Escape tactics of two syntopic forms of the *Lacerta perspicillata* complex with different colour patterns

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Abstract: It has been suggested that dorsal colour patterns and defence strategies could have coevolved in reptiles, the striped species being more prone to flee compared with the spotted species that rely more on crypsis. Because of the confounding effects of phylogeny and habitat, we compared closely related forms that share the same habitats and predation pressures but display different patterns. The spotted (*chabanaudi*) and the striped (*pellegrini*) forms of the *Lacerta perspicillata* (= *Teira perspicillata*) Duméril and Bibron, 1839 complex are reproductively isolated in a locality where they live in syntopy. The responses of lizards to a direct attack by a predator, simulated by the approach of a researcher, were investigated. Both forms displayed divergent antipredatory behaviours (escaping and recovering) to optimize survival. *Chabanaudi* lizards showed longer approach distances and took more time to abandon shelter than *pellegrini* lizards when the effects of temperature and of distance fled were removed. Reappearance was related with previous flight in *chabanaudi* but with thermal quality of the refuge in *pellegrini*. Although both used similar refuges, *chabanaudi* selected bigger rocks that were less accessible to terrestrial predators but were more prone to bird attacks, whereas *pellegrini* selected fragmented rocks that faced more terrestrial predation. Our results support the hypothesis of coevolution between pattern and antipredatory behaviour.

Résumé : On a suggéré que, chez les reptiles, il a pu y avoir une coévolution des patrons de coloration dorsale et des stratégies de défense; les espèces rayées sont plus enclines à fuir, alors que les espèces tachetées comptent plus sur le camouflage. À cause des effets confondants de la phylogénie et de l'habitat, nous avons comparé des formes fortement apparentées vivant dans les mêmes habitats et soumises aux mêmes pressions de prédation, mais présentant des patrons différents de coloration. Les formes tachetée (*chabanaudi*) et rayée (*pellegrini*) du complexe de *Lacerta perspicillata* (= *Teira perspicillata*) Duméril et Bibron, 1839 sont isolées génétiquement dans une localité où elles vivent en syntopie. Nous avons observé les réactions des lézards à une attaque directe d'un prédateur simulée par l'approche d'un chercheur. Les deux formes ont des comportements anti-prédateurs différents (fuite et retour) pour optimiser leur survie. Les lézards *chabanaudi* ont des distances d'approche plus longues et prennent plus de temps à abandonner leur refuge que les lézards *pellegrini*, une fois retirés les effets de la température et de la distance de la fuite. Le retour de l'animal est relié à la fuite précédente chez *chabanaudi*, mais à la qualité thermique du refuge chez *pellegrini*. Bien que les deux formes utilisent des refuges semblables, les *chabanaudi* choisissent des rochers plus grands moins accessibles aux prédateurs terrestres, mais plus ouverts aux attaques des oiseaux, alors que les *pellegrini* sélectionnent des rochers fragmentés qui les exposent à plus de prédation terrestre. Nos résultats appuient l'hypothèse de la coévolution des patterns de coloration et des comportements anti-prédateurs.

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Introduction

Reptile colour patterns represent an adaptive compromise between different selective forces (communication, thermoregulation, feeding, predator avoidance, etc.) that often act in opposite directions (Cooper and Greenberg 1992). Because such pressures feasibly change with sex, reproductive activity, and age, sexual dimorphism and seasonal and ontogenetic variations in pattern have been recorded for many reptile species (reviewed in Cooper and Greenberg 1992). Moreover, body parts can be affected differently. Thus, in diurnal species preyed upon by visual predators coming from above, the ventral and lateral sides are often related with social signalling, whereas the dorsal pattern is more moulded by predation pressure (Greene 1988; Stuart-Fox and Ord 2004). This is especially true for small lizards like lacertids because (*i*) colour pattern does not significantly affect thermoregulation of small body sizes (Hailey 1982; Stevenson 1985; Tosini et al. 1991); (*ii*) predation pressure typically increases when size decreases (Valverde 1967; Jaksić et al. 1982; Martín and López 1996); and (*iii*) they lack other defensive devices like spikes or venom and only the adults of the biggest species display aggressive behaviours (Márquez and Cejudo 2000). Under such circumstances, individual lizards may choose between two alternative strategies: escape or crypsis (Greene 1988). This dichotomy has attracted considerable attention because the ecological consequences may differ considerably. A trade-off between the risks of capture and the costs of fleeing has been proposed (Martín and López 1999*a*, 1999*b*; Martín 2002). Models predict that a prey will escape only either when predators pose a serious threat to survivorship or when costs of fleeing are acceptable in terms of fitness. Lizards should optimize their behaviours according to both pressures. They should decrease the opportunities of being detected but increase the possibilities of escaping from predators when seen and should decide when to use each strategy (Martín 2002). Associated behaviours would include immobility and associated postures in the first case, and adequate flight speed, routes, and evaluation of potential shelters in the second (Cooper and Greenberg 1992).

