*Folia Zool.* – 56(3): 225–234 (2007)

# Biogeography of small terrestrial vertebrates on the Adriatic landbridge islands

Boris KRYŠTUFEK[1]* and Eduard KLETEČKI[2]

[1] *Science and Research Centre, University of Primorska, Garibaldijeva 1, SI-6000 Koper, Slovenia; e-mail: boris.krystufek@zrs.upr.si*

[2] *Croatian Natural History Museum, Demetrova 1, HR-1000 Zagreb, Croatia; e-mail: Eduard.Kletecki@hpm.hr*

Received 24 May 2007; Accepted 20 September 2007

Abstract. Species–area relationships and nestedness patterns were studied in three groups of small terrestrial vertebrates (mammals, reptiles, amphibians) on 14 landbridge islands of the eastern Adriatic. Islands ranged in surface area between 15 and 410 km$^2$ and contained from eight to 36 species from a total species pool of 48. Reptiles were the most species rich group ($S$ = 28), and had more species than mammals ($S$ = 13) and amphibians ($S$ = 7) combined. Island surface area predicted species richness best in reptiles ($r^2 = 0.79$) and most poorly in amphibians ($r^2 = 0.52$). Mammals showed a significantly lower slope of the species–area curve than amphibians and reptiles, and thus accumulated species counts with increase in area at the lowest rate. Nestedness patterns in all groups were significantly more organised than expected by chance. Amphibian nested structure points to extinction dominated and well insularised populations with no subsequent recolonisations. Frequent unexpected presences and absences in the nestedness patterns of mammals and reptiles suggest complex biogeographic histories for these two groups, with several factors putatively in operation: heterogeneity in habitats and the original source fauna, post-isolation immigrations and differential extinction rate due to human-caused habitat degradation.

**Key words**: Amphibia, Reptilia, Mammalia, species–area relationship, nestedness pattern, island biogeography

## Introduction

During the last glacial cycle a sufficient volume of water had been removed from the ocean basins and stored in the continental ice sheets to reduce global sea level by around 135 m (Bell & Walker 2005). Such a transgression exposed the entire bottom of the northern Adriatic Sea and the present day islands were part of the mainland throughout the Würm glacial cycle (Rodić 1970). Following climatic amelioration, global ice volumes reduced by more than 50 per cent at approximately 11,500 years BP when the seashore was still 60 m lower than the current one (Bell & Walker 2005). Adriatic islands, as we know them today, have thus been isolated from the mainland for approximately 10,000 years. It is safe to assume that the islands of the Adriatic archipelago first supported unbalanced faunas, which subsequently relaxed to equilibrium in accordance with the model of insular biogeography (MacArthur & Wilson 1967). Contrary to an earlier expectation of extinction as a random process, the order of species extinction is highly determined, and small islands lose more species than larger ones (Brown 1986). As a consequence, island faunas, produced by fragmentation of a formerly continuous habitat that supported common species pools prior to inundation by glacial meltwater, are commonly made up of non-random subsets of the total available species pool (Cutler 1991).

Insular faunas of the landlocked Mediterranean Sea have already attracted considerable attention. Oceanic-like Mediterranean islands, effectively isolated since the Messinian

---

*Corresponding author

Salinity Crisis (McKenzie 1999), were of particular interest to students because of their high endemism on the one hand and a chain of human-caused extinctions since the early Holocene on the other (Alcover et al. 1999). The focus of this paper is pattern of small terrestrial vertebrates (mammals, reptiles and amphibians) on landbridge islands off the eastern Adriatic coast. All these taxonomic groups are poor colonisers across sea barriers and their passive transportation to an island, other than by humans, was probably an exceptional and stochastic event once the island faunas relaxed to equilibrium. Because vertebrate groups differ in energy demands and in life cycle (Eisenberg & Harris 1989) they have different resilience to extinction in fragments. It is thus a plausible assumption that patterns of island biogeography also differ among the three groups. Differences between groups were assessed by applying two metrics: species–area relationship and nestedness.

The species–area relationship is based on the tendency of larger areas to support more species. When both variables are transformed to logarithms, a bi-variate plot aligns the data along a straight line, thus allowing the application of simple statistical tests for comparisons (Rosenzweig 1996). Because the islands of the Adriatic archipelago differ substantially in their size, we tested the power of the island's surface area to predict species richness in different vertebrate groups.

