




INVITED PAPER

Specialist versus Generalist at the Intraspecific Level: Functional Morphology and Substrate Preference of *Mediodactylus kotschy* Geckos

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Synopsis Populations of the same species occupying different microhabitats can either exhibit generalized traits across them or display intraspecific variability, adapting to each microhabitat in order to maximize performance. Intraspecific variability contributes to the generation of diversity, following selection and adaptation, and understanding such variability is important for comprehending how individuals choose their microhabitats. Compared with interspecific variability, however, intraspecific variability in functional morphology and its relationship with microhabitat preference and use have been relatively little studied. Here we examined whether populations of the gecko *Mediodactylus kotschy* that differ in the substrates they occupy display habitat-specific behaviors and differing morphologies associated with functional adaptation to their microhabitats. We collected 207 geckos from under or on rocks or on trees from seven populations in Greece. On large islands individuals occupy both substrates; whereas small islets are devoid of trees and the geckos are restricted to rocks, while on the mainland they are only found on trees. We determined gecko substrate preferences in the laboratory, together with their clinging abilities to the different substrates. We measured their limbs, digits, and claws and assessed how these measurements relate to clinging ability. Geckos from all populations preferred the tree made available to them, but this preference was not statistically significant. Geckos from both large and small islands clung better to the tree than to the rock in the laboratory, while those from the mainland clung similarly to both substrates. Geckos collected from trees had longer manual digits and hind limbs. Geckos collected from large and small islands had taller (longer on the dorso-ventral axis; henceforth “deeper”) claws. Longer digits and deeper but shorter claws were associated with a better ability to cling to rocks. Our findings suggest that while *M. kotschy* is potentially preferentially arboreal, due to the great variation and plasticity it possesses, it can successfully also exploit the habitats available on the smallest, treeless islets in the Aegean Sea. Our study suggests that the dichotomous use of generalist versus specialist in describing species’ habitat use is oversimplified, and we suggest the use of a generalist–specialist gradient instead.

Introduction

The microhabitat of an organism determines both the abiotic and biotic conditions that it experiences (Davis and Stamps 2004). Traits of individuals within populations of species with wide geographic distributions, occupying different microhabitats, often vary according to the characteristics of their

microhabitats (Bolnick et al. 2003). They may thus evolve specialized traits in order to thrive in unique microhabitats (Futuyma and Moreno 1988; Herrel et al. 2001; Kolbe 2015; Kamath and Losos 2017; Taylor et al. 2018; Donihue et al. 2020a, 2020b). Conversely, individuals within populations may exhibit generalized traits throughout their range, enabling them to

exploit multiple microhabitats (Bolnick et al. 2007; Chavarie et al. 2016; Dehnhard et al. 2020). Whether individuals exist in their microhabitat based on exaptation of functional traits, or locally adapt through phenotypic changes to increase fitness, or whether selection eliminates unsuitable phenotypes from the microhabitat, is still subject to debate (Edelaar et al. 2008, 2017; Nicolaus and Edelaar 2018). Nonetheless, the idea that habitat preference and use interact with trait variation and may promote the local adaptation of traits in various taxa has been strongly supported (Ravigné et al. 2009; Ospina-Garcés et al. 2018; Yoshikawa et al. 2018).

Comprehending how traits vary within and between populations is key to understanding how animals have adapted to their microhabitats (Howes and Loughheed 2004). Studying microhabitat-induced trait variation can benefit our understanding of how species have attained their geographical ranges and what traits are important for successful invasion and establishment in new niches and habitats (e.g., Miller et al. 2017; Falvey et al. 2020). Much research has focused on interspecific functionally advantageous morphological traits of lizards that reflect responses to particular microhabitats (Scheers and Van Damme 2002; Goodman et al. 2008; Fuller et al. 2011; Tulli et al. 2011; Clemente et al. 2013; Hagey et al. 2017; Boronow et al. 2018). Members of some reptile clades (e.g., iguanians, Tulli et al. 2009; Losos 2011; Yuan et al. 2019, 2020; geckos, Riedel et al. 2020; varanids, D'Amore et al. 2018) have been assigned to “ecomorphs”—groups of species with distinct body, limb, and claw shapes that represent putative adaptations to the substrate they inhabit. Some ecomorphs have been found to have broadly similar morphological characteristics across clades (Herrel et al. 2002; Crandell et al. 2014; Hagey et al. 2017; Yuan et al. 2020). Tree-dwellers are generally characterized by short limbs and digits and highly curved hook-like claws (deriving from a larger deviation of the inner trace of the claw from a straight line), while terrestrial and saxicolous species have been found to possess longer limbs, digits and claws, and straighter claws (deriving from a smaller deviation of the inner trace of the claw from a straight line; Herrel et al. 2002; Tulli et al. 2009; Hagey et al. 2017; D'Amore et al. 2018; Yuan et al. 2019, 2020). Similar studies at the intraspecific level, however, are uncommon, especially for lizards (but see Herrel et al. 2001; Howes and Loughheed 2004; Collins et al. 2015). Although linking functional morphology with habitat preference of lizard populations is important for understanding the evolutionary processes of microhabitat use and population

dynamics, to the best of our knowledge this has never previously been attempted under controlled laboratory conditions.

