ORIGINAL ARTICLE

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Effect of competition on habitat utilization in two temperate climate gecko species

Abstract Competition over spatial niche utilisation is one of most common competitive interactions between species in sympatry. Moreover, competitive interactions may involve age classes, and can fluctuate temporally. Consequently, evasive strategies that enable co-existence are likely to be important in the evolution of species assemblages. Here we investigate a system of two co-existing species of temperate geckos with similar ecologies (the house gecko, *Hemidactylus turcicus* and the wall gecko, *Tarentola mauritanica*), providing an opportunity to study the effect of species interactions. Juveniles and adults of both species were investigated throughout their daily and annual cycle to explore the effect of inter- and intra-specific interactions on microhabitat use. The two species showed differences in habitat use for both age classes in sympatry. In sympatry, *T. mauritanica* uses more open habitats and is more active. In contrast, *H. turcicus* is found in more closed habitats, closer to the ground and to vegetation cover. In allopatry, *H. turcicus* was observed in more open habitats, closer to the ground, and to vegetation cover, when compared to the population in sympatry with *T. mauritanica*. These differences in habitat usage were significant for both age classes. Moreover, there were differences, both in sympatry and in allopatry, between age classes that were dependent on season. In conclusion, the presence of a competitor induces a spatial shift in individuals of both age classes of *H. turcicus*. Observed plasticity in habitat utilisation in both age classes of *H. turcicus* is used to argue for the invasive potential of this species.

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Introduction

An animal's niche is a complex ecological phenomenon that can be subdivided into several dimensions (Pianka 1974; Schoener 1974a). Differences in the ecological and physiological requirements of an individual will determine its position in the different spatial and temporal components of a niche. The selection of suitable habitats, fulfilling requirements for food, safety, heat and reproduction is of great importance for all organisms (Daly et al. 2007). However, the co-existence of species may result in an overlap in optimal habitat requirements (i.e. spatial niche) and represents one of the most common forms of species interactions (Schoener 1974b). If the overlap between two interacting species is too great, the demands for similar resources will conflict and may negatively affect either both, or only one of the two species interacting (Downes and Bauwens 2002; Kumstátová et al. 2004; Merkle et al. 2009).

To overcome the potentially negative effects of niche partitioning, many sympatric species evolve strategies that allow co-existence in a same area (Vitt and Zani 1998; Grbac and Brnin 2006; De Pinho et al. 2009). Such strategies usually involve niche shifts or character displacement that enables niche shifts (Schoener 1975; Schoener et al. 2005). Evasive strategies have been documented in many co-existing, ecologically similar species of both animals and plants and appear to be a general mechanism to avoid competition (Schoener 1983; Luiselli 2006). Plasticity in resource use is likely an important characteristic in the process of co-evolution in sympatric populations and enables flexibility in spatial, trophic or temporal niches, thus allowing successful co-existence. If there is no niche divergence, competitive interactions may result in lowered body condition, health status, and fitness of a subdominant species that may ultimately lead to its local extinction (Luh and

Pimm 1993; Hunt and Bonsall 2009; Dangremond et al. 2010). As competitive interactions are the result of ecological similarity in requirements, these are often the most intensive among individuals of the same species (Pough et al. 2001). As such, not only heterospecific, but also conspecific niche shifts can occur and may result in differences in niche utilisation between juvenile and adult individuals (Lima and Moreira 1993; Brischoux et al. 2009) or between the sexes (Marquet et al. 1990; Doughty and Shine 1995; Brecko et al. 2008).

Interspecific interactions and niche shift are frequently studied using reptiles (usually lizards) as model species (Pianka 1969; Huey and Pianka 1977; Werner et al. 2005), and there are many cases where species with similar ecological requirements appear to co-exist. For example, Huey and Pianka (Huey and Pianka 1977; Pianka and Huey 1978) reported patterns of niche overlap and competition between scincid and gekkonid lizards living in the Kalahari Desert and suggested that differences in microhabitat utilisation may be important in structuring these communities.

Two species of nocturnal, insectivorous geckos, the house gecko (*Hemidactylus turcicus* Linnaeus 1758) and the moorish gecko (*Tarentola mauritanica* Linnaeus 1758) are often found inhabiting the same areas in Mediterranean human-modified habitats (Arnold and Ovenden 2002). These geckos share many biological characteristics, which can be expected to result in interspecific competition. However, morphological and behavioural differences between these two species may allow them to utilise specific temporal and spatial niches and thus reduce the potentially negative effects of interspecific competition (Selcer 1986; Arad et al. 1997; Johnson et al. 2005; Hódar et al. 2006). Since *H. turcicus* and *T. mauritanica* have coexisted in Mediterranean habitats for a long time, it can be assumed that competition avoidance strategies exist in the areas of sympatry. However, the mechanisms that allow the coexistence of these two species remain unknown (Capula and Luiselli 1994; Luiselli and Capizzi 1999).

Here, we examined the influence of the presence of *T. mauritanica* on habitat utilisation of *H. turcicus* by examining populations of *H. turcicus* in sympatry and allopatry on two geographically close and structurally similar islands in the Eastern Adriatic. Moreover, we explored habitat utilisation in different age classes for both species to reveal potential intraspecific niche shifts in the presence of competition. Our aim was to answer two main questions: (1) are there any differences in habitat utilisation between sympatric populations of *T. mauritanica* and *H. turcicus* on the island of Hvar, and (2) are there differences in habitat utilisation between a sympatric population of *H. turcicus* on the island of Hvar and a population of *H. turcicus* in allopatry on the island of Vis.

Insights into the behavioural patterns of both species and the selection of a specific well-defined study area allowed the monitoring of these species throughout their diurnal and annual cycle. Previous studies on interspecies interactions suggest that larger species are usually better and dominant competitors (Schoener 1975, 1983; Kjoss and Litvaitis 2001; Merkle et al. 2009). Consequently, we predict that the larger and more aggressive *T. mauritanica* will induce a habitat shift in the smaller *H. turcicus* in sympatry. Previous authors have demonstrated differences between adults and juveniles in niche utilisation (Downes and Shine 1998; Brischoux et al. 2009), influences of adults of one species on the juveniles of another species in sympatry (Museth et al. 2010), and competition between juveniles of two sympatric species (McGrath and Lewis 2007) led us to predict that habitat use would be different between juvenile and adult geckos in both species, and that these differences are dependent on the presence of a potential competitor.

