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Competitive Exclusion between Insular *Lacerta* Species (Sauria, Lacertidae)

Notes on Experimental Introductions

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Summary. Competetive exclusion between *Lacerta sicula* and *L. melisellensis* characterizes the small islands of the Adriatic Sea.

In 1958 and 1959 M. Radovanović introduced *Lacerta sicula* or *Lacerta melisellensis* onto islands exclusively occupied by the other species. During the summer of 1971 follow-up observations were made on three of these islands, two of which completely lacked representatives of the introduced species. On the third island, the introduced species appears to be replacing the native form. Minor habitat differences permit coexistence, however the situation is dynamic and probably not at equilibrium. A reciprocal introduction involving the two species on the islands of Pod Kopište and Pod Mrčaru is announced.

The theory of island biogeography (MacArthur and Wilson, 1967) is based heavily on data from bird distributions. The theory is highly successful in predicting bird species diversity as a function of land area and distance from the source of propagules. Anomalies exist, however, when the theory is applied to island lizards. Williams (1969) and others have pointed out that some islands occupied by species of *Anolis* have many fewer species than expected, and Soulé (1966) remarked that *Sator* seems to exclude most species in closely related genera. Thus, it appears that competitive exclusion may be more important in determining community structure in lizards than birds.

Observational data alone will not suffice to illuminate the mechanisms of competitive exclusion in vertebrates. One experimental approach is the introduction of a species on an island already occupied by another.

We describe some follow-up observations of such experiments involving lizards of the genus *Lacerta* that began in 1958—59 (Radovanović, 1965). We record a similar experiment begun by us in 1971.

Lacerta melisellensis and *L. sicula* are broadly distributed along the Adriatic coast of Yugoslavia, and on its numerous islands. Although both species are reported from some of the largest islands, e.g. Čiovo, Krk, Pag, Pašman, and Ugljan (measuring tens to hundreds of sq. km.), they were never sympatric on 46 smaller islands, 28 with *melisellensis* and 18 with *sicula* (Radovanović, 1959). The hypothesis of Radovanović (1956, 1959) was that the generally more robust *L. sicula* of Italian origin was invading the range of the Adriatic autochthon *L. melisellensis*, and that on small islands where *sicula* gained a foothold, *melisellensis* was being replaced through competitive exclusion. To test this hypothesis, he made four experimental introductions. In August, 1958, he introduced *L. melisellensis* onto a small island exclusively occupied by *L. sicula*. The following year he introduced *L. sicula* onto three islands exclusively occupied by *melisellensis*. Several years later he revisited these islands (Radovanović, 1965). During an extensive collecting trip to the Adriatic Islands in August, 1971, we revisited three of his experimental islands. Original data and our observations are summarized in Table 1.

Our observations extend those of Radovanović for site 1 (Mali Obrovanj), confirm his observations for site 4 (Koromašna), but negate his observations for site 3 (Krpeljina).

On Koromašna we found only *L. sicula*, the original inhibitant, indicating failure of the introduced *L. melisellensis*. A single specimen was collected with a salmon colored belly, a character widespread in *melisellensis* but not observed by us in *sicula*. This might suggest hybridization but electrophoretic comparison of proteins of this specimen shows it to have the *sicula* patterns for seven proteins that differ in the two species: aldolase, two esterases, supernatant glutamicoxaloacetic transaminase, general protein, supernatant isocitric dehydrogenase, and malic enzyme (see also Gorman, 1972).

On a thorough visit to Krpeljina we saw large numbers of *L. melisellensis* (20 specimens collected) and no *L. sicula* which indicated the failure of the *sicula* introduction. This observation is completely contrary to the trend observed by Radovanović (1965) who claimed that the native *L. melisellensis* had been almost entirely replaced in the five years that elapsed between introduction and observation[1].

1 Because there are hundreds of Adriatic Islands, and some duplication of names, one might argue that we or Radovanović did not find Krpeljina. This is improbable, for the island is clearly marked on nautical charts, lies due S. of Kornat, as Radovanović described, and is not close to other small islands.

Table 1. Summary of Radovanović's introductions and their follow-up

Site no.	Island	Size (approx. m)	Native species	Introduced species and its source	Date of introduction	Follow-up	
						Radavanović	Present study
1.	Mali Obrovanj	80 × 50	*L. melisellensis*	*L. sicula* from Pakoštane 3 males 4 females	5/28/1959	9/25/1964 Similar numbers of both species	8/24/1971 12 *L. melisellensis* 33 *L. sicula*
2.	Dajnice (S. of Žut)	100 × 50	*L. melisellensis*	*L. sicula* from Pakoštane 2 males 5 females	5/28/1959	7/17/1964 *L. melisellensis* is abundant; *L. sicula* is less so but numerous	Not visited
3.	Krpeljina (S. of Kornat)	200 × 50	*L. melisellensis*	*L. sicula* from Rakita near Vrgada 3 males 2 females 5 juveniles	5/30/1959	7/18/1964 *L. sicula* completely prevalent *L. melisellensis* almost entirely replaced	8/20/1971 20 *L. melisellensis* caught; no *sicula* seen
4.	Koromašna (E. of Zirje)	300 × 150	*L. sicula*	*L. melisellensis* from Mali Kamešnjak, S. Kakan 12, unspecified age and sex	8/21/1958	5/16/1965 *L. sicula* only; no *melisellensis*	8/24/1971 15 *L. sicula* no *melisellensis* seen One possible hybrid

