Short Notes

Flight initiation distance in relation to substratum type, sex, reproductive status and tail condition in two lacertids with contrasting habits

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Abstract. Flight initiation distance in relation to substratum type, sex, reproductive status and tail condition was studied in two lacertid lizards with contrasting habits: the ground-dwelling common lizard *Zootoca vivipara* and the rupicolous Horvath's rock lizard *Iberolacerta horvathi*. These species were studied in sympatric populations in a mountain area in North-Eastern Italy, Tarvisio Forest. Mean escape distance was significantly higher in *I. horvathi* than in *Z. vivipara*. In both species there were significant differences between sexes, with males escaping at longer distances than females but there were no significant differences between adults and subadults. In both species there were no differences in escape distance of females in different reproductive states. In *Z. vivipara* specimens with broken tails escaped at a shorter distance than individuals with intact tails. Substratum type had a significant effect on escape distance in both species.

How close should an animal allow a potential predator to approach before fleeing to a refuge? This is a crucial question for the survival of most animal population, but it has been only rarely tested on vertebrate species up to now (e.g. Kramer and Bonenfant, 1997; Martín and López, 2000a, b). Antipredatory behaviour is essential, especially in those animal species which are basal or intermediate in a trophic chain. Lizards are among the most widely predated organisms in the temperate zone ecosystems, being preyed upon by a variety of predators including birds of prey, carnivorous mammals, snakes, etc. (e.g., see Agrimi and Luiselli, 1994; Martín and López, 1996). Indeed, there is a great wealth of studies investigating the es-

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cape strategy of lizards and the costs associated to it (Cooper, 1997, 2000, 2005; Martín and López, 1999a; Martín, 2000; Cooper et al., 2003; Diego-Rasilla, 2003), but very few of these studies investigated the flight initiation distance (i.e. the linear distance between the approaching predator and the lizard prey at the time of first lizard's movement in response to the predatory attack). For instance it has been demonstrated that gravid females lizard of the live-bearing Zootoca vivipara allow a human predator to approach closer and flee less far than their non-reproductive conspecifics, this probably being due to them being hampered in locomotion by the weight of their clutch (Bauwens and Thoen, 1981). In addition, flight initiation distance was demonstrated to increase weakly with starting distance (i.e. with the distance separating predator and prey when the predator begins to approach) in a few species (e.g., Sceloporus virgatus) but not in other species (e.g., Urosaurus ornatus) (Cooper, 2005).

In this paper we analyse the correlates of flight initiation distance in two sympatric lacertid lizards with contrasted life-history traits,

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the ground-dwelling common lizard (*Zootoca vivipara*) and the rupicolous Horvath's rock lizard (*Iberolacerta horvathi*), to analyse whether the different ecological traits of these lizards (rupicolous versus terrestrial habits; oviparous versus live-bearing reproductive mode) may influence the lizard's responses towards an approaching predator.

The field study was carried out during July-August 1996 in a mountainous area in north-eastern Italy (Tarvisio Forest, province of Udine; 46°26'N, 13°31'E, 1100 m a.s.l.). The habitat consisted of stonepiles and ruins of old buildings at the border of coniferous forests and Fagus sylvatica forests, surrounded by detrital stony cones and rocky spots. The climate was typically alpine, with prolonged snow cover each year (usually from late November to late April). The study area was already used for long-term ecological studies on the snakes (e.g., Luiselli, 1995; Luiselli et al., 1996). The two studied species are abundant in this area; Zootoca vivipara was observed especially on ground or on tree stumps, whereas Iberolacerta horvathi on nearly vertical rocky spots. Both species were important prey sources for the snakes Coronella austriaca (Luiselli et al., 1996) and Vipera berus (Luiselli, 2006), and likely for some species of birds of prey (e.g., Buteo buteo) (Capizzi et al., unpublished) at the study area.

