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DISTRIBUTION OF REPTILES AND AMPHIBIANS IN THE NATURE PARK LASTOVO ARCHIPELAGO: POSSIBLE UNDERLYING BIOTIC AND ABIOTIC CAUSES

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In this paper we examine the distribution of amphibians and reptiles over the islands of the newly founded Lastovo Archipelago Nature Park (Lastovsko otočje), Croatia. On several field trips between 1996 and 2008, we encountered five species of lizards (*Podarcis sicula*, *P. melisellensis*, *Dalmatolacerta oxycephala*, *Hemidactylus turcicus* and *Pseudopus apodus*), one species of snake (*Dolichophis caspius*), one species of sea turtle (*Caretta caretta*) and one species of toad (*Bufo viridis*). We confirm literature data on the presence of some of these species on different islands of the archipelago, and add distributional records for several other islands and islets. Logistic regression analyses show that the variables predicting presence/absence from different islands vary among species. Within species, populations from different islands noticeably vary in body size and shape, scalation, dorsal and ventral coloration, behaviour and density. This observation adds to the value of the study area as a »natural laboratory« for future research into the ecology and evolution of island populations. Although most species seem to be doing well presently, we list a number of possible hazards and concerns.

Keywords: distributional records, species occurrence, degree of isolation, Croatia, Adriatic, island biogeography

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U ovom radu istražujemo distribuciju vodozemaca i gmazova novoosnovanog Parka prirode »Lastovsko otočje«, Hrvatska. Tijekom višestrukih terenskih posjeta u periodu od 1996. do 2008. godine zabilježili smo pet vrsta guštera (*Podarcis sicula*, *P. melisellensis*, *Dalmatolacerta oxycephala*, *Hemidactylus turcicus* i *Pseudopus apodus*), jednu vrstu zmije (*Dolichophis caspius*), jednu vrstu morske kornjače (*Caretta caretta*) i jednu vrstu žabe (*Bufo viridis*). Potvrdili smo prisutnost određenih vrsta na pojedinim otocima Lastovskog otočja, te dodali nalaze na mnogim drugim otocima i otočićima. Logističkom regresijskom analizom smo pokazali da varijable koje predviđaju prisutnost / odsutnost s različitih otoka variraju između vrsta. Unutar vrste, populacije s različitih otoka zapaženo variraju u veličini i obliku tijela, broju i izgledu pločica, ledđnoj i trbušnoj obojenosti, ponašanju i gustoći. Ova opažanja povećavaju vrijednost istraživanog područja kao »prirodnog laboratorija« za buduća istraživanja ekologije i evolucije otočkih populacija. Iako se čini je većina vrsta u dobrom stanju, navodimo listu mogućih opasnih i zabrinjavajućih čimbenika.

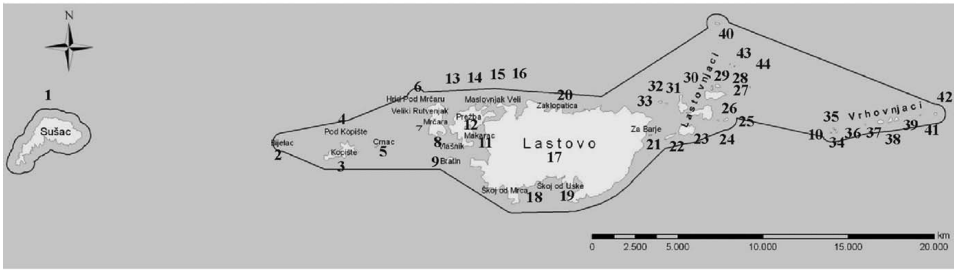
Ključne riječi: distribucija vrsta, stupanj izolacije

INTRODUCTION

In September 2006, the Croatian parliament declared the Lastovo Archipelago (Lastovsko otočje) a Nature Park, thus granting protection to the natural richness of an area covering 195 km^2. Besides 143 km^2 of superb marine habitat, the new nature Park also encloses 52 km^2 of terrestrial environments on Lastovo, Sušac and 42 smaller islands (Fig. 1). The main island of Lastovo consists of wooded hills (mostly holm oaks, *Quercus ilex* and Aleppo pines, *Pinus halepensis*), and typical karst fields (»poljes«). Of the smaller islands, some are wooded, while on others the vegetation is restricted to Mediterranean herbs (mainly *Crithmum maritimum*, *Silene inflata*, *Lotus edulis*, *Portulaca oleracea*, *Chenopodium* spp., *Cynodon dactylon*) and/or shrubs (*Pistacia lenticus*, *Juniperus communis*).