Species distribution patterns within naturally fragmented habitats often exhibit patterns of pronounced nestedness (Patterson & Atmar 1986). Given a set of replicate habitats with faunas varying in species richness, less species-rich faunas tend to be subsets of more species-rich faunas. In the case of perfectly nested subsets, a species present in a given fauna is also present in all more species-rich faunas. If a species is absent from a fauna, it is also missing from all less species-rich faunas. Extinction is believed to play a major role in producing the observed nested substructure (Wright et al. 1998), consequently insight into the nestedness pattern within an archipelago has the potential to reconstruct the faunal extinction sequence and to predict vulnerability of species to forthcoming extinctions (Cutler 1991).

## Material and Methods

The eastern Adriatic Sea abounds with islands that run parallel to the coast and are actually ridges of submerged Dinaric Mountains. The great majority of islands are very small and only 67 of them are ≥ 1 km$^2$ in surface area; the area of 29 islands exceeds 10 km$^2$, while only eight islands are larger than 100 km$^2$ (Rodić 1970). Fourteen islands were selected (Fig. 1) that provided data for small terrestrial vertebrates: amphibians (Anura and Caudata), reptiles (Testudines, Amphisbenia, Lacertilia, and Serpentes), and small terrestrial mammals (Erinaceomorpha, Soricomorpha, Rodentia). Information was gathered from published sources (Tvrtković et al. 1985, Petrov 1992, Tvrtković 1993, Lončar 2005), collections of the Slovenian Museum of Natural History (Ljubljana) and the Croatian Museum of Natural History (Zagreb), and unpublished field records by the authors. Taxonomy and nomenclature follow Wilson & Reeder (2005) for mammals and Janev Hutinec et al. (2006) for amphibians and reptiles. Published information was carefully checked and dubious records were rejected. Taxonomic issues for green lizards are not settled yet in the study area. The traditional division into *Lacerta viridis* and *L. trilineata* was followed, thus ignoring the recently recognised *L. bilineata* whose range is still poorly understood (Tvrtković et al. 1998). The end product of these efforts was a presence–absence matrix of 14 islands × 48 species.

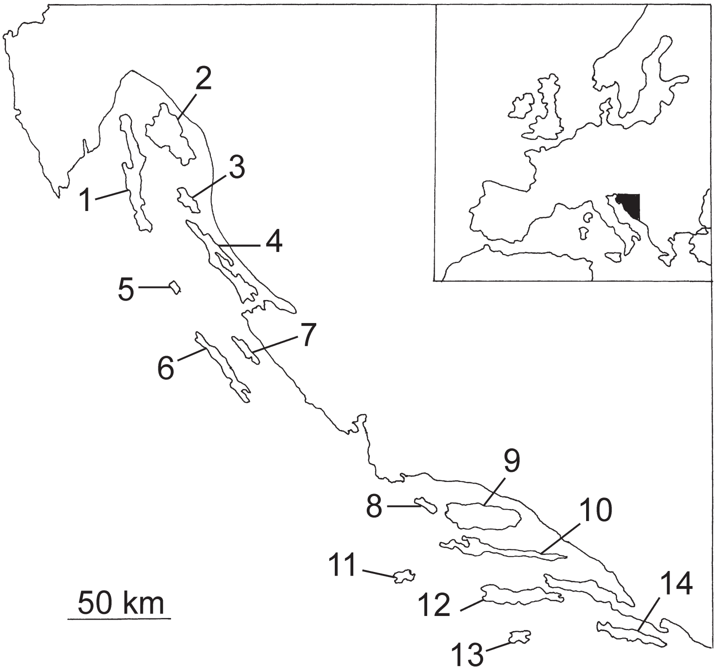

**Fig. 1.** Map of the north-eastern Adriatic coast with islands considered in this study. Right upper insert indicates position of study area in Europe. Islands (surface area in parentheses; in km$^2$): 1 – Cres (404), 2 – Krk (410), 3 – Rab (91), 4 – Pag (285), 5 – Silba (15), 6 – Dugi (114), 7 – Ugljan (52), 8 – Šolta (59), 9 – Brač (395), 10 – Hvar (300), 11 – Lastovo (47), 12 – Korčula (276), 13 – Vis (90), 14 – Mljet (100).

Species–area relationship was assessed by the Arrhenius equation (Rosenzweig 1996): $\log S = c + z \log A$, where $S$ is species richness, $A$ is surface area, $c$ is the intercept and $z$ is the slope of the curve. Original variables were transformed into base 10 logarithms and tests were performed using STATISTICA 5.5 (Statsoft Inc. 1999).