Moreover, after retreating to a shelter, the so-called recovery behaviour (i.e., the decisions on when and how to come out; Martín and López 1999*b*) would also be optimized. In this case, the fitness trade-off would be between the costs of staying in the refuge at suboptimal temperature for physiological functions and the benefit of diminishing predation risk, both being time-dependent (Martín and López 1999*b*). The lizard's decision would then depend on the intensity of the risk and the quality of the refuge (Cooper 1998, Martín and López, 1999*b*). Time lost for other activities, especially reproduction (Martín et al. 2003), should also be taken into account. Escape and recovery behaviours may be linked because the intensity of the risk and the refuge chosen may depend on the escape strategy previously adopted.

Dorsal colour patterns, frequently associated with microhabitat selection (Van der Winden et al. 1995), constitute, in fact, ways of enhancing such strategies. However, like the antipredatory behaviours, such strategies are also alternative because what makes a lizard cryptic when immobile often allows predators to view it when moving and vice-

versa (Jackson et al. 1976). In this context, it has long been suggested that dorsal colour patterns and defence strategies could be coupled (Heathwole 1968; Johnson 1970). Although this mainly refers to escape behaviour, colour pattern could also be important for recovery because predation risk after emergence from the refuge would also be different. In any case, evidence on evolutionary covariation between pattern and behaviour is already available. In a multivariate study correlating pattern and behavioural variables based on a data set of 132 snake taxa, Jackson et al. (1976) concluded that uniform and striped patterns were found in species with flight tactics rather than with defence tactics, whereas irregular banding and blotched or spotted species relied more on crypsis and aggressive defence. Additional studies have even demonstrated that, in polymorphic species, patterns and behaviours may be selectively and genetically coupled (Beatson 1976; Brodie 1989; King 1993; Forsman and Shine 1995). Although no similar studies have been carried out for lacertid lizards, ontogenetic covariation between pattern and antipredator behaviour has already been demonstrated for the lacertid *Acanthodactylus beershebensis* Moravec, Baha-El Din, Seligmann, Sivan and Werner, 1999 (Hawlena et al. 2007). In this species, striped juveniles with brightly coloured tails are more active than spotted, dull-tailed adults. Because of the confounding effects of historical constraints and habitat availability (Johnson 1970; Jaksić and Núñez 1979; Avery et al. 1987; Bulova 1994; Labra and Leonard 1999; Smith and Lemos-Espinal 2005), a valid way to test the hypothesis of covariation would be to analyse phylogenetically closely related species that share similar habitats and predation pressures but display substantially different patterns.

The Moroccan rock lizards, currently assigned to *Lacerta perspicillata* (= *Teira perspicillata*) Duméril and Bibron, 1839, are small lacertids that inhabit the mountains of Morocco and western Algeria (Bons and Geniez 1996; Schleich et al. 1996), with an introduced population in Menorca, Balearic islands (Perera 2002). Recent investigations have revealed a complex panorama of forms that are genetically and morphologically heterogeneous, but are grouped into two main phylogenetic lineages with highly divergent mtDNA haplotypes (Harris et al. 2003; Perera et al. 2007). Nevertheless, at the population level, there is no general correspondence between the genetic variation and the colour patterns traditionally used for subspecies assignation (Bons and Geniez 1996). Previous research showed that the spotted (*chabanaudi*) and the striped (*pellegrini*) morphs live in strict syntopy in a locality of the Middle Atlas, Morocco (Harris et al. 2003). An analysis of 52 adult lizards from this locality revealed no individuals with intermediate patterns, morphological distinctiveness for other characters (linear measurements and scalation), and full correspondence between morphs and haplotypes (Perera et al. 2007). Such evidence, clearly indicating lack of gene flow between both entities, indicates that they behave as distinct species at least in this site, although further research in other areas still needs to be done to completely resolve the systematics of this group. Thus, the name "form" is used hereinafter to refer to these entities.

The aim of this study was to evaluate whether such drastic pattern differences between two phylogenetically related

