Effects of environmental factors vs. inside constraints on the escape behaviour of Schreibers green lizards (Lacerta schreiberi)

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Summary

Predation is one of the major selection pressures that determine the behaviour of animals (Lima 1988). But the predation risk of a specimen can depend on a lot of factors and the animals can compensate their behaviour fitting to the situation and have very flexible escape behaviour. Environmental and inside factors equally can infuence the decision of the prey when and where escape. In our study we testing int he field whether among the sex, season, microhabitat type, refuge distance and escape angle which are the real important factors on the antipredator behaviour of Lacerta schreiberi. We found that the inside factors (sex, season) have not any effect for the escape behaviour, solely the environmental factors have influence for the approach distance. In herbal substrate approach distance depend on the refuge distance but there is no relationship between this two distance on rock substrateAnalysing the effect of interaction of the refuge distance and escape angle for the approach distance we found if the animal is close to the refuge, they permit the predator close to them independent on escape angle, if the escape angle is high the lizards permit the predator close independent on the refuge distance, but if the escape angle is low and the refuge is far the animals begin escape early.

Introduction

The predation is the one of the most important selectional pressures, that determines the form (Endler, 1991) and behavior of animals (Lima, 1998), because the major key of surviving of the animals is how big are the odds (likelyhood) to avoid the predators and how big are the odds (likelyhood) to survive their attacks (Ydenberg and Dill 1986, Lima and Dill 1990). Animals are always under predation risk, they have to choose when and how to escape from the predators, when and how to engage in social and reproductive activitiesand when and how to feed (Lima and Dill 1990). The escaping can be very costly, because the moving is awareness, energy used and because with this behavior the animal can loose sources. Consequently, escaping will occur when the costs of staying exceed the costs of escaping (Ydenberg and Dill, 1986; Cooper and Frederick 2007). Investigating the antipredator behaviour there are two approaching models. In one of these, the refuge using where the hiding time is the major variable, and in the other, the escape behaviour where is investigated the relative positions (locations) of the prey and the predator and the approach distance (AD) is the major variable. In this study we will analyze the effects of external and internal factors on escape behaviour, concretely on AD and refuge distance.

The AD is influenced by several factors such as microhabitat type (vegetation cover) (Martín and López, 1995; Snell et al. 1988; Majláth and Majláthova 2009), predator characteristics (Bulova 1994; Burger and Gochfield 1993; Cooper 1997a,d; 1998, 1999; Cooper et al. 2003; Martín and López 1996, 1999, 2003) refuge and obstacles (Domenici et al. 2011), the relative position of the predator, the prey and the refuge, behaviour of the predator, the frequency of attacking, locomotor performance of the prey (Braña 1993; Martín 1996), gender of the prey, conspicuousness of the prey, the season (reproduction or not), body temperature (Bulova 1994; Losos 1988), body size (Martín and López 2003), age (Whiting et al. 2003), presence of conspecifics or food, extent of body armor (Losos et al. 2002) and autotomy. Thanks to these factors behaviour of lizards is very flexible.

In dense vegetation the AD is generally shorter than in rocky habitat, because the animal can use cryptic behaviour, while in rocky habitats the animals are more conspicuous. This result was found in the case of large Psammodromus (*Psammodromus algirus)* (Martín and López, 1995), lava lizard *Tropidurus albemalensis* (Snell et al. 1988), and Western Green lizard (*Lacerta viridis)* (Majláth and Majláthova, 2009). But there is no any effect of environment on the escape behavior of ground skink *Scincella lateralis* (Smith 1997).

Most lizards and some mammals use refuges that can have serious effect for the escape behavior. Reaching a safe refuge seems to be more beneficial than generating other escape tactics when the refuge is nearby (Domenici et al. 2011). Some animals, for example side-blotched lizard *(Uta stansburiana)* have different escape tactics when the refuge is available near and when is not (Zani et al. 2009).