Gekkotans have evolved very disparate morphologies, including limb loss to permit efficient burrowing, webbed digits to prevent sinking in sand, and skin flaps that enable gliding (Bauer and Russell 1991; Young et al. 2002; Gamble et al. 2012; Wall and Shine 2013). Many gecko lineages have evolved subdigital adhesive toepads of diverse shapes, enabling them, together with claws, to climb and cling effectively to both smooth and rough surfaces (Gamble et al. 2012; Naylor and Higham 2019). These functionally advantageous morphological traits are associated with the successful occupation of a variety of substrates by geckos, including trees, leaves, rocks, and both sands and heavier soils (Higham and Russell 2010; Romijn et al. 2014). Many geckos (e.g., *Cyrtodactylus* with over 300 described species; Uetz and Freed Hošek 2020), however, do not possess adhesive toepads (i.e., possess the ancestral lizard phenotype) but are nevertheless able to climb trees and rocks and occupy and efficiently move over different substrates (e.g., Higham and Jayne 2004; Kulyomina et al. 2019).

Mediodactylus kotschy is a small (mean snout-vent-length [SVL] 42.2 ± 4.3 mm, mean mass 2.7 ± 0.9 g, Itescu et al. 2017), padless, catheymeral, and insectivorous gecko, ranging from the southern Balkans, throughout Greece, including the Cyclades and North Aegean archipelagos (Kotsakiozi et al. 2018; Lymberakis et al. 2018). In the Peloponnese region (mainland Greece) *M. kotschy* is almost exclusively arboreal (Schwarz et al. 2016; Fig. 1), while on the small, treeless Aegean islands it is exclusively saxicolous, inhabiting rocks, stone piles, and dry-stone walls (Beutler 1981; Valakos et al. 2008; Schwarz et al. 2016; Fig. 1). Interestingly, on the large Aegean islands (e.g., Naxos, Paros, and Skyros) *M. kotschy* is both arboreal and saxicolous (R. Schwarz, personal observation), with individuals occupying natural rocky areas, dry-stone walls, trees, and external walls of buildings (Beutler 1981; R. Schwarz, Y. Itescu, and P. Pafilis, personal observation; Fig. 1). However, whether individuals move among different substrates or remain their entire life on the same one is unknown.

Here we sought to determine whether *M. kotschy* exhibits specialized behavioral, morphological, and functional putative adaptations to the substrates it inhabits, or whether these traits are generalized across populations. In other words, we examined whether *M. kotschy* is a “Jack of all trades, master of none,” or whether it has become specialized to the