Perfectly nested patterns are unusual, and several metrics have been devised to measure the fit of a given presence–absence matrix to the nested subset model. Each of these metrics has merits, and the results are highly correlated (Cutler 1998, Wright et al. 1998). We assessed nestedness by $T$ metrics (Atmar & Patterson 1993); this method is based on counting holes and outliers (unexpected absences and presences, respectively) and by weighting them by the size of the faunas and the incidences of the species involved (Cutler 1998). A matrix of perfect order assumes a system temperature of 0°C, and no discernible occurrence order remains at 100°C. Thus, the warmer the island, the more it deviates from perfect nestedness. The statistical significance of the nestedness pattern was determined by comparing the $T$ index of the island pattern with random matrices generated through Monte Carlo simulation (2000 runs). Calculations were performed using the “Nestedness Temperature Calculator” program (Atmar & Patterson 1995). The nestedness calculator package performs poorly when the input matrix has checkerboard patterns; it also assumes that each species has an equal chance of occurring in a habitat patch and thus ignores possible artefacts of passive sampling. As such, it is sensitive to Type I errors, i.e. it detects significant results in random datasets (Fischer & Lindenmayer 2002). Probabilities of finding random matrices with the same or lower temperature were thus tested also with the BINMATEST algorithm, which is based on more conservative null models. BINMATNEST reorders the input matrix in such a way that, if fragment size/isolation plays a role in determining community structure, there will be a significant rank correlation between the size/isolation of the fragments and the way that they are ordered in the packed matrix (Rodríguez-Gironés & Santamaría 2006).

## Results

### Species richness

Islands ranged in surface area between 15 and 410 km$^2$ (Fig. 1) and contained from 10 to 39 species from a total species pool of 48 (Appendix). Reptiles were the most species-rich group ($S$ = 28), and had more island species than mammals ($S$ = 13) and amphibians ($S$ = 7) combined. Thus on all islands at least half of the small terrestrial vertebrate species were reptiles. No amphibians were recorded on the island of Ugljan, while mammals and reptiles had representatives on each island studied. Five species (*Podarcis melisellensis, Telescopus falax, Hierophis gemonensis, Mus musculus, Rattus rattus*) were widespread across the archipelago, while six reptiles (*Podarcis muralis, Typhlops vermicularis, Blanus strauchi, Dolichophis caspius, Platyceps najadum, Hierophis viridiflavus*) and two mammals (*Talpa europaea, Crocidura leucodon*) were restricted to a single island each.

### Species–area relationships

Island surface area predicted species richness in all three vertebrate groups but fit differed substantially among groups (Fig. 2). Area predicted 79% of the variance in reptilian species richness as opposed to 52% in amphibians; this proportion was intermediate in mammals (69%). Several islands had substantially higher or lower number of species than expected from their size, but there was little congruency among vertebrate groups. The number of amphibians and mammals on Rab was substantially higher than predicted by its area, while Vis had lower species richness than expected for its size in all three groups.

Species–area regression curves were of different intercept and different slope, depending on the group (Fig. 2). The slope differed significantly between groups (ANCOVA, F = 83.07, df = 2,37, $P \ll 0.0001$) and was the lowest in mammals. Not surprisingly, the intercept was the lowest in amphibians, a group with the smallest total species pool, and the highest in the most species rich, reptiles. Consequently, the total species pool was a predictor of species number on an island.

### Nestedness patterns

Nestedness patterns in all vertebrate groups were significantly cooler (i.e. more organised) than expected by chance, and both algorithms resulted in comparable temperatures (Table 1). It is thus safe to conclude that species composition on smaller islands is not random but structured, thus a result of predictable processes. System temperature was particularly low in amphibians (Table 1), while the nestedness patterns in reptiles and mammals revealed many unexpected presences and absences (Appendix). Note that unexpected presences and absences appear in pairs on the opposite sides of the occurrence boundary threshold and coalesce towards it as the matrix cools. Such a pattern is indicative of idiosyncratic

