuracy, and less hesitation (Rowe and Owings, 1990). Lizards such as *Anolis lineatopus* also tend to flee sooner as the temperature decreases (Rand, 1964). Nonetheless, we can not rule out the influence of other factors on the variation in ED, such as an increase in the importance of the perching site to foraging or finding mates during the midday.

The most puzzling aspect of our results is the observation that adults tend to escape when the experimenter was at a greater distance than did juveniles. Martin et al. (2005) found similar results in a study of the escape behavior of the green frog (*Rana perezi*), with smaller frogs appearing to rely on crypsis more than large frogs by allowing shorter escape distances. If viewed in terms of a trade-off between present and future reproductive success, juveniles have the highest interest in staying alive and therefore should escape sooner. Moreover, since males are territorial, there is a clear conflict between territorial defense and avoiding predators; a hiding territorial resident is unable to monitor its ter-

ritory and to defend it from conspecific intrusions. In this case, we would predict that ED should be smaller in territorial males (e.g. Diaz-Duarte, 1999). Even though females are not territorial in this species (Patto and Pie, unpublished results), the disruption of mate searching activities should affect ED in the same fashion. Why did adults attempt to escape sooner? Predators could be more motivated to pursue and attack larger prey, and the observed pattern would be the result of a size-dependent predation strategy. Alternatively, predators could be equally motivated to pursue any prey item, but larger prey could be more easily detected than smaller prey. Detailed experimental studies are necessary to discriminate between those hypotheses.

ACKNOWLEDGEMENTS

We thank C.F.B. Haddad and D. Rosa-Feres for valuable discussion. This work was funded by CNPq – Conselho Nacional de Desenvolvimento Científico e Tecnológico (CEGP) and Fundação Coordenação de Aperfeicoamento de Pessoal de Nível Superior – CAPES (MRP), and was carried out while the authors were part of the Graduate Program in Ecology of the Campinas State University.

REFERENCES

Arnold, S.J., Bennett, A.F. (1984): Behavioural variation in natural populations. III: antipredator displays in the garter snake *Thamnophis radix*. Anim. Behav. **32**: 1108-1118.

Bennet, A.F. (1980): The thermal dependence of lizard behaviour. Anim. Behav. **28**: 752-762.

Cooper, W.E. (2003): Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. Ethology **109**: 617-626.

Curio, E. (1976): The Ethology of predation. Springer-Verlag, New York.

Diaz-Duarte, R. (1999): Anti-predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. Proc. R. Soc. Lond B **266**: 2457-2464.

Edmunds, M. (1974): Defense in Animals. Longman Group Limited, New York.

Heckrotte, C. (1967): Relations of body temperature, size, and crawling speed of the common garter snake, *Thamnophis s. sirtalis*. Copeia **1967**: 759-763.

Heyer, W.R., Rand, S.A., Cruz, C.A.G., Peixoto, O.L., Nelson, C.E. (1990): Frogs of Boraceia. Arq. Zool., São Paulo **31**: 231-410.

Kavaliers, M., Choleris, E. (2001): Antipredator responses and defensive behavior: ecological and ethological approaches for the neurosciences. Neurosci. Biobehav. Rev. **25**: 577-586.

Kramer, D.L., Bonenfant, M. (1997): Direction of predator approach and the decision to flee to a refuge. Anim Behav. **54**: 289-295.

Lillywhite, H.B. (1987): Temperature, energetics, and physiological ecology. In: Snakes: Ecology and Evolutionary Biology, p. 25-91. Siegel, R.A., Collins, J.T., Novak, S.S., Eds, Macmillan, New York.

Lima, S.L., Dill, L.M. (1990): Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619-640.

Martin, J., de Neve, L., Fargallo, J.A., Polo, V., Soler, M. (2004): Factors affecting the escape behaviour of juvenile chinstrap penguins, *Pygoscelis antarctica*, in response to human disturbance Polar Biol. **27**: 775-781.

Martin, J., Luque-Larena, J.J, Lopez, P. (2005): Factors affecting escape behavior of Iberian green frogs (*Rana perezi*). Can. J. Zool. **83**: 1189-1194.

Pie, M.R. (2005): Signal evolution in prey recognition systems. Behav. Proc. **68**: 47-50.

Rand, A.S. (1964): Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology **45**: 863-864.

Rowe, M.P., Owings, D.H. (1990): Probing, assessment and management during interactions between ground squirrels and rattlesnakes. I. Risks related to rattlesnake size and body temperature. Ethology **86**: 237-249.

Schieffelin, C.D., de Queiroz, A. (1991): Temperature and defense in the common garter snake: warmer snakes are more aggressive than cold snakes. Herpetologica **47**: 230-237.

Welton, N.J., McNamara, J.M., Houston, A.I. (2003): Assessing predation risk: optimal behaviour and rules of thumb. Theor. Popul. Biol. **64**: 417-430.

Whiting, M.J. (2002): Field experiments on intersexual differences in predation risk and escape behaviour in the lizard *Platysaurus broadleyi*. Amphibia-Reptilia **23**: 119-124.