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Original scientific paper

Habitat use of sympatric populations of *Podarcis sicula* and *P. melisellensis* on a small Adriatic island

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Key words: habitat use, competitive exclusion, *Podarcis sicula*, *Podarcis melisellensis*, island

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Abstract

Background and Purpose: *Competitive exclusion is thought to be involved in the distribution of the lizards* Podarcis sicula *and* P. melisellensis (Lacertidae) *along the Adriatic coastal region of Croatia. It is hypothesized that robust and aggressive* P. sicula *colonized the East Adriatic coast and numerous islands, where it replaced* P. melisellensis *by direct behavioral interference.*

Material and Methods: *Here we report on a study of habitat selection of sympatric populations of* P. sicula *and* P. melisellensis *on the small Adriatic island of Vrgada. We examine differences in habitat usage by the two species during summer and fall, and evaluate lizard sighting frequency in different habitat categories in relation to their availability.*

Results: *The two species differed significantly in habitat use;* P. sicula *used more frequently houses and walls in village, fields and rocks near sea, whereas* P. melisellensis *preferred all types of stonewalls.* P. sicula *showed the highest niche breadth, and was also the most abundant species. The observed sighting frequency of both species in different habitat categories differed significantly from their availability. Although variation in habitat use between summer and fall was detected in both species, the between-species difference in habitat occupation was consistent in both seasons.*

Conclusion: *The observed differences in habitat preferences between the sympatric populations of two species are qualitatively similar to those exhibited on islands inhabited by only one of both species. This suggests that differences in habitat use are species-specific and may delay or even prevent complete exclusion.*

INTRODUCTION

Interspecific competition occurs when individuals of two species reduce one another's growth or reproductive rates through utilization of common resources *(1)*. The Gause Principle poses that species with similar needs for the same limiting resources cannot coexist in the same place *(2, 3)*. This implies that highly similar species must evolve differences along some niche dimension to coexist in the same area *(1)*. Alternatively, the competitively inferior species may be forced to use suboptimal resources to minimize interactions with the dominant species. This process, known as »competitive exclusion« *(1, 4)*, can ultimately result in an allopatric distribution throughout most of the range of the species involved.

Competitive exclusion is thought to be involved in the distribution of the Lacertid lizards *Podarcis sicula* and *P. melisellensis* along the

Adriatic coastal region of Croatia. These two species are small lacertid lizards that are highly similar in many ecological characteristics; both are active foragers feeding mainly on arthropods, diurnal active basking heliotherms, and they exhibit a highly similar behavioral repertoire. While *P. sicula* is distributed throughout the central Mediterranean region and was introduced in many other locations, *P. melisellensis* is restricted to the East Adriatic coastal region and adjacent Croatian islands *(5)*.

Distributional data show that only one of both species is present on Croatian islands, except on a few bigger islands (surface area > 15 km^2) *(6)*.

Several authors suggested that *P. sicula* of Italian origin colonised the East Adriatic coast and numerous islands, where it replaced the less robust and aggressive *P. melisellensis* through competitive exclusion by direct behavioural interference *(6, 7, 8)*. Radovanović *(7)* tested this hypothesis by experimentally introducing *P. sicula* onto 3 islets exclusively occupied by *P. melisellensis*, and by introducing *P. melisellensis* on one islet exclusively inhabited by *P. sicula*. He visited the islands five years later and concluded that *P. sicula* had become numerous on islands where it was introduced, whereas *P. melisellensis* was not present on the islet where it was introduced *(7, 8)*. Nevo *et al. (8)* revisited three of the experimental islands in 1971 and partially confirmed the findings of Radovanović *(7)*. Nevo *et al. (8)* also expanded the introduction experiment on two additional Adriatic islands. They introduced *P. sicula* on the island Pod Mrčaru, which was originally occupied by *P. melisellensis*, and introduced *P. melisellensis* on Pod Kopište, originally inhabited solely by *P. sicula* island. Thirty years later (2001) we visited Pod Mrčaru and observed a very dense population of *P. sicula* but no *P. melisellensis* (Grbac, pers. observations.). This observation was recently (2004) confirmed by R. Van Damme and colleagues (R. Van Damme, pers. communication). Thus, *P. sicula* gained a foothold, and sometimes even replaced *P. melisellensis*, on some but not all of the islets where it was introduced, whereas introductions of *P. melisellensis* were seemingly not successful. Together, these data provide rather equivocal support for the hypothesis that *P. sicula* competitively excludes *P. melisellensis* in Adriatic islands.

