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Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource

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Although rapid adaptive changes in morphology on ecological time scales are now well documented in natural populations, the effects of such changes on whole-organism performance capacity and the consequences on ecological dynamics at the population level are often unclear. Here we show how lizards have rapidly evolved differences in head morphology, bite strength, and digestive tract structure after experimental introduction into a novel environment. Despite the short time scale (≈36 years) since this introduction, these changes in morphology and performance parallel those typically documented among species and even families of lizards in both the type and extent of their specialization. Moreover, these changes have occurred side-by-side with dramatic changes in population density and social structure, providing a compelling example of how the invasion of a novel habitat can evolutionarily drive multiple aspects of the phenotype.

bite force | diet | evolution | gut structure

Recent reviews have illustrated how rapid adaptive evolution is common and may be considered the rule rather than the exception in some cases (1, 2). Experimental introductions of populations in novel environments have provided some of the strongest evidence for natural selection and adaptive divergence on ecological time scales (3–6). However, little is known about the degree to which the observed changes in morphology may affect the population structure and behavioral ecology of organisms through the mediating effects of whole-organism performance (7, 8). Consequently, our understanding of how rapid phenotypic changes affect ecological processes at the population level is limited (2, 9). Moreover, despite the fact that microevolutionary responses to environmental changes have been well documented, the unpredictability and reversibility of changes of morphological traits in fluctuating environments (10, 11) have raised questions regarding how these microscale changes can lead to the emergence of novel structures as seen on macroevolutionary scales (2).

Here we address these issues by examining the outcome of a remarkable 36-year experimental introduction with the lizard *Podarcis sicula*. In 1971 five adult pairs of this species were moved from the small islet of Pod Kopište (0.09 km^2) to the nearby Pod Mrčaru (0.03 km^2) by Nevo and coworkers (12). Both islets lie in the middle of the South Adriatic Sea near the larger island of Lastovo and belong to Croatia. Although the islet of Pod Mrčaru was originally inhabited by another lacertid lizard species (*Podarcis melisellensis*), repeated visits (twice yearly over the past three years, beginning in 2004) show that this species has become extinct on Pod Mrčaru. Genetic mitochondrial DNA analyses indicate that the lizards currently on Pod Mrčaru are indeed *P. sicula* and are genetically indistinguishable from lizards from the source population [supporting information (SI) Fig. 5].

Morphometric data describing head size and shape show that both males and females of the two populations differ significantly in head morphology [MANOVA; males: Wilks's $\lambda = 0.463$, $F_{9,115} = 14.81$, $P < 0.001$; females: Wilks's $\lambda = 0.425$, $F_{9,123} = 18.45$, $P < 0.001$ (Table 1 and Fig. 1)] with lizards on Pod Mrčaru having longer, wider, and taller heads than lizards on Pod Kopište (Table 1 and Fig. 1). Differences between populations are not merely the result of differences in overall size but represent distinct changes in head shape [MANCOVA with SVL as covariate; males: slopes, Wilks's $\lambda = 0.918$, $F_{6,131} = 1.96$, $P = 0.08$; intercepts, Wilks's $\lambda = 0.387$, $F_{6,132} = 34.88$, $P < 0.001$; females: slopes, Wilks's $\lambda = 0.983$, $F_{8,122} = 0.25$, $P = 0.98$; intercepts, Wilks's $\lambda = 0.754$, $F_{8,123} = 5.02$, $P < 0.001$; juveniles: slopes, Wilks's $\lambda = 0.969$, $F_{6,39} = 0.21$, $P = 0.97$; intercepts, Wilks's $\lambda = 0.498$, $F_{6,40} = 6.72$, $P < 0.001$ (Table 1 and Fig. 1)].

Differences in head size and shape also translate into significant differences in bite force between populations (males: $F_{1,44} = 4.93$, $P = 0.03$; females: $F_{1,38} = 16.94$, $P < 0.01$). Whereas the difference in bite force is the result of overall head size differences in females (ANCOVA; slopes, $F_{1,36} = 0.02$, $P = 0.91$; intercepts, $F_{1,37} = 1.55$, $P = 0.22$), in males size variation does not explain the difference in bite force (ANCOVA; slopes, $F_{1,42} = 0.25$, $P = 0.62$; intercepts, $F_{1,43} = 18.42$, $P < 0.01$).