Materials and methods

Study species and site

The house gecko (*Hemidactylus turcicus*) and the moorish gecko (*Tarentola mauritanica*) are two typical gekkonid lizards. Both species are insectivores, mainly nocturnal and associated typically with vertical surfaces. They live in warm, dry areas, and often thrive in modified, anthropogenic landscapes, including olive grows and vineyards, stone walls, cliffs, rocks, ruins, and houses. *Tarentola mauritanica* can grow up to 20 cm in total length and employs a typical sit-and-wait foraging behaviour. Moreover, it is reported to be territorial and aggressive towards conspecifics (Carretero 2008). *Hemidactylus turcicus* is smaller (up to 10 cm in total length) and, in contrast to *T. mauritanica*, is reported have a more active foraging style (Capula and Luiselli 1994). *Hemidactylus turcicus* is more social, and can achieve relatively high population densities (Punzo 2001; Locey and Stone 2006). Differences in activity patterns are also noticeable; while *H. turcicus* appears to be an exclusively nocturnal and crepuscular animal, *T. mauritanica* shows significant diurnal activity in both foraging and thermoregulatory behaviour (Arnold and Ovenden 2002).

Both species inhabit coastal areas of the Mediterranean Sea including the Adriatic coast. In the Croatian part of the Eastern Adriatic, *H. turcicus* is widespread through costal areas and on islands, while *T. mauritanica* is present only on the island of Hvar and in the town of Zadar. On both locations species are sympatric (M. Lončar, 2005, unpublished data). Two islands in Eastern Adriatic coast were selected for this study: the islands Hvar and Vis. Whereas both gecko species are present in sympatry on the island of Hvar, island of Vis contains only *H. turcicus*. The island of Hvar is elongated, orientated diagonally relative to the mainland and is 68 km long. Its area is 299.66 km^2, and highest point of the island is 626 m. The study area on the island of Hvar is approximately 30 km from the mainland, but, at the nearest point, the island is only 4 km away from the mainland. The island of Vis is smaller than the island of

Hvar, with its longest axis being only 17 km and its surface area 91.5 km^2. The highest point of the island of Vis is 587 m, similar to that of Hvar. Given the small distance between these two islands ($\pm$ 20 km apart), microclimate and vegetation are very similar. The climate is typical Mediterranean, with long, hot summers and mild winters. The main vegetation type on both islands is macchia with forests, composed of typical central Mediterranean plant species: lentisc and turpentine tree shrubs (*Pistacia lentiscus* and *P. terebinthus*), junipers (*Juniperus macrocarpa*, *J. phoenicea*), strawberry tree (*Arbutus undeo*), holm oak (*Quercus ilex*), Aleppo pine (*Pinus halepensis*) and rock roses (*Cistus* sp.). Both islands have abandoned and active agricultural areas that include mainly olive growths and vineyards. Our study areas on Hvar (43°10′55″N; 16°35′31″E) and Vis (43°02′48″N; 16°12′09″E) include similar anthropogenic habitats, with stone walls, field cottages, water wells and rock piles.

Relative population densities of *H. turcicus* (observed geckos during field surveys and recalculated as number of geckos per square metre) were greater for the allopatric population on the island of Vis (0.13 adults/m^2 and 0.014 juveniles/m^2) compared to those of sympatric population on the island of Hvar (0.022 adults/m^2 and 0.009 juveniles/m^2). *Tarentola mauritanica* showed lower densities than the sympatric population of *H. turcicus* (0.012 adults/m^2 and 0.001 juveniles/m^2) (D.L. et al., unpublished data).

Surveys and habitat sampling

Our study was conducted from April 2002 to December 2006. The survey was not constant throughout the year. Instead, some months were skipped in a particular year, and surveys for those were made during the following year. In total, three independent data sets, from different years, were collected for each month. During monthly surveys, a 24-h period of observation was held on each island and search effort was standardised. During each observation bout, transects were walked and suitable habitats were surveyed for geckos along each transect. On both islands, transects consisted of a variety of different habitats used by geckos throughout their annual cycle. To ensure that the majority of habitats available and used by geckos were included in transects, preliminary observations were performed in 2002. Transects comprised several different locations suitable for geckos (field cottages, stonewalls, water wells, etc.) separated by unfavourable habitat (e.g. meadow, road, vineyard). On the island of Hvar, a total of 51 survey locations were distributed along a transect of 3.2 km, and 21 on the island of Vis, distributed on a 1.1 km long transect. Each 24-h period of observation was divided into four sections: morning (70 min before to 2 h after sunrise), daytime, evening (2 h before to 70 min after sunset) and night. The survey locations were inspected for geckos during each section of the day. Since morning and evening periods were shorter than day and night, a reduced number of locations were inspected during those sections. However, the locations inspected were constant through all of the surveys and are thus comparable across months and years. Geckos were spotted visually using head lamps while inspecting cottages, water wells, and other hiding places. For each gecko observed, we recorded the month, time of day, species, age (adult-juveniles), habitat (7 categories), microhabitat (24 categories), substrate (9 categories), type of behaviour (6 categories), cardinal direction (5 categories), position (inside or outside of shelter place, 3 categories), height from the ground, the distance from/inside a shelter, the distance from/inside vegetation, and the inclination (see Appendix). All habitat categories were present on both islands. Age classes were distinguished visually by size. Geckos were classified as juveniles if they were too small to be sexually active (*H. turcicus* $\leq$ 4 cm; *T. mauritanica* $\leq$ 5.5 cm; D.L. personal observation; Atzori et al. 2007). There is some error associated with the visual identification of age classes which was, however, reduced by the prior experience of the observer and the fact that visual estimation was performed by the same observer over the course of study.