The effect of the relative position of the predator, the prey and the refuge is one of the most important factor that affects the escape behaviour. How close allow an animal to approach a predator is strongly dependent on the distance to refuge and of how big is the angle between the refuge and predator from the prey. Usually, in most environments, the approach distance and the refuge distance have positive relationship (Cooper 1997a; 2000; Stankovich and Blumstein 2005; but see Cooper and Wilson 2007) If we take into the modell the escape angle, the situation becomes more complex. The escape angle can depend on sensory performance constraints, acute changes in environmental factors, direct manipulation of sensory structures, availability and position of refuge(s) and obstacles, presence of conspecifics. If there is a refuge, the most safe escape direction is direct to the refuge or the midway between maximizing distance from the predator and reaching the refuge in the shortest time (Domenici et al. 2011a). For example in the lizard *Uta stansburiana*, when the predator approached, lizards ran nonrandomly toward the nearest refuge, but when the animal was beyond ~15 m from the refuge the escape behavior of lizards changed to nondirectional running without hiding (Zani et al. 2009). In case of Broad-headed skink *(Plestiodon (Eumeces) laticeps)* the approach distance increased with distance and angle to refuge (Cooper, 1997). Investigating escape behaviour of Eastern woodchuck *(Marmota monax)*, showed the same results (Kramer and Bonenfant 1997).

Behaviour of the predator is very important for the prey to feel himself in danger or not. If the predator directly approach the animal and/or turn toward the prey, the lizards flee before than the approaching of the predator is indirectly or turn award from the lizard in broad-headed skink (*Plestiodon laticeps)*, keeled earless lizard *(Holbrookia propinqua)*, desert iguana *(Dipsosaurus dorsalis)* and Lilford’s wall lizard *(Podarcis lilfordi)* (Cooper 1997a,b,c; Cooper 1998; Cooper 2003; Cooper et al. 2010) .

Locomotor performance of the lizard (Braña 1993; Martín 1996) also can effect escape behaviour. In a lot of species the males, for example common flat lizard *(Platysaurus intermedius wilhelmi)* (Lailvaux et al. 2003) and some *Cnemidophorus* species (Cullum 1998), are faster than females. Consequently, usually the different sexes of these species have different escape tactics.

There are very big difference between the predators whose hunt for lizards. Avian predators rely on visual active searching, whereas snakes and mammals rely mainly on chemical cues to locate prey. Diurnal raptors use UV wavelength as a hunting cue (Viitala et al. 1995; Honkavaara et al. 2002).

Predators often show strong male bias in prey with males outnumbering females to a significant extent (Cade 1960, Lindberg 1983, Moller et al. 2011). For example predation of western green lizards (*Lacerta bilineata*) by Eurasian kestrel is male-biased (Constantini et al 2007), but in sand lizards (*Lacerta agilis*), both sexes are equally selected by avian predators (Olsson 1993), but here the difference between males and females was not so strong, than for *Lacerta bilineata*. Males of many lizards have conspicous breeding colors that are important for status signalling or sex recognition (Cooper and Greenberg 1992). However these signals decrease crypsis and cause a higher susceptibility to predators (Moller 1989; Magnhagen 1991; Forsman and Shine 1995) and for this it can sign that for these animals suffer higher predation risk (e.g. Stuart-Fox et al. 2003; Husak et al. 2006). But they can compensate this higher risk by modifying their antipredator behaviour (Lima and Dill 1990; Magnhagen 1991) for example by longer AD. Most studies show that visual conspicuousness of male coloration correlates positively with shyness (Forsman and Appelqvist 1998; Martín and López 1999b; Hedrick 2000; Cuadrado et al. 2001; Lindström et al. 2007), but there are some exceptions (Godin and Dugatkin 1996) and in some lizards, AD vary among species, being inversely correlated with the degree of cryptic coloration (Heatwole 1968; Johnson 1970), or within a species as a function of the degree of conspicuousness in different microhabitats (Cooper 1998). In several cases there are differences between the escape tactics of males and females. For example males of green anole lizard *(Anolis carolinensis), Platysaurus intermedius wilhelmi, Psammodromus algirus* have longer AD than females. *Lacerta viridis* males have longer AD than females before and after the mating season, but during the mating season are similar. However, for example, in *Scincella lateralis,*striped plateau lizard *Sceloporus virgatus* or Broadley's flat lizard *(Platysaurus broadleyi)* there are not any difference in AD between sexes, in spite that they have dichromatic coloration.

Predator sometimes need the stimulus of a moving prey to attack (Brodie et al. 1974). It would be advantageous to wait as long as possible before responding to a predator. If the lizard was initially stationary and moved too soon, it might be attacked when otherwise it might be bypassed. Lizards may assess that the probability of being detected (i.e. predation risk) is different according to their relative conspicuousness and decide when to escape accordingly (Ydenberg and Dill 1986).