Reptiles, especially lizards, make up an important and conspicuous part of the fauna of this archipelago. On many of the islands, lizards are the most abundant, if not the sole terrestrial vertebrates. As such, they most likely play a vital role in the islands' community dynamics, as important secondary consumers, but probably also as pollinators (cf. ELVERS, 1977; TRAVESET & SÁEZ, 1997; NYHAGEN *et al*., 2001) and dispersal agents (cf. VALIDO & NOGALES, 1994; PÉREZ-MELLADO & TRAVESET, 1999) for the local flowering plants. From a scientific point of view, lizards on islands have proved excellent models for studying a variety of ecological and evolutionary questions (e.g. island biogeography: DARLINGTON, 1957; extinction and colonisation dynamics: SPILLER *et al*., 1998; food web dynamics: SPILLER & SCHOENER, 2007; morphological evolution: LOSOS *et al*., 2001; MALHOTRA & THORPE, 1991; genetic differentiation: THORPE *et al*., 1994).

The reptiles and amphibians of the Lastovo Archipelago have received considerable attention. The unusual diversity of the Balkan herpetofauna attracted early herpetologists such as Franz WERNER (1892, 1902, 1908), Otto VON TOMASINI (1894), Paul KAMMERER (1926), Robert MERTENS (1937), and especially Milán RADOVANOVIĆ (1951, 1954, 1956, 1964). These pioneers noted the remarkable variability of the in-



1. Sušac	12. Prežba	23. Kručica	34. Mala Sestrica
2. Bijelac	13. Mali Rutvenjak	24. Mali Golubinjak	35. Vela Sestrica
3. Kopište	14. Veli Rutenvenjak	25. Veli Golubinjak	36. Mrkljenta
4. Pod Kopište	15. Mali Maslovnjak	26. Češvinica	37. Smokvica
5. Crnac	16. Veli Maslovnjak	27. Saplun	38. Donji Vlašnik
6. Pod Mrčaru	17. Lastovo	28. Veli Arženjak	39. Srednji Vlašnik
7. Mrčara	18. škoj od Mrca	29. Mali Arženjak	40. Tajan Veli
8. Vlašnik	19. Hrid Uska	30. Stomorina	41. Hrid Mrjenta
9. Bratin	20. Zaklopatica	31. Gornij Lukovac	42. Glavat
10. Hrid Bratač	21. Barje	32. Srednji Lukovac	43. Hrid Mrkljenta Crna
11. Makarac	22. Petrovac	33. Mali Lukovac	44. Hrid Mrkljenta Bijela

Fig. 1. Map of the islands belonging to the Lastovo Archipelago Nature Park. Numbers refer to islands in columns.

sular forms and proposed the first hypotheses on their taxonomy, distribution and evolution. In the 1970s, lizard populations of the archipelago were sampled in a pioneering study regarding the evolution of genetic diversity on islands (GORMAN *et al*. 1975, CLOVER 1979) and two of the smaller islands were involved in a reciprocal translocation experiment, set-up to test the hypothesis of competitive exclusion between two *Podarcis* species (NEVO *et al*., 1972). More recently, lizard populations on Lastovo and surrounding islands featured in studies on functional ecology and behavioural ecology (IRSCHICK *et al*., 2005; HUYGHE *et al*., 2007; VERVUST *et al*., 2007, 2008a,b; BRECKO *et al*., 2008). A follow-up on the reciprocal transplant experiment revealed surprisingly fast evolutionary morphological and physiological differentiation (VERVUST *et al*., 2007; HERREL *et al*., 2008). PODNAR and co-workers (2004, 2005, 2006) sampled several of the *Podarcis* populations in the area as part of a broad-scale phylogeographical study of the genus using mitochondrial DNA. One of their main conclusions was that many of the subspecies described by earlier taxonomists based on morphological differences do not hold in the light of genetic evidence. Both the *P. melisellensis* and *P. sicula* populations in the area seem to belong to homogenous, distinctive clades within the respective species, further adding to the uniqueness of the archipelago's herpetofauna.

Despite this long-standing interest in the amphibian and reptile community of the Nature Park, many uncertainties remain. Many of the smaller islands do not figure in distributional lists, and others have not been investigated for decades. Given the natural instability of island populations (HANSKI & GILPIN, 1991) and their vulnerability to anthropogenic perturbation (CASE *et al*., 1992), an update of the distribution data seemed warranted. Moreover, possibly because of problems with the identification of the different species, historical accounts of species presence contradict one

another on several occasions. The reliability of the (older) literature is also jeopardized by the confusing geographical nomenclature of land bodies in the Adriatic Sea. Many islands and islets are known under different names, and often the same name is used for different islands.