Downes and Bauwens experimentally tested the mechanistic basis of the hypothesis, that direct behavioral interference is responsible for the putative competitive exclusion. Using newborn lizards of similar size, they showed that when individuals of both species were reared together, *P. sicula* were more aggressive and dominant, used better thermal microhabitats, and grew faster than *P. melisellensis*. These observations indicate that asymmetric aggressive interactions between hatchlings of the two species result in a reduction of an important fitness component (i.e., growth rate) of *P. melisellensis*, and are consistent with the hypothesis that direct behavioral interference by *P. sicula* is the mechanistic basis of the competitive exclusion of *P. melisellensis*.

An additional prediction of the hypothesis of competitive exclusion is that on islands inhabited by the two species, they should diverge in ecological and/or morphological characteristics (i.e., »character displacement«, *(10)*). This prediction has not been addressed in detail, presumably due to the scarcity of situations where the two species occur sympatrically. Only Nevo *at al. (8)* mention that they found differences in habitat preferences between the two species on the same island, suggesting that those differences may delay complete exclusion.

Here we report on a study of habitat selection of sympatric populations of *P. sicula* and *P. melisellensis* on the small Adriatic island of Vrgada. We examined the difference in habitat usage by the two species during summer and fall, and evaluated lizard sighting frequency in different habitat categories in relation to their availability. We compared our results with those of Raynor *(11)* which were mostly collected on islands inhabited by only one of the two species. This qualitative comparison indicated to what extent the differences in habitat usage by the two species reflect species-specific habitat preferences or, alternatively, reveal ecological segregation induced by competitive processes.

MATERIALS AND METHODS

Study area and field procedures

We conducted our study on Vrgada, a small island (surface area = 3.7 km^2) in the central part of the Adriatic Sea (Croatia). We recorded the presence of lizards in different habitat categories while we walked along a fixed transect of 3500 m length. The transect was a footpath that ran from the coast to the interior of the island and back. It covered all major habitats found on the island, starting in the island's only village, along the seaside and then through fields and along stonewalls, shrubs and woods in the central part of the island.

We walked the transect line 1.5 times per day during 8 summer days (between 21 July and 2 August, 2000) and 8 days (between 23 September and 10 October, 2000). Observations were carried out on alternating days during either morning or afternoon. Because weather conditions were highly similar on consecutive days, we joined observations from the morning period with those of the afternoon period on the following day, resulting in observations that covered the entire lizard activity period during 4 days in summer (7:00 – 20:00 h MET) and 4 days in fall (8:00–19:00 h MET).

Upon sighting of an adult lizard, we recorded species, sex, time of day and habitat type. We distinguished between the following 10 habitat categories: **1)** village (houses and walls); **2)** cultivated fields with olive and fig trees; **3)** grassland with low (<10 cm) grasses (dominant species: *Brachypodium ramosum* and *Lagurus ovatus*) or high (>10 cm) grasses (dominant species: *Dactylis glomerata*, *Stipa bromoides*, *Avene fatua* and *Haymaldia villosa*); **4)** grassland with shrubs of *Helichrysum italicum*, *Carlina* *corymbosa*, *Inula viscosa* and *Cystus villosus*;; **5)** dense shrubs of *Juniperus oxycedrus*, *J.phoenicaea*, *Pistacia lentiscus*, *P. terebrintus*, *Q.uercus ilex* and *Pinus halepensis,* and shrubs of *C. villosus*, *J. oxycedrus* and *J. ilex* in the *P. halepensis* wood; **6)** solitary olive trees, *Q.ilex* and *P. halepensis*; **7)** dry stonewall in the pine wood or in the shrub of *Hedera helix*, *Smilax aspera*, *Pistacia sp.*, *J. oxycedrus,* *Q.ilex* and *P. halepensis*; **8)** dry stonewall in grassland; **9)** dry stonewall; **10)** rocks with scattered *Helichrysum italycum* bushes near the seaside.