Fig. 1. Schematic representation of the relationships between variables in both forms of the *Lacerta perspicillata* complex in the study area. $\oplus$ is a positive partial correlation; $\ominus$ are negative partial correlations; the remaining relationships are not significant. T_a, air temperature; T_s, substrate temperature; T_r, refuge temperature.
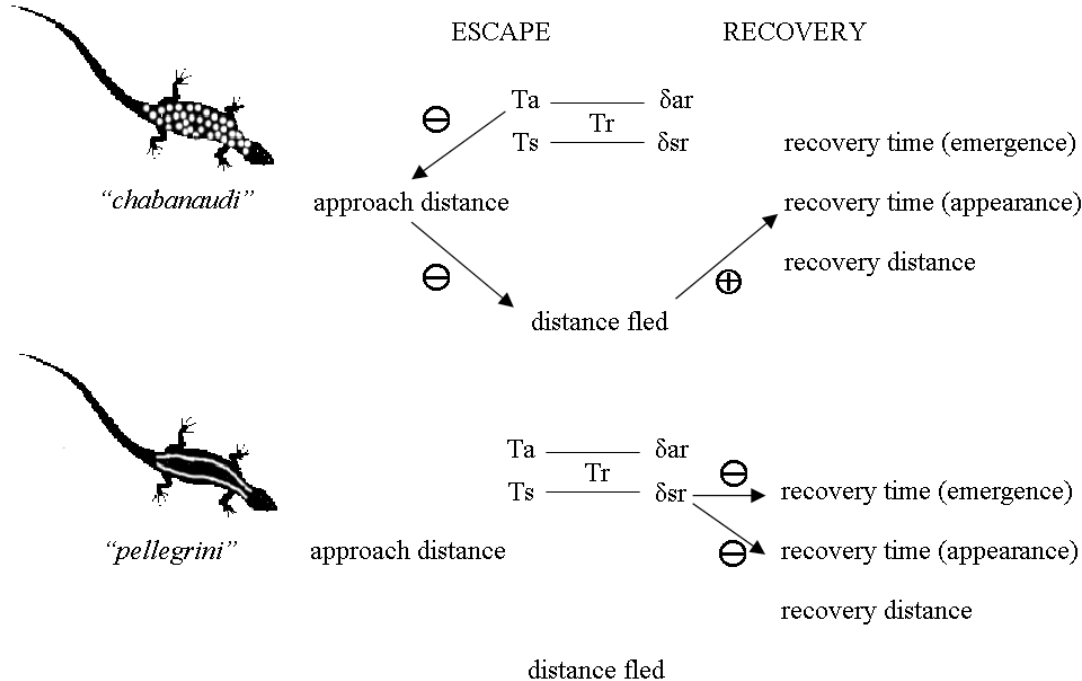
but reproductively isolated lizard forms correspond to divergent antipredator behaviours (escape and recovery) and microhabitat selection. Additionally, intersexual and ontogenetic variation in defensive behaviour within each form based on colour variation was also tested.

Materials and methods

Study site and organisms

This study was conducted in the contact zone between the spotted and the striped morphs of the *L. perpicillata* complex in the Tazzeka Natural Park, near Taza (34°13′N, 4°1′W; altitude 1000 m), where they constitute genetically distinct forms (Perera et al. 2007). The area is characterized by a steep, southeast-oriented slope covered by evergreen oak forest, junipers, and *Pistacia* bushes. The herbaceous stratum is strongly degraded by goat overgrazing. Abundant rock blocks of various sizes that had fallen from the mountain cliffs are scattered throughout the whole area. Because of their calcareous composition, they are full of crevices and holes that are often connected, providing excellent refuges for these saxicolous lizards.

This contact zone probably represents a narrow overlap between the *chabanaudi* form that occupies the lower altitudes and the *pellegrini* form that is found higher up in the mountains. At this site, the two forms had similar densities, shared the same habitats, and were even observed closer than 1 m from each other (Harris et al. 2003). Individuals of both forms can be unambiguously distinguished based on pattern by an experienced observer at a distance (see pictures in Bons and Geniez 1996 and in Harris et al. 2003). Spotted *chabanaudi* were slightly bigger (10 males: 59.95 ± 3.92 m (mean ± SE) snout–vent length (SVL); 5 females:

56.00 ± 4.49 m SVL) than striped *pellegrini* (6 males: 52.58 ± 0.79 m SVL; 13 females: 50.23 ± 0.96 m SVL), and both showed a male-biased sexual size dimorphism (Perera et al. 2007). Lizards were not weighed for this study, but body masses of adults from Menorca ranged from 1.8–4.4 g in males to 1.1–3.8 g in females (Perera 2005). Immatures of both forms were also spotted or striped. However, they also presented bright green–yellow tails, the *pellegrini* retaining this colour longer in its adult stage (M.A. Carretero, unpublished data).

Other less-abundant lizards in the study area were the lacertids *Lacerta tangitana* Boulenger, 1887, *Podarcis vaucheri* Boulenger, 1905, and *Psammodromus algirus* L., 1758, as well as the geckonid *Tarentola mauritanica* L., 1758 and the agamid *Agama impalearis* Boettger, 1874. Although the adults of all these species could predate on immature Moroccan rock lizards, the horseshoe whip snake (*Hemorrhois hippocrepis* L., 1758), the chough (*Pyrrhocorax pyrrhocorax* (L., 1758)), and the Eurasian kestrel (*Falco tinnunculus* L., 1758), as well as unidentified mustelids observed in the area, probably constitute effective predators (Schleich et al. 1996).