In this paper, we report our observations on amphibians and reptiles of the Lastovo Archipelago Nature Park during repeated visits of the islands in the period spanning 1996-2008. We also attempt to explain the presence/occurrence of the more common species on the constituting islands, using variables of the biotic and abiotic environment. We hope that these observations will be helpful for future conservational practice and for further scientific work on the nature Park's herpetofauna.

MATERIAL AND METHODS

Data were gathered during multiple visits to the archipelago in the years 1996, 1997, 1998 and 2001 (IG, NT) and 2004, 2006, 2007 and 2008 (BV, JB, RVD). Habitats on the main island of Lastovo were censused both during the day and at night; the smaller islands were visited during daytime only. Weather conditions were always such to permit activity. We also frequently turned over rocks and stones to look for inactive specimens. The number of man-hours searched varied among islands and ranged between 10 and 650, but we are confident not to have missed any species on the islands visited. To permit identification, animals were caught by noose, by hand or in traps (plastic bottles with reversed necks) baited with soft fruits (peach or grapes). They were released at the exact place where they were caught.

We used stepwise logistic regression analysis to examine which biotic and abiotic factors can predict the presence/absence of *Podarcis melisellensis*, *Dalmatolacerta oxycephala* and *Hemidactylus turcicus* from the sampled islands in the Nature Park. We considered the following characteristics: island surface area, island perimeter, distance to the main island (Lastovo) and maximal height of the island. Island surface area and perimeter were taken from LEDER *et al*. (2004) for most of the larger islands. For islands not listed in this paper, we digitised the perimeter from digital copies of a nautical map (Admirality Charts, The United Kingdom Hydrographic Office, Taunton, UK, scale 1:100 000) and then obtained its length and the area of the island using the tpsDig software (R. J. Rohlf, http://life.bio.sunysb.edu/morph/). We used the same software to measure the smallest distance to the nearest point on Lastovo Island, and to estimate the area of land within circles with radius of 500 and 1000 m, placed at the centre of mass on the island. The latter variables are considered indicative for the island's »degree of isolation«. The maximal height of each island was taken from a nautical map. »Presence of competitors« and »presence of buildings« (inhabited or recently abandoned) were introduced as dichotomous biotic factors. Because stepwise regression methods tend to »overfit« the data to noise, we used the Bayesian Information Criterion (BIC) to select the most parsimonious model explaining the variation in the dependent variable.

To avoid problems of multicolinearity among dependent variables in the logistic regression analyses, we introduced the Area, Perimeter, Distance, Land500 and Land1000 variables (log10-transformed) into a principal components analysis, using

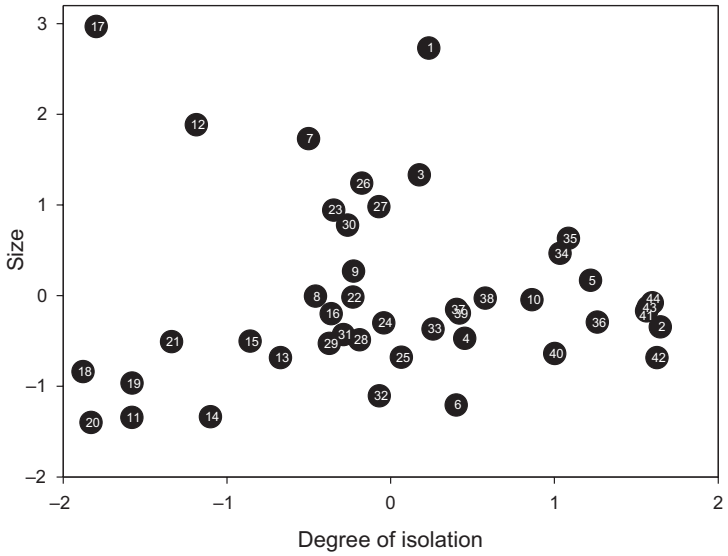


Fig. 2. Projections of the islands on the first principal component plane. The first axis (X-axis) is an »isolation« axis, islands to the right being more remote. The second axis is a »size« axis, running from small (bottom) to large (top) surface area. The numbers on the symbols are the same as those listed in Fig. 1.

the Varimax rotation method. This resulted in two composite variables that explained 67% and 21% of the total initial variation, respectively. The first composite variable correlated positively with Distance (r = +0.84) and negatively with Land500 (r = –0.77), Land1000 (r = –0.90), and we will refer to it as »Degree of isolation«. The second axis correlated positively with Area (r = +0.96) and Perimeter (r = +0.96) and we will name it »Size«. The distribution of the islands within the first principal components plane is illustrated in Fig. 2.