Loss of benefits of mating or mate-guarding can be a strong effect for AD of the predator, because earlier running can be very costly for the males, because his opportunity for mating decrease. And for this in a lot of cases the males, if they are with females, the AD become shorter than when they are alone. There are some experimental evidence for this theory, for example in case of *Eumeces laticeps* (Cooper 1997, 1999), *Psammodromus algirus* (Martín and López 1999) or *Sceloporus virgatus* (Cooper 2007). Similarly, the males involved in agonistic encounters with other males have shorter AD, because they have to defense their sources from the other males, for example in Peter's lava lizard *(Tropidurus hispidus)* (Diaz-Uriarte 1999), *Sceloporus virgatus* (Cooper 2007) or *Eumeces laticeps* (Cooper 1999). If prey have opportunity to feed they have shorter AD than those lacking feeding opportunities for example in *Eumeces laticeps* (Cooper 2000), Bonaire whiptail lizard *(Cnemidophorus murinus)* (Cooper et al. 2003), *Podarcis lilfordi* (Cooper and Perez-Mellado 2004), or eastern grey squirrel *(Sciurus carolinensis)* (Dill and Houtmon 1989).

If escape behavior is energetically costly, it should be especially important for ectotherm animals, such as lizards, where the body temperature is influenced by the environment (Huey 1982). In lower ambient temperature lizard have lower body temperature that cause lower running speed and for this some lizard species compensate distances to nearest safe place by having longer escape distances (Snell et al. 1988; Dill and Houtman 1989; Cooper 1997; Ekner et al. 2008). However, since usage of refuges may be costly for lizards because they can decrease body temperature (Sih 1992), the escape decisions can be affected by thermal costs of refuges (Martín and López 2000b).

We examined the escape behaviour of Schreiber's green lizard (*Lacerta schreiberi*), a large (130 mm maximum snout-to-vent length, SVL) diurnal lacertid lizard found in the northwest, west, and central areas of the Iberian Peninsula (Pérez-Mellado 1998; Marco 2002). For human observers, adult male lizards *L. schreiberi* have predominantly green dorsal coloration with small black spots, yellow chest, and ventral coloration and bright blue head coloration (at least the throat and the mental scales). Coloration is especially intense during the breeding season (Pérez-Mellado 1998; Salvador 1988). Females have brown, or less often, dark green dorsal coloration, with large black spots, pale yellow ventral coloration, and light brown head coloration with black spots. This species is non-territorial and polygynous (Marco and Perez-Mellado 1999).

We previously know about escape behaviour of *L. schreiberi*, that the sex have not any effect on refuge use. The hiding time is dependent on the external temperature and the temperature of the refuge. When initial external temperatures are higher and lizards have higher thermal inertia, lizards can spend longer times inside refuges before reaching a 'critical' low body temperature. However, when refuge temperature was low lizards did not decrease refuge use. If low refuge temperatures increased risk upon emerging because lizards had lower escape performance, lizards would need to compensate by remaining in a refuge for longer to scan the surroundings before emerging to ensure that the risk of a new attack decreased. Therefore, when deciding refuge use, *L. schreiberi* lizards seem to consider physiological costs of being at low temperatures and also the risk of emerging with low escape performance (REF).

One of the closest kin of *L. schreiberi*, the European green lizard (*L. viridis*) have sex-related escape behaviour and changes a lot as the season progress. At the beginning of the season, females stay in close proximity to refuges and hide immediately after being disturbed. The distance from refuge is larger in males and they use microhabitat protrusions to hide. The approach distances are bigger in males. During the mating period, approach distances of females and males equalize and they hide in microhabitat refuge. After the mating period, the approach distance of females decreases, whereas that of males increases (Majláth and Majláthová 2009).

In this study we examined which factors are more important in determining the escape behaviour of *L. schreiberi*, whether the pair- searching has any effect for fleeing and differences between the two sexes or this behaviour depend only on environmental variables, such as vegetation, refuge distance and escape angle.

Our predictions were that (i), because male *L. shreiberi* should experience higher predation risk, they will compensate the escape behaviour and will have different escape strategies than females and (ii) the pair-searching will affect at least the escape behaviour of males compared with their behaviour after the mating season has finished.

Matherials and Methods

The study was performed during summer 2008 and spring 2009 at a large pine forest area ('Valle de La Fuenfría') in the Guadarrama mountains (40^{o}44' N, 4^{o}02' W; Madrid Province, Spain). The dominant vegetation consists of *Pinus sylvestris* forest, with shrubs such as *Juniperus communis* and *Cytisus scoparius*. In this area, Schreiber's green lizards (*L. schreiberi*) are active from March to September, mate in April–May, and produce a single clutch during June (Marco and Pérez-Mellado, 1990). Lizards occupy relatively moist well vegetated areas often close to streams (Pérez-Mellado, 1998). In this area the most frequent predator of *Lacerta schreiberi* are common kestrel *(Falco tinnunculus),* grass snake *(Natrix natrix)* and cat *(Felis catu*s) (personal observations).