Lizards were approached to quantify their escape distance (precision \pm 5 cm), then were captured and individually marked by toe-clipping to avoid data pseudoreplication (Hurlbert, 1984). We walked slowly through the study area on a linear path bypassing the zone in which we were looking for lizards between 9:00 and 13:00 (GMT) until an adult lizard was sighted. Upon spotting a lizard, we attempted to approach the animal by walking directly towards it at the same medium speed (approximately 45 m/min), simulating a predatory attack (see also Martin and López, 1999b). On capture, we identified them to species, sex, age (adults or subadults, depending on the development level of their secondary sexual characters), and recorded their SVL with callipers (to the nearest 0.1 mm), tail condition (whether whole, broken or regenerated), and reproductive status (pregnant or not, if females). We also defined habitat at the initiation of the flight, microhabitat type at the initiation of the flight, and time of day. Habitats at the initiation of the flight were categorized as follows: (i) ruins, i.e. the dilapidated cement walls of old buildings bombed during the first World War (1914-1919) and currently colonized by trees, bushes and tall grass, (ii) 'torbiera', i.e. a typically Alpine swamped area surrounded by tall grass, (iii) forest, i.e. the Swiss mountain pinewoods mixed with Fagus sp. forested territories that dominate the landscape of the study area; (iv) 'ghiaione', i.e. detrital cones colonized mainly by Pinus mugo trees and with substratum constituted mainly by large stones and rocks. The following microhabitat types were defined: (i) grass, (ii) leaves, (iii) stone, (iv) rock, (v) wood (i.e. piles of cut trees which are regularly found in the lizards' habitat and are actively used by lizards for basking), and (vi) sheet iron (this is a typical basking substratum of the ruins habitat, because it is a remain of the human manufactures at the time when the buildings were at work).

Data were processed by a Statistica version 6.4 PC package, with all tests being two-tailed and alpha set at 5%. We used parametric tests, given that all the variables were normally distributed or were log-transformed to achieve normality. We used several one-way ANOVA sets to establish eventual differences between groups, i.e. between species, sexes, etc.

Overall, we recorded escape distance and its ecological and morphological correlates in 81 *I. horvathi* and 87 *Z. vivipara*. Mean escape distance was 162.38 ± 72.5 cm in *I. horvathi* and 132.19 ± 57.1 cm in *Z. vivipara*. The two species differed significantly in terms of mean escape distance (one-way ANOVA: $F_{1,166} = 9.06, P < 0.005$). In both species there were no differences between climbing and ground-dwelling lizard regarding the mean escape distance (*I. horvathi*: $F_{1,79} = 1.725, P =$ 0.193; 70/11 climbing/on ground; *Z. vivipara*: $F_{1,81} = 0.297, P = 0.587$; 25/58 climbing/on ground).

The summarized data of the escape distances divided by sex and by species is given in table 1. In both species there were significant differences between sexes (*I. horvathi*: $F_{1,70} = 5.16$, P < 0.03; *Z. vivipara*: $F_{1,66} = 14.33$, P < 0.001), with males escaping at longer distances than females, but there were no significant differences between adults and subadults (*I. horvathi*: $F_{1,79} = 1.61$, P = 0.207; *Z. vivipara*: $F_{1,85} = 0.011$, P = 0.918).

In both species there were no significant differences regarding the reproductive status effects on the escape distance of females (*Z. vivipara*: $F_{1,25} = 1.615$, P = 0.216; *I. horvathi*: $F_{1,27} = 2.896$, P = 0.1). On the other hand, there was a significant effect of tail condition on *Z. vivipara* escape distance with specimens with broken tails escaping at a shorter distance than individuals with intact tails (90.32 ± 38.7 vs 146.4 ± 55.5; $F_{1,85} = 19.198$, P <0.001), but not in *I. horvathi* ($F_{1,78} = 0.778$, P = 0.381). Substratum type had a significant effect on escape distance in both species (*Z. vivipara*: $F_{5,81} = 3.74$, P < 0.005; *I. horvathi*: Short Notes