We grouped our data into four seasons: winter (December, January and February), spring (March, April and May), summer (June, July and August) and autumn (September, October and November). Time of day was grouped into four distinct categories: morning, day, evening and night.

Statistical analysis

We analysed two different data sets: (1) data for *T. mauritanica* and *H. turcicus* in sympatry on Hvar; and (2) data from populations of *H. turcicus* on Hvar and Vis. Prior to analysis, continuous data were log$_{10}$-transformed. To reduce the dimensionality of our data set, we performed factor analyses with varimax rotation on all measured microhabitat characteristics (i.e. habitat, microhabitat, substrate, type of behavior, cardinal direction, position, height from the ground, the distance from/inside a shelter, the distance from/inside vegetation, and the inclination). Extracted factor scores with eigenvalues greater than one were saved and used in a MANCOVA with island (Hvar vs Vis), species (*H. turcicus* vs *T. mauritanica*) and age class (adult vs juvenile) as fixed factors, and season and time of day as covariates. Prior to analysis, factor scores were checked for assumptions of normality and homoscedascity. The level of significance used in the analysis was set at 0.05. All non-significant interactions were removed from the final model. All analyses were performed using SPSS v. 17.0 (SPSS, Chicago, IL).

Results

In total, data on habitat preference for 6,197 geckos were collected over the 4-year period of study. More

Table 1 Number of geckos observed on the islands of Hvar and Vis classified by species, age, year and season. *TM Tarentola mauritanica*, *HT Hemidactilus turcicus*, *Ad* adults, *Juv* Juveniles

Island	Species	Season	Year									All years		Position[a]			
			2003		2004		2005		2006						Inside		0ut	
			Ad	Juv	Ad	Juv	Ad	Juv	Ad	Juv	Ad	Juv	Ad	Juv	Ad	Juv
Hvar	TM	Spring	100	11	96	27	89	28	19	10	304	76	187	33	117	43
		Summer	180	23	32	12	150	14	71	9	433	58	161	25	272	33
		Autumn	64	49	0	0	61	54	51	40	176	143	106	68	70	75
		Winter	36	17	26	11	79	25	29	22	170	75	150	52	20	23
	HT	Spring	105	22	139	28	113	32	22	15	379	97	312	83	67	14
		Summer	73	11	34	9	107	21	64	23	278	64	156	21	122	43
		Autumn	80	27	0	0	134	88	58	58	272	173	250	134	22	39
		Winter	27	1	40	3	74	31	64	55	205	90	199	82	6	8
Vis	HT	Spring	260	31	463	30	235	13	40	1	998	75	886	46	112	29
		Summer	133	19	61	19	98	7	52	5	344	50	99	8	245	42
		Autumn	300	45	0	0	305	60	93	42	698	147	603	100	95	47
		Winter	111	8	265	7	205	24	220	52	801	91	801	89	0	2
Total												6197				

[a]The position of the geckos relative to hiding places is also presented

Table 2 Factor loadings resulting from a factor analysis with varimax rotation on habitat data of geckos observed during a 24-h cycle throughout all seasons for two species of geckos (*H. turcicus* and *T. mauritanica*) found in sympatry

	Factor		
	1	2	3
Eigenvalue	3.3	1.62	1.23
% of variance explained	32.89	16.19	12.26
Habitat	0.283	−0.057	0.761[a]
In-out	−0.877[a]	0.178	0.076
Microhabitat	−0.736[a]	0.230	−0.284
Substrate	−0.104	0.101	0.799[a]
Activity	0.721[a]	−0.063	0.000
Orientation	0.007	0.216	0.257
Height	−0.121	0.870[a]	0.184
Log (inside-outside) (lower is inside)	0.656	−0.261	0.102
Log (dist to veg) (lower is under veg)	−0.387	0.803[a]	−0.119
Log (inclination)	0.563	0.240	−0.443

[a]Indicate factor loadings greater than 0.7

detailed information about the number of geckos observed and some general habitat preferences are given in Table 1.

A factor analysis performed on micro-habitat data during the 24-h cycle through all seasons for both species of geckos (sympatry) on the island of Hvar retained three factors that jointly explained 61.34% of the variation in the data (Table 2; Fig. 1). Type of behavior was strongly positively orientated, and in-out and microhabitat were strongly negatively correlated with the first factor. The second factor showed strong and positive correlations with height and distance to vegetation. The third factor was strongly and positively correlated with habitat and substrate.

A MANCOVA performed on the micro-habitat data for both species of geckos on the island of Hvar, during a 24-h cycle, for all seasons, indicated significant differences between species and age classes, as well as a significant seasonal (co-variate) effect. The two-way interaction between species and age class was also significant (Table 3).

Subsequent univariate ANCOVA's indicated significant differences between species on factors one ($F_{1,2314}$ = 110.28, $P < 0.001$), two ($F_{1,2314}$ = 6.77, $P = 0.009$) and three ($F_{1,2314}$ = 589.33, $P < 0.001$) (Fig. 2a). Indeed, *T. mauritanica* is found frequently outside hiding places and more often uses open habitats and microhabitats. Also, it can be found at greater heights as well as farther from the vegetation cover. Furthermore, it performs behaviours associated with high scores in our analysis, like activity and basking, more frequently. It uses substrates that are convenient for warming and basking like wooden debris, bark or plastic, more often. In contrast, *H. turcicus* is found in closer proximity to the ground and near or under vegetation cover. Moreover, it preferentially uses closed habitats like water wells and field cottages. Differences between age classes were significant on factor one only ($F_{1,2314}$ = 5.38, $P = 0.02$). This implies that juveniles of both species are more active and perform thermoregulatory behaviours (like basking and indirect warming) more often compared to adults. Juveniles of both species use open microhabitats more frequently and venture away from hiding places and vegetation cover. The seasonal effect was significant on factors one ($F_{1,2314}$ = 86.1, $P < 0.001$) and two ($F_{1,2314}$ = 49.13, $P < 0.001$). Season had a significant effect on the type of behaviour, microhabitat selection and distance to hiding place and vegetation cover in both species. Interaction effects of species and age class were significant on factors two ($F_{1,2314}$ = 7.82, $P = 0.005$) and three ($F_{1,2314}$ = 4.74, $P = 0.03$), indicating that the habitat use of age classes was not identical for both species.