We observed 44 adult females and 12 males in August 2008 and 36 males and 23 females in May 2009. We searched for lizards between 1000 and 2000 h. The weather was sunny, warm and unwindy during observations. We simulated a mammal predator by simulating attacks made by the same person wearing the same clothes. This is the conventional method, because lizards identify humans as a natural predator (Braña 1993, Bulova 1994, Martín and López 1995, Kramer and Bonenfant 1997, Cooper 1997a,b,c, 1998, Martín and López 1999a,b, Martín et al. 2003, Amo et al. 2003, 2005). The females were not gravid or were in a very early stadium of gravidity, so this factor could not affect to their escape behaviour.

The observer walked at the same moderate speed (about 1m/sec) until an adult Schreiber's green lizard was located. After this the observer approached the lizard directly at the same moderate speed (about 0,6 m/s) and observed the direction of escape and the type of refuge used. We noted the sex of animals and the following escape behaviour variables: (i) approach distance: distance between prey and predator that provoked escaping (ii) refuge distance: distance between prey and refuge (Figure 1.) (iii) escape angle: the angle formed by two lines (the line between the prey and the predator and the line between the prey and the first stopping point when escaping) an escape angle of 0° indicated the direction of escaping directly away from the predator, while 180° was the direction of escaping towards the predator.(Figure 2.)

The observations were made in different parts of the field area, so we considered that chance of repeated observations of the same individuals was very low, hence we considered data as independent (Bulova 1994, Martín and López 1995, Cooper 1997b, Amo et al. 2005). We analysed the effect of sex, season, and approach distance for the indirect risk taking by lizards (refuge distance), and the effect of inside factors (sex, season) and outside factors (microhabitat type: grass or rock substrate, fleeing angle, refuge distance) for the direct risk taking (approach distance). For this two analysis we used General Linear Model ANCOVA Backward Stepwise Model Selection with SPSS 17.0.1 (SPSS, Chicago, IL, USA) program.

Results

The lizards meanly shove off 141,27cm (sd:135,50cm) from the refuge, the less distance from the was 5cm and the biggest 1020cm. The animals meanly allow close to them 134,34cm (sd:99,54) and the less approach distance was 0cm (the animal allowed to touch her and just after escaped) and the longest was 410cm. Meanly they escaped in 54,16 degree (sd: 38,61). The less degree was 0^{o} and biggest 160^{o}.

Analysing the effects of factors for the refuge distance we did not find any significant effects for the refuge distance. Thus, neither sex and season nor microhabitat type have no any effect for that the lizards how far venture from the refuge.

We found that the microhabitat type, refuge distance and the interaction of microhabitat type and the refuge distance have very strong significant effects ($p<0.001$) for the approaching distance, furthermore the interaction of refuge distance and escape angle was also significant ($p=0.011$) (Table 1.). Testing the interaction of microhabitat type and refuge distance we found that the approach distance depended on the refuge distance in grass substrates ($t=4.658$, $p<0.001$)(Figure 4.), but there was no significant relationship between these two distances on rock substrates ($t=-1.272$, $p=0.215$)(Figure 5). Analysing the effect of the interaction of refuge distance and escape angle for the approach distance we found that if the animal was close to the refuge, they permited the predator to approach close to them independent of escape angle if the escape angle was high the lizards permited the predator to approach close independent on refuge distance, but if the escape angle is low and the refuge was far the animals began escape early (Figure 3.).

Discussion

From the results we can see that the escape behaviour of the Schreiber's green lizards is determined by only external factors, the internal status of the lizards affect neither the approach distance nor determined how long was the distance that the lizards dare to shove out from the refuge.

Investigating the effect of sex, season and microhabitat on the refuge distance we did not find any significant effect. Similar results were found in the lizard *Psammodromus algirus* where neither the sex nor age of lizards affected the refuge distance (Martín and López 1995).