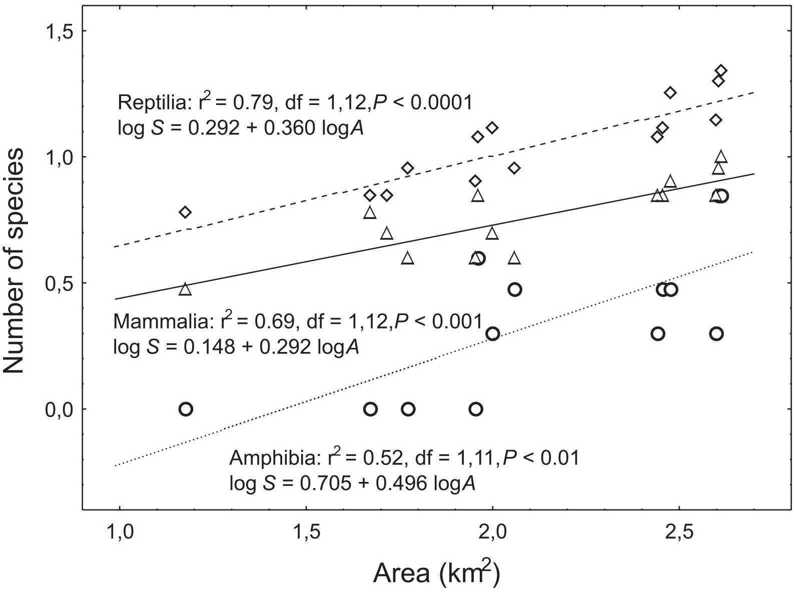

**Fig. 2.** Species–area curves for three vertebrate groups from the Adriatic islands. Circles – amphibians, diamonds – reptiles, triangles – mammals. The plot emphasises that the curves follow Arrhenius equations of the form $\log_{10} S = c + z \log_{10} A$. See text for further explanation.

distributions of species among the islands of the archipelago. Idiosyncratic species generate specifically higher temperatures than the matrix as whole due to their disconnection from the biogeographic events within the archipelago.

**Table 1.** Summary of nestedness analysis of Adriatic island vertebrate matrices. Parameters were estimated using the “Nestedness Temperature Calculator” program and the BINMATEST algorithm. *T* – system temperature; *P* – probability that Monte Carlo-derived simulations would generate a matrix of equal or lower temperature than that observed in a system.

| | Temp. Calculator | | BINMATEST | |
|---|---|---|---|---|
| | *T* | *P* < | *T* | *P* < |
| Amphibia | 0.80° | $10^{-2}$ | 0.74° | $10^{-5}$ |
| Reptilia | 18.39° | $10^{-10}$ | 15.94° | $10^{-5}$ |
| Mammalia | 15.46° | $10^{-5}$ | 13.21° | $10^{-5}$ |

## Discussion

Our results show that small vertebrate assemblages on the Adriatic islands are structured and thus non-random. Area alone predicted the number of species on an island fairly accurately but the coefficient of determination differed among groups. Goodness-of-fit was modest in amphibians ($r^2 = 0.52$) but good in reptiles ($r^2 = 0.79$). This probably reflects fundamental differences in habitat requirements between the two groups, which prefer habitats on the opposite extremes of the mesic–xeric gradient. Amphibians are limited to moist areas and require freshwater for spawning (Eisenberg & Harris 1989). Such habitats are scarce in the karstified limestone bedrock with a predominantly underground water outlet

(Gams 1974). Species depending on patchy resources are often vulnerable to extinction, especially when those resources are unpredictable in time or space (Meffe & Carroll 1997). Drought years, for instance, can cause crash of amphibian populations dependent on ephemeral wetlands, and the effects of such extremes are probably more detrimental on small islands with restricted habitat patchiness. We thus suggest for amphibians that the island surface area is largely a surrogate for habitat diversity and consequently for the availability of critical resources. Steep slope of the species–area regression curve in amphibians is possibly indicative of a rapid decline in habitat diversity with decrease in island surface area.

Contrary to amphibians, island area was a much better predictor of reptilian species richness. Reptilian diversity peaks sharply in the European Mediterranean, while amphibians attain highest species densities further north (Meliadou & Troumbis 1997). Differences in latitudinal species richness between the two groups point to their habitat preferences. A warm climate with high annual variation of precipitation, which is typical of the European Mediterranean, suits reptiles (Meliadou & Troumbis 1997). As a consequence, reptilian assemblages are probably governed by island surface area to a much larger degree than by other environmental factors.