A factor analysis performed on micro-habitat data during the 24-h cycle through all seasons comparing sympatric (Hvar) and allopatric (Vis) populations of *H. turcicus* retained three factors that jointly explained
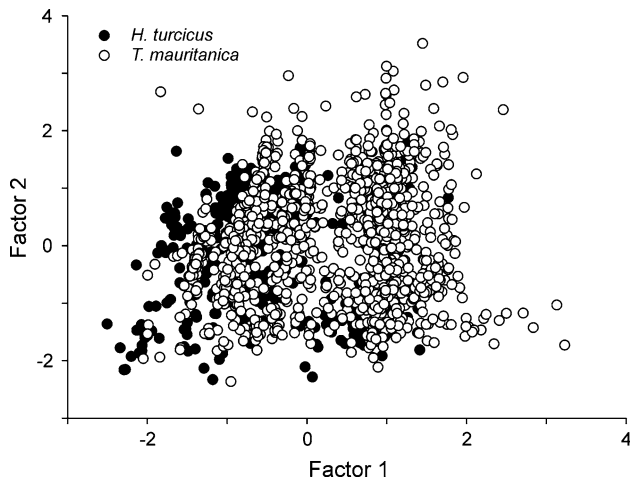
Fig. 1 Scatter plot illustrating the results of a factor analysis performed on the microhabitat data for two species of geckos (*Hemidactilus turcicus* and *Tarentola mauritanica*) occurring in sympatry on the island of Hvar

Table 3 Results of MANCOVA performed on micro-habitat data during a 24-h cycle for all seasons. The level of significance used in analysis was 0.05

Effect	Wilks' lambda	df	F	P
MANCOVA on micro-habitat data for two species of geckos on the island of Hvar				
Species	0.75	3, 2312	261.71	<0.001
Age classes	0.99	3, 2312	4.15	0.006
Season (co-variate)	0.94	3, 2312	45.37	<0.001
Species × age classes	0.99	3, 2312	4.08	0.007
MANCOVA on the factor scores on microhabitat data for allopatric and sympatric population of *H. turcicus*				
Island	0.95	3, 3235	53.98	<0.001
Age classes	0.97	3, 3235	27.69	<0.001
Season (co-variate)	0.87	3, 3235	155.54	<0.001
Time of day (co-variate)	0.95	3, 3235	58.16	<0.001
Species × age classes	0.98	3, 3235	20.97	<0.001

67.52% of the variation in the data (Table 4). In-out, microhabitat, height and distance to vegetation were strongly positively correlated, while distance to hiding place was strongly negatively correlated with the first factor. Substrate was strongly positively correlated with second factor, and inclination was strongly positively correlated with the third factor.

A MANCOVA performed on the factor scores on microhabitat data for allopatric and sympatric populations of *H. turcicus* indicated significant differences between populations on different islands and age classes with significant seasonal (co-variate) and time of day (co-variate) effects. The two-way interaction between islands and age classes was also significant (Table 3).

Subsequent univariate ANCOVA's indicated significant differences between populations inhabiting different islands on factors one ($F_{1,3237} = 24.26$, $P < 0.001$), two ($F_{1,3237} = 113.15$, $P < 0.001$), and three ($F_{1,3237} = 24.76$, $P < 0.001$) (Fig. 2b). The individuals from the population inhabiting the island of Hvar were more often
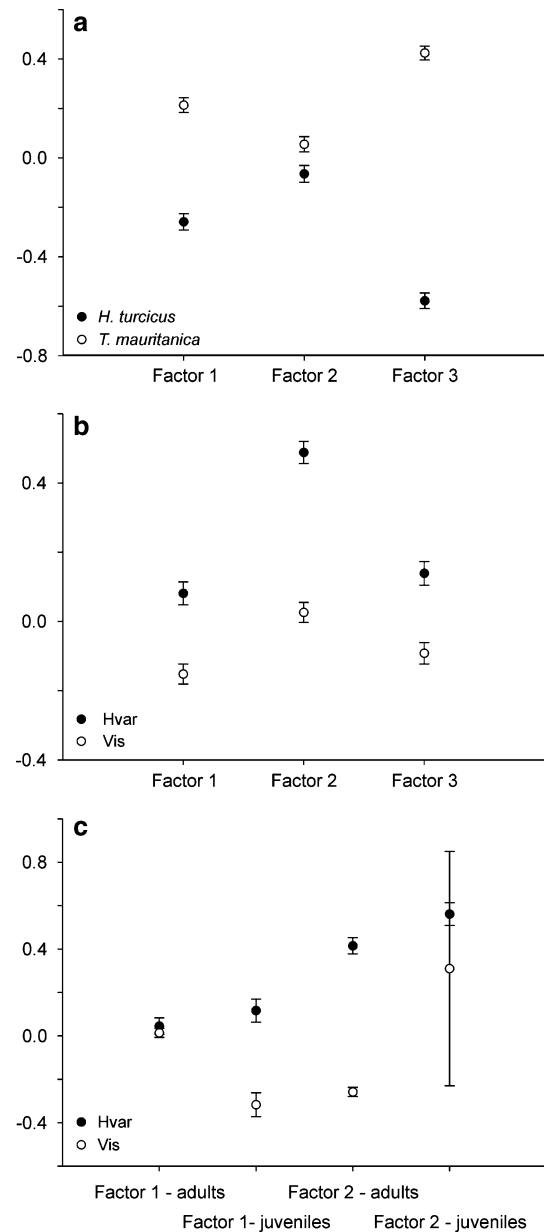