Several studies show that the more conspicous animals suffer higher predation risk. (Stuart-Fox et al. 2003; Husak et al. 2006) In case of dichromatic lizards, in many lizards the more conspicuous males modify their escape strategy, because they suffer a higher predation risk, and begin to flee earlier than females. *Lacerta schreiberi* is a tipical sexually dichromatic species and a very similar and close relative to the lizard, Western green lizard (*Lacerta bilineata)* where males suffer higher predation risk (Constantini et al. 2007), but in our study we did not find any effect of sex on AD. This result is similar to that found in the lizards *Scincella lateralis* (Smith 1997), *Sceloporus virgatus* (Smith 1996; Cooper and Wilson 2007), *Platysaurus broadley* (Whiting 2002), zebra-tailed lizard *(Callisaurus draconoides)* (Bulova 1994), cape spinytail iguana *(Ctenosaurus hemilopha)* (Blázquez et al.1997), *Holbrookia propinqua* (Cooper 2003), tropical tree lizard (*Urosaurus bicarinatus),* Gadow's spiny lizard *(Sceloporus gadoviae),* Anahuacan Bunchgrass Lizard *(Sceloporus anahuacus),* cleft lizard *Sceloporus mucronatus* (Smith and Lemos-Espinal 2005).The lack of sexual differences in our study species might be expalined if males could escape faster than females, as it occurs in a lot of species (Lailvaus et al.2005; Cullum 1998) and escape to the same distance than females but runing faster.

Our other results showed that the season have not any effect on AD. Similarly, *Scincella lateralis* (Smith 1997) do not differ their escape behaviour between seasons, but for example *Lacerta viridis* have shorter AD during the mating season (Majláth and Majláthova 2009).

From our above results we can see that not only for the refuge use of *Lacerta schreiberi*, but also for the escape behaviour tehre are no effects of the inside state (constraints). But the environmental factors are very important in determining escape tactics and cause very flexible fleeing behaviour.

One of the most important factor is the microhabitat, because lizards in palces with less vegetations do not allow to approach close the predators. It is not surprising, in many cases a simialr result was found, for example *Psammodromus algirus* (Martín and López, 1995), *Tropidurus albemalensis* (Snell et al. 1988), *Lacerta viridis* (Majláth and Majláthova, 2009). But in the two types of microhabitats the animals have two diffent escape tactics. In grass substrate the approach distance depend on the refuge distance, but do not in rock substrate. In the rocky field the animals no shove out from the refuge 2,2 m (except 2 times, see the figure x), but inside this part, the animals begin to run randomly. It could be that it is really not random, but depend on something that we did not measure. For example we did not know the actual body temperature of the animals and the colder animals have to run earlier, or it might also be explained by the variation caused by shy-bold differences between different individual lizards. Maybe this more or less 2 m is the distance where the lizards can use the maximum locomotor performance and without any grass obstacles the lizards can run direct to the refuge and inside this circle lizards feel himself in safe. There was a similar result investigating the escape behaviour of Sceloporus virgatus. The animals did not go far than 1 m from the refuge, but inside this circle the refuge distance have not any effect on AD (Cooper and Wilson 2007).

The other dominant factor affecting the AD is the refuge distance. Many studies have found similar results and not just for lizard but birds and mammals, for example *Plestiodon laticeps* or *Marmota monax* (Cooper 1997, 2000; Stankowich and Blumstein 2005, Kramer and Bonefant 1997). But in our study the refuge angle also is an important factor in the relationship between refuge distance and AD. We found that if the animal is close to the refuge, they permit the predator to approach close to them independent on escape angle, if the escape angle is high the lizards permit the predatorto approach close independent on the refuge distance (if it is longer than 0.5 m), but if the escape angle is low and the refuge is far the animals begin escape early (See figure 3.). These results are totally logical because if the lizards are close to the refuge (more or less 0.5 m), they can run to the refuge very fast independent on the position of predator. If the escape angle is low, that is the direction is opened to the refuge, but if this is far the lizards allow long AD, such as it has been found in many studies (Cooper 1997a; 2000; Stankovich and Blumstein 2005). But if the escape angle is high, that is the lizards have to run towards to the predator, and the refuge is far than 0.5m, animals allow to approach close to them the predators. They run to direct to the refuge even if predator is there, because it seems to be safer than run away to an unknown refuge, because there could be another predator or an agressive conspecific (Amo et al. 2005). In this situation the animal change its escape tactic and try to be unobserved with cryptic colour and/or movelessness and they run just at that moment when the predator perceive them. In case of *Eumeces laticeps* there was opponent result, the approach distance increased with distance and angle to refuge, the animals begin to start before if they have to run in direction of predator. And if the predator is between the refuge and prey, the lizard escape away from the predator to an unsafe refuge (Cooper 1997).