The most obvious difference between endothermic mammals and ectothermic amphibians and reptiles was in the lower slope of the species–area curve in the former. Mammals thus accumulated species counts at substantially slower rates with the increase in the island surface area. Because of their low basal metabolic rate amphibians and reptiles do not require the same energy from the environment per unit body mass as do endothermic vertebrates, consequently they can exist at substantially higher biomass densities. Lower densities of mammals predispose them to more frequent local extinction events (Eisenberg & Harris 1989), which is most evident on islands (Case & Cody 1983). It is also noteworthy that, under the Mediterranean climate, the mammal assemblages show poor resilience to increased aridity and habitat degradation. Voles (Arvicolinae), the group that is effectively filtered along the mesic–xeric gradient on the coastal slopes of the Adriatic (Dinaric) mountains (Kryštufek & Griffiths 1999), are entirely absent from the islands. When compared with coastal assemblages, the mammalian species pool of the archipelago is much more impoverished (13 island species v. 27 coastal species; cf. Petrov 1992) than is the case in reptiles (28 v. c. 30; Džukić & Kalezić 2004, Lončar 2005). Amphibians were intermediate in this respect (7 v. c. 10; Tvrtković & Kletečki 1993, Džukić & Kalezić 2004).

Nestedness patterns in all vertebrate groups were significantly more organised than expected by chance. Species composition on smaller islands is thus not random but rather results from a predictable process. A perfectly nested matrix of the fauna of an archipelago points to extinction dominated island faunas with no subsequent recolonisations (Atmar & Patterson 1993). The amphibian nestedness structure thus suggests a highly ordered and perfectly replicable extinction sequence. Such predictability allows a tentative ranking of species according to their resilience to population fragmentation in karstic habitats. *Bufo viridis* seems to be the most resilient, while *Triturus vulgaris, Bombina variegata* and *Rana dalmatina* are likely to be most vulnerable in this respect. Under this presumption the above species should exercise different patterns of occupancy in karstic habitats on the mainland as well. In fact, a faunal survey of Mt. Velebit (north-eastern Adriatic coast) showed *B. viridis* to be found in a much larger number of localities (15) than either *R. dalmatina* (six localities), *B. variegata* (four localities) or *T. vulgaris* (two localities; data from Tvrtković & Kletečki 1993).

The north-to-south distance across the archipelago is approximately 350 km. Our data set thus unavoidably violates some of the assumptions that govern the development of the metric of nestedness and its theory: uniformity in habitat heterogeneity, lack of significant clinal gradation, equal isolation for all species, and a uniform common source fauna (Cutler 1991, Atmar & Patterson 1993). Northern islands are in general colder and wetter (on Krk the mean annual temperature is 13.9°C and annual rainfall amounts to 1475 mm), while southern islands are warmer and drier (a temperature of 16.1°C and precipitation of 690 mm on Hvar; Rodić 1970). Unexpected absences and presences, however, were so widespread in mammals and reptiles that they cannot be ascribed merely to lack of environmental homogeneity across the archipelago. For example, the hedgehog (*Erinaceus roumanicus*), a habitat generalist (Petrov 1992) that inhabits the smallest island considered in this study (Silba), is absent from several larger islands, including Cres with relatively well preserved pristine habitats. The pattern seen in several species is particularly puzzling. *Apodemus epimelas*, for instance, was most probably part of the original source fauna for the entire region (Kowalski 2001); it prefers bare rocky habitats (Petrov 1992), which are widespread throughout the archipelago, is not much affected by the island surface area (cf. its presence on Šolta), and was unlikely to have been passively transported to islands by humans (cf. Storch 2004). Species that are so clearly idiosyncratic were most likely disconnected from the system-wide biogeography of the archipelago by various ecological mechanisms.

Idiosyncratic distributions are frequently generated by post-isolation immigration (Cutler 1991). Considering the long history of human presence in the Adriatic archipelago, unintentional transportation of animals among the islands and from the mainland to the archipelago is likely to have shifted species composition. Distances are short, both between the islands and to the mainland (Fig. 1). Human-aided post-isolation immigration is the most plausible explanation for the presence in the archipelago of two murids (*Mus musculus* and *Rattus rattus*). Fossil evidence does not suggest either of these rodents to be part of the original source fauna (Kowalski 2001), however they are now more widespread than any other mammal species. Passive transportation is a more parsimonious explanation than an isolated relict occurrence in several other species as well, for instance the unexpected presence of *Tarentola mauritanica* on Ugljan. This mechanism might be also in operation in three idiosyncratic reptiles (*Dolichophis caspius*, *Typhlops vermicularis* and *Blanus strauchi*), which are absent from the eastern Adriatic coast; consequently their presence in the archipelago is the subject of various speculative explanations (Janev Hutinec et al. 2006).