We estimated availability of the different habitat categories by recording the presence of each habitat type at 10 m intervals along the entire length of the transect. We sampled available habitats separately during summer and fall. Because the availability of the distinct habitat categories did not differ between the two seasons, we lumped the data to obtain a more robust estimate of habitat availability.

Statistical analyses

We grouped observations in three daily time periods: morning (before 12:00 h), mid-day (12:00 – 15:59 h) and afternoon (after 16:00 h).

For each species we estimated niche breadth along the habitat axis using the standardized Shannon-Wiener index:

$$J' = -\frac{\Sigma p_i \ln p_i}{\ln n}$$

with p_i the proportion of observations within the i^{th} habitat category, and n the number of habitat types distinguished (=10). Values of J' range between 0 and 1.

We employed frequency dependent statistical tests (chi-square, log-linear models of frequency tables) to identify significant associations among variables, using a probability of $p \leq 0.05$ as the standard criterion of statistical significance.

RESULTS

We initially used four-way log-linear analyses of frequency tables, including the factors habitat species, season and sex or time period. The analysis including sex as a factor, revealed a significant association between sex and species ($Chi^2 = 13.95$, df=1, $p<0.001$). Actually, we saw more females than males of *P. sicula* and more males than females of *P. melisellensis*. However, none of the higher order interactions with the factors habitat and species was significant, indicating that males and females of both species did not differ in habitat use. The analysis that included the factor time period indicated a significant interaction between time period and season ($Chi^2=66.38$, df=2, $p<0.001$). During summer we saw more lizards during morning (49%) and afternoon (38%) periods than during mid-day (13%) whereas during autumn we saw more lizards during mid-day (47%), than during morning (32%) and afternoon (21%) periods. The higher order interactions with the factors habitat and species were not significant, indicating that habitat use by both species was similar at all time periods.

Results of these initial analyses justify omission of the factors sex and time period from further analyses to concentrate on results of the log linear model with the variables habitat, species and season.

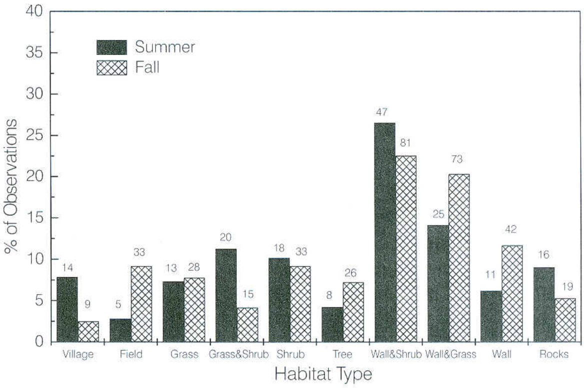


Figure 1. *Habitat use by* P. sicula *and* P. melisselensis *(data lumped) during summer and fall. Numbers above bars indicate sample sizes.*

The use of distinct habitat categories differed in the two seasons ($Chi^2=33.71$, df=9, $p<0.001$; Figure 1). During summer, we saw more lizards in the village, in grassland with shrubs, on rocks near the sea and, to a lesser extent, on stonewalls with shrubs. In the fall, lizards were often seen in the field, on the open stonewall, and to a lesser extent on trees and stonewalls in grassland. Nevertheless, the absence of a significant interaction effect between the variables habitat, species and season ($Chi^2=6.52$, df=9, $p>0.5$), indicates that the difference in habitat choice between summer and fall was similar in the two species.