The most interesting observation was on Mali Obrovanj. This was the smallest of the introduction islands, measuring approximately 80 m × 50 m. Five years after the introduction of seven *L. sicula*, Radovanović (1965) reported approximately equal numbers of the two species. We found that *sicula* was decidedly the more abundant, accounting for 33 of 45 lizards observed. Despite the small size of the island, the two species were found in different habitats. Most of the *L. sicula* were obseved in the relatively open periphery of the island. The periphery is sparsely covered by small bushes of *Crithmum maritimum* and *Salicornia* sp. The island's center is covered heavily by a thicket of low bushes and shrubs, including *Quercus ilex, Pistacia lentiscus, Pinus halepensis, Juniperus excelsa, Smilax excelsa* and grasses. Virtually all of the *L. melisellensis* were found in this central area. Thus, differences in habitat preference may delay complete exclusion, and the process of replacement is not so rapid as implied by Radovanović's 1965 study. That exclusion eventually will occur is our prediction based on the observed fact that there are no small islands naturally harboring both species.

The relatively large island of Čiovo (28.8 sq. km.) illustrates how the two species may co-exist with limited direct competition. Čiovo lies adjacent to the mainland city of Trogir, separated by only a narrow strait of water (and connected by a bridge). We found *L. melisellensis* in agricultural areas near Gornji Okrug away from heavy habitation. However, about 2 km away, in the town of Čiovo, we observed that *L. sicula* was well established. A similar observation was made by Radovanović (1960).

We add a further observational note. Since both *L. melisellensis* and *L. sicula* could be transported to new islands, naturally or by man, it is of interest to compare our observations with those of Radovanović, some of his dating back to 1936 (Radovanović, 1956, 1959). In all cases where we revisited an island that he had been to, we found only the species that he reported (except the introduction island of Krpeljina, see above). However, there were some islands where he failed to see any *Lacerta* (Radovanović, 1959) where we found *L. melisellensis* in low densities; two such islands were Kornat and Lavsa. We predict that careful collecting will show one or the other species on all the large islands.

An Experimental Reciprocal Introduction

L. melisellensis occupies the southern Adriatic Islands of Yugoslavia with *L. sicula* completely absent, except for several islands due west of Lastovo where the situation is reversed. Because *sicula* is common along the Italian mainland on the western side of the Adriatic, it appears that over-water colonization from the Italian mainland may account for