Our data show that *P. sicula* lizards consume more plant material on Pod Mrčaru compared with the ancestral population on Pod Kopište. Analysis of stomach contents shows marked differences in diet between populations in both spring ($F_{1,204} = 22.9$, $P < 0.01$) and summer ($F_{1,74} = 103.13$, $P < 0.01$) but no differences in diet between sexes in either population ($F_{1,202} = 1.36$, $P = 0.24$). Seasonal differences in diet were significant in lizards from the introduced population (Pod Mrčaru, $F_{1,184} = 30.31$, $P < 0.01$) with plants composing between 34% (spring) and 61% (summer) of the total volume of the food eaten (Fig. 2). In contrast, plant consumption was low (7% to 4%) and did not differ seasonally for lizards from the source population (Pod Kopište, $F_{1,94} = 0.33$, $P = 0.57$). Moreover, ≈50% of the plant matter eaten year round by lizards from Pod Mrčaru consists of items with high cellulose content such as leaves and stems (Fig. 3).

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Data deposition: The sequences reported in this paper have been deposited in the GenBank database [accession nos. EU362067–EU362088 (the 16S rDNA fragment) and EU362089–EU362110 (the 12S rDNA fragment).

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Table 1. Phenotypic, performance, and ecological divergence for two populations of *P. sicula* 36 years after the introduction of 10 individuals in a new environment

			Pod Kopište		Pod Mrčaru	
	Haldanes, m/f	Darwins, m/f	Male	Female	Male	Female
SVL, mm	0.044/0.045	2,713/3,350	63.06 ± 4.68	56.80 ± 5.30	69.54 ± 2.86	64.08 ± 2.93
Mass, g	0.028/0.034	6,384/9,441	5.07 ± 1.37	3.36 ± 1.16	6.38 ± 1.42	4.72 ± 1.24
Head length, mm	0.045/0.049	2,978/3,209	14.67 ± 1.08	12.25 ± 0.84	16.33 ± 0.77	13.75 ± 0.64
Head width, mm	0.046/0.051	3,359/3,799	8.09 ± 0.67	6.55 ± 0.46	9.13 ± 0.42	7.51 ± 0.38
Head height, mm	0.048/0.048	4,326/4,228	6.29 ± 0.59	5.12 ± 0.46	7.35 ± 0.43	5.95 ± 0.38
Lower jaw length, mm	0.045/0.048	2,936/3,349	15.70 ± 1.23	12.80 ± 0.94	17.45 ± 0.72	14.44 ± 0.71
Jaw outlever, mm	0.045/0.049	2,972/3,463	14.17 ± 1.10	11.60 ± 0.87	15.77 ± 0.65	13.14 ± 0.62
Snout length, mm	0.045/0.049	2,841/3,339	10.40 ± 0.78	8.77 ± 0.64	11.52 ± 0.47	9.89 ± 0.45
Open inlever, mm	0.016/0.011	2,417/2,223	1.54 ± 0.31	1.20 ± 0.16	1.68 ± 0.28	1.30 ± 0.27
Close inlever, mm	0.039/0.039	3,403/3,844	3.76 ± 0.39	2.83 ± 0.29	4.25 ± 0.31	3.25 ± 0.30
Bite force, N	0.007/0.018	3,690/8,170	9.85 ± 2.29	4.99 ± 1.61	11.25 ± 2.42	6.70 ± 1.90
% of plants			9 ± 7	4 ± 5	60 ± 34	48 ± 23

Lizards were transplanted from Pod Kopište to Pod Mrčaru. Table entries are means ± standard deviations. Divergence rates are indicated for males (m) and females (f) separately. SVL, snout-vent length.