Fig. 2 Factor loadings values (*y* axis) resulting from factor analyses with varimax rotation on microhabitat characteristics illustrating differences in microhabitat utilisation. **a** Graph illustrating differences in microhabitat use between *H. turcicus* and *T. mauritanica* on the island of Hvar. **b** Graph illustrating differences in microhabitat use between *H. turcicus* occurring in sympatry with *T. mauritanica* on island of Hvar versus in allopatry on island of Vis. **c** Graph illustrating differences in habitat use of *H. turcicus* of different age classes in sympatry and allopatry

associated with closed microhabitats, were more often found inside the shelters, at greater heights and further away from vegetation cover. Individuals of the population from the island of Hvar were found on substrates like metal, wood or plastic more often, and were more orientated toward western and southern exposures. Age class differences were significant on factors one ($F_{1,3237} = 8.69$, $P = 0.003$) and two

Table 4 Factor loadings resulting from a factor analysis with varimax rotation performed on the habitat data of geckos observed during the 24-h cycle through all seasons for sympatric (Hvar) and allopatric (Vis) populations of *H. turcicus*

| | Factor | | |
	1	2	3
Eigenvalue	4.333	1.4	1.018
% of variance explained	43.33	14.00	10.18
Habitat	−0.087	0.550	0.011
In-out	0.903[a]	−0.131	−0.172
Microhabitat	0.861[a]	−0.244	−0.065
Substrate	−0.089	0.786[a]	−0.255
Activity	−0.678	0.379	0.230
Orientation	−0.280	0.673	0.073
Height	0.735[a]	0.119	0.439
Log (inside-outside) (lower is inside)	−0.754[a]	0.152	0.306
Log (dist to veg) (lower is under veg)	0.766[a]	−0.285	0.114
Log (inclination plus)	−0.148	−0.134	0.858[a]

[a] Factor loadings greater than 0.7

($F_{1,3237} = 67.66$, $P < 0.001$) (Fig. 2c). Adults on both islands were found more often in closed microhabitats, inside hiding places, at greater heights and at greater distance from vegetation. However, juveniles on both islands chose substrates like metal, wood, plastic or other types of man-made debris more often. The seasonal effect was significant on factors one ($F_{1,3237} = 266.8$, $P < 0.001$), two ($F_{1,3237} = 90.77$, $P < 0.001$) and three ($F_{1,3237} = 65.24$, $P < 0.001$). In addition, time of day was significant on factors one ($F_{1,3237} = 161.77$, $P < 0.001$) and three ($F_{1,3237} = 8.59$, $P = 0.003$). This implies that both seasonal changes and daytime cycle have a significant effect on microhabitat utilisation, distance to hiding place and vegetation cover; and the choice of height, substrate and cardinal direction. The two-way interaction between island and age class was significant on factors one ($F_{1,3237} = 20.99$, $P < 0.001$), two ($F_{1,3237} = 23.64$, $P < 0.001$) and three ($F_{1,3237} = 19.16$, $P < 0.001$), indicating that the age classes used different microhabitats on the two islands.

Discussion

A previous study on relative population densities comparing *T. mauritanica* and *H. turcicus* indicated lower population densities of *H. turcicus* in sympatry (Hvar), as compared to the populations in allopatry (Vis). Moreover, populations in syntopy showed lower population densities than population in allotopy on the same island (Hvar), and allotopic populations on Hvar showed lower densities than allopatric populations on Vis, indicating a strong effect of the presence of *T. mauritanica* on *H. turcicus*. (D.L. et al., unpublished data) The results of the present study reveal differences in habitat and microhabitat use of these same two gecko species in sympatry. Moreover, differences in habitat use can be demonstrated between populations of *H. turcicus* in allopatry (Vis) versus those on Hvar in sympatry with *T. mauritanica* (Fig. 2).

Species differences in sympatry

Our results suggest differentiation in habitat use among these two species in sympatry (Table 3; Fig. 2a). Differences in microhabitat use in ecologically similar species in sympatry are common (Reinert 1984; Kumstátová et al. 2004; Daly et al. 2007; Yamauchi and Miki 2009; Chillo et al. 2010). Although spatial segregation is often suggested as one of the mechanisms allowing the coexistence between different species (Schoener 1974a, b), it is unlikely that sympatric species are completely spatially isolated and, in many cases, some degree of spatial overlap does occur (Schoener 1983). Thus, even if our data suggest segregation on a small spatial scale between *T. mauritanica* and *H. turcicus* in sympatry, it is unlikely that competition does not occur at all. More likely, the reported microhabitat differences function to decrease the competitive interactions between *T. mauritanica* and *H. turcicus*. Moreover, the observed differences in habitat usage may stem from the species-specific biological requirements, as suggested previously (Gill et al. 1994a, b; Punzo 2001; Hitchcock and McBrayer 2006). Consequently, the ecological differences between these species may allow their coexistence in communal habitats. A spatial niche shift, like that reported here, has been observed previously in other sympatric associations of ecologically similar species (Schoener 1975; Pianka and Huey 1978; Grbac and Brnin 2006). Our data are similar to that reported for habitat use in the tree pipit (*Anthus trivialis*) and meadow pipit (*A. pratensis*) at sympatric versus allopatric localities (Kumstátová et al. 2004). These two related passerines show differences in habitat use in allopatry, and express niche shifts when occurring in sympatry, similar to what we observed in our two studied geckos.

Allopatric versus sympatric populations of *H. turcicus*

Habitat divergence between allopatric and sympatric populations of *H. turcicus* may originate from the presence or absence of the potential competitor, *T. mauritanica*. (Table 3; Fig. 2b). Previous studies on *T. mauritanica* and *H. turcicus* in sympatry suggested similarity in niche occupation between species (Capula and Luiselli 1994; Luiselli and Capizzi 1999). Moreover, our data on relative population densities suggests competitive interactions between *T. mauritanica* and *H. turcicus* (D.L. et al., unpublished data). Although the habitat analysis presented here suggests differences in spatial niche in sympatry, to test whether the presence of a potential competitor affects habitat use, one must compare populations in different competitive scenarios (sympatry vs allopatry). Our data show that *H. turcicus*

in allopatry uses all types of microhabitats needed to fulfil its ecological demands. In sympatry, *H. turcicus* can be observed more in closed habitats like water wells and field cottages, the types of habitat that are usually avoided by the heliophilous and more active *T. mauritanica*. Changes in spatial niche in allopatry as compared to sympatry, like that observed in this study, have been reported for a wide variety of taxa including insects (Honkavaara et al. 2011), amphibians (Rice et al. 2009), and birds (Kirschel et al. 2009) and suggests that this may be a general phenomenon. However, the observed habitat difference in sympatric versus allopatric populations of *H. turcicus* may potentially be related to differences in available microhabitats between the two islands. Indeed, islands show slight differences in field cottage and stonewall constructions. As these differences are generally minor and do not reflect the observed differences in habitat use, it is likely that observed differences in spatial niche are driven by the presence of competition between two ecologically similar species, with *T. mauritanica* being dominant over *H. turcicus*.