RESULTS

During our stays in the Lastovsko otočje Nature Park, we encountered five species of lizards (*Podarcis sicula*, *P. melisellensis*, *Dalmatolacerta oxycephala*, *Hemidactylus turcicus* and *Pseudopus apodus*), one species of snake (*Dolichophis caspius*), one species of sea turtle (*Caretta caretta*) and one amphibian (*Bufo viridis*). We also found one single specimen of Hermann's tortoise (*Testudo hermanni*), which was most probably released from captivity.

Podarcis sicula

Populations of the Italian wall lizard (*Podarcis sicula pelagosae* Rafinesque – Schmaltz, 1810 – originally described as *P. s. cazzae* Schreiber, 1912, but put in synonymy with *P. s. pelagosae* Rafinesque – Schmaltz, 1810 by HENLE & KLAVER in 1986,

and later with *P. s. adriatica* (Werner, 1902) by PODNAR LEŠIĆ & TVRTKOVIĆ, 2006), occur on the western islands of the archipelago: Šušac Island (Cazza: KOLOMBATOVIĆ, 1903; KAMMERER, 1926; PODNAR *et al*., 2005), Bijelac (KAMMERER 1926), Kopište (KAMMERER, 1926), Pod Kopište (KAMMERER, 1926; NEVO *et al*., 1972; PODNAR *et al*., 2005) and Pod Mrčaru (NEVO *et al*., 1972; GORMAN *et al*., 1975; VERVUST *et al*., 2007; HERREL *et al*., 2008). The presence of the species on the latter islet is remarkable, as it was introduced there in the context of an ecological experiment in 1971 (NEVO *et al*., 1972). Although the founder population consisted of ten adult specimens (five males and five females) only, the species has successfully colonized the island, eradicating the original population of *Podarcis melisellensis* in the process. The newly founded population of *P. sicula* on Pod Mrčaru is extremely dense and differs considerably from its source on Pod Kopište in aspects of average body size and shape (VERVUST *et al*., 2007), pholidosis (VERVUST *et al*., 2008a), physiological performance (VERVUST *et al*., 2007; HERREL *et al*., 2008) and behaviour (Vervust *et al*., 2007, submitted).

Podarcis melisellensis

We confirm the presence of the Dalmatian wall lizard (*Podarcis melisellensis* Braun, 1877) on Mrčara (KAMMERER, 1926), Mali Rutvenjak (KAMMERER, 1926), Veli Rutvenjak (KAMMERER, 1926), Lastovo (WERNER, 1902; KAMMERER, 1926; RADOVANOVIĆ, 1956; PODNAR *et al*., 2004), Tajan Veli (KAMMERER, 1926), Vela Sestrica (KAMMERER, 1926; PODNAR *et al*. 2004), Smokvica (KAMMERER, 1926), Srednji Vlašnik (KAMMERER, 1926; PODNAR *et al*., 2004), Stomorina (PODNAR *et al*., 2004), Kručica (PODNAR *et al*., 2004) and Glavat (KAMMERER, 1926; PODNAR *et al*., 2004). In addition, we report the following new distributional records for this species: Vlašnik, Bratin, Makarac, Prežba, Mali Maslinjak, Veli Maslinjak, Zaklopatica, Petrovac, Češvinica, Saplun, Veli Arženjak, Mali Arženjak, Gornji Lukovac, Srednji Lukovac and Srednji Vlaški. As mentioned above, *Podarcis sicula* has replaced *P. melisellensis* completely on Pod Mrčaru (KAMMERER, 1926; RADOVANOVIĆ, 1956; NEVO *et al*., 1972; TIEDEMANN & HENLE, 1986). The species is very varied in coloration. A dark, reticular dorsal coloration pattern is characteristic of *P. melisellensis* on Veli Rutvenjak, an observation already made by Kammerer back in 1926. We did find specimens with similar dorsal patterns on Makarac, Mali and Veli Maslinjak. On Srednji Lukovac, we found a (semi) melanistic population of *P. melisellensis*. The population of Lastovo Island exhibits an intriguing polymorphism in vent color; males may have white, yellow or orange colored bellies, females are usually white or yellow (HUYGHE *et al*., 2007; BRECKO *et al*., 2008). On the smaller islands, one or more of these color morphs seem to be missing. Specimens on Glavat, for instance, all have a white-greenish vent color (as mentioned by KAMMERER 1926, p. 72), whereas on Tajan Veli and Češvinica all individuals of both sexes have reddish bellies (also noted by KAMMERER 1926, p. 73). On Vela Sestrica, males have red bellies, while all females are white (again as observed by KAMMERER 1926, p. 72). Although we have no quantitative data to support this, populations clearly also differ strongly in density and shyness. For example, on Češvinica the lizards occur in very high densities and are extremely tame. The Srednji Lukovac population is also dense, but the animals are extremely shy and difficult to capture. The nearby island of Gornji Lukovac also harbors high densities, but lizards are obviously less shy. On the other hand, Mali and Veli Arženjak and Saplun harbors low densities and lizards are extremely shy.