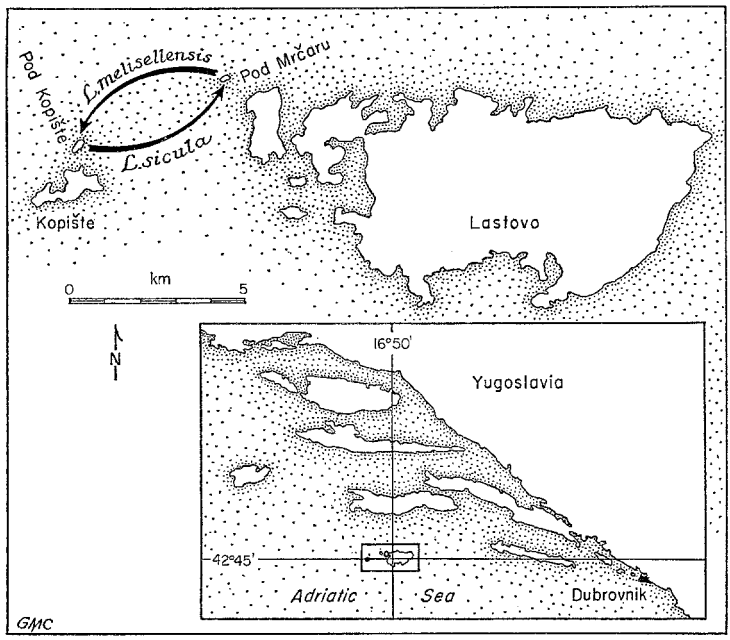

Fig. 1. Site of the experimental introductions

sicula on these southern islands. At the latitude of Lastovo there is a discrete border between the two species. *L. melisellensis* inhabits the Yugoslav mainland, Lastovo, and the small islands to the west, including Pod Mrčaru; there is then a water gap of approximately 4.5 km, followed by islands occupied by *L. sicula* which extends west to the Italian mainland (Fig. 1). The island of Pod Kopište is the *sicula* island closest to a *melisellensis* island. Pod Mrčaru and Pod Kopište are similar in size, habitats, and population densities (extremely high) of their native *Lacerta*. We felt that this was an ideal pair of islands for experimental introduction to study inter-specific competition. Furthermore, we wanted a better control over the introduced animals than was provided by Radovanović. Thus, we provide habitat descriptions, live weights, measurements, and short descriptions of the introduced animals, and similar data for population samples of the native lizards (Table 2).

Pod Mrčaru is a small island (about 0.03 sq. km)[2] rising to about 20 meters and comprised of organogenic limestone. Plant cover consists

2 Areas of Pod Mrčaru, Pod Kopište and Kopište are estimated from the hydrographic chart No. 212, "Lastovo", Hidrografski Institut Jugoslavenske ratne mornarice — Split, published 1 April, 1951, new edition, 1 June 1966. Altitudes were estimated by eye.

Table 2. Body size data for native and introduced specimens in the reciprocal introduction experiment

A. Native populations' samples

Island species	Sex	n	Weight (in g)		Snout to vent length (in mm)	
			$\bar{x}$	s.d.	$\bar{x}$	s.d.
Pod Mrčaru						
Lacerta melisellensis	♂	16	5.13	0.73	63.44	3.5
	♀	40	2.92	0.62	55.70	6.15
Pod Kopište						
Lacerta sicula	♂	31	5.47	0.66	62.58	2.06
	♀	42	3.47	0.71	56.02	4.22

B. Introduced specimens selected from population samples

Species	Sex	n	Weight		Length	
			$\bar{x}$	range	$\bar{x}$	range
L. melisellensis	♂	5	6.94	6.6–7.1	66.6	64–69
	♀	5	3.52	3.2–3.9	59.6	54–61
L. sicula	♂	5	6.04	5.0–6.8	65.4	61–68
	♀	5	3.92	3.6–4.5	58.0	56–61

mainly of annuals including *Silene inflata*, *Lotus* sp., *Portulaca oleracea*, *Chenopodium murale*, other Chenopodiaceae and *Cynodon dactlyon* in the center, and *Crithmum maritimum* in the periphery. Land snails abound. There are two species of *Lacerta* on the island. *L. melisellensis* is predominant in the center of the island in association with plant cover, and *L. oxycephala* on the periphery of the island primarily on rocky cliffs[3]. Males of this population of *melisellensis* all had bright orange bellies (the species is highly variable for color and pattern), females had white bellies. Their backs are patterned on a brown ground color.

3 *L. oxycephala* is so distinctive in its habitat preferences and general body shape that it rarely enters into discussions of competitive exclusion involving *L. sicula* and *L. melisellensis*. The situation is somewhat more interesting, because *oxycephala* and *melisellensis* are broadly sympatric even on tiny islands, whereas we failed to find *oxycephala* sympatric with *sicula* with but one exception, the island of Kopište (about 1 sq. km) where *sicula* was seen in great numbers (about 70 collected) and a single *oxycephala* was observed on cliffs at the edge of the shore. The possibility that *sicula* is excluding *oxycephala* bears investigation.

Pod Kopište is a somewhat larger "small" island (about 0.09 sq. km.) rising to about 30 meters consisting of dolomitic limestone. Low bushes of *Pistacia lentiscus* and *Juniperus excelsa*, and grass cover of *Cynodon dactlyon*, several Chenopodiaceae, and *Asparagus* sp. grow in the center of the island, and *Crithmum maritimum* in the periphery. Land snails of the same species as on Pod Mrčaru are also found. *Lacerta sicula* was the only lizard species found on the island. They appeared faster, more alert, and more aggressive (when captured) than the *L. melisellensis* on Pod Mrčaru. Of about 70 specimens collected, all were brown dorsally except two that were green. Ventral coloration of males and females is white.

On 14 August, 1971, five adult pairs of *L. sicula* from Pod Kopište were introduced onto the geographic center of Pod Mrčaru, and reciprocally, five adult pairs of *L. melisellensis* from Pod Mrčaru were introduced to the center of Pod Kopište. The introduced lizards of both species were approximately of equivalent size (Table 2). At the time of introduction the breeding season seemed to have terminated, and it will not be until the Spring of 1972 that the introduced lizards will be able to add to their numbers.

It is our hope that we or other biologists can follow the dynamics of these introductions over a period of years to gain further insight into the competitive dynamics between *L. melisellensis* and *L. sicula*.

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