	n	Mean	Min	Max	Std. err.	Std. Dev.	Climbing	Ground	IT	BT
Z. vivipara										
Total	87	132.19	25	300	6.1	57.1	25	62	65	22
Males	39	153.49	75	300	9.2	57.6	7	32	33	6
Females	29	104.35	45	202	8.5	45.8	14	15	17	12
Subadults	19	136.54	25	250	12.7	60.9	4	15	15	4
I. horvathi										
Total	81	162.38	38	400	8.1	72.48	70	11	53	24
Males	40	175.05	50	360	11.9	75.3	35	5	27	13
Females	32	138.44	38	272	10.2	57.4	29	3	18	14
Subadults	9	191.22	73	400	30.0	90.0	6	3	8	1

Table 1. Summary of the means (and dispersion measures) of the escape distances (cm) in the two study species at the study area. Symbols: IT = intact tail, BT = tailless or broken tail.

 $F_{3,77} = 4.882$, P < 0.005). Tukey HSD posthoc test revealed that in *Z. vivipara* the only significant differences were between sheet iron and rock (sheet iron > rock) and between sheet iron and stone (sheet iron > stone), whereas in *I. horvathi* the only significant differences were between stone and rock (stone > rock) and between stone and leaves (stone > leaves).

The effect of habitat type on escape distance was not tested for *I. horvathi* given that all these lizards were captured only in a single habitat type (forest). On the other hand, there was a significant effect of the habitat type on the escape distance of *Z. vivipara* ($F_{3,83} = 4.21$, P < 0.01), and Tukey HSD post-hoc test indicated that the escape distance was significantly higher in 'torbiera' than in ruins.

Our study highlighted noteworthy differences between species regarding their escaping response to an approaching potential predator. To begin with, the flight initiation distance of Iberolacerta horvathi exceeded that of Zootoca vivipara. This interspecific differences does not seem to be related to the predominant climbing habits of I. horvathi: indeed there were not statistical differences between climbed and ground-dwelling individuals. On the contrary it seems more plausible that the observed differences were linked to species-specific antipredatory strategies, and also to eventual temperature differences (e.g., Rand, 1964; Hertz et al., 1982; Brana, 1993), a factor which was not measured in the present study. The different

strategies could depend on the fact *Z. vivipara* is a cryptically coloured, slow-moving ground lizard, whereas *I. horvathi* is a much quicker, conspicuously coloured climbing lizard. It is possible that *Z. vivipara* relies more on its cryptic colouration than on its running ability to escape predation. Moreover, *Z. vivipara* was observed exclusively in bushy habitat which could act itself as a refugia due to the presence of leaf litter and consequently allow lizards to flee at a shorter distance.

Another important trait which remarkably differed between species was the sex-linked flight initiation distance: the sexes showed an escaping strategy clearly different with males escaping at a longer distance than females, showing a similar pattern in both species. We suggest that this pattern may depend on the higher conspicuousness of the males because of both coloration patterns (Lapini, 2006) and behavioural displays in lizards (e.g., Martins, 1991, 1992, and references therein).

Concerning Z. vivipara, although the pregnant females are conspicuously heavier than males and non-reproductive females (hence, likely slower), there was no apparent effect of pregnancy on the flight initiation distance. A similar pattern was also seen in *I. horvathi*. This is in agreement with Rugiero's (1997) data on the lacertid *Podarcis muralis*, but clearly in contrast with the findings by Bauwens and Thoen (1981) on *Z. vivipara* from Belgium. This may be in part due to the fact that Belgian *Z. vivipara* are life-bearing whereas conspecific from the study area (belonging to the subspecies *carniolica*) are oviparous (Mayer et al., 2000) as also *I. horvathi* (Lapini, 2006) and *Podarcis muralis* (Bruno and Maugeri, 1977) are.