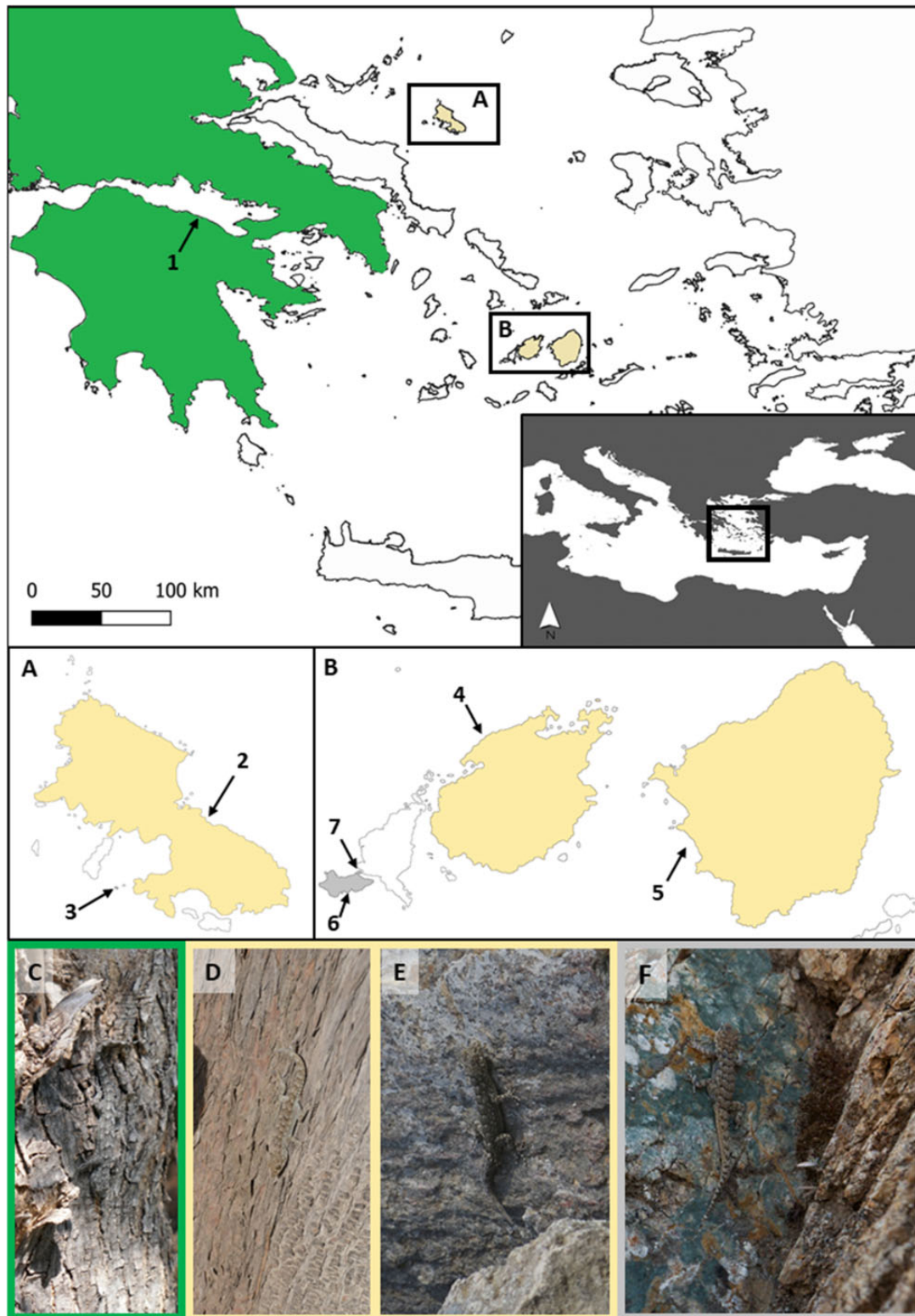


Fig. 1 Map of habitats sampled during the fieldwork seasons between April and June 2017–2019. The arrows indicate the island/islet or site on the mainland where we collected geckos. Main panel: (1) Peloponnese (Kamari). Inset **A**: (2) Skyros island; (3) Exo Diavates islet. Inset **B**: (4) Paros island; (5) Naxos island; (6) Despotiko islet; (7) Tsimintiri islet. “Tree” habitat type (green) refers to the mainland (1), where geckos are almost exclusively found on trees (**C**, taken by R.S. in Kamari, Peloponnese); “mixed” habitat types (yellow; 2, 4, 5) refers to large islands where geckos are found on both trees (**D**, taken by S.M. on Kimolos island) and rocks (**E**, taken by R.S. on Naxos island); “Rock” habitat types (gray) refer to small, treeless islets, where geckos are found only on or under rocks (3, 6, 7, **F**, taken by Alex Slavenko on Serifos island).

available substrates in the different habitats. To the best of our knowledge this is the first attempt to evaluate the relationship between a padless gecko's substrate preference and use and its functional morphology, in a controlled environment (Higham et al. 2019).

We hypothesized that geckos have adapted to the substrate they occupy by evolving traits that maximize their performance on these substrates. We thus predicted that individuals would prefer the substrate on which they are found in nature; that their morphology would suit this substrate; and that they would cling better to it. More specifically we predicted that

- (1) Geckos that inhabit trees on the mainland, where both substrates exist, would prefer trees over rocks in the laboratory; that their morphology would be adapted to tree climbing; and they would be able to better cling to trees. Further, we predicted that geckos inhabiting trees would exhibit traits associated with lowering their center of gravity (Van Damme et al. 1997). Thus, we predicted that they would have shorter limbs and digits, as well as shorter, deeper, and more curved, hook-like claws, in order to exert greater clinging force without expending more energy, as claws can interlock with protrusions or depressions on the substrate and are able to penetrate a soft substrate.
- (2) Geckos from small islets, where there are no trees and where only rocks are available for shelter, would choose rocks over trees for shelter in the laboratory, and would be able to cling to rocks more effectively than to trees. Because they are found both in rock crevices and on the ground under the rocks, we predicted that their claw morphology would be more similar to that found to be prevalent in terrestrial species (Tulli et al. 2009): longer limbs and digits, and shallower, longer and straighter claws.
- (3) On large islands, where both trees and rocks are found and geckos are frequently encountered on both substrates, they would not prefer either substrate, but cling equally well to both trees and rocks and feature an intermediate morphology suited to clinging to both substrates. Thus, we predicted that these geckos would possess longer limbs and digits than those from the mainland, and shorter, deeper, and more curved claws than those from small islets.

Alternatively, it is possible that *M. kotschyi* is preferentially arboreal and only inhabits rocks where trees are not present; or if it is displaced into rocky habitats by fierce intraspecific competition on islands (e.g., Pafilis et al. 2009; Itescu et al. 2017). Under such a scenario, we predicted that all geckos would exhibit morphological characteristics reflective of suitability to arboreal situations, regardless of the substrate from which they had been collected.

Materials and methods

Data collection

We collected 211 *M. kotschyi* individuals of both sexes (146 females and 65 males) between April and June 2017–2019 under permit no. 71BA4653Π8-267, ΩM4X4653Π8-2OE, and 7M7T4653Π8-ΠA5 issued by the Ministry of the Environment of Greece. Geckos were collected by hand or with a noose, either by upending rocks and catching inactive geckos underneath, or by locating them on tree bark, outside their shelter (most were on the trunk and larger branches, up to a height of 1.5 m above the ground). Both the mainland and the large islands we sampled are characterized by a mosaic of olive tree groves and almond trees (see Fig. 3 in Hartmann and Bougas 1970; Papanastasis et al. 2009), and we found geckos on both these tree types. Other trees at these sites include walnut, oak, carob, and pistachio (Papanastasis et al. 2009), but we never found geckos on these tree types. The small islets are treeless. The rock types available on all the sites we sampled were marble, schist, and alluvium (Higgins and Higgins 1996). We treated all geckos collected from the same island (even when collected at several sites) as belonging to a single population. In total we sampled six insular and one mainland population (Fig. 1 and Supplementary Table S1).

