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MELANISM AND FORAGING BEHAVIOUR IN AN INTERTIDAL POPULATION OF THE MADEIRAN LIZARD PODARCIS (=LACERTA) DUGESII (MILNE-EDWARDS, 1829)

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The Madeiran lizard *Podarcis* (=*Lacerta*) *dugesii* (Milne-Edwards) is a common lacertid 'wall' lizard occurring throughout the Madeiran archipelago, particularly in the orchards and vineyards of the main island where it occurs in large numbers and has been regarded as an agricultural pest for centuries by the Madeirans (Forster, 1777). *P. dugesii* is omnivorous, eating vegetation, fruit and even nectar as well as insects and other terrestrial invertebrates (Elvers, 1977, 1978; Sadek, 1981; Beyhl, 1990).

P. dugesii is a polymorphic, adaptable species that occurs in a variety of morphological types and colours (Cook, 1979; Crisp *et al.*, 1979) and is found at all altitudes in Madeira, from sea level where air temperatures range between about 18°C in winter and 32°C in the summer, to mountainous areas up to 1850 m where summer temperatures may be as low as 20°C and snow falls in the winter.

The investigation reported here was carried out on a melanic population of *P. dugesii* that was seen to be exploiting the intertidal zone, an unusual ecological niche particularly given the high-energy (i.e. exposed to heavy wave action), stony nature of Madeiran shores.

The study was carried out at a beach at Caniço, Southern Madeira, about 15 km east of Funchal. The whole beach, about 1 km long, consists of small outcrops of dark coloured lava interspersed with long stretches of mixed dark grey boulders, cobbles and pebbles. These latter portions of the beach were regularly resorted by the advancing and receding tides since Madeira features strong breezes and heavy oceanic swells. The jumble of boulders, cobbles and pebbles was generally at least 0.3 m thick and overlaid coarse gravel. Although the uppermost layers of this substratum rapidly dried out on sunny days, the deeper layers were always damp. Most of the dampness was due to seawater, but there were some freshwater inputs to the beach too. In common with most of such high energy boulder/ pebble beaches there was little sign of animal life save for substantial numbers of an isopod, *Ligia italica* Fabricius. *L. italica* is a large (<16 mm body length in females; Vandel, 1960) plant and debris-eating isopod and browses particularly (in daylight hours) upon lichens, microbial films and, on large boulders and fixed rocks, upon green macroalgae (especially *Cladophora* sp.). Lizards that were black dorsally and blue-grey ventrally were seen in the intertidal zone during most daytime visits to the beach at Caniço, though sightings were rare before mid-morning. They occurred from the top of the shore down to about low water neap tide level though they were never seen nearer to the water's edge than about 1-2 m.

Melanism. To determine whether the 'intertidal' population differed in colour and morphology from the 'terrestrial' population, 115 lizards (58 'intertidal'; 57 'terrestrial') were collected (between 15.11.93 and 16.2.94) in fruit-baited bucket traps set in the intertidal zone and nearby terrestrial area (pyroclastic pebbles and earth, with some vegetation). Measurements were made to the nearest mm: snout-vent length (SVL), tail length (TL; only for specimens with undamaged tails.); and to the nearest 0.1 mm: head width (HW), right forearm length (RFAL) and length of 4th digit of right forelimb (FIL; 'finger length'). The colour of lizards was ranked on a scale from 0-5 (5 being completely black, 0 being sand-coloured). This study confirmed that intertidal lizards were almost black (mean score = 4.4, SD = 0.5, n=58), while terrestrial lizards were dark brown (mean score = 3.1, SD = 0.6, n=57); the difference was statistically highly significant (Mann-Whitney U-test: U = 2293, P < 0.001). Intertidal lizards were also significantly bigger (mean SVL=58.0 mm SD=7.0, n=58) than terrestrial lizards (mean SVL= 51.8 mm, SD = 9.4, n=57; Mann-Whitney U-test: U = 2293, P<0.001). There was a weak, but significant, influence of body size on colour rank (colour score = 0.05 SVL + 1.16; $r^2 = 0.24$, P < 0.001). However, ANCOVA established that, for the same body length, intertidal lizards were always darker than terrestrial animals (P<0.001). To correct for body size, slopes and elevations of the regressions of TL, HW, RFAL and FIL on SVL were compared for both lizard groups. No differences in slopes were detected (ANCOVA, homogeneity of slopes) for any of the measurements. However, for a given SVL, intertidal lizards had longer tails and longer fingers than terrestrial lizards as there were significant differences in elevations for TL (ANCOVA: F = 11.6, n = 105, P < 0.001) and FIL (ANCOVA: F = 18.9, n = 113, P < 0.001). The regression equations are listed in Table 1.