Species leakage between islands, however, cannot be a universal explanation for all the idiosyncrasies in the archipelago. It is probable that not all species were initially dispersed throughout the region; consequently not all fragments began with precisely the same complement of species. *Lacerta oxycephala*, for instance, is restricted to the southern part of the study area, both on the mainland and on the islands (Džukić & Kalezić 2004). Consequently its absence from the northern part of the archipelago is more likely to reflect heterogeneity of the original source fauna than regional post-isolation extinctions. In addition insular ecosystems have been profoundly transformed following initial colonisation of the islands by humans (Grove & Rackham 2001). Modern humans appeared in the Mediterranean islands less than 8000 years BP (Alcover et al. 1999); consequently it is a plausible assumption that insularised vertebrate faunas faced habitat degradation relatively shortly after they relaxed to equilibrium. Some of the gaps in nestedness patterns thus probably reflect post-isolation local extinctions due to subsequent destruction of habitats.

Clearly, various factors were responsible for the current patterns of small terrestrial vertebrates in the Adriatic islands: heterogeneity in habitats and the original source fauna, inconsistent extinction sequences on all fragments, post-isolation immigrations and differential extinction rates due to human-caused habitat degradation. These factors filtered species according to their resilience to surface area, aridity and habitat degradation. With the lack of supplementary information, it is hard to judge exactly which of these mechanisms was responsible for the observed species composition on individual islands. Regardless of this, different groups show unique patterns, which reflect their life-history strategies.

Acknowledgements

We thank Jan Zima for constructive criticism on an earlier draft.

## LITERATURE

Alcover J.A., Seguí B. & Bover P. 1999: Extinctions and local disappearances of vertebrates in the West Mediterranean islands. In: MacPhee R.D.S. (ed.), Extinctions in near time: causes, contexts, and consequences. *Kluwer Academic Publ., New York: 165–188.*

Atmar W. & Patterson B.D. 1993: The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia 96: 373–382.*

Atmar W. & Patterson B.D. 1995: The Nestedness Temperature Calculator: a visual basic program, including 294 presence-absence matrices. Version: March, 2004. *AICS Research, Inc., University Park, NM and The Field Museum, Chicago, IL.*

Bell M. & Walker M.J.C. 2005: Late Quaternary environmental change. Physical and human perspective. 2nd ed. *Pearson Prentice Hall, London.*

Brown J.H. 1986: Two decades of interaction between the MacArthur-Wilson model and complexities of mammalian distributions. *Biol. J. Linn. Soc. 28: 231–251.*

Case T.J. & Cody M.L. 1983: Island biogeography in the Sea of Cortes. *University of California Press, Berkeley.*

Cutler A. 1991: Nested faunas and extinction in fragmented habitats. *Cons. Biol. 5: 496–505.*

Cutler A. 1998: Nested patterns of species distribution: process and implications. In: McKinney M.L. & Drake J.A. (eds), Biodiversity dynamics: turnover of populations, taxa, and communities. *Columbia University Press, New York: 212–231.*

Džukić G. & Kalezić M. 2004: The biodiversity of amphibians and reptiles in the Balkan peninsula. In: Griffiths H.I., Kryštufek B. & Reed J.M. (eds), Balkan Biodiversity: Pattern and Process in the European Hotspot. *Kluwer Academic Press, Dordrecht: 167–192.*

Eisenberg J.F. & Harris L.D. 1989: Conservation: a consideration of evolution, population, and life history. In: Western D. & Pearl M. (eds), Conservation for the twenty-first century. *Oxford University Press, NewYork: 99–108.*

Fischer J. & Lindenmeyer D.B. 2002: Treating the nestedness temperature calculator as a “black box” can lead to false conclusions. *Oikos 99: 193–199.*

Gams I. 1974: [Karst]. *Slovenska matica, Ljubljana (in Slovene).*

Grove A.T. & Rackham O. 2001: The nature of Mediterranean Europe: An ecological history. *Yale University Press, New Haven.*

Janev Hutinec B., Kletečki E., Lazar B., Podnar Lešić M., Skejić J., Tadić Z. & Tvrtković N. 2006: Red book of amphibians and reptiles of Croatia. *Ministry of Culture, Zagreb.*

Kowalski K. 2001: Pleistocene rodents of Europe. *Folia Quat. 72: 3–389.*

Kryštufek B. & Griffiths H.I. 1999: Mediterranean v. continental small mammal communities and the environmental degradation of the Dinaric Alps. *J. Biogeogr. 26: 167–177.*

Lončar M. 2005: [Distribution of reptiles in Croatia; collection of Croatian Natural History Museum]. *University in Zagreb, Zagreb. Unpublished BSc Thesis (in Croatian).*

MacArthur R.H. & Wilson E.O. 1967: The theory of island biogeography. Monographs in Population Biology 1. *Princeton University Press, Princeton.*