In our study we could see that in the escape behaviour of *Lacerta schreiberi* there are role only for the outside factors and nothing for the inside, similarly the refuge use of this species. Likely, this statement could change if the animals meet actual inside constraints, such as food or conspecifics, when they really lost the sources after escaping (Dill and Houtmon 1989; Cooper 1997b; 1999b, 2000; 2007; Martín and López 1999). But without these effects the most important factors of approach distance of *L. schreiberi* are the microhabitat type, the refuge distance and refuge angle.

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Appendix I.

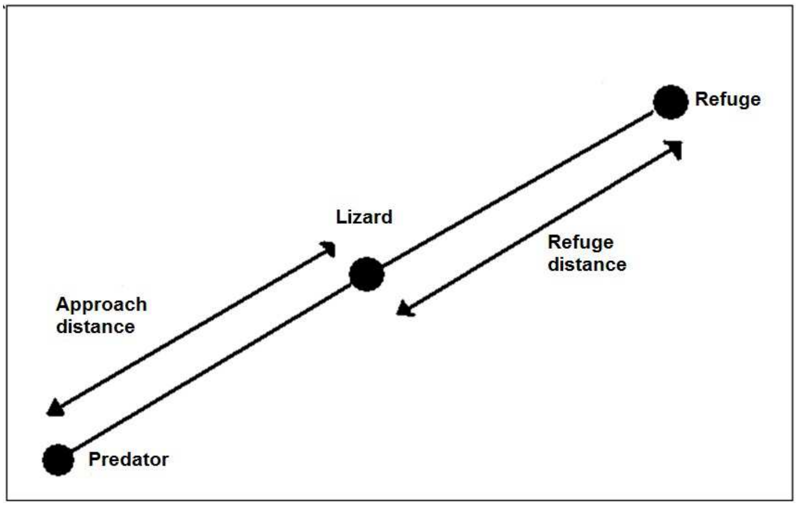


Figure 1. Representation of Approach distance and Refuge distance. Approach distance: distance between prey and predator that provoke escaping Refuge distance: distance between prey and refuge.

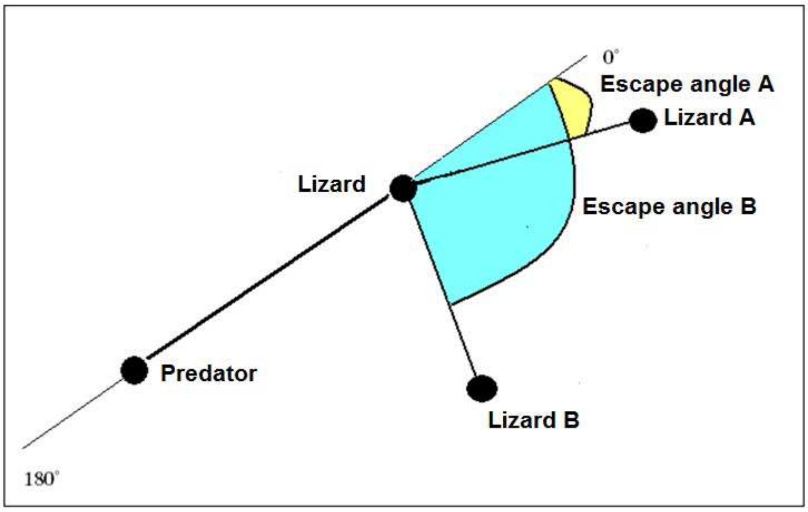


Figure 2. Measuring of escape angle. Escape angle A: lizard escaping away from the predator. Escaping angle B: lizard escape towards the predator.

Appendix II.