Field methods

Lizards were observed during 3 consecutive days in late April 2005, within the reproductive season (Schleich et al. 1996; Perera 2005), between 0900 and 1500 GMT (activity time). One of the researchers (M.A.C.), who always wore the same clothes, walked a slow and fairly constant pace following a random route and made all of the observations, while two others farther back recorded the lizard's behavioural variables and the related abiotic variables (Martín and López 1999*a*; Martín 2002). The transect was designed to prevent either repetitive observations of the same individ-

Table 1. Descriptive statistics of the behavioural variables by form and class of *Lacerta perspicillata* in the study area.

Form and class (N)	Approach distance (m)	Distance fled (m)	T_a (°C)	T_s (°C)	T_r (°C)	δ_{ar}	δ_{sr}	Recovery time (s)		Recovery distance (cm)
								Appearance	Emergence	
Chabanaudi										
Adult males (19)	2.30±0.27	0.28±0.04	18.5±0.7	27.7±0.9	21.1±0.9	0.10±0.02	0.14±0.02	70±15	74±15	0.05±0.03
Adult females (9)	1.86±0.34	0.51±0.22	18.5±0.7	29.9±1.4	20.8±1.4	0.08±0.03	0.18±0.05	135±23	136±22	0.09±0.08
Immatures (12)	1.16±0.29	0.50±0.21	21.5±1.1	30.7±1.1	23.3±1.0	0.10±0.02	0.14±0.02	73±20	84±21	0.20±0.07
Total (40)	1.86±0.19	0.40±0.08	19.4±0.5	29.1±0.7	21.7±0.6	0.09±0.01	0.15±0.02	86±11	91±11	0.11±0.03
Pellegrini										
Adult males (19)	1.39±0.16	0.48±0.13	19.6±0.5	30.7±0.9	21.2±1.0	0.09±0.02	0.19±0.03	72±14	72±14	0.22±0.07
Adult females (16)	1.57±0.21	0.26±0.07	18.6±0.6	29.8±1.0	23.2±0.8	0.11±0.02	0.15±0.02	56±13	64±15	0.12±0.06
Immatures (13)	1.34±0.22	0.27±0.08	21.1±0.5	29.6±1.3	21.9±1.0	0.08±0.01	0.15±0.02	39±15	40±15	0.11±0.04
Total (48)	1.44±0.11	0.35±0.06	19.7±0.3	30.1±0.6	22.1±0.6	0.09±0.01	0.16±0.01	58±8	61±9	0.16±0.04

Note: Values are means ± SE. See the Materials and methods section to calculate the thermal costs (δ_{ar} and δ_{sr}) of the refuge relative to air (T_a) and substrate (T_s) temperatures.

ual or observations of interacting lizards, factors that might modify the lizard's escape behaviour (Marcellini and Jenssen 1991; Cooper 1997; Labra and Leonard 1999; Martín and López 2001, 2003; Cooper and Vitt 2002; Martín et al. 2003; López et al. 2005). For the same reason, lizards with more recently broken tails were not taken into account (Martín and Salvador 1997; Martín and Avery 1998), although those with long regenerated tails were considered, as it was assumed that their escape behaviour did not differ much from those with intact tails (see Rugiero (1997) for *Podarcis muralis* Laurenti, 1768, which is also a saxicolous lacertid). No differences between forms in the proportion with regenerated tails were recorded (21.43% in *chabanaudi* and 20% in *pellegrini*). We also assumed minimal differences in the nutritional status between individuals. Each observation could be assigned to a form (spotted is *chabanaudi* and striped is *pellegrini*) and a class (adult male or adult female or immature), the latter according to the criteria of Carretero and Llorente (1993).