A model that includes »Presence of *P. sicula*«, »Maximal height of the island« and »Degree of Isolation« best predicts the presence/absence of *P. melisellenis* on the islands within the Nature Park (fit of final model: Nagelkerke-pseudo $r^2 = 0.78$, BIC = 36.93, $\chi^2_3 = 37.7$, $P < 0.001$). »Island size« and »Presence of building« did not enter the final equation. Inspection of the model's parameters learns that *P. melisellensis* is more likely to be absent from islands that are remote (parameter estimate for Degree of isolation: B = –1.678), have a limited maximal height (Maximal height: B = –15.93) and contain no *P. sicula* (B = –36.81). The model successfully predicts the species' occurrence in 38 of the 44 islands (91%). The model places *P. melisellensis* on Crnac and D. Vlašnik, where we failed to find the species, and predicts its absence from Mali Arženjak, where in reality we observed it.

Dalmatolacerta oxycephala

The sharp-headed lizard (*Dalmatolacerta oxycephala* Duméril and Bibron, 1839) inhabits most islands of the Lastovsko otočje Nature Park. We confirmed this species' presence on Lastovo (WERNER, 1892, 1908; KOLOMBATOVIC, 1903; MÜLLER, 1902; RÖSSLER, 1919; KARAMAN, 1921, 1939; KAMMERER, 1926; RADOVANOVIĆ, 1951, 1954, 1956), Veli Rutvenjak (KAMMERER, 1926; RADOVANOVIC, 1956), Mali Rutvenjak (KAMMERER, 1926; RADOVANOVIĆ, 1956), Pod Mrčaru (KAMMERER, 1926; RADOVANOVIĆ, 1956; NEVO *et al*. 1972, GORMAN *et al*. 1975), Kopište (KAMMERER, 1926; Radovanović, 1951), Mrčara (Kammerer, 1926), Tajan Veli (Kammerer, 1926), Vela and Mala Sestrica (KAMMERER, 1926), Smokvica (KAMMERER, 1926), Glavat (KAMMERER, 1926) and Sušac (KOLOMBATOVIĆ, 1903; WERNER, 1908; KAMMERER, 1926). In addition, we found the species on Vlašnik, Bratin, Makarac, Prežba, Mali Maslinjak, Veli Maslinjak, Zaklopatica, Petrovac, Kručica, Češvinica, Saplun, Veli Arženjak, Mali Arženjak, Stomorina, Gornji Lukovac, Srednji Lukovac, Srednji Vlaški, Mali and Veli Golubinjak. As far as we know, all these constitute new distributional records.

The most parsimonious model for *D. oxycephala* contains only »Maximal height of the island« as a useful predictor (fit of final model: Nagelkerke-pseudo $r^2 = 0.48$, BIC = 34.66, $\chi^2_1 = 18.13$, $P < 0.001$). The model predicts that species will be absent from very flat islands only (Fig. 3). In seven islands (Bijelac, Pod Kopište, Crnac, Skoj od Mrca, Hr. Uska, Barje, D. Vlašnik), we could not confirm the existence of populations *D. oxycephala* where it was predicted by the model. In three other islands (Mali Golubinjak., Sestrica Vela and Mala) there exist populations where the model predicts none.

Densities of *D. oxycephala* apparently vary considerably among islands. Although the occurrence of other lacertids does not appear in the species' presence/absence model, it is clear that *P. melisellensis* and especially *P. sicula* specimens are competitively superior over *D. oxycephala.* We noted that on small islands were species co-occur, *D. oxycephala* often retreats to the peripheral zone of almost barren rocks. Even there, it can often be seen chased by individuals of the *Podarcis* species. The idea that interspecific competition may constrain the density and distribution of *D. oxycephala* within islands is further corroborated by the fact that on two particularly harsh islands (Mali and Veli Golubinjak) without *Podarcis*, the species occurs in very high density.