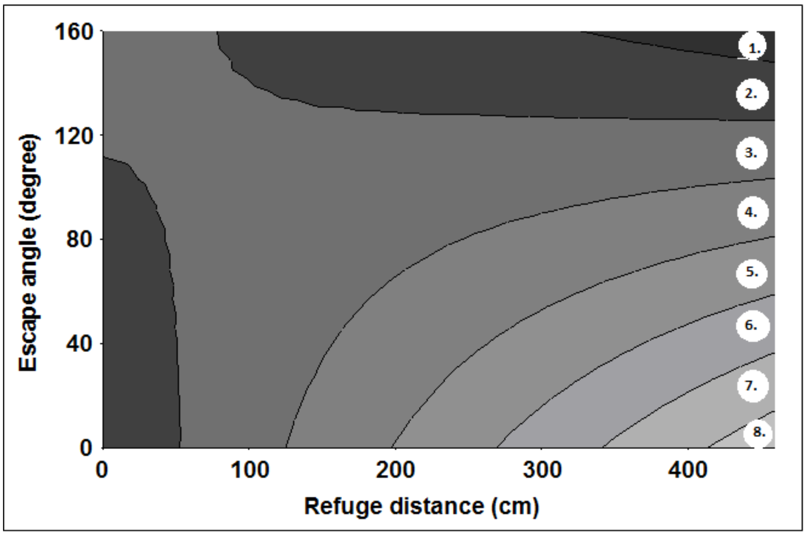


Figure 3. The relationship of the escape angle, the approach distance and refuge distance. The colour code of approach distance (1. 0-50cm, 2. 50-100cm, 3. 100-150cm, 4. 150-200cm, 5. 200-250cm, 6. 250-300cm, 7. 300-350cm, 8. 350-400cm). The equation of the relationship: z:= 0,744*x + 0,352*y - 0,006*x*y.

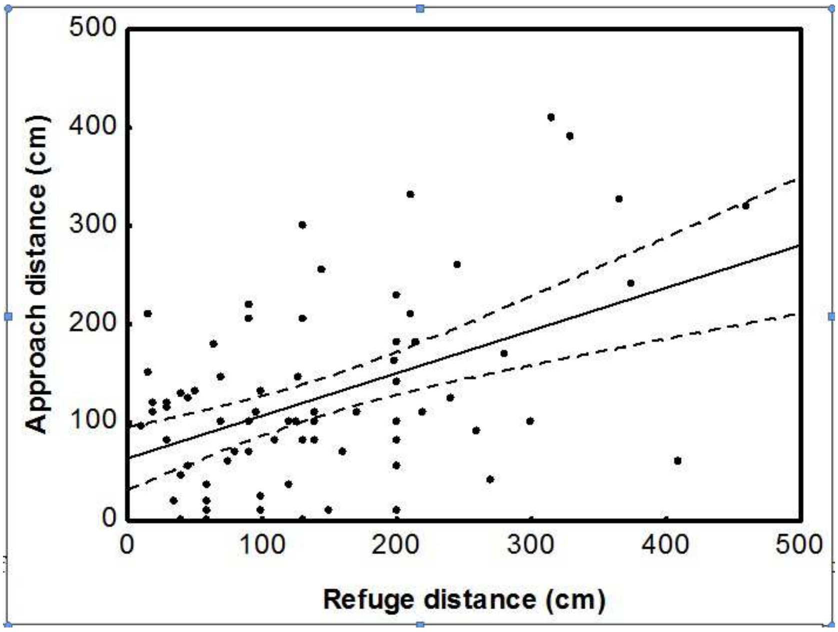


Figure 4. The relationship between the refuge use and the approach distance in substrate microhabitat type.

Appendix III.