However this scenario appear to be complicated by the substratum type and the tail status. With regard to the substratum type effects on the escape distance, other studies attained contrasted conclusions (Ydenberg and Dill, 1986; Martín and López, 2000a). In the light of the unpredictability of the substratum effects on lizard escape distance, we prefer to avoid discussing more in depth of our results, but we take the opportunity to call this issue to general attention, given that there was in any case a true effect of the type of substratum (and, more in general, microhabitat type) on the lizard escaping strategies. We just suggest that our lizards started to flee earlier in microhabitats where they were presumably more visible to potential predators. Moreover, theoretical models of escape behaviour suggest that the optimal distance at which an animal starts to flee (approach distance) increases with distance to the refuge (Ydenberg and Dill, 1986; Dill and Houtman, 1989; Bonenfant and Kramer, 1996; Cooper, 1997). Thus, the presence of abundant leaf litter in bushy habitat, although it is not a safe refuge because predator could still locate concealed prey (Martín and López, 2000a), would condition the escape decisions towards a shorter fleeing distance for Z. vivipara than for I. horvathi which inhabits habitats with sparse or absent vegetation cover. Escape strategy of our Z. vivipara agrees with findings on the same species assessed by Bauwens and Thoen (1981) and could be compared to that revealed in Psammodromus algirus in bushy habitat by Martín and López (2000a), whereas I. horvathi escapes from predators by fleeing towards the nearest available refuge, and its flight initiation distance varies depending on the distance of available refuges, a same behaviour observed in several lizards species inhabiting heterogeneous habitats (Cooper, 1997). Unfortunately we did not

record the refuge distance of our lizards, thus we can not investigate the correlates between initial flight distance and relative animal distance from his refuge.

With regard to tail condition effects on flight initiation distance, it is hypothesized that tail loss may alter the escape tactics of lizards (Formanowicz et al., 1990; Smith, 1996) because tail loss could constitute a significant disadvantage for a lizard as it decreases its sprint performance (Ballinger et al., 1979; Punzo, 1992; Dial and Fitzpatrick, 1984). Thus, tailess specimens should change their behaviour towards crypsis rather than flight as main escape tactic, a defensive strategy in that they remain motionless and rely on the camouflage of their cryptic dorsal colouration (Formanowicz et al., 1990; Smith, 1996). Our data on Z. vivipara agree with this prediction, as the tailess lizards escaped at much shorter distance than tailed individuals, possibly when they feel their predator has definitely discovered their position and is ready to attack. On the other hand, our data on I. horvathi falsified the above hypothesis, as also did data by Rugiero (1997) on another rupicolous species (Podarcis muralis). Therefore, we predict that a shift in escape strategy by tailess lizards may occur on ground-dwelling species but less likely in climbing, rupicolous species.

Acknowledgements. We thank Claudio Anibaldi (Roma), Massimo Capula (Roma), and Lorenzo Rugiero (Roma) for much helpful cooperation in the field, and useful suggestions on the manuscript. James Harris (Porto) and two anonymous reviewers critically reviewed and considerably improved a earlier draft of this manuscript.

References

- Agrimi, U., Luiselli, L. (1994): Ecology of the snake Coronella girondica (Reptilia: Colubridae) in central Italy. Vie Milieu 44: 203-210.
- Ballinger, R.E., Nietfeldt, J.W., Krupa, J.J. (1979): An experimental analysis of the role of the tail in attaining high speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacertilia). Herpetologica 35: 114-116.
- Bauwens, D., Thoen, C. (1981): Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. J. Anim. Ecol. **50**: 733-743.