Intraspecific differences in habitat use

Interestingly, in both species, independent of the presence of a potential competitor, we observed different habitat use between age classes (Table 3). Juvenile geckos more often used open habitats, and venture into microhabitats rarely occupied by adults. Other studies have similarly demonstrated that juveniles differ in spatial niche from adult conspecifics (Blouin-Demers et al. 2007). One of the arguments put forward to explain this difference is the avoidance of predation by adults on juveniles (Pough et al. 2001). Alternatively, avoidance of competition with adults (Brischoux et al. 2009), population dispersion strategies (Punzo 2001), or lack of experience in young animals have been suggested as explanations for this pattern (Pough et al. 2001). One of the most studied European lizard species, *Lacerta agilis*, shows similar ontogenic shifts in microhabitat usage. Young individuals typically use open habitats like meadows, while adults are usually found in vicinity of bushes that can be used as shelters. These differences in habitat use suggest behavioural interactions between adults and juveniles. Meadows do not provide enough shelter for adult lizards and thick grass may disturb their locomotion, while juveniles avoid habitats occupied by adults and find enough cover in meadows (Amat et al. 2003; Nemes et al. 2006). The results of our study suggest that such behavioural strategies may also be employed in the gecko species studied here. Our results also indicate that the difference in microhabitat use between age classes in sympatry is species specific, implying that, when occurring in the same habitat, the two age classes of each species each have their unique requirements, resulting in a decrease in intra-, but also interspecies competitive interactions. In addition, age class-related differences in habitat use detected in *H. turcicus* are

island specific. This result implies a spatial niche shift between age classes in *H. turcicus* in the absence of the competitively superior *T. mauritanica*.

Interestingly, not only is the habitat use in both age classes of *H. turcicus* affected by the presence of *T. mauritanica*, but both age classes also show a shift in habitat use in allopatry compared to sympatry (Fig. 2c). Niche widening in the absence of competition is a well-documented phenomenon (Rice et al. 2009). The habitat shift observed in this study illustrates how profound is the influence of the presence of the competitively superior *T. mauritanica* on *H. turcicus*. In many species, the presence of a sympatric heterospecific influences only one age class. For example, a study on the interactions between two similar trout species implied negative competitive interactions in juveniles but not adults (McGrath and Lewis 2007). Yet, other studies indicate competitive interactions occurring principally between adults (Török and Tóth 1999). In some cases, interspecific age class-related interactions were reported with adults of one species influencing juveniles of the other species (Museth et al. 2010).

The ability of *H. turcicus* to adapt its habitat requirements in both age classes may be an explanation for its invasive potential. This species is known to have invaded distant areas that are far outside its natural geographic area, mostly by means of human-based dispersal (Selcer 1986; Locey and Stone 2006). Our study on spatial niche shifts suggests a potential origin of the ecological plasticity allowing *H. turcicus* to adapt to the new environment. Since in its native geographic range *H. turcicus* often enters into competition with *T. mauritanica*, it would seem beneficial for *H. turcicus* to retain some level of plasticity that allows coexistence with a competitively stronger heterospecifics. Moreover, our results suggest that this plasticity is characteristic of both adults and juveniles.

Effect of covariates (season and time of day)

Finally, our results also indicate a significant seasonal effect on the spatial niche utilisation between species in sympatry, as well as among populations of *H. turcicus* in sympatry versus allopatry. Such a temporally fluctuating utilisation of the available habitat has been reported for many different taxa (Pianka 1969; Ricklefs et al. 1981; Pough et al. 2001) and may further impose demands on flexibility in habitat use.

However, it is important to point out the lack of a significant effect of the time of the day in the sympatric population on Hvar. This implies that both species have similar behavioural patterns during the course of the day. Nevertheless, both species exhibit similar oscillations in habitat utilisation, showing greater movements during the night hours and staying near hiding places during daytime. In addition, both species demonstrate positive thermoregulatory behaviour during daytime hours, but with different thermoregulatory strategies (direct sunlight basking vs convective heating). Inter-

estingly, our results indicate difference in habitat utilisation between sympatric versus allopatric populations of *H. turcicus*. This implies that two populations differ not only in the seasonal characteristics of habitat preferences, but also in a way of habitat utilisation on a daily basis. Such differences could be the result of different climate and ecological characteristics between islands, but are likely affected by the presence of another gecko species on the island of Hvar.

In summary, the data presented here indicate habitat segregation in sympatry, as well as release of competitive restraints in allopatry in the subordinate species. Given the often complicated mechanisms of interspecies interactions and species co-existence (Ricklefs et al. 1981; Pough et al. 2001; Merkle et al. 2009), our data may add to a better understanding of these processes. Whereas our data suggest effects of competition on habitat use in *H. turcicus*, further studies including other components of the ecological niche such as diet and temperature are needed to better understand the ecological strategies of this species that allow it to coexist with *T. mauritanica*.

Appendix

(See Table 5).