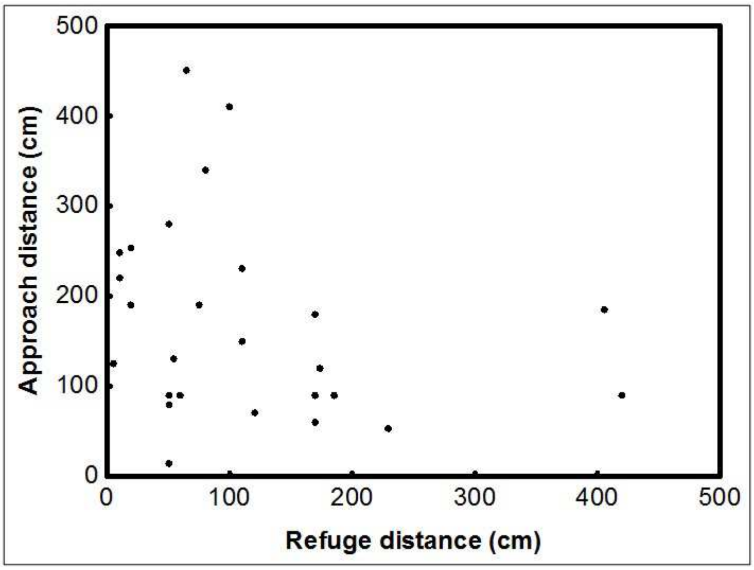
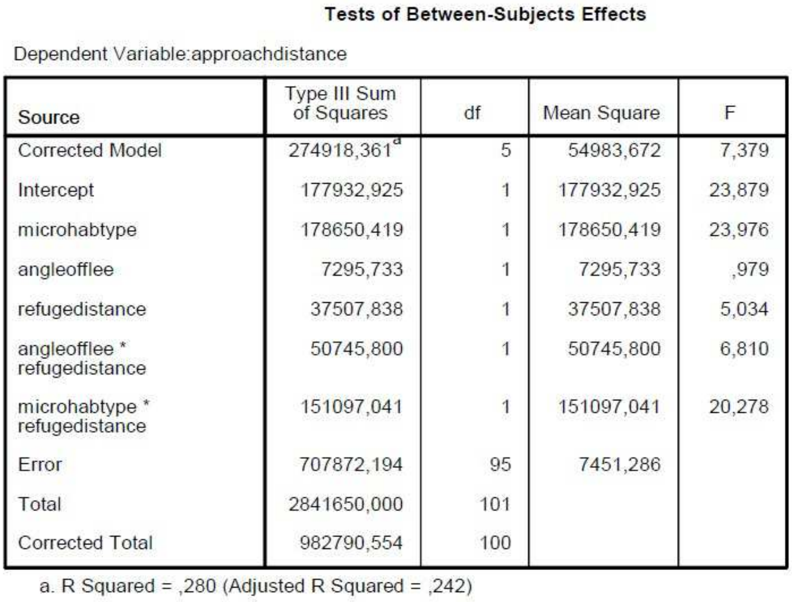


Figure 5. The relationship between the approach distance and refuge distance in rock microhabitat type.

Appendix IV.

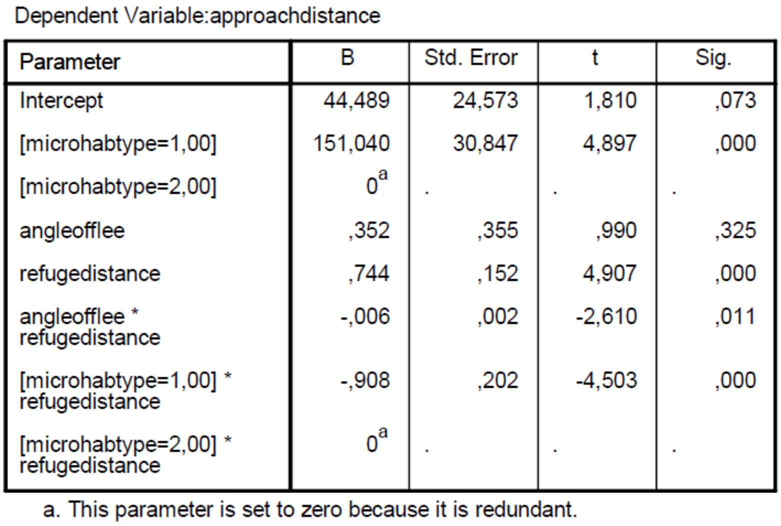


Tests of Between-Subjects Effects

Dependent Variable:approachdistance

Source	Type III Sum of Squares	df	Mean Square	F
Corrected Model	274918,361[a]	5	54983,672	7,379
Intercept	177932,925	1	177932,925	23,879
microhabtype	178650,419	1	178650,419	23,976
angleofflee	7295,733	1	7295,733	,979
refugedistance	37507,838	1	37507,838	5,034
angleofflee * refugedistance	50745,800	1	50745,800	6,810
microhabtype * refugedistance	151097,041	1	151097,041	20,278
Error	707872,194	95	7451,286	
Total	2841650,000	101		
Corrected Total	982790,554	100		

a. R Squared = ,280 (Adjusted R Squared = ,242)



Dependent Variable:approachdistance

Parameter	B	Std. Error	t	Sig.
Intercept	44,489	24,573	1,810	,073
[microhabtype=1,00]	151,040	30,847	4,897	,000
[microhabtype=2,00]	0[a]	.	.	.
angleofflee	,352	,355	,990	,325
refugedistance	,744	,152	4,907	,000
angleofflee * refugedistance	-,006	,002	-2,610	,011
[microhabtype=1,00] * refugedistance	-,908	,202	-4,503	,000
[microhabtype=2,00] * refugedistance	0[a]	.	.	.

a. This parameter is set to zero because it is redundant.

Table 1. Result of General Linear Model ANCOVA Backward Stepwise Model Selection for the external and internal factors of escape behaviour.