The relative observation frequency of two species was similar in both seasons ($Chi^2=2.3$, df=1, $p>0.1$), although we always saw more individuals animals of *P. sicula* than of *P. melisellensis*; in fall 2.6 times and during summer 3.7 times more *P. sicula*.

The two species differed significantly in habitat use ($Chi^2 = 92.79$, df=9, $p<0.0001$). *P. sicula* used more frequently houses and walls in the village, fields, shrubs, trees and rocks near the sea, while *P. melisellensis* was seen more frequently on all types of walls, except those in the village (Figure 2). The observed habitat niche breadth was considerably higher in *P. sicula* ($J' = 0.963$) than in *P. melisellensis* ($J' = 0.698$). This difference primarily reflects more equal spreading of observations of *P. sicula* among distinct habitat categories, while a large proportion of *P. melisellensis* were observed in only three habitats (82% of observations in the habitats stonewall in shrub or wood, stonewall in grassland and dry stonewall; Figure 2).

The observed sighting frequency of *P. sicula* in different habitat categories differed significantly from their

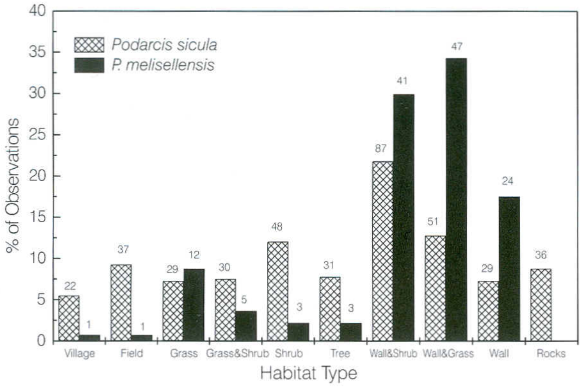
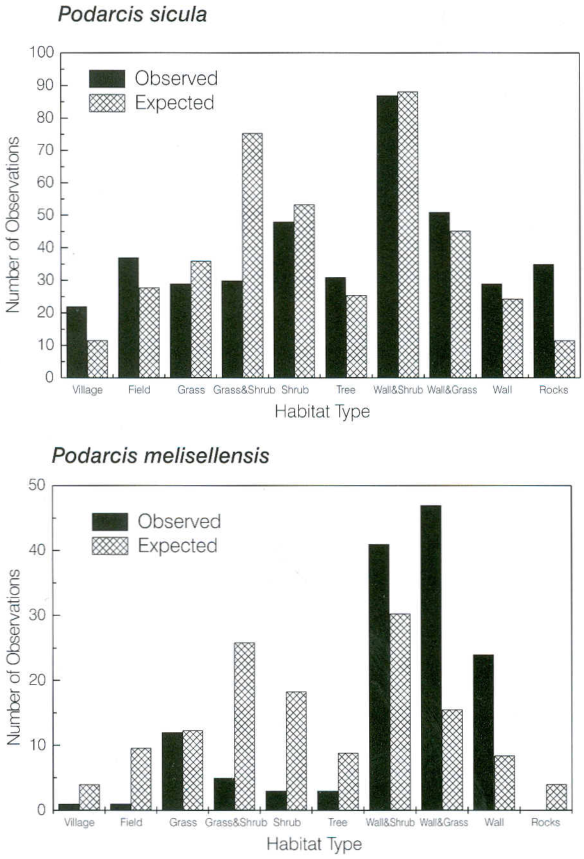


Figure 2. *Habitat use by* Podarcis sicula *and* P. melisellensis. *Numbers above bars indicate sample sizes.*

availability (Chi^2 = 91.58, df=9, $p < 0.001$). We saw more *P. sicula* on rocks near the sea, on houses in the village, in fields, and to a lesser extent on trees, stonewalls and stonewalls in grassland. *P. sicula* avoided grasslands with shrub and to a lesser extent grasslands and shrubs (Figure 3).