Table 5 Categories and subcategories of habitat used in measuring habitat utilisation for *H. turcicus* and *T. mauritanica* on island of Hvar (populations in sympatry) and island of Vis (*H. turcicus* population in allopatry)

Category of habitat	Sub-category of habitat	Description
Habitat		General habitat types
	Water well	
	Field cottage	
	Field doors	Specific constructions that include wooden doors, two columns and small roof above doors. Intensively used by geckos
	Wall	All types of walls and stonewalls
	Tree	
	Column	Power columns or field marks of column form
	Near to ground habitat	Ground, grass, piles of rocks or twigs, man-made debris.
Position	Outside	Position inside or outside of shelter place
	At the entrance	
	Inside	
Microhabitat		Various types of microhabitat used by geckos
Open habitats		Habitats that were open or offer minimal protection from weather conditions and predators
	Ground	
	Log	
	Stone	
	Wall	
	Under stone/board	
	Inside hole	Shallow holes at open habitats
	Near ceiling	
	Ceiling	
Closed habitats		Inside closed habitats that offers protection from environmental conditions, i.e. inside field cottage
	Wall	
	Board	
	Ground	
	Under stone/board	
	Inside hole	
	In crevice	Crevices are defined as all types of holes deep enough that geckos can hide from weather conditions and predators
	Anthropogenic debris	Old clothes, piles of twigs, glasses, old boxes with tools
	Near ceiling/ceiling	
Inside water well entrance		Water well entrances, usually used as warming spots
	Wall	
	Under panel	
	Panel	
Inside water well		Very stable conditions, ideal hiding places from weather conditions
	Wall	
	Near ceiling	
	Inside hole	
	Ceiling	

Table 5 continued

Category of habitat	Sub-category of habitat	Description
Substrate		
	Old cloth	
	Paper	
	Concrete	
	Stone-concrete	
	Stone	
	Wood	
	Brick	
	Plastic, glass	
	Metal	
	Tile	
	Dirt, grass	
Type of behavior		
	Still	
	Still/active	Geckos found standing still outside the typical hiding places, i.e. on wall inside field cottage during cold day
	Active	
	Eating	
	Warming	
	Still/warming	Inactive, non-moving geckos that chose warming positions, i.e. inside water well entrance during winter months
	Sun bathing	
Cardinal direction		
	None	Geckos found in the middle of field cottage or water well had no general cardinal direction
	North	
	East	
	West	
	South	

References

Amat F, Llorente GA, Carretero MA (2003) A preliminary study on thermal ecology, activity times and microhabitat use of *Lacerta agilis* (Squamata: Lacertidae) in the Pyrenees. Folia Zool 52:413–422

Arad Z, Schwarzbaum A, Werner Y (1997) Temperature selection and thermoregulation in the Moorish gecko, *Tarentola mauritanica*. Amphibia Reptilia 69:269–282

Arnold EN, Ovenden D (2002) A field guide to the reptiles and amphibians of Britain and Europe, 2nd edn. Harper Collins, London

Atzori A, Berti F, Cencetti T, Fornasiero S, Tamburini M, Zuffi MAL (2007) Advances in methodologies of sexing and marking less dimorphic gekkonid lizards: the study case of the Moorish gecko, *Tarentola mauritanica*. Amphibia Reptilia 28:449–454

Blouin-Demers G, Bjorgan LPG, Weatherhead PJ (2007) Changes in habitat use and movement patterns with body size in black ratsnakes (*Elaphe obsoleta*). Herpetologica 63:421–429

Brecko J, Huyghe K, Vanhooydonck B, Herrel A, Grbac I, Van Damme R (2008) Functional and ecological relevance of intraspecific variation in body size and shape in a lizard, *Podarcis melisellensis*. Biol J Linn Soc 94:251–264

Brischoux F, Bonnet X, Shine R (2009) Determinants of dietary specialization: a comparison of two sympatric species of sea snakes. Oikos 118:145–151

Capula M, Luiselli L (1994) Tropic niche overlap in sympatric *Tarentola mauritanica* and *Hemidactylus turcicus*: a preliminary study. Herpetol J 4:24–25

Carretero MA (2008) Preferred temperatures of *Tarentola mauritanica* in spring. Acta Herpetol 3:57–64

Chillo V, Rodríguez D, Ojeda AR (2010) Niche partitioning and coexistence between two mammalian herbivores in the dry chaco of Argentina. Acta Oecol 36:611–616

Daly BD, Dickman CR, Crowther MS (2007) Selection of habitat components by two species of agamid lizards in sandridge desert, central Australia. Austral Ecol 32:825–833

Dangremond EM, Pardini EA, Knight TM (2010) Apparent competition with an invasive plant hastens the extinction of an endangered lupine. Ecology 91:2261–2271

De Pinho WF, Colli GR, Vitt LJ (2009) Determinants of assemblage structure in Neotropical dry forest lizards. Aust Ecol 34:97–115

Doughty P, Shine R (1995) Life in two dimensions: natural history of the southern leaf-tailed gecko, *Phyllurus platurus*. Herpetologica 51:193–201

Downes S, Bauwens D (2002) An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species. Anim Behav 63:1037–1046

Downes S, Shine R (1998) Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. Anim Behav 55:1387–1396

Gill MJ, Guerrero F, Perez-Mellado V (1994a) Diel variation in preferred body temperatures of the Moorish gecko *Tarentola mauritanica* during summer. Herpetol J 4:56–59

Gill MJ, Guerrero F, Perez-Mellado V (1994b) Seasonal variation in diet composition and prey selection in the mediterranean gecko *Tarentola mauritanica*. Isr J Zool 40:61–74

Grbac I, Brnin K (2006) Habitat use of sympatric populations of *Podarcis sicula* and *P. melisellensis* on a small Adriatic island. Period Biol 108:177–182

Hitchcock MA, McBrayer LD (2006) Thermoregulation in nocturnal ectotherms: seasonal and intraspecific variation in the Mediterranean Gecko (*Hemidactylus turcicus*). J Herpetol 40:185–195

Hódar JA, Pleguezuelos JM, Villafranca C, Frenandes-Cardenete JR (2006) Foraging mode of the Moorish gecko *Tarentola mauritanica* in an arid environment: inferences from abiotic setting, prey availability and dietary composition. J Arid Environ 65:83–93