Once a lizard was identified with binoculars (>5 m away), the observer walked directly towards it to simulate an attack until it had retreated into a refuge. The usual response of the lizard was to make a short run straight to the refuge and hide inside. The approach distance (between the observer and the lizard when the latter started to move) and the distance fled (between the place from where the lizard started to move and the refuge) were recorded. Because escape routes were systematically short (see Results) and in a straight line, measuring the total trajectory was not necessary. After the lizard hid, from a distance (>5 m) sufficient to leave the lizard undisturbed, the time of appearance (snout visible) and emergence (more than the mid-body outside the refuge) were recorded to characterize the recovery behaviour (according to Martín and López 1999*a*, 1999*b*). To optimize the fieldwork effort, the duration of observation was limited to 3 min. This period was considered reasonable, since most of the lizards (>96%) reappeared before that time limit. The remaining lizards were assumed to have appeared but remained undetected. Since the points of hiding and appearance/emergence were often different because of the complex architecture of the crevices, the distance between both points (recovery distance) was also measured. Because escape and recovery behaviours may be thermodependent (Losos 1988; Rocha and Bergallo 1990; Bulova 1994; Cooper 2000), the air (10 cm above ground, T_a) and substrate temperatures (T_s) at the sighting point, as well as the temperature of the refuge (T_r) were recorded immediately after the lizard's emergence. Except for the first one, which was measured with a digital thermometer (Digitron® 3208K) with the bulb shaded, an infrared thermometer (Raytek® Raynger ST80 ProPlus) was used to minimize lizard disturbance inside the crevices. Body temperature (T_b) of the lizard was not recorded because the normal thermocouple thermometers required collecting, and hence disturbing, the lizard, and the infrared thermometer could not be accurately directed at the lizard given the working distances and the light conditions. Nevertheless, T_b is highly correlated with both T_a and T_s in lacertids (Castilla et al. 1999), including members of the *L. perpicillata* complex (Perera 2005). Accuracy values of the measurements were 1 s for the duration of observations, 1 cm for the dis-

Table 2. MANCOVA, MANOVA, ANCOVA, and ANOVA comparisons of behavioural variables between forms and classes of *L. perspicillata* in the study area.

		All lizards			Adults		
Dependent variable	(Covariates), factors	$F*$ or Wilks' λ	df	P	$F*$ or Wilks' λ	df	P
Escape behaviour							
Approach distance	(Distance fled)	7.91*	1, 80	0.006	2.26*	1, 57	0.14
	(T_a)	0.05*	1, 80	0.82	0.001*	1, 57	0.97
	Form	2.23*	1, 80	0.14	4.54*	1, 57	0.04
	Class	3.01*	2, 80	0.05	0.23*	1, 57	0.63
	Form × class	1.32*	2, 80	0.27	0.55*	1, 57	0.46
Approach distance	Form	0.22*	1, 82	0.22	4.38*	1, 59	0.04
	Class	3.29*	2, 82	0.04	0.20*	1, 59	0.20
	Form × class	2.28*	2, 28	0.11	0.26*	1, 59	0.27
Distance fled	Form	0.72*	1, 82	0.40	0.05*	1, 59	0.81
	Class	0.03*	2, 82	0.97	0.04*	1, 59	0.84
	Form × class	2.07*	2, 28	0.13	3.37*	1, 59	0.07
Recovery (rec.) behaviour							
Rec. time (appearance) + rec. time (emergence) + rec. distance	(Distance fled)	1.17	3, 78	0.23	0.70*	3, 55	0.56
	(δ_{ar})	0.65	3, 78	0.59	0.69*	3, 55	0.56
	Form	4.15	3, 78	0.009	4.59	3, 55	0.03
	Class	1.03	6, 156	0.41	0.78	3, 55	0.51
	Form × class	2.38	6, 156	0.03	2.33	3, 55	0.08
Rec. time (appearance) + rec. time (emergence) + rec. distance	Form	3.38	3, 80	0.02	4.17	3, 57	0.01
	Class	1.06	6, 160	0.39	0.83	3, 57	0.48
	Form × class	2.63	6, 160	0.02	3.04	3, 57	0.04
Rec. time (appearance)	Form	5.92*	1, 80	0.02	3.97*	1, 57	0.05
	Class	2.38*	2, 80	0.10	1.06*	1, 57	0.31
	Form × class	1.89*	2, 80	0.16	3.97*	1, 57	0.05
Rec. time (emergence)	Form	5.96*	1, 80	0.34	3.53*	1, 57	0.06
	Class	2.48*	2, 80	0.62	1.52*	1, 57	0.22
	Form × class	1.54*	2, 80	0.22	2.97*	1, 57	0.09
Rec. distance	Form	0.34*	1, 80	0.56	2.82*	1, 57	0.10
	Class	0.62*	2, 80	0.54	0.33*	1, 57	0.57
	Form × class	0.64*	2, 80	0.20	1.38*	1, 57	0.24

tances, and 0.1 °C for the temperatures. For every observation, the habitat associated was classified as ground, big (>2 m height) or small rocks, trees, or bushes, whereas the refuge used was classified as big (>50 cm width) or small crevices, vegetation, or trunks.

Statistical analyses

A logarithm transformation was used to normalize the data. Levene's tests ($p < 0.01$ in all cases) was used to assess the homocedasticity of the data. Log-linear models were used to test for differences in habitat and refuge use by the forms and the classes. Significance level for rejection of the null hypothesis was set at 0.05 and all tests were two-tailed. Data are presented as means ± SE.