We assigned each gecko to one of three habitat categorizations according to the habitat in which it had been found (hereafter “habitat type”) according to geographic origin: “trees” (mainland site), “rocks” (small islets), and “mixed” (large islands): (1) All geckos from the mainland (Peloponnese region; 32 individuals) were encountered on trees, even though rocks were present around and in the vicinity of the trees. Hence all these were assigned to the “tree” habitat type; (2) Geckos collected from small islets (Tsimintiri, Exo Diavates, and Despotiko; 49 individuals) were found only on or under rocks, as trees are absent, and these were assigned to the “rock” habitat

type; (3) Geckos from large islands (Naxos, Paros, and Skyros) were collected from either trees (30 individuals) or rocks (100 individuals; Fig. 1). On these islands we sampled sites where trees were scarce and sites where both substrates were available. Geckos from large islands were assigned to the “mixed” habitat.

We recorded the substrate on which each gecko was caught (tree or rock). We then transferred them to the University of Athens, housed them individually in terraria maintained at room temperature of 28°C supplemented by heating lamps, and provided them with food and water *ad lib* and vitamin and mineral supplements. Not all geckos were used for each experiment because the experiments and measurements were conducted over the course of 3 years and different individuals were caught each year. Some individuals were released back to nature after the experiments while the majority were sacrificed and deposited in the Herpetological Collection of the Zoological Museum of the National and Kapodistrian University of Athens.

Substrate preference experiment

All trials took place during the day, throughout August 2017, between 10:00–14:00 or 14:00–18:00 (individuals were randomly selected for either the first or second session). We performed habitat preference experiments for 60 female *M. kotschy* (18, 13, and 28 geckos from “rock,” “tree,” and “mixed” habitat types, respectively), by placing each, in turn, inside a 1×1 m plexiglass soil-lined enclosure containing a marble rock (40 cm wide × 40 cm high; Stelios Lozios, personal communication) and an almond tree stump (30 cm diameter × 1.5 m high). Both rock and tree types were those upon which we had found the geckos in nature (i.e., marble and almond), both on large islands and on the mainland. At the beginning of the experiment we placed each gecko on the floor of the arena, equidistant from the rock and the tree. We filmed each gecko from two angles for 4 h in the arena using two HD web cameras that covered the location of the geckos throughout the entire trial. The first hour of the experiment was regarded as an acclimation period and not analyzed (Rodríguez-Prieto et al. 2011). Thus, the data for analysis comprised 180 min. At the beginning of each filming session we recorded the temperature of the tree and of the rock to ensure that the gecko’s choice between these two substrates was not thermoregulatory. Both substrates always had the same temperature. We analyzed the camera footage to record the time that each gecko spent on each substrate (under/on the rock, on the tree, and on the ground) throughout

the experiment. We used the time (in minutes) spent on each substrate as a measure of individual substrate preference.

Clinging ability to different substrates

During May 2018 and June 2019 we examined the clinging ability to rock and tree surfaces of 86 geckos (22, 23, and 41 males and females from “rock,” “tree,” and “mixed” habitat types, respectively) from the seven populations. We accomplished this by measuring the maximum force required to detach them from each substrate (Zani 2000; Tulli et al. 2011; Kolbe 2015).

Geckos were allowed to bask under incandescent lamps for 30 min before each trial. We attached each gecko to a 50 g Pesola spring balance by a harness placed around its abdomen (Zani 2000; Tulli et al. 2011; Kolbe 2015). We then placed the gecko onto the test substrate and, after it had grasped the surface with all digits, R.S. drew the scale horizontally backward at an even speed. Each gecko was tested three times on each substrate (tree and rock), with at least a 5-h interval between trials. The order of the trials was randomized. We filmed the scale during each trial using a video camera, to record the force required to cause the lizard to lose contact with the substrate. The weight at which it lost its grip was recorded as its clinging ability. We chose the maximum force recorded during the three trials as a measure of clinging performance for each substrate.

Morphology

We measured the SVL, fore and hind limb lengths, and the fourth manual and pedal digits (Supplementary Fig. S1) of 196 geckos (40, 30, and 126, males and females from “rock,” “tree,” and “mixed” habitat types, respectively) using callipers to 0.01 mm precision. The geckos were weighed using Pesola spring scales to 0.2 g precision. We placed their fore and hind feet on millimeter-scale paper and took photographs of a total of 82 digits (second manual and third pedal) and 77 claws. Using ImageJ software (Schneider et al. 2012) we measured digit (second manual and third pedal) length and claw dorso-ventral and proximodistal lengths, and the length of the claw’s ventral arch (Supplementary Fig. S2). We calculated claw curvature by dividing the ventral arch length of the claw by the proximodistal claw length, measured from the base of the claw to its tip (Supplementary Fig. S2). Live animals could not be photographed with a stereo microscope, and the resulting low-resolution photographs therefore prevented us from assessing claw curvature using methods such as geometric morphometrics (Tinius and Russell 2017). We measured digits and

claws of the second and fourth manual digits and the third and fourth pedal digits, because these were the digits that we had observed participating most in substrate grasping and are thus presumably the functionally most important ones for clinging (Zani 2000; Tulli et al. 2011). Not all the geckos we caught were photographed for claw measurements as some photographs were not sufficiently clear for this, and some geckos had broken or missing claws.

Statistical analyses

All data pertaining to the experiments and measurements are summarized in the [Supplementary Materials \(Supplementary Table S1\)](#). To test our hypotheses, we constructed nested mixed-effects models using the “lme” function from the “nlme” package (Pinheiro et al. 2020), unless stated otherwise. To determine which relationship contrasts were significant we performed a “Tukey” HSD *post hoc* test on the model, using the function “emmeans” implemented in the package “emmeans” (Lenth 2020). All statistical analyses were performed with R v3.6.2 (R Core Team 2019). The statistical analysis’ R script is provided in full in the Supplementary Materials ([Online Appendix S1](#)).