McKenzie J.A. 1999: From desert to deluge in the Mediterranean. *Nature 400: 613–614.*

Meffe G.K. & Carroll C.R. 1997: Principles of conservation biology. 2nd ed. *Sinauer Associates, Sunderland.*

Meliadou A. & Troumbis A.Y. 1997: Aspects of heterogeneity in the distribution of diversity of the European herpetofauna. *Acta Oecol. 18: 393–412.*

Patterson B.D. & Atmar W. 1986: Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc. 28: 65–82.*

Petrov B.M. 1992: Mammals of Yugoslavia: Insectivores and rodents. *Natural History Museum in Belgrade, Special Issue 13: 1–186.*

Rodić D.P. 1970: [Geography of Yugoslavia I]. *Naučna knjiga, Beograd (in Serbian).*

Rodríguez-Gironés M. & Santamaría L. 2006: A new algorithm to calculate the nestedness temperature of presence-absence matrix. *J. Biogeogr. 33: 924–935.*

Rosenzweig M.L. 1996: Species diversity in space and time. *Cambridge University Press, Cambridge.*

Storch G. 2004: Late Pleistocene rodent dispersal in the Balkans. In: Griffiths H.I., Kryštufek B. & Reed J.M. (eds), Balkan Biodiversity: Pattern and Process in the European Hotspot. *Kluwer Academic Press, Dordrecht: 135–145.*

Tvrtković N. 1993: [Zoogeographic and synecological relations of selected reptiles, amphibians and mammals in terrestrial ecosystems of northeastern Adriatic coast and its hinterland]. *University in Zagreb, Zagreb. Unpublished PhD Thesis (in Croatian).*

Tvrtković N. & Kletečki E. 1993: Vertebrates of the Velebit Mountain (Croatia). Part I: Amphibians. *Nat. Croat. 2: 27–46.*

Tvrtković N., Dulić B. & Mrakovčić M. 1985: Distribution of Insectivora and Rodentia on the north-east Adriatic coast (Yugoslavia). *Acta Zool. Fennica 170: 201–203.*

Tvrtković N., Lazar B., Tome S. & Grbac I. 1998: The western green lizard *Lacerta (viridis) bilineata* Daudin, 1804 (Sauria: Lacertidae) in Slovenia and Croatia. *Nat. Croat. 7: 363–369.*

Wilson D.E. & Reeder D.M. 2005: Mammal species of the World: A taxonomic and geographic reference. 3rd ed. *John Hopkins University Press, Baltimore.*

Wright D.H., Patterson B.D., Mikkelson G.M., Cutler A. & Atmar W. 1998: A comparative analysis of nested subset patterns of species composition. *Oecologia 113: 1–20.*

**Appendix.** Presence–absence matrices of species richness (rows) according to island (columns) in three vertebrate groups. Matrices have been packed into a state of maximum nestedness. The hospitability of islands is ordered starting from the left (most hospitable), and species' niches are ordered from the top (the widest niche). The leftmost island is judged to be the most hospitable one, and the topmost species are the ones whose niche requirements are the most common and prevalent. Framed cells are on the occurrence boundary threshold. Note that species on the boundary threshold are near their absolute minimum sustainable population sizes and are at great risk of extinction. *S* – number of species on the island. For island identities see Fig. 1.

| **Amphibia** | 1 | 2 | 3 | 6 | 4 | 10 | 9 | 14 | 12 | 11 | 13 | 5 | 8 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bufo viridis* | × | × | × | × | × | × | × | × | × | × | × | × | × |
| *Hyla arborea* | × | × | × | × | × | × | × |  | × |  |  |  |  |
| *Rana ridibunda* | × | × | × |  | × |  |  | × |  |  |  |  |  |
| *Bufo bufo* | × | × | × | × |  | × |  |  |  |  |  |  |  |
| *Triturus vulgaris* | × | × |  |  |  |  |  |  |  |  |  |  |  |
| *Bombina variegata* | × | × |  |  |  |  |  |  |  |  |  |  |  |
| *Rana dalmatina* | × | × |  |  |  |  |  |  |  |  |  |  |  |
| *S* | 7 | 7 | 4 | 3 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 1 |