Sighting frequency of *P. melisellensis* also differed significantly from availability of distinct habitats (Chi^2 = 144.14, df=9, $p < 0.001$). *P. melisellensis* used different types of stonewalls more frequently than expected, they avoided grasslands with shrubs, fields, trees and houses in the village, and they were not observed on rocks near the sea (Figure 3).


Podarcis sicula

Podarcis melisellensis

Figure 3. *Observed and expected observations of* Podarcis sicula *and* P. melisellensis *in different habitat types. The expected number of observations was based on the availability of the different habitat types.*

DISSCUSION

P. sicula and *P. melisellensis* are known to occur sympatrically on only a few of the larger (> 15 km^2) Adriatic islands *(6)*. Thus, we used the rare opportunity to study sympatric populations of the two species on a rather small island. We lack precise information on the history of the two species on Vrgada. Both Radovanović *(6)* and Raynor *(11)* mention the presence of only *P. sicula* on this island. Hence, they may have overlooked *P. melisellensis* during their short-term visit to Vrgada, or the current presence of *P. melisellensis* could reflect a recent colonization of the island. However, the latter would represent a hitherto unreported case of successful colonization by *P. melisellensis* of an island inhabited by *P. sicula*. As other islands near Vrgada (e.g., Obrovanj, Murvenjak, Vrtlac) are inhabited by *P. melisellensis*, we assume that the co-occurrence of both species on Vrgada results from historical colonization by *P. sicula*.

Our results indicate that the two species differed in habitat usage and differed clearly in habitat preferences. *P. sicula* was clearly more abundant and was much more diverse in its habitat use than *P.melisellensis*. *P. sicula* more frequently used houses and walls in village, fields and rocks near the sea, while *P.melisellensis* was seen most often on different types of stonewalls. *P. sicula* clearly preferred habitats near human habitation (village and fields) and at the periphery of the island (village and rocks near sea), whereas these habitat types were avoided by *P.melisellensis* which preferred walls located in the interior of the island. These results are comparable, at least qualitatively, with the findings of *Nevo et al. (8)* on the relatively large island of Čiovo (ca 29 km^2). They observed *P.melisellensis* in agricultural areas away from human habitation, whereas *P. sicula* was well established in the town.

We studied lizards during two seasons (summer and fall) that differ considerably in thermal heat loads. During summer, lizards showed a bimodal daily activity pattern, whereas in fall the activity pattern was clearly unimodal. Adjustment of activity time is one of the main behavioral mechanisms of temperature regulation in lizards *(12, 13, 14)*. We also observed differences in habitat use between the two seasons. During summer lizards preferred more sheltered habitats like grasslands with shrubs, stonewalls with shrubs and houses and walls in the village, but also rocks near the sea which are relatively open habitats. In fall, we saw relatively more lizards in open sites like fields, stonewalls, stonewalls in grassland and on the trees. The sheltered habitats preferred in summer are structurally more heterogeneous and thereby probably more favorable in terms of thermoregulatory abilities than structurally less heterogeneous open fields and stonewalls *(15)*. The presence of shrubs, or houses and walls in the village, creates a sun-shade gradient that facilitates thermoregulation by shuttling, which is especially important during hot summer days. In early fall, when environmental temperatures are not so constraining, lizards used more open habitats and open stonewalls. Nevertheless, stonewalls also provide ample thermoregulatory possibilities through the adoption of basking postures, adjustment of orientation towards the sun and enhancing heat gain through conduction with the sun-warmed substrate *(14, 16, 17, 18, 19)*. Despite the observed seasonal variation in activity rhythms and habitat use, we found no indication that this affected the difference in habitat use by the two species. Hence, the observed difference in habitat use between *P. sicula* and *P. melisellensis* existed and was similar throughout a considerable part (summer and fall) of the annual activity period.