Substrate preference

To determine whether the geckos preferred the substrate from which they had been collected (trees/rocks), and whether their choice depended on their specific habitat type (i.e., “trees,” “rocks,” or “mixed”), we constructed a zero-inflated nested generalized mixed effects model using the function `glmmTMB` from the package “glmmTMB” (Brooks et al. 2017). We used the number of minutes spent by each individual on the rock, ground, and tree in the laboratory (three numbers per individual, summing to 180 min) as the response. During the 3-h test, 32%, 35%, and 18% of the geckos did not spend any time on the ground, the rock, or the tree, respectively. As this meant that ca. 30% of the data for this experiment contained zeros, we used a zero-inflated model. We included the substrate (rock/tree), the mass of each gecko, and the interaction between them, as well as the original substrate (tree/rock) and the habitat type from which the geckos were caught in nature (large and small islands and the mainland) as fixed effects. We accounted for the fact that each individual gecko presents three data points (number of minutes spent on each substrate) by nesting the substrate type in the gecko’s identification number. The gecko identification numbers were subsequently nested within the islands they were collected from, to account for any

variation that may have resulted from the individuals evolving on different islands. We treated our entire nesting design as a random effect. Test session time (morning or afternoon) did not influence the preference of the geckos (not shown); thus we pooled the data for the two sessions. All geckos tested in the substrate preference experiment were adult females.

Clinging ability

To determine whether geckos collected from different substrates and habitat types can cling to one substrate better than the other we ran two models, using the maximum clinging ability (over three trials) of each gecko to each substrate as the response. In both models we included the substrate of each trial (tree or rock) along with the mass and sex of each gecko as fixed effects. We used mass and not SVL to account for the fact that clinging force was measured using a spring scale, and thus including mass in the model eliminates the effect of the individual’s mass (although adding both predictors did not qualitatively change the outcome of the tests; results not shown). In one model we used the original substrate on which the gecko had been found in nature (rock/tree) and in the second, the habitat type (“rock,” “tree,” and “mixed”), as additional fixed effects. To account for the fact that each individual was tested on both substrates, we nested the substrate identity in the gecko identification number. To account for potential island-specific variation we further nested the individual geckos (gecko identification number) within the islands from which they had been collected. The entire nesting design was designated as a random effect. To correct for heteroskedasticity, we included the VarPower variance function implemented in the nlme package, evaluating mass and sex (Zuur et al. 2009). Upon residual and model fit inspection, we identified gecko no. #RS58 from the mainland (Peloponnese) as an extreme outlier, in that it performed poorly in the clinging experiment to the rock relative to its mass. We thus omitted this individual from the analyses (although including it did not change the results qualitatively).

Morphology

We determined whether gecko morphology differed among individuals collected from the different substrates (rock/tree) and different habitat types (rocks/trees/mixed) by constructing a model for each morphological characteristic (forelimb, hind limb, digit length, and proximodistal and dorso-ventral claw length and curvature) separately as the response. The substrate and habitat type from which the gecko

had been collected, its sex, mass, and SVL, were used as fixed effects. To account for potential island-specific variation, we nested the gecko identification number within the islands from which they had been collected, and assigned this nesting design as a random effect. We used a backward stepwise elimination model selection procedure based on P -value ($\alpha < 0.05$) for each model.

Morphology and clinging ability

To determine whether morphological characteristics are associated with the clinging ability for each substrate, we constructed two models in which we tested the maximum clinging ability of geckos for each substrate as the response. In each model we used forelimb length, hind limb length, digit length, claw dorso-ventral length, claw proximodistal length, claw curvature, sex, SVL, and body mass as fixed effects. To account for potential island-specific variation we nested the gecko identification number within the islands from which they had been collected, and assigned this nesting design as a random effect. We used a backward stepwise elimination model selection procedure based on P -value ($\alpha < 0.05$) for each model.

Results

Substrate preference

Geckos in the experimental arena spent, on average, nearly twice as much time on the tree than on the rock (103.6 ± 9.6 min on the tree versus 57.3 ± 9.3 min on the rock; Fig. 2A), but the difference was not statistically significant (Tukey's HSD, t -ratio = 1.90, $df = 152$, $P = 0.14$). This pattern, although not significant, was evident regardless of the substrate or habitat type from which geckos had been collected (Fig. 2B and C and Supplementary Table S2A and B). Geckos preferred the tree ($z = 7.1$, $P < 0.0001$) or the rock ($z = 5.1$, $P < 0.0001$) to remaining on the ground (mean number of minutes on the ground = 19.0 ± 4.2 , Fig. 2A). Body mass had no significant effect on the geckos' preference ($t = -0.20$, $P = 0.84$).