The thermoregulatory costs of retreating to a refuge were estimated using the thermal-quality formula (Hertz et al. 1993; Scheers and Van Damme 2002) applied here as $\delta_{ar} = \frac{|T_a - T_r|}{T_a + T_r}$; $\delta_{sr} = \frac{|T_s - T_r|}{T_s + T_r}$, where δ_{ar} and δ_{sr} were the costs associated with air (T_a) and substrate (T_s) temperatures, respectively, and T_r is the refuge temperature. Both variables were considered because these lizards can use both radiation and conduction from the substrate as heat sources (Perera 2005).

Multiple regression analysis was used to test two specific

models in which the putative variables could modify the antipredator behaviour (see Fig. 1). In the case of escape behaviour, approach distance was regressed against the distance fled, the air and substrate temperatures, and the two estimations of thermal costs; in the case of the recovery behaviour, recovery times and distances were regressed against the approach distance and the distance previously fled, as well as against the two estimations of thermal costs. Multiple analyses of variance and covariance (MANOVA and MANCOVA, respectively), with form and class as factors, were performed for each behavioural variable, first in isolation and then considering the variable interactions by using the subsequent significant independent variables of the multiple regression analysis as covariates.

Results

Behavioural variables were collected from a total of 88 lizards: 40 corresponding to *chabanaudi* and 48 to *pellegrini* (Table 1).

Escape behaviour

In *chabanaudi* lizards, the approach distance was inversely correlated with distance fled ($\beta = -0.41$; $t_{[36]} = -2.87$, $p =$

Fig. 2. Variation in the approach distances (m) after a logarithm transformation, with form and class as variables, of the *L. perspicillata* complex in the study area. The values are means + SE.
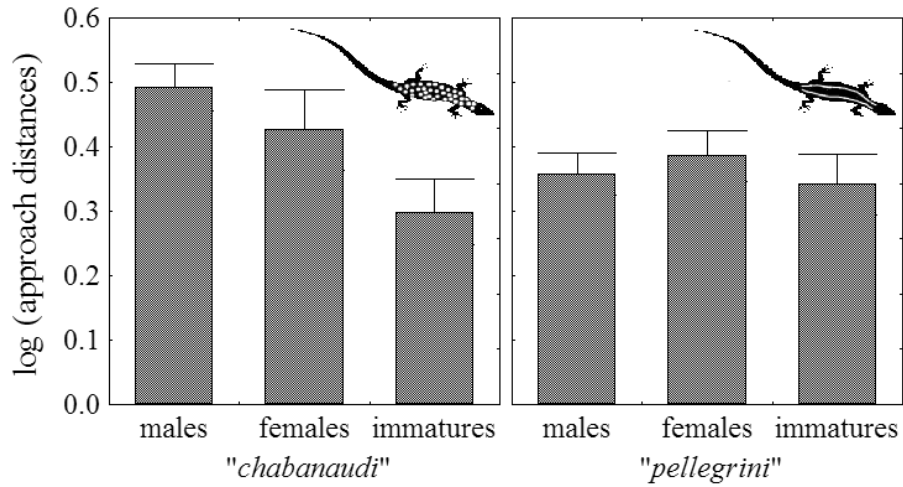
Table 3. Habitat and refuge use by form and class of *L. perspicillata* in the study area.

	Chabanaudi				*Pellegrini*			
	Adult males	Adult females	Immatures	Total	Adult males	Adult females	Immatures	Total
Habitat								
Ground	—	—	—	—	—	—	1	1
Small rocks	4	1	2	7	11	7	5	23
Big rocks	13	6	9	28	7	8	6	21
Trees	2	2	—	4	—	—	—	—
Bushes	0	0	1	1	1	1	1	3
Refuge								
Small crevices	9	5	7	21	6	8	8	22
Big crevices	6	2	4	12	10	7	3	20
Vegetation	2	1	1	4	3	1	2	6
Trunks	2	1	—	3	—	—	—	—
Total	19	9	12	40	19	16	13	48

0.006) and, to a lesser extent, with T_a ($\beta = -0.40$, $t_{[36]} = -2.59$, $p = 0.01$) but not with T_s or with both estimations of the thermal costs. In fact, immatures of both forms were found at higher T_a (not T_s) than the adults (form: $F_{[1, 82]} = 0.52$; $p = 0.52$; class: $F_{[2, 82]} = 8.85$, $p = 0.002$; form × class: $F_{[2, 82]} = 0.59$, $p = 0.56$). Consequently, although such correlations were not detected for *pellegrini*, the analyses were run while correcting for approach distance, which was considered the main target variable for both covariates (Table 2, Fig. 2). When considering all lizards, the corrected approach distance only showed variation between adults and juveniles, the latter escaping from shorter distances. However, when the analysis was restricted to adults, *chabanaudi* lizards escaped from longer distances than *pellegrini* without variation between sexes (Table 2). The comparison of the uncorrected approach distances produced essentially the same results (Table 2). No significant differences were found for the absolute distances fled (Table 2).