Does the observed difference in habitat usage reflect divergence induced by competitive processes, or is it merely the result of species-specific differences in habitat preferences? To answer this question, comparable studies are required in islands that are similar in habitat availability to Vrgada, but inhabited by either of the two species. Such studies are not available, although the report of Raynor *(11)* provides some indication. This author studied habitat use of the two species on six islands inhabited by *P. sicula*, four islands occupied by *P. melisellensis* and one island where the two species co-occured. Raynor *(11)* presents the lumped results for all islands, but it seems reasonable to assume that the majority of his observations were from islands inhabited by only one species. He found that *P. sicula* was much more diverse in its choice of habitats and was observed most often in vegetated and open land near human habitation, whereas *P. melisellensis* was seen most frequently on dry stonewalls, especially overgrown and collapsed ones, often away from human habitation. Our results from Vrgada, where the two species occur sympatrically, concur quite well with those of Raynor *(11),* suggesting that the observed difference in habitat usage between the two species reflects, at least to some extent, species-specific differences in habitat preferences.

It is generally assumed that a dominant species will force the subordinate to use less favorable microhabitats. Arnold *(18)* hypothesized for syntopic lacertid lizards on Mediterranean islands that dominant species occupy terrestrial, vegetated and horizontal habitats, whereas the subordinate species is mostly confined to rocks, walls and other vertical microhabitats. Our results correspond to some extent to this general idea. *P. sicula* preferred some »horizontal« habitats, like fields and rocks near the sea, while *P.melisellensis* showed strong preference for stonewalls. However, *P. sicula* also preferred walls in the village. On the other hand, neither *P. melisellensis* nor *P. sicula* are clearly climbing species like *Lacerta oxycephala*, a third lacertid species that often co-occurs with *P. sicula* or *P. melisellensis* on Adriatic islands. Schreers and Van Damme *(19)* studied the usage and the thermal quality of habitats occupied by the predominantly ground-dwelling *P.melisellensis* and the climbing *L. oxycephala*. They demonstrated that the »horizontal« habitat of *P. melisellensis* possesses a higher overall absolute thermal quality over the »vertical« habitat of *L. oxycephala*.

Under experimental laboratory conditions, Downes & Bauwens *(9)* showed that in mixed-species pairs, juvenile *P. sicula* were more aggressive and used better thermal microhabitats than *P. melisellensis*, whereas differences in thermal microhabitat usage were less pronounced in homospecific pairs. As a consequence, *P. sicula* grew faster and *P. melisellensis* slower, in heterospecific than in homospecific pairs. This study shows that interactions occur between juveniles of both species, and that these may affect growth rate, an important fitness component in lizards *(9)*. Hence, the occurrence of competitive exclusion of *P. melisellensis* by *P.sicula* cannot be disregarded. However, and as suggested by Nevo *et al. (8)* and Raynor *(11),* differences between species in habitat preferences may delay or even avoid competitive exclusion, at least on islands where sufficiently large patches of the preferred habitats of the two species are available.

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Distributional data show that only one of both species is present on Croatian islands, except on a few bigger islands (surface area > 15 km^2) *(6)*.

Several authors suggested that *P. sicula* of Italian origin colonised the East Adriatic coast and numerous islands, where it replaced the less robust and aggressive *P. melisellensis* through competitive exclusion by direct behavioural interference *(6, 7, 8)*. Radovanović *(7)* tested this hypothesis by experimentally introducing *P. sicula* onto 3 islets exclusively occupied by *P. melisellensis*, and by introducing *P. melisellensis* on one islet exclusively inhabited by *P. sicula*. He visited the islands five years later and concluded that *P. sicula* had become numerous on islands where it was introduced, whereas *P. melisellensis* was not present on the islet where it was introduced *(7, 8)*. Nevo *et al. (8)* revisited three of the experimental islands in 1971 and partially confirmed the findings of Radovanović *(7)*. Nevo *et al. (8)* also expanded the introduction experiment on two additional Adriatic islands. They introduced *P. sicula* on the island Pod Mrčaru, which was originally occupied by *P. melisellensis*, and introduced *P. melisellensis* on Pod Kopište, originally inhabited solely by *P. sicula* island. Thirty years later (2001) we visited Pod Mrčaru and observed a very dense population of *P. sicula* but no *P. melisellensis* (Grbac, pers. observations.). This observation was recently (2004) confirmed by R. Van Damme and colleagues (R. Van Damme, pers. communication). Thus, *P. sicula* gained a foothold, and sometimes even replaced *P. melisellensis*, on some but not all of the islets where it was introduced, whereas introductions of *P. melisellensis* were seemingly not successful. Together, these data provide rather equivocal support for the hypothesis that *P. sicula* competitively excludes *P. melisellensis* in Adriatic islands.