Clinging ability

Clinging ability (corrected for mass and sex) to the tree for geckos collected from rocks was 62% greater than their clinging ability to the rock ($n = 51$, $t = 6.84$, $P < 0.0001$, Fig. 3A and Supplementary Table S3a). However, there was no difference in the clinging ability of geckos collected from trees to either substrate ($n = 34$, $t = 0.85$, $P = 0.40$), although their clinging abilities to both substrates

were higher than the clinging abilities of geckos collected from rocks clinging to the rock (Tukey's HSD, rock-rock: $t = 2.95$, $P = 0.02$; tree-rock: $t = 3.48$, $P = 0.005$, Fig. 3A). The clinging ability of geckos to the tree was 67% ($n = 22$, $t = 3.49$, $P = 0.0008$) and 77% ($n = 41$, $t = 4.87$, $P < 0.0001$) higher than those recorded for the rocks for geckos collected from small and large islands, respectively (Fig. 3B and Supplementary Table S3b). However, there was no difference in the clinging ability of geckos collected from the mainland to either substrate ($n = 22$, $t = 0.63$, $P = 0.53$, Fig. 3B and Supplementary Table S3b).

Morphology

Corrected for SVL (but not for mass, Supplementary Table S4), the hind limbs and second manual digits of geckos collected from trees were longer than those of geckos collected from rocks by 12% ($t = 2.12$, $P = 0.04$) and 18% ($t = 3.77$, $P = 0.0003$), respectively (Supplementary Table S4). The claws of the third pedal digits of geckos collected from large islands ("mixed") were deeper by 75% ($t = 2.91$, $P = 0.04$) compared with those collected from the mainland ("trees"), but did not differ from the claws of geckos collected from small islets ("rocks"; $t = -0.10$, $P = 0.92$, Supplementary Table S4). The claws of the fourth pedal digits of geckos collected from large ("mixed") and small islets ("rocks") were deeper by 60% ($t = 5.78$, $P = 0.004$), and 57% ($t = 4.44$, $P = 0.01$), respectively, compared with those of geckos collected from the mainland ("trees"; Supplementary Table S4). The forelimbs, digit lengths of the third pedal digit and the fourth digits of the manus and pes, the claw proximodistal lengths, and claw curvatures did not differ among geckos collected from the different substrates or habitats (Supplementary Table S4).

Morphology and clinging ability

Shorter and deeper claws of the fourth pedal digits were associated with a better clinging ability to the rock (corrected for SVL, Supplementary Table S5), while shorter claws of the third pedal digits were associated with a better clinging ability to both the tree and the rock (Supplementary Table S5). Longer fourth manual and pedal digits were associated with better clinging ability to the rock (Supplementary Table S5). The morphologies of the second manual digit and claw, forelimb and hind limb lengths, and claw curvature were not significantly associated with clinging ability to either substrate (Supplementary Table S5).

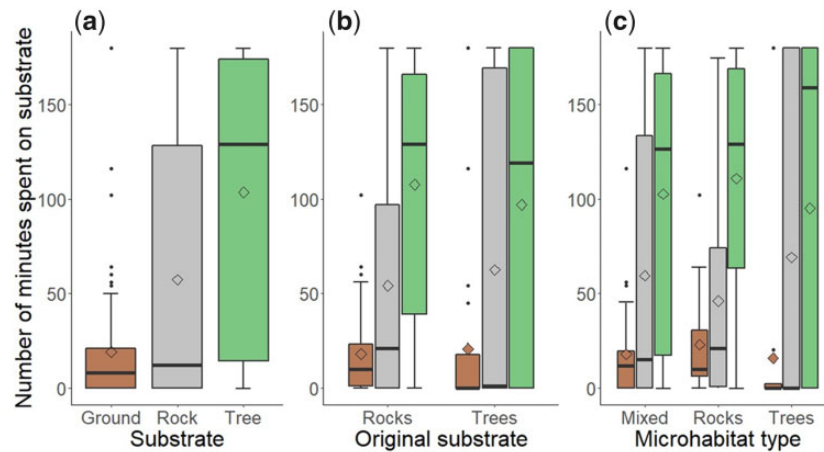


Fig. 2 Boxplots displaying the number of minutes that geckos spent on the ground (brown), rock (gray), and tree (green) in the laboratory (a), in relation to the habitat type (b) and original substrate (c) from which they were collected. Diamonds show the means and the bold lines show the median. Boxes represent the interquartile (third–first) range, whiskers represent the minimum and maximum, and dots depict outliers. The means, SE, n , and Tukey's HSD *post hoc* results are provided in [Supplementary Table S2](#).

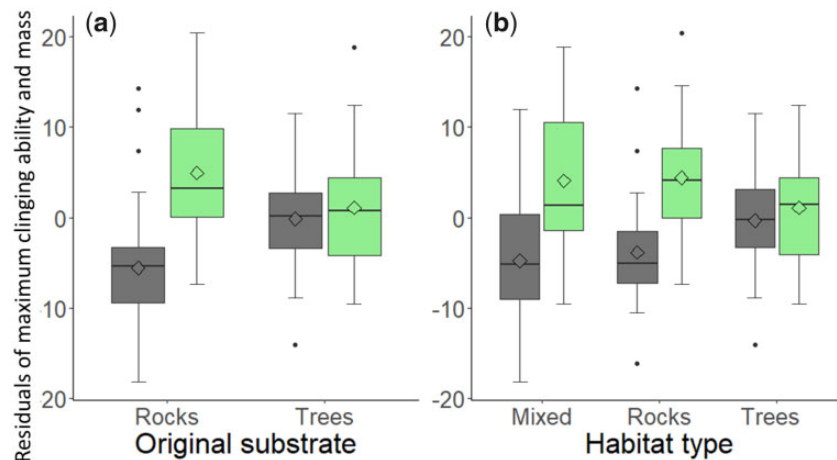


Fig. 3 Boxplots of the maximum clinging ability of geckos (corrected for body mass) to the rock (gray) and tree (green) in the laboratory, among geckos collected from the different substrates (a) and habitat types (b). Diamonds show the means and the bold lines show the median. Boxes represent the interquartile (first–third) range, whiskers represent the minimum and maximum, and dots depict outliers. The model's numerical results are presented in [Supplementary Table S3](#).