Recovery behaviour

Correlations between variables describing recovery behaviour and other variables were found. In *chabanaudi*, time for appearance (not for emergence) was correlated with the dis-

tance previously fled (appearance vs. distance fled: $\beta = 0.35$, $t_{[35]} = 2.04$, $p = 0.04$) but not with both estimations of thermal costs. In contrast, in *pellegrini*, both emergence and appearance were inversely correlated with thermal costs associated with the substrate temperature (emergence vs. δ_{sr}: $\beta = -0.33$, $t_{[43]} = -2.17$, $p = 0.03$; appearance vs. δ_{sr}: $\beta = 0.35$, $t_{[43]} = -2.29$, $p = 0.03$), but not with the distance fled or with the costs associated the air temperature. For both forms, the recovery distance was uncorrelated with any of the variables recorded. Consequently, the recovery times were corrected for distance fled and substrate–refuge thermal costs in the analyses. Results indicated overall differences in recovery behaviour between forms and ontogenic differences that are stronger in *chabanudi* than in "*pelegrini*" (Table 2). Having retreated inside a refuge, *chabanaudi* lizards remained there relatively longer than *pellegrini* lizards, both for reappearance and for emergence (Table 2). The uncorrected times for reappearance and emergence were still delayed for *chabanaudi* than for *pellegrini* (Table 2). No differences in the recovery distances were detected (Table 2).

Behaviour and habitat

Both forms used big and small refuges in similar propor-

Table 4. Results of the log-linear analysis on habitat use (big and small rocks) and refuge use (big and small crevices) by form (*chabanaudi* and *pellegrini*) and class of *L. perspicillata*.

Factor	df	Partial χ^2	p	Marginal χ^2	p	Maximum likelihood χ^2	Pearson's χ^2	p
Form	1	0.75	0.39	0.75	0.39			
Class	2	2.05	0.36	2.05	0.36			
Refuge	1	1.68	0.19	1.68	0.19			
Habitat	1	6.79	0.009	6.79	0.009			
Form × class	2	1.71	0.42	1.83	0.40			
Form × refuge	1	1.35	0.25	0.61	0.44			
Form × habitat	1	8.35	0.004	7.72	0.005			
Class × refuge	2	2.48	0.29	2.28	0.32			
Class × habitat	2	0.35	0.84	0.26	0.88			
Refuge × habitat	1	2.07	0.15	1.13	0.29			
Form × class × refuge	2	2.05	0.36	1.80	0.41			
Form × class × habitat	2	1.83	0.40	0.62	0.73			
Form × refuge × habitat	1	3.22	0.07	1.96	0.16			
Class × refuge × habitat	2	1.49	0.47	2.04	0.36			
Log-linear model (factor)								
Automatic (habitat)	18					23.89		0.16
	18						26.68	0.46
Forced (form × habitat)	20					19.90		0.46
	20						18.34	0.57

tions but had microhabitat differences, with *pellegrini* tending to occupy smaller rocks than *chabanaudi* (Table 3). No evidence of differential use of habitats and refuges either between adults and juveniles or between males and females was found (Table 4). When considering all the individuals, no significant differences between forms and habitats arose for the different behavioural variables. However, when immatures were excluded from the analyses, the approach distance was higher for *chabanaudi* than for *pellegrini* either on big or on small rocks. This happened both using the absolute values (form: $F_{[1,53]} = 8.32$, $p = 0.006$; habitat: $F_{[1,53]} = 0.60$, $p = 0.44$; form × habitat: $F_{[1,53]} = 0.48$, $p = 0.49$) and after correcting for the distance fled and T_a (form: $F_{[1,51]} = 7.52$, $p = 0.008$; habitat: $F_{[1,51]} = 0.67$, $p = 0.42$; form × habitat: $F_{[1,51]} = 0.47$, $p = 0.49$). Finally, the only four lizards observed climbing trees with bare trunks were all *chabanaudi*. Of these four lizards, three simply climbed the trunks higher (>6 m) to the oak canopy when disturbed.

Discussion

The two forms of the *L. perspicillata* complex display divergent antipredatory behaviours. Differences included the wariness of the lizards both escaping and recovering, with *chabanaudi* being more shy than *pellegrini* under the same environmental conditions. However, since both forms were present and equally abundant, both strategies should be interpreted as alternative. Therefore, compensatory mechanisms, including colour pattern and microhabitat use, should exist in each case.

Our results supplement reasonably well the evidence already available for other lacertids. For instance, Moroccan rock lizards escaped from longer distances and ran to more distant refuges when environmental temperatures were low as reported for other lacertids (Carrascal et al. 1992; Braña 1993; Martín and López 1995; Diego-Rasilla 2003). How-

ever, such factors did not account for the differences between both forms because *chabanaudi* lizards still showed longer approach distances than did *pellegrini* for the same temperatures and distances fled. Moreover, differences in thermal inertia are negligible for lizards less than 10 g (Hailey 1982; Stevenson 1985), thus the slight body size differences between *chabanaudi* and *pellegrini* are also irrelevant. Presumably, immatures compensated for shorter approach distances than adults by being active at higher temperatures and probably running relatively faster (but see Martín and López 1995), and by deflecting predators' attention to their coloured tails (Hawlena et al. 2007).