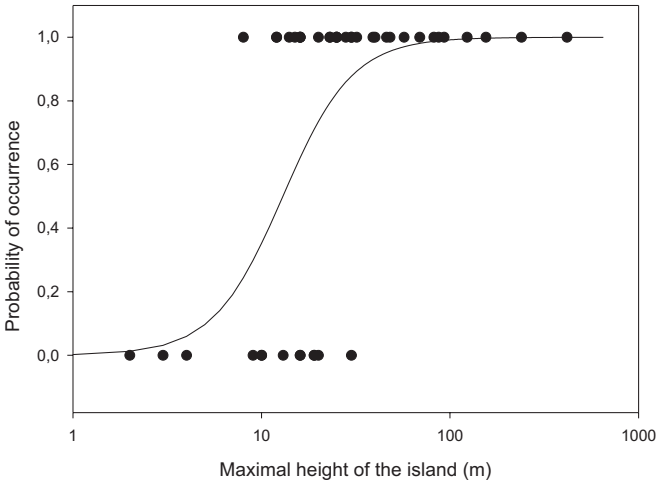


Fig. 3. Effect of island height on the probability of occurrence of *Dalmatolacerta oxycephala*.

Hemidactylus turcicus

The Mediterranean house gecko or Turkish gecko (*Hemidactylus turcicus* Linnaeus, 1758) was found on Lastovo (WERNER, 1908; KAMMERER, 1926; KARAMAN, 1939), Prežba, Glavat, Mrčara, Srednji Lukovac and Sušac (Cazza: KOLOMBATOVIĆ, 1903).

Confirming its man-driven distributional pattern, the only independent variable that enters the equation predicting this species' presence/absence is »Presence of buildings« (fit of final model: Nagelkerke pseudo r2 = 0.81, BIC = 38.8, χ^2_1 = 25.75, P < 0.001). Islands with inhabited or recently abandoned human constructions (n = 5) all house populations of this species, while most uninhabited islands (n = 38) do not. The only island without buildings where *H. turcicus* was found is Lukovac Sr.

Pseudopus apodus

The presence of European glass lizards (*Pseudopus apodus* Pallas, 1775) on the main island of Lastovo has been documented long time ago (WERNER, 1908; KARAMAN, 1939; RADOVANOVIĆ, 1964). This species was restricted only to Lastovo. We encountered these large lizards in great numbers, especially in spring, and mostly in cultivated areas near human habituation, such as vineyards.

Dolichophis caspius

The Caspian whip snake (*Dolichophis caspius* Gmelin, 1789) has been reported from Lastovo (WERNER, 1902, 1903, 1904, 1908, 1913; SCHREIBER 1912; ZFMK – collection; RADOVANOVIĆ, 1964) and from Kopište (KAMMERER, 1926). We can confirm these distributional records, and we also found the species on Mrčara. We could not corroborate this snake's current presence on Sušac Island (KAMMERER, 1926). People from the island's lighthouse remember its probable extermination in the recent past.

Hierophis viridiflavus

POZZI (1966) mentions the western whip snake (*Hierophis viridiflavus* Lacépède, 1789) on Sušac. We did not encounter this species there or anywhere else in the Lastovo Archipelago.

Testudo hermanni

Although KLETECKI (2006) reported Hermann's tortoise (*Testudo hermanni* Gmelin, 1789) from Lastovo Island, we are unable to confirm its natural occurrence on Lastovo Island. Local farmers also deny its presence. We found one tortoise specimen in Lokavje polje (Lastovo) in 1997, and several captive tortoises in 2007 and 2008 (closed gardens in Ubli, Lastovo and Zaklopatica), which were presumably brought from the mainland.

Caretta caretta, Chelonia mydas, Dermochelys coriacea

Sea turtles are commonly observed in the seas Archipelago. LAZAR & TVRTKOVIĆ (1995) reported 18 sightings between 1989 and 1993, including the observation of a school of about 30 specimens of *Caretta caretta* westward from Lastovo Island, in the winter of 1990. In the summer of 2007 we observed one loggerhead turtle (*Caretta caretta* Linnaeus, 1758) in the strait between Pod Mrčaru and Pod Kopište. We never observed the more rare green turtle (*Chelonia mydas* Linnaeus, 1758) or leatherback turtle (*Dermochelys coriacea* Vandelli, 1761), but it should be noted that our censuses primarily centered on terrestrial reptiles.