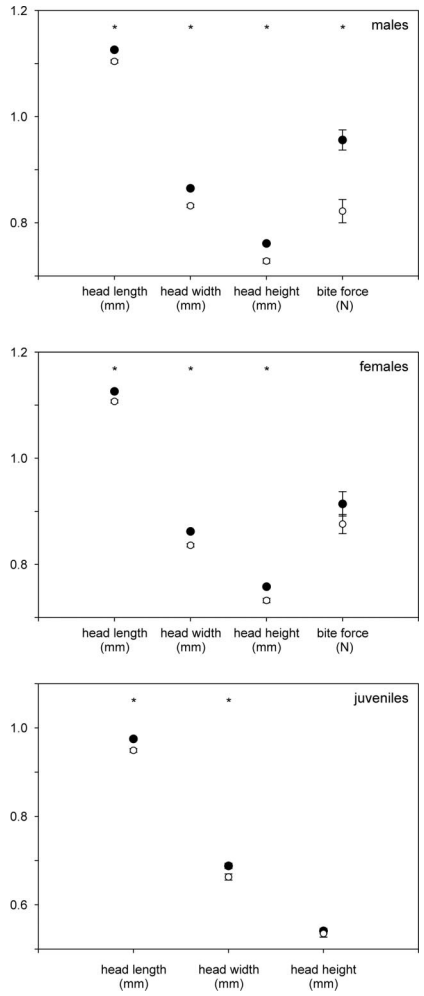

Fig. 1. Graphs illustrating differences in aspects of head morphology and bite force for male (*Top*), female (*Middle*), and juvenile (*Bottom*) lizards from two populations (filled symbols, Pod Mrčaru; open symbols, Pod Kopište) having diverged for 36 years. On the graphs, the size-adjusted means are represented, thus illustrating body-size-independent variation in morphology and bite force. Population differences are highly significant and show how lizards on Pod Mrčaru generally have bigger heads and greater bite forces. The *y* axis gives the $\log_{10}$-transformed size-adjusted head dimensions and bite force. Error bars depict 1 standard deviation. Asterisks depict significant differences between populations.

This shift to a predominantly plant-based diet has resulted in the dramatic evolution of intestinal morphology. Morphological analysis of preserved specimens shows the presence of cecal valves (Fig. 4) in all individuals, including a hatchling (26.4-mm snout-vent length, umbilical scar present) and a very young juvenile (33.11-mm snout-vent length) examined from Pod Mrčaru. These valves are similar in overall appearance and structure to those found in herbivorous lacertid, agamid, and iguanid lizards (13, 14) and are not found in other populations of *P. sicula* (13) or in *P. melisellensis*. Cecal valves slow down food passage and provide for fermenting chambers, allowing commensal microorganisms to convert cellulose to volatile fatty acids (15, 16). Indeed, in the lizards from Pod Mrčaru, nematodes were common in the hindgut but absent from individuals from Pod Kopište. The fact that <1% of all currently known species of squamates have cecal valves (13, 14) illustrates the unusual nature of these structures in this population. The evolution of these structures has likely gone hand in hand with a novel association between *P. sicula* on Pod Mrčaru and a set of microorganisms assuring the digestion of cellulose as is suggested by the presence of nematodes in the hindgut of individuals from Pod Mrčaru.

Our data show that in only 36 years (≈30 generations) the experimental introduction of a small propagule of lizards (five males and five females) into a novel environment has resulted in large differences in external morphology with high phenotypic divergence rates (17) up to 8,593 darwins or 0.049 haldanes [Table 1; note, however, that these are synchronic rates (1) and assume no additional colonization of the island by *P. sicula*]. Moreover, the invasion of a novel environment has resulted in the evolution of a novel phenotypic character that is rarely observed in lizards and that cannot be quantified by such metrics. More importantly, the observed morphological changes appear adaptive because they result in an increase in bite performance in both sexes. Because plants are tough, fibrous materials, high bite forces may allow lizards to crop smaller pieces from larger plants (13, 18) and thus may help the breakdown of the indigestible cell walls (19, 20). Previous data show that lizards that include plant matter into their diet do indeed have higher bite forces (13, 18). Interestingly, phenotypic divergence rates are higher for females (the sex with the smallest heads and lowest bite forces) than males, suggesting that selection for high bite forces is directly related to the inclusion of tough and fibrous items into the diet. Additionally, functional components of the jaw system related to jaw opening (e.g., the inlever for jaw opening) show much lower divergence rates, again suggesting