Differences in wariness between the two forms were even more distinctive. The *chabanaudi* lizards took more time to abandon their shelter than did the *pellegrini* lizards. Appearance was related to previous flight in *chabanaudi* lizards, and both emergence and appearance correlated with thermal quality of the refuge (Martín and López 1999b) in the *pellegrini* lizards. This divergent result cannot be attributed to the limited sample size, as the number of lizards observed was similar in both cases. Apparently, *pellegrini* lizards could be warranted in abandoning their thermally better refuges and still be able to move rapidly (Avery et al. 1987; Avery and Bond 1989), whereas *chabanaudi* would be more sensitive to the disturbance, would stay in safer but thermally poorer refuges, and could afford to bask longer afterwards.

Both forms were extremely shy compared with other lacertids, including those living sympatrically (Martín and López 1995, 2001, 2003; Diego-Rasilla 2003; M.A. Carretero, unpublished data). Apparently, a very wary behaviour constitutes the best strategy for those lizards restricted to open rocky surfaces where they can be easily detected by visual predators (Arnold 1987, 1999; Vitt et al. 2002). Nevertheless, forms differed in the way they used the rocky landscape. Although both used similar refuges, the *chabanaudi* lizards selected big rocks that could be less accessible to ter-

restrial predators (mammals and those ophidians relying more on visual cues such as the Montpellier snake, *Malpolon monspessulanus* Hermann, 1804) but more prone to bird attacks (Vitt et al. 2002), whereas the *pellegrini* lizards used more fragmented rocks that face inverse predation pressures. Under this scenario, the two distinctive colour patterns would also be in concert with alternative strategies of habitat use.

If the evidence coming from snakes (Jackson et al. 1976) is applicable to lacertids, the spotted pattern would perform better with immobile lizards that rely on crypsis. In fact, during the transects many static *chabanaudi* were almost invisible at long distances as expected for a bird attacking on open, vertical surfaces, including trunks (see also Schleich et al. 1996). On the other hand, the striped pattern of lizards has also been considered cryptic if related to vegetated situations (Van der Winden et al. 1995; Arnold 1999; Carretero 2002). However, almost no *pellegrini* lizards were seen in association with plant cover, but were seen restricted to rocks. Again, if the snake model is valid, the striped form should be more active because stripes would prevent the determination of the exact position of a moving prey (Jackson et al. 1976). This strategy seems more suitable in more complex habitats consisting of small rocks where more intense terrestrial predation may take place.

Interestingly, immature *chabanaudi* were more similar in terms of escape distances to adult and immature *pellegrini* than to adult *chabanaudi*. A coloured tail may deflect the predator's attention to a nonvital, renewable part of the body that is compensating for slower escape speeds (Arnold 1988) when the associated costs (i.e., reproduction) are still low (Vitt and Cooper 1986). However, this device is effective only with active lizards, as the tail is not shown when appearing from the refuge and provides little advantage for a static animal because it disrupts crypsis (Hawlena et al. 2007). The parallel ontogenic change in escape behaviour and conspicuousness, which is more dramatic in *chabanaudi* than in *pellegrini*, also reasonably fits with our predictions.

In summary, the results from the field experiments carried out with the two sympatric forms in Taza support the hypothesis of coevolution between pattern and antipredatory behaviour (including microhabitat selection) being also compatible with a coupled ontogenic change of such traits within each form. Nevertheless, at least some precautions must be taken when interpreting these results. First, the antipredator behaviour accounts for a part of a lizard's normal life. Field experiments were designed to investigate what lizards did after being detected by a predator. However, most of the time lizards are looking for food, thermoregulatory sites, sexual partners, etc., and such behaviours may also be selected to minimize predation risk. Colour pattern will also play an important role. Behavioural patterns of both forms when not directly threatened by a predator should be investigated. On the other hand, it is not clear to what extent the interaction between the forms (i.e., character displacement) and the evolutionary history contribute to the behavioural differences that we found. At present, only indirect evidence is available. For instance, the diet differed more between both forms in Taza than between populations of the complex from different Moroccan sites, which suggests competitive interactions and probably different forag-ing strategies (Perera et al. 2006). Further investigations, including manipulative experiments with natural predators, comparative behavioural studies between sites and forms, and the completion of the evolutionary phylogeny of this group should be carried out to corroborate the hypothesis of coevolution between pattern and antipredator behaviour in this lizard group.

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