Bufo viridis

We found large numbers of green toad (*Bufo viridis* Laurenti, 1768) on Lastovo Island (WERNER, 1908; KAMMERER, 1926; RADOVANOVIĆ, 1956). Breeding occurs in fresh water ponds found on Vino Polje (Ubli) and Lokavje (Lastovo). Most probably because of the lack of fresh water, this species is absent from all smaller islands of the Archipelago.

DISCUSSION

Our results on the occurrence of reptilian and amphibian species within the Lastovo Archipelago are in general agreement with earlier findings. We were able to confirm the presence of the distinct species on most of the islands that had been visited by earlier students, although some of the records in the literature date from considerable time ago. That we also report a fair amount of »new« distributional data probably reflects the fact that previous expeditions did not land on the islands and islets in question, and most surely does not indicate recent colonisation.

In addition, our statistical analyses suggest that the occurrence (or absence) from some of the more widely distributed species can be predicted on the basis of a few environmental variables, which make sense considering the natural history of the species in question. For instance, the presence of both *P. melisellensis* and *D. oxycephala* requires islands to be sufficiently high, probably because lizards on lower is-

lands run the risk of being swept into sea by waves during storms. The finding that the presence of *P. sicula* is fatal for *P. melisellensis* is in agreement with the old idea that competitive exclusion prevents these two ecologically similar species to co-exist on most smaller islands (RADOVANOVIĆ, 1956; NEVO *et al.*, 1972). The syntopy of *D. oxycephala* with *P. melisellensis* species on many of the islands suggests a smaller niche overlap between these two species. However, these simple presence/absence censuses do not assure that there is no competition at all. Our observations on the peripheral distribution of *D. oxycephala* on islands inhabited by *P. melisellensis* (or *P. sicula*) and the frequent aggressive interactions suggest quite the opposite. They indicate that *D. oxycephala* on these islands is restricting its fundamental niche breadth, in an attempt to make the best of a bad situation. Comparing the realized niche widths of *D. oxycephala* along different resource axes (thermal, trophic, microhabitat, etc) on islands with and without competing *Podarcis* species would be a valuable line of research. It would also be of great interest whether the presence of these competitors also translates in altered life history and demographic characteristics.

The fact that most historically reported populations were still present when we censused the area, and the fact that models with (mostly) natural variables predict the distribution of the species well, may suggest that the Archipelago's terrestrial herpetofauna is doing well. With the clear exception of the *P. melisellensis* population on Pod Mrčaru, none of the insular populations seems to have gone extinct in the last few decades. The remarkable observation that populations on some of the smaller islands exhibit particular features (coloration, degrees of shyness) already described by authors many decades ago, adds to the belief that the populations are stable and have not been replaced or invaded by conspecifics from other islands. It will be most instructive to learn about the phylogenetic relationships between the different island populations. However, we wish to stress again that our current data do not fully allow assessing the well being of the amphibian and reptilian populations in the area. We merely report presence/absence. Future studies should gauge more reliable indicators of vulnerability, such as population densities, genetic diversity, physiological condition etc.

Meanwhile, several observations warrant some disquietude. First, the rapid disappearance of *P. melisellensis* from Pod Mrčaru following introduction of *P. sicula* demonstrates how fast and drastically invasive species may affect indigenous populations. The Italian wall lizard is renowned in this respect; it has displaced several other lacertid species on islands and other habitats throughout the Mediterranean (CAPULA, 1993; ARNOLD, 1997; CAPULA *et al.*, 2002). It seems not unlikely that the current populations of the species on Sušac, Kopište and Pod Kopište have also replaced native *P. melisellensis* populations in historical times. Adding to its threat as an invasive species is the fact that perhaps more than any other lacertid, *P. sicula* feels at home in anthropogenic habitats. This probably aids its accidental dispersal to islands aboard vessels (PODNAR *et al.*, 2004). If it is a goal to protect the native populations of *P. melisellensis* in the Lastovo Archipelago, measures should be taken to prevent *P. sicula* from expanding its distribution eastwards Pod Mrčaru.