**Appendix.** Continued.

| **Reptilia** | 2 | 1 | 10 | 9 | 14 | 4 | 3 | 12 | 6 | 8 | 13 | 11 | 7 | 5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Podarcis melisellensis* | × | × | × | × | × | × | × | × | × | × | × | × | × | × |
| *Telescopus fallax* | × | × | × | × | × | × | × | × | × | × | × | × | × | × |
| *Hierophis gemonensis* | × | × | × | × | × | × | × | × | × | × | × | × | × | × |
| *Hemidactylus turcicus* | × | × | × | × | × | × | × | × | × | × | × | × |  |  |
| *Pseudopus apodus* | × | × | × | × | × | × | × |  | × | × | × | × |  | × |
| *Malpolon monspessulanum* | × | × | × | × | × | × |  | × | × | × |  |  | × |  |
| *Natrix natrix* | × | × | × | × |  | × | × | × | × | × |  |  |  |  |
| *Elaphe quatuorlineata* | × | × | × |  | × |  | × | × |  |  | × |  |  | × |
| *Zamenis longissimus* | × | × | × | × | × |  | × |  |  | × |  |  | × |  |
| *Podarcis sicula* | × | × | × |  |  | × | × |  |  |  |  |  | × | × |
| *Lacerta trilineata* | × | × | × | × |  | × | × | × |  |  |  |  |  |  |
| *Testudo hermanni* | × | × | × | × | × | × |  | × |  |  |  |  |  |  |
| *Zamenis situla* | × | × | × |  |  | × |  | × | × |  | × |  |  |  |
| *Vipera ammodytes* | × |  | × | × | × | × |  | × |  | × |  |  |  |  |
| *Lacerta oxycephala* |  |  | × | × | × |  |  | × |  |  | × | × |  |  |
| *Tarentola mauritanica* | × | × | × | × |  |  |  |  |  |  |  |  | × |  |
| *Emys orbicularis* | × | × |  |  | × | × | × |  |  |  |  |  |  |  |
| *Algyroides nigropunctatus* | × | × |  |  |  |  | × |  |  |  |  |  |  |  |
| *Coronella austriaca* | × |  |  | × | × |  |  |  |  |  |  |  |  |  |
| *Natrix tessellata* | × | × |  |  |  |  |  |  |  |  |  |  |  |  |
| *Lacerta viridis* |  | × | × |  |  |  |  |  |  |  |  |  |  |  |
| *Dolichophis caspius* |  |  |  |  |  |  |  |  |  |  |  | × |  |  |
| *Anguis fragilis* | × | × |  |  |  |  |  |  |  |  |  |  |  |  |
| *Typhlops vermicularis* |  |  |  |  |  |  |  |  | × |  |  |  |  |  |
| *Blanus strauchi* |  |  | × |  |  |  |  |  |  |  |  |  |  |  |
| *Hierophis viridiflavus* | × |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Podarcis muralis* |  | × |  |  |  |  |  |  |  |  |  |  |  |  |
| *Platyceps najadum* | × |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *S* | 22 | 20 | 18 | 14 | 13 | 13 | 12 | 12 | 9 | 9 | 8 | 7 | 7 | 6 |

| **Mammalia** | 2 | 1 | 10 | 3 | 9 | 4 | 12 | 11 | 7 | 14 | 13 | 6 | 8 | 5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Mus musculus* | × | × | × | × | × | × | × | × | × | × | × | × | × | × |
| *Rattus rattus* | × | × | × | × | × | × | × | × | × | × | × | × | × | × |
| *Apodemus sylvaticus* | × | × | × | × | × | × | × | × | × |  | × | × | × |  |
| *Crocidura suaveolens* | × | × | × | × | × | × | × | × | × |  |  | × |  |  |
| *Erinaceus roumanicus* | × |  | × | × | × | × |  | × | × | × | × |  |  | × |
| *Glis glis* | × | × | × |  | × |  | × |  |  | × |  |  |  |  |
| *Suncus etruscus* | × | × | × | × |  | × |  |  |  |  |  |  |  |  |
| *Eliomys quercinus* | × |  | × |  | × | × | × | × |  |  |  |  |  |  |
| *Apodemus epimelas* |  |  |  |  |  |  | × |  |  | × |  |  | × |  |
| *Apodemus flavicollis* |  | × |  | × |  |  |  |  |  |  |  |  |  |  |
| *Sciurus vulgaris* | × | × |  |  |  |  |  |  |  |  |  |  |  |  |
| *Crocidura leucodon* | × |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Talpa europaea* |  | × |  |  |  |  |  |  |  |  |  |  |  |  |
| *S* | 10 | 9 | 8 | 7 | 7 | 7 | 7 | 6 | 5 | 5 | 4 | 4 | 4 | 3 |