Downes and Bauwens experimentally tested the mechanistic basis of the hypothesis, that direct behavioral interference is responsible for the putative competitive exclusion. Using newborn lizards of similar size, they showed that when individuals of both species were reared together, *P. sicula* were more aggressive and dominant, used better thermal microhabitats, and grew faster than *P. melisellensis*. These observations indicate that asymmetric aggressive interactions between hatchlings of the two species result in a reduction of an important fitness component (i.e., growth rate) of *P. melisellensis*, and are consistent with the hypothesis that direct behavioral interference by *P. sicula* is the mechanistic basis of the competitive exclusion of *P. melisellensis*.

An additional prediction of the hypothesis of competitive exclusion is that on islands inhabited by the two species, they should diverge in ecological and/or morphological characteristics (i.e., »character displacement«, *(10)*). This prediction has not been addressed in detail, presumably due to the scarcity of situations where the two species occur sympatrically. Only Nevo *at al. (8)* mention that they found differences in habitat preferences between the two species on the same island, suggesting that those differences may delay complete exclusion.

Here we report on a study of habitat selection of sympatric populations of *P. sicula* and *P. melisellensis* on the small Adriatic island of Vrgada. We examined the difference in habitat usage by the two species during summer and fall, and evaluated lizard sighting frequency in different habitat categories in relation to their availability. We compared our results with those of Raynor *(11)* which were mostly collected on islands inhabited by only one of the two species. This qualitative comparison indicated to what extent the differences in habitat usage by the two species reflect species-specific habitat preferences or, alternatively, reveal ecological segregation induced by competitive processes.

MATERIALS AND METHODS

Study area and field procedures

We conducted our study on Vrgada, a small island (surface area = 3.7 km^2) in the central part of the Adriatic Sea (Croatia). We recorded the presence of lizards in different habitat categories while we walked along a fixed transect of 3500 m length. The transect was a footpath that ran from the coast to the interior of the island and back. It covered all major habitats found on the island, starting in the island's only village, along the seaside and then through fields and along stonewalls, shrubs and woods in the central part of the island.

We walked the transect line 1.5 times per day during 8 summer days (between 21 July and 2 August, 2000) and 8 days (between 23 September and 10 October, 2000). Observations were carried out on alternating days during either morning or afternoon. Because weather conditions were highly similar on consecutive days, we joined observations from the morning period with those of the afternoon period on the following day, resulting in observations that covered the entire lizard activity period during 4 days in summer (7:00 – 20:00 h MET) and 4 days in fall (8:00–19:00 h MET).

Upon sighting of an adult lizard, we recorded species, sex, time of day and habitat type. We distinguished between the following 10 habitat categories: **1)** village (houses and walls); **2)** cultivated fields with olive and fig trees; **3)** grassland with low (<10 cm) grasses (dominant species: *Brachypodium ramosum* and *Lagurus ovatus*) or high (>10 cm) grasses (dominant species: *Dactylis glomerata*, *Stipa bromoides*, *Avene fatua* and *Haymaldia villosa*); **4)** grassland with shrubs of *Helichrysum italicum*, *Carlina*