Second, preliminary observations on several islands suggest that lizards may suffer from the introduction of mammals, whether intended (e.g. sheep, goats) or

accidental (e.g. rats, cats). Grazing by sheep or goats may considerably alter an island's physical habitat structure, often leading to a decrease in the availability of vegetative protection against aerial predators (VERVUST *et al*., 2007). This may lead to increased predation pressure and, unless the lizards can adapt to this new circumstances (VERVUST *et al*., 2007), may result in reduced viability of the population. In addition, we noted that lizards on islands with sheep tend to have higher ectoparasite (tick) loads. Although we have no direct evidence for any effects on the condition of the lizards, this may constitute an additional burden. Rats and cats can predate lizards (KAMMERER, 1926). A few islands in the archipelago that are frequently visited (e.g. Saplun, Mrcara) by locals and tourists for recreational purposes carry considerable amounts of trash and may therefore house threatening populations of rats. Littering should be prevented as much as possible. Cats presumably present a hazard in populated areas of Lastovo only. Preliminary observations showed a much higher incidence of tail breaks in *P. melisellensis* from the town of Pasadur compared to a rural site in the centre of the island (Huyghe, personal communication).

Third, many islands of the archipelago are breeding places for gulls, mainly yellow legged gulls (*Larus michahellis*). Despite the generalist feeding habits of this species, pellets often contain remnants of lizards (Vervust, unpubl.). However, lizards on islands with high densities of breeding gulls are not less shy compared to populations on islands with lower densities (e.g. VERVUST *et al*., 2007; unpubl.). The presence of gulls may even relax predation pressure on lizards because gulls tend to chase away other, perhaps more dangerous bird predators, and this benefit may outweigh the putative greater risk of predation by the gulls themselves (WHEELWRIGHT *et al*., 1997). Some authors (e.g. KAMMERER, 1926) has even suggested a mutualistic relationship between breeding seagulls and lacertid lizards, in which the gulls would refrain from attacking lizards near their nest because they would help reduce the chicks' ectoparasite load (GRUBER, 1986; SALVADOR, 1986). This is contradicted by the experimental study of CASTILLA & LABRA (1998), who showed that the predation intensity on *Podarcis atrata* increased near a gull colony. Overall, the importance of gulls as predators of lizards is debated (e.g. MARTINEZ-RICA & CIRER, 1982; PÉREZ-MELLADO *et al*., 1997) and demands investigation.

One of the most intriguing aspects of the Archipelago's herpetofauna is the high degree of interpopulational differences in body size, shape, coloration, behaviour and density. Insular populations can diverge from their source on the mainland or nearby islands for a variety of reasons, genetic and plastic, adaptive and non-adaptive, but the exact pressures and mechanisms involved are rarely known (for a recent review, see WHITTAKER & FERNÁNDOZ-PALACIOS, 2007). The Lastovo Archipelago may constitute an excellent natural laboratory (sensu WHITTAKER, 2003) in which to study these matters. Earlier herpetologists (references above) have used the differences in size, scalation and colour to delineate subspecies of *P. melisellensis* and *P. sicula*. However, their intraspecific classification is not well supported by recent studies using mitochondrial DNA (PODNAR *et al*., 2004; 2005). Further genetic analyses using different regions of the genome will be necessary to learn the exact relationships among the different island populations. Such information will be most valuable in analyses of evolutionary patterns, as well as for conservational decisions.

The disparate distribution of smaller lizards over the whole of the Archipelago is fascinating, but the main island of Lastovo also holds a number of interesting herps. *Pseudopus apodus* was seen on Lastovo Island only. Also elsewhere in the Adriatic, this species seem restricted to larger bodies of land (SČERBAK & BÖHME, 1993). The European glass lizard is extremely abundant, especially near human settlements. Lastovo seems an ideal study area to learn more of the biology of this elusive species. Locals are known to kill legless lizards. Here's an excellent opportunity for nature education; farmers should be explained that this species is harmless and valuable because it eats snails. The status of *D. caspius* is difficult to assess because of its secretive habits. It does not seem to suffer from deliberate persecution, as locals are aware that it is non-poisonous. The increased availability of asphalted roads may present a problem as the warmth of the road in the evening attracts snakes that consequently get run over by traffic.

We also encountered numerous individuals of *Bufo viridis* on Lastovo. This species is apparently thriving, but this situation may change rapidly through the loss of suitable habitat (especially breeding ponds and wetlands) due to drainage (COLLINS & STORFER, 2003). A number of relatively small measures (e.g. creation/maintenance of breeding pools) could easily help prevent such calamity.

In summary, the Lastovo Archipelago Nature Park is home to a most interesting collection of reptilian and amphibian populations. We hope that our observations will instigate further research into the system and may provide a basis for conservational plans and practices.

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