Discussion

Our hypothesis, that *M. kotschy* has specialized in its habitats to maximize its performance on the available substrates, was overall refuted. Although the tested geckos did, on average, spend twice as much time on the tree than on the rock, the differences were not statistically significant. Counter to our prediction, the habitat from which the geckos were collected did not influence their preference for the tree or rock substrates in the substrate preference experiment. These results demonstrate that individuals of this species are neither rigidly associated with the substrate they usually occupy in nature nor specifically adapted to it, and that they will use substrates

that are not present in their natural environment. This implies that these geckos are opportunistic in their habitat use, which agrees with their widespread distribution and the high densities they reach within their range (Valakos et al. 2008; Schwarz et al. 2016; Itescu et al. 2018). This, potentially along with its preference for trees (albeit not statistically significant in our analyses, and thus requiring further examination), may explain why *M. kotschy* was observed by Pafilis et al. (2020) on olive trees planted on the small (<1 km²) islet of Monolia in the Lichadonissia Archipelago.

The lack of a significantly strong substrate preference by the tested geckos in the laboratory, while in nature they are either restricted to rocks due to the

absence of trees on small islets, or strongly prefer trees on the mainland, may be due to an ecological factor, such as predation pressure. While on the mainland predation pressure is predicted to be higher, on small islets it is more relaxed (Itescu et al. 2017, 2018), and thus the use of rocks probably does not result in a reduction in fitness. Similarly, a relaxed predation pressure on large islands with both trees and rocks may permit geckos to frequent both substrates and to occupy rocks much more often on such islands than on the mainland (Schwarz et al. 2016). As no other lizard species fills exclusively the arboreal niche on the mainland, competitive exclusion is unlikely. A further examination of the role of predation pressure as a potential driver of substrate preference might shed more light on the evolution of substrate preference and use in this species.

Geckos collected from trees featured longer second manual digits and hind limbs, counter to our predictions that tree-climbing geckos would have shorter digits and limbs, allowing them to maintain their center of gravity close to the tree (Van Damme et al. 1997). The longer second manual digits and hind limbs, however, did not increase the geckos' ability to cling to the tree; and thus this trait variation may not be functionally relevant to clinging performance but may be due to another, untested, factor. Instead, longer fourth manual and pedal digits were positively associated with a better ability to cling to rocks, without any significant difference between individuals caught on rocks or trees. As these latter digits are the longest, and based on previous research which found that longer digits improved clinging ability (Tulli et al. 2011), it is possible that they participate in and contribute to the exertion of the clinging force more than the other digits. This finding indirectly supports our prediction that geckos collected from rocks will have longer digits, which will enhance their ability to cling to rocks. It is however possible, since we tested the clinging ability of geckos pulled horizontally backward, that some digits participate more in this way of clinging while others participate more in clinging when the gecko is hanging upside down or facing the ground. Recording the orientation of the geckos on the substrates they occupy along with a biomechanical study on why longer digits enhance clinging ability may help future studies assess whether this claim is valid.

Our claw morphometry results, however, counter our predictions. The claws of the pedal digits of geckos originating from the mainland, where they mostly occupy trees, were shorter than those of geckos collected from large and small islets, where they occupy also, or only, rocks. Even though the

claws of the fourth manual digits did not significantly vary among populations, deeper claws were significantly associated with a better ability to cling to rocks. Claw proximodistal lengths did not significantly differ among populations, but shorter claws were associated with a better clinging ability to either both substrates (third pedal digit) or only to the rock (fourth manual digit). Our results thus imply that deeper and shorter claws are more associated with saxicolous individuals than with arboreal ones, and are therefore of greater benefit in clinging performance on rock, contrary to our predictions.

Tulli et al. (2011) suggested that claw morphometry of *Liolaemus* lizards may be more important than limb length for climbing and clinging to trees and rocks; and that selection on limb length of scansorial lizards will be weaker than selection on claw morphology. If true, this could explain our results for geckos. Lizards occupying narrow perches often have short limbs, to enhance balance (Losos et al. 1993; Macrini and Irschick 1998; Vanhooydonck and Van Damme 2001; Goodman et al. 2007), but this is not the case in *M. kotschyi*. Consequently, we suggest that these geckos are not as sensitive as other lizards to the same speed versus balance trade-offs (similar to the findings of Hagey et al. 2017), because, similarly to many other geckos, they rely more on camouflage than they do on speed. Thus, their limb morphology may not be under the same selection pressures as in lizards that rely mostly on flight for predator avoidance. Furthermore, *M. kotschyi* is seldom found on thin branches, usually preferring the trunk or one of the main wider branches (R. Schwarz, Y. Itescu, and S. Meiri, personal observation). A similar pattern of longer hind limbs associated with arboreal species climbing tree trunks and wider branches was found by Grizante et al. (2010) for tropidurine lizards. The reason for this is that, as also previously described for geckos, arboreal species lower their center of gravity by means of a sprawled posture rather than by developing shorter limbs (Zhuang and Higham 2016). This may also be the case for *M. kotschyi*, but further data on its body posture on the different substrates are needed.