These data show that the intertidal population differs significantly in both colour and morphology from its terrestrial near-neighbours. The differences in morphology might, perhaps, have been explained by a difference in sex ratio, since Sadek (1981) reported

TABLE 1. Regression equations of tail length (TL), head width (HW), right forearm length (RFAL) and finger length (FIL) on snout-vent length (SVL) for intertidal and terrestrial lizards or, if ANCOVA stated no difference between regressions, for pooled data.

Variable	Slope	Constant	r^2	Р
TL(intertidal)	1.41	13.04	0.49	< 0.001
TL (terrestrial)	1.62	9.09	0.64	< 0.001
HW (pooled)	0.08	0.98	0.58	< 0.001
RFAL(pooled)	0.20	-0.44	0.67	< 0.001
FIL(intertidal)	0.10	0.56	0.50	< 0.001
FIL(terrestrial)	0.10	0.21	0.83	< 0.001

that females have relatively shorter tails and hind legs than males. However, although the lizards of this study were not sexed directly, the head width data were analysed (c.f. Sadek, *op. cit.*) and this analysis showed that there was no significant difference in sex ratio between the populations, reinforcing the hypothesis that the intertidal population of lizards is morphologically distinct.

Foraging behaviour. Specimens of *P. dugesii* were regularly seen along the whole of the beach; direct visual observation of their behaviour was carried out whenever possible over a period of two weeks in the summer of 1993. Four melanic specimens of *P. dugesii* were trapped in a banana-baited trap at mid-tide level. The banana bait was wrapped in perforated plastic film so that it could be smelt, but not eaten. One of the animals was sacrificed humanely for dissection and analysis of stomach contents; the others were held separately unfed for 24 hr so that their droppings could be collected. These three animals were then offered specimens of *L. italica* and their behaviour was observed.

On several occasions intertidal lizards were seen to eat discarded fruit remnants (particularly banana skins) left behind by tourists. However, they were also seen to exhibit alertness whenever specimens of Ligia were visible nearby. Often they were seen to stalk isopods, but usually disappeared from view in the jumble of beach pebbles before food capture was observed. However, on the afternoon of 17.8.93 two black lizards were seen to capture and eat Ligia. One caught a single isopod (capture and handling taking 5 s), but the other first chased two large groups (n>20) of isopods without success, ceasing pursuit within 0.2-0.4 m. It then chased, caught and swallowed a large isopod (catching and handling time 10 s), rested for 60 s before jumping in the air to catch a dipteran fly. It ate another Ligia before disappearing into the pebble substratum in pursuit of another isopod.

The single animal dissected was a mature male (overall length 134 mm; snout-to-vent length 61 mm). On dissection the stomach contents were found to consist wholly of five large, partly digested *Ligia*. The isopods were in pieces; all of the heads were separate from the bodies. The droppings of the three other captured lizards revealed the following material:

Lizard 1: Parts of the exoskeleton of a large cockroach (attracted into the banana-baited trap?), several parts of *Ligia* exoskeleton, particularly the eyes, plus a small piece of polythene sheet.

Lizard 2: Droppings contained *Ligia* exoskeleton pieces, two dipteran pupal cases, and parts of a large cockroach.