Honkavaara J, Dunn DW, Ilvonen S, Suhonen J (2011) Sympatric shift in a male sexual ornament in the damselfly *Calopteryx splendens*. J Evol Biol 24:139–145. doi:10.1111/j.1420-9101.2010.02146.x

Huey RB, Pianka ER (1977) Patterns of niche overlap among broadly sympatric versus narrowly sympatric Kalahari lizards (Scincidae: *Mabuya*). Ecology 58:19–28

Hunt JFG, Bonsall MB (2009) The effects of colonization, extinction and competition on co-existence in metacommunities. J Anim Ecol 78:866–879

Johnson J, McBrayer LD, Saenz D (2005) Allometry, sexual size dimorphism, and niche partitioning in the Mediterranean gecko (*Hemidactylus turcicus*). Southwest Nat 50:435–439. doi:10.1894/0038-4909(2005)050[0435:ASSDAN]2.0.CO;2

Kirschel ANG, Blumstein DT, Smith TB (2009) Character displacement of song and morphology in African tinkerbirds. Proc Natl Acad Sci USA 106:8256–8261

Kjoss V, Litvaitis J (2001) Community structure of snakes in a human-dominated landscape. Biol Conserv 98:285–292

Kumstátová T, Brinke T, Tomková S, Fuchs R, Petrusek A (2004) Habitat preferences of tree pipit (*Anthus trivialis*) and meadow pipit (*A. pratensis*) at sympatric and allopatric localities. J Ornithol 145:334–342. doi:10.1007/s10336-004-0048-3

Lima A, Moreira G (1993) Effects of prey size and foraging mode on the ontogenetic change in feeding niche of *Colostethus stephani* (Anura: Dendrobatidae). Oecologia 95:93–120

Locey KJ, Stone PA (2006) Factors affecting range expansion in the introduced Mediterranean gecko, *Hemidactylus turcicus*. J Herpetol 40:526–530

Luh HK, Pimm SL (1993) The assembly of ecological communities: a minimalist approach. J Anim Ecol 62:749–765

Luiselli L (2006) Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos 114:193–211

Luiselli L, Capizzi D (1999) Ecological distribution of the geckos *Tarentola mauritanica* and *Hemidactylus turcicus* in the urban area of Rome in relation to age of buildings and condition of the walls. J Herpetol 33:316–319

Marquet PA, Bozinovic F, Medel RG, Werner YL, Jaksic FM (1990) Ecology of *Garthia gaudichaudi*, a gecko endemic to the semiarid region of Chile. J Herpetol 24:431–434

McGrath CC, Lewis WM Jr (2007) Competition and predation as mechanisms for displacement of Greenback Cutthroat Trout by Brook Trout. Trans Am Fish Soc 136:1381–1392

Merkle JA, Stahler DR, Smith DW (2009) Interference competition between gray wolves and coyotes in Yellowstone National Park. Can J Zool 87:56–63

Museth J, Borgstrøm R, Brittain JE (2010) Diet overlap between introduced European minnow (*Phoxinus phoxinus*) and young brown trout (*Salmo trutta*) in the lake, Øvre Heimdalsvatn: a result of abundantresources or forced niche overlap? Hydrobiologia 642:93–100. doi:10.1007/s10750-010-0162-6

Nemes S, Vogrin M, Hartel T, Öllerer K (2006) Habitat selection at the sand lizard (*Lacerta agilis*): ontogenetic shifts. N West J Zool 2:17–26

Pianka ER (1969) Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology 50:1012–1030

Pianka ER (1974) Niche overlap and diffuse competition. Proc Natl Acad Sci USA 71:2141–2145

Pianka ER, Huey RB (1978) Comparative ecology, resource utilisation and niche segregation among gekkonid lizards in the Southern Kalahari. Copeia 4:691–701

Pough FH, Andrews RM, Cadle JE, Crump ML, Savitzky AH, Wells KD (2001) Herpetology, 2nd edn. Prentice-Hall, Englewood Cliffs, NJ

Punzo F (2001) The Mediterranean gecko, *Hemidactylus turcicus*: life in an urban landscape. Fla Sci 64:56–66

Reinert HK (1984) Habitat variation within sympatric snake populations. Ecology 65:1673–1682

Rice AM, Leichty AR, Pfennig DW (2009) Parallel evolution and ecological selection: replicated character displacement in spadefoot toads. Proc R Soc B 276:4189–4196. doi:10.1098/rspb.2009.1337

Ricklefs RE, Cochran D, Pianka ER (1981) A morphological analysis of the structure of communities of lizards in desert habitats. Ecology 62:1474–1483

Schoener TW (1974a) The compression hypothesis and temporal resource partitioning. Proc Natl Acad Sci USA 71:4169–4172

Schoener TW (1974b) Resource partitioning in ecological communities. Science 185:27–39

Schoener TW (1975) Presence and absence of habitat shift in some widespread lizard species. Ecol Monogr 45:233–258

Schoener TW (1983) Field experiments on interspecific competition. Am Nat 122:240–285

Schoener TW, Losos JB, Spiller DA (2005) Island biogeography of populations: an introduced species transform survival patterns. Science 310:1807–1809. doi:10.1126/science.1120165

Selcer KW (1986) Life history of a successful colonizer: the Mediterranean gecko, *Hemidactylus turcicus*, in Southern Texas. Copeia 4:956–962

Török J, Tóth L (1999) Asymmetric competition between two tit species: a reciprocial removal experiment. J Anim Ecol 68:338–345

Vitt LJ, Zani PA (1998) Prey use among sympatric lizard species in lowland rain forest of Nicaragua. J Trop Ecol 14:537–559

Werner YL, Takahashi H, Mautz WJ, Ota H (2005) Behavior of the terrestrial nocturnal lizards *Goniurosaurus kuroiwae kuroiwae* and *Eublepharis macularius* (Reptilia: Eublepharidae) in a thigmothermal gradient. J Ther Biol 30:247–254. doi:10.1016/j.jtherbio.2004.12.004

Yamauchi A, Miki T (2009) Intraspecific niche flexibility facilitates species coexistence in a competitive community with a fluctuating environment. Oikos 118:55–66