- Brana, F. (1993): Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. Oikos **66**: 216-222.
- Bruno, S., Maugeri, S. (1977): Rettili d'Italia. Martello, Milano.
- Cooper, W.E. Jr. (1997): Escape by refuging prey, the broadheaded skink (*Eumeces laticeps*). Can. J. Zool. **75**: 943-947.
- Cooper, W.E. Jr. (2000): Effect of temperature on escape behavior by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia propinqua*). Behaviour **137**: 1299-1315.
- Cooper, W.E. Jr. (2005): When and how do predator starting distances affect flight initiation distances? Can. J. Zool. **83**: 1045-1050.
- Cooper, W.E. Jr., Perez-Mellado, V., Baird, T., Baird, T.A., Caldwell, J.P., Vitt, L.J. (2003): Effects of risk, cost and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. Behav. Ecol. 14: 288-293.
- Dial, B.E., Fitzpatrick, L.C. (1984): Predator escape success in tailed versus tailess *Scincella lateralis* (Sauria: Scincidae). Anim. Behav. **32**: 301-302.
- Diego-Rasilla, F.J. (2003): Influence of predation pressure on the escape behaviour of *Podarcis muralis* lizards. Behav. Proc. **63**: 1-7.
- Formanowicz, D.R. Jr., Brodie, E.D. Jr., Bradley, P.J. (1990): Behavioural compensation for tail loss in the ground skink, *Scincella lateralis*. Anim. Behav. 40: 782-784.
- Hertz, P.E., Huey, R.B., Nevo, E. (1982): Fight versus flight: Body temperature influences defensive responses of lizards. Anim. Behav. **30**: 676-679.
- Hurlbert, S.H. (1984): Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187-211.
- Kramer, D.L., Bonenfant, M. (1997): Direction of predator approach and the decision to flee to a refuge. Anim. Behav. 54: 284-295.
- Lapini, L. (2006): Anfibi e Rettili nel Parco Naturale delle Dolomiti Friulane. Museo Friulano di Storia Naturale, Udine.
- Luiselli, L. (1995): The mating strategy of the European adder, *Vipera berus*. Acta Oecol. **16**: 375-388.
- Luiselli, L. (2006): Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos **114**: 193-211.
- Luiselli, L., Capula, M., Shine, R. (1996): Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps. Oecologia **106**: 100-110.

- Martín, J. (2002): Behaviour under predation risk: optimisation of escape decisions in lacertid lizards. Rev. Esp. Herp. 2002: 71-78.
- Martín, J., López, P. (1996): Avian predation on a large lizard (*Lacerta lepida*) found at low population densities in Mediterranean habitats: an analysis of bird diets. Copeia **1996**: 722-726.
- Martín, J., López, P. (1999a): An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. Oikos **65**: 328-333.
- Martín, J., López, P. (1999b): Nuptial coloration and mate guarding affect escape decisions of male lizards *Psammodromus algirus*. Ethology **105**: 439-447.
- Martín, J., López, P. (2000a): Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammodromus algirus*. Can. J. Zool. **78**: 265-270.
- Martín, J., López, P. (2000b): Costs of refuge use affect escape decisions of iberian rock lizards *Lacerta monticola*. Ethology **106**: 483-492.
- Martins, E.P. (1991): A field study of individual and sex differences in the push-up display of the Sagebrush Lizard, *Sceloporus graciosus*. Anim. Behav. 41: 403-416.
- Martins, E.P. (1992): Structure, function and evolution of the *Sceloporus* push-up display. Unpubl. Ph.D. Thesis, University of Wisconsin, Madison.
- Mayer, W., Böhme, W., Tiedemann, F., Bischoff, W. (2000): On oviparous populations of *Zootoca vivipara* (Jacquin, 1787) in south-eastern Central Europe and their phylogenetic relationship to neighbouring viviparous and South-west European oviparous populations. Herpetozoa 13: 59-69.
- Punzo, F. (1982): Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uta notata*. J. Herpetol. **16**: 329-331.
- Rand, A.S. (1964): Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology 54: 863-864.
- Rugiero, L. (1997): Tail loss and escape behaviour in the common wall lizard *Podarcis muralis* Laurenti, 1768. Herpetozoa 10: 149-152.
- Smith, G.R. (1996): Correlates of approach distance in the Striped Plateau Lizard (*Sceloporus virgatus*). Herp. J. 6: 56-58.
- Ydenberg, R.C., Dill, L.M. (1986): The economics of fleeing from predators. Adv. Stud. Behav. 16: 229-249.

Received: July 27, 2006. Accepted: October 6, 2006.