Contrary to our prediction, it seems that, overall, most of the geckos we investigated (those collected from large and small islands), were better able to cling to the tree than to the rock, even if there are no trees in their natural habitat. Why individuals that occupy trees are able to cling equally well to both trees and rocks, and why such individuals can cling to rocks better than geckos collected from rocks, cannot be explained by our morphological findings, because most characteristics were associated

with enhanced clinging ability to rocks. Because tree bark tends to be softer than rock, it is possible that the geckos' claws are able to penetrate the bark, and become more firmly anchored, whereas they can only interdigitate with asperities on the rock surface and may thus be more easily dislodged. A better ability to cling to the tree may also result from the tree presenting a rougher surface than the rock, enabling the geckos to achieve greater traction, in contrast to what has been found for toepad-bearing geckos (Vanhooydonck et al. 2005; Higham et al. 2019). Metamorphic rocks, such as the marble used in this study, tend to have a relatively uniform texture due to their equidimensional mineral grains, and are thus usually smoother than the surfaces of most sedimentary rocks (Pedernana et al. 2017). They may also be smoother than the bark of some trees, depending on the asperity height and density (Higham et al. 2019). Previous studies have found that deeper claws are correlated with an increased ability to cling to rough surfaces (Zani 2000; Tulli et al. 2011). Research seldom distinguishes between tree and rock surfaces, but rather between smooth and rough surfaces (Herrel et al. 2001, 2002; Vanhooydonck et al. 2005; Tulli et al. 2011, 2012; Naylor and Higham 2019; Pillai et al. 2020). Both the rock and the tree can be considered to present rough surfaces, but if the tree was rougher than the rock we used (both taken from actual gecko habitats) this would help to explain why the geckos could better cling to it. Furthermore, small asperities on tree trunk surface, particularly on trees such as olive or almond, may provide a better traction for gecko claws and thus improve their ability to cling. Future studies on the microstructure of either substrate, the skeletal features of the claws, and the biophysics of clinging performance of padless geckos may enhance our understanding on this relationship between substrate, form, and function.

Even though some differences in morphology exist among populations, only a few of them appear to benefit the clinging ability of the geckos on the different substrates. Although there was no significant preference for either substrate, a strong preference for the trees was observed across populations, as well as a better clinging ability to the tree in most geckos. We therefore consider that our findings support the hypothesis that *M. kotschy* is preferentially arboreal in essence, but inhabits rocks where trees are not found, or when it is displaced into rocky habitats by fierce intraspecific competition on islands, where predation pressure is lower. Some *Mediodactylus* species are saxicolous (e.g., *M. amictopholis* and *M. heterocercus*), while others are

arboreal (e.g., *M. orientalis* and *M. sagittifer*), and some (e.g., *M. russowii* and *M. kotschy*) inhabit both substrates (Schwarz et al. 2016; Meiri 2018). Reconstructing the ancestral state of *Mediodactylus* species in their use of substrate may shed more light on whether *M. kotschy* is ancestrally saxicolous or arboreal.

Because there were some morphological differences among the populations collected from the different substrates and habitats, and because these traits are not generalized (i.e., similar) across populations, *M. kotschy* may appear to have specialized in its habitats. These differences, however, do not appear to be functionally important in relation to the observations made, and thus specialization of these morphological traits is unlikely in this case. These geckos also seem to prefer trees and to be able to cling to them better, which again may point to specialization. Their preference, however, was insignificant, and the mainland geckos we predicted would have specialized to trees performed equally well on both substrates. *Mediodactylus kotschy* thus seems to be neither a generalist nor a specialist *per se*. It is probable that its great variation in a suite of morphological, ecological, and life-history traits (Valakos and Vlachopoulos 1989; Valakos and Polymeni 1990; Slavenko et al. 2015; Itescu et al. 2017, 2018; Schwarz et al. 2020) has contributed to it becoming the most common reptile on the Aegean Islands, occupying even the smallest of islets. Our study suggests that the dichotomy of the specialist versus generalist categorization may be inadequate and oversimplified when describing the ecology and population dynamics of a species. This dichotomy of specialists versus generalists has also been criticized previously (Van Tienderen 1997; WallisDeVries 2014), as species can be generalists in some aspects and specialists in others (Dennis 2010; Dennis et al. 2011; Loxdale et al. 2011). *Mediodactylus kotschy* for instance, may be more specialized to trees in its clinging performance and its preference of trees, but have a generalized morphology. Consequently, describing species on a specialist–generalist continuum rather than a dichotomy (Habel and Schmitt 2012; Carnicer et al. 2013; Dappporto and Dennis 2013) would seem to offer a better approach and may improve our ability to describe behavioral and morphological patterns in ecology. Further intraspecific studies that incorporate functional morphology and behavior are needed in order to better understand the evolution of populations within the habitats they occupy, and to uncover how they expand their ranges or invade new territories.

Author contributions

R.S., S.M., and D.G.C. conceived the ideas and designed the methodology. R.S., G.S., P.P., A.A., and Y.I. collected the data. R.S. analyzed the data. R.S. and S.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

The data supporting this article are available in the article and in its Online [Supplementary Material](#).

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Conflict of interest

The authors declare that there is no conflict of interest.

Supplementary data

[Supplementary data](#) are available at *ICB* online.

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