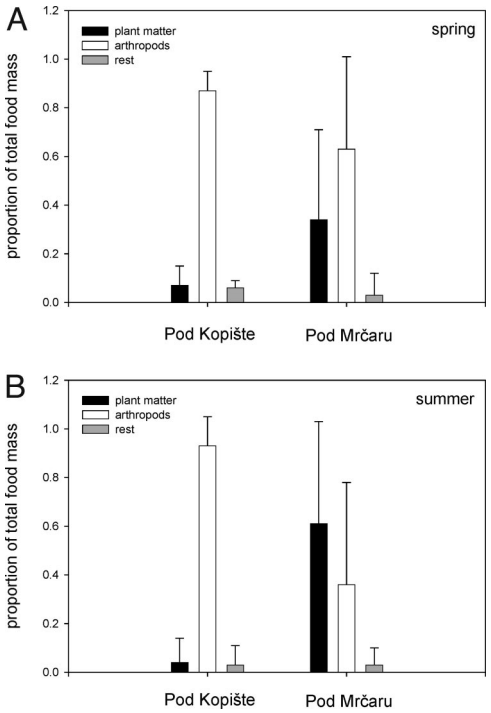

Fig. 2. Graphs illustrating differences in diet between populations in spring (*A*) and summer (*B*). Differences in the proportions of plants (black bars), invertebrate prey (white), and rest fraction (gray) are highly significant between populations. Seasonal differences in diet were highly significant on Pod Mrčaru but not on Pod Kopište. Error bars depict 1 standard deviation.

that morphological changes are specifically associated with the ability to bite hard and the increased consumption of plant matter (Table 1).

The relatively large fraction of leaves included into the diet of lizards in the introduced population of Pod Mrčaru has apparently also resulted in the evolution of cecal valves, a structure previously unreported for this species and rare in this family and scleroglossan lizards in general (13, 14, 18). Our data also add to the growing number of studies suggesting that the inclusion of plant matter into the diet of small temperate lizards may be more common than previously thought (21, 22). Moreover, our data show not only rapid, directional changes in quantitative phenotypic traits related to the inclusion of plant matter into the diet, but also the evolution of novel morphological structures on

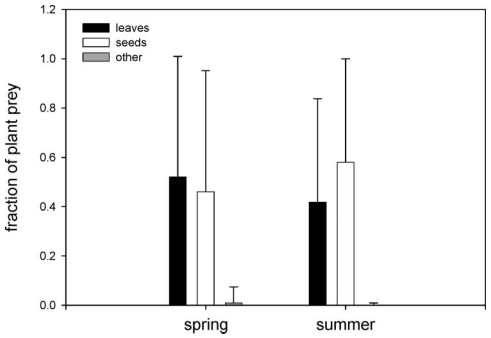

Fig. 3. Bar graph illustrating the fraction of plant prey in the diet of lizards from Pod Mrčaru consisting of leaves (black), seeds (white), and other plant material (gray). Fibrous, indigestible materials such as leaves compose a large fraction of the diet in both spring and summer. Error bars depict 1 standard deviation.

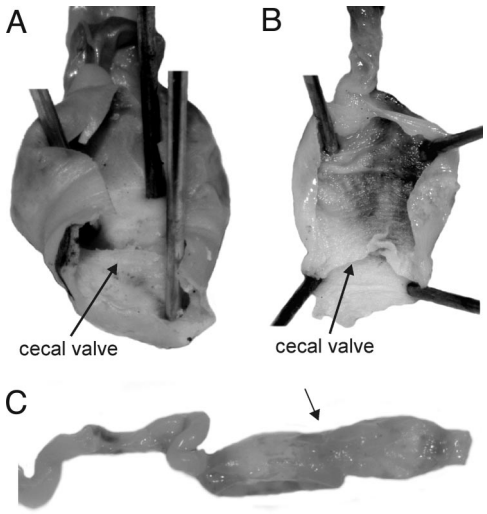

Fig. 4. Photographs illustrating the cecal valves in a male (*A*), a female (*B*), and a hatchling (*C*) *P. sicula* from Pod Mrčaru. Note the thick cecal wall and pronounced ridges. The arrow in *C* indicates the position of the cecal valve in a hatchling as seen from the outside.

extremely short time scales. Although the presence of cecal valves and large heads in hatchlings and juveniles suggests a genetic basis for these differences, further studies investigating the potential role of phenotypic plasticity and/or maternal effects in the divergence between populations are needed.

The inclusion of plant matter into diet may have had profound effects on the population structure as well. Because of the larger food base available and the increase in the predictability of the food source, lizard densities on Pod Mrčaru are much greater (0.01 versus 0.05 lizards per trap per hour, caught in unbaited traps, on Pod Kopiste and Pod Mrčaru, respectively). This, in turn, likely affected the social structure, and lizards on Pod Mrčaru do no longer appear to defend territories. Moreover, changes in foraging style (browsing versus active pursuit of mobile prey) and social structure may also have resulted in the dramatic changes in limb proportions and maximal sprint speed previously documented for this population (23). Thus, our data show how rapid phenotypic changes may affect population structure and dynamics through their effect on behavioral ecology and life history of animals. They also show that rapid evolution can result in changes in both qualitative and quantitative characters.

Methods

Samples and Phylogenetic Analysis. Islands were visited in spring and summer of 2004, 2005, and 2006. Lizards were caught by noose and transported to the field laboratory or measured *in situ*. Small tail clips (±4 mm) were taken from all individuals and stored in 100% ethanol for genetic analysis. To corroborate morphological identifications, a subset of specimens from both islands (Pod Kopište, $n = 8$; Pod Mrčaru, $n = 7$) and a set of reference specimens of *P. melisellensis* from Lastovo Island ($n = 7$) were subjected to DNA sequence analysis. Total genomic DNA was extracted by using the QIAamp DNA Mini Kit (Qiagen). Two mitochondrial DNA fragments (12S rDNA and 16S rDNA) were amplified by PCR by using the primer pairs 12SaL (5′-AAACTGGGATTAGATACCCCACTAT-3′) and 12SaH (5′-GAGGGTGACGGGCGGTGTGT-3′) for the 12S fragment (modified from ref. 24) and 16Sar (5′-CCGGTCTGAACTCAGATCACGT-3′) and 16Sbr (5′-CGCCTGTTTAACAAAAACAT-3′) for the 16S fragment (25). PCRs were performed in a total volume of 25 μl, containing 200 μM of each dNTP, 0.2 μM of each primer, 2.5 μl of TaqPCR buffer (10×), 1.25 units of *Taq* polymerase (Qiagen *Taq* for 12S and Sigma REDTaq for 16S), and DNA template (1 μl for 12S and 3 μl for 16S). The PCR protocols started with an initial DNA denaturation at 95°C (5 min) and ended with a final extension step of 5 min at 72°C. Amplification was done in 35 cycles of 95°C (1 min), 50°C (1 min), and 72°C (2 min) for 12S and 95°C (45 s), 46°C (45 s), and 72°C (90 s) for

16S. PCR products were purified with the GFX PCR DNA and Gel Band Purification Kit of Amersham Biosciences and sequenced by using the Big Dye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems) on an AB 3130 XL Genetic Analyzer. Sequences were edited and aligned with BioEdit software (26). The MEGA v4 (27) was used to calculate pairwise Jukes–Cantor distances and to construct a neighbor-joining tree based on a concatenated alignment of both gene fragments, including all published data of specimens for which both gene fragments were available in the GenBank database (28, 29) and with *Podarcis muralis* as outgroup (SI Fig. 5). Branch support was obtained by 1,000 bootstrap replicates.

Morphology and Performance. Snout-vent length, head dimensions, and body mass were measured for 258 adult lizards in the spring of 2004 and 2006 (Pod Kopište, $n = 100$; Pod Mrčaru, $n = 158$). Snout-vent length and head dimensions were measured by using digital calipers, and body mass was measured by using a digital scale. Variables measured included head length, head width, head height, and lower jaw length as overall head size indicators. Additionally, biomechanically relevant measurements including the jaw outlever, the inlever for jaw opening and jaw closing, and snout length were measured as described elsewhere (30). Bite forces were measured in 100 lizards (Pod Kopište, $n = 42$; Pod Mrčaru, $n = 58$) during the spring of 2004 using a Kistler force transducer set in a custom-built holder and connected to a Kistler charge amplifier (30, 31). Lizards were induced to bite the transducer five times, and the maximal value was retained for analysis. All morphological and performance data were $\log_{10}$-transformed before analysis. Divergence rates for morphology and performance were calculated in darwins and haldanes as suggested previously (17).

Diet Analysis. A total of 330 lizards (Pod Kopište, $n = 119$; Pod Mrčaru, $n = 211$) were stomach-flushed by using previously described methods (30), and stomach contents were stored in 70% ethanol. The stomach contents were analyzed down to order for invertebrate. Plant matter was divided in leaves, seeds, and a rest fraction. All invertebrate prey were measured ($\pm$0.01 mm) and weighed ($\pm$0.01 mg). Plant fractions were weighed separately, and seeds were both measured and weighed. Unidentifiable items were weighed together as a single group. The relative proportion of plant, arthropod, and the remainder were calculated per individual and arcsine-transformed before analysis.

Lizard Abundance. To get a relative assessment of lizard abundance, an array of 20 plastic cups was randomly placed across the island and left overnight. The next day lizards were retrieved from the traps, counted, measured, and released.

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