Lizard 3: Beetle elytrae and large numbers of *Ligia* eyes.

The three animals held captive after trapping took specimens of *Ligia* offered to them immediately after collection of droppings (i.e. when they had fasted for 24 hr). They were subsequently held for several months during which they were fed exclusively on a diet of *Ligia* and talitrid amphipods.

In conclusion, the observations recorded in this study indicate that there is a separate population of melanic P. dugesii that forages entirely or predominantly between the tidemarks at Caniço, Madeira, the most important item of diet being the large, amphibious isopod L. italica. The population appears to be readily separable from nearby terrestrial populations by virtue of its black coloration, though there are subtle morphological differences too. Although Sadek (1981) included 'beach' populations in his study of the diet of P. dugesii on Madeira, he makes no reference to melanic lizards on the main island of Madeira, and it seems likely that he caught supralittoral/terrestrial predators rather than intertidal foragers, particularly as the diet of his 'beach' specimens was dominated by ants, beetles, flies and amphipods (which may well have been terrestrial talitrids, common on Madeira (Dahl, 1967)). Both Crisp et al. (1979) and Bischoff et al. (1989) also fail to mention melanic lizards on the main island of Madeira.

Other carnivorous lizard species are known to forage entirely within the intertidal zones of islands: *Anolis agazzi* and *Diploglossus haycocki* which both eat intertidal crustaceans on the Isla Malpelo, Colombia, and the skink *Cryptoblepharus boutoni* which eats insects, crustaceans and juvenile fish on Madagascar (Fricke, 1970), migrating up and down the shore in similar fashion to *P. dugesii*. Although no other lacertid lizard has been reported to use the intertidal zone in this fashion, such behaviour might be expected from other wall lizards living on islands (e.g. in the eastern Mediterranean) where *L. italica* is to be found.

The following factors may have encouraged the development of intertidal foraging on Madeira. On most Atlantic coastlines the productivity of cobble/pebble beaches is dominated by strandlines at the top of the shore where rotting wrack supports a diverse talitrid

amphipod and insect (dipterans and beetles) fauna. Such strandlines are less important on a volcanic island like Madeira whose seaweed beds are very limited in extent. Instead, the dominant animals are large L. italica that feed on green algae on boulders and in pools, but also eat detritus, lichens and microbial films as they move up and down with the tide. On most eastern north Atlantic shores a different member of the genus is found, Ligia oceanica L. (see Vandel, 1960 for discussion). However, L. oceanica is a nocturnal species (Nicholls, 1931) that hides under stones throughout the day, whereas L. italica (at least on Madeira) is a day-active isopod that hides at night when predatory grapsid crabs (mainly Pachygrapsus maurus) are numerous and active on the wet rocks. Lizards are diurnal visual foragers, too slow-moving in the cool of the night to catch fast-moving animals, so the daytime coincidence of P. dugesii and its isopod prey is important. Additionally, in most coastal intertidal environments there is an alternation of predatory influences with fish and crabs dominating when the tide is in, and sea birds dominating when the tide is out, at least during the day. On Madeira the influence of birds on the intertidal zone is very limited since the number of resident seabirds is low (e.g. Jepson & Zonfrillo 1988), there are no members of the crow family on Madeira (Bannerman & Bannerman, 1965) and even migrant waders are sparse (Zonfrillo, pers. comm.). Both P. dugesii and its prey avoid predation at high tide and/or night by moving off the shore or hiding amongst the pebbles of the substratum; they can both exploit the intertidal zone during the day with little or none of the risk that they would face during the day if there were more wading birds, or if corvids were present.

The reliance of a population of *P. dugesii* on a diet of intertidal isopods poses a number of interesting questions regarding salt and water regulation. No data concerning the osmoregulatory capacity of L. italica appear to have been published, but the related L. oceanica, L. occidentalis and L. pallasii are all powerful osmoregulators at low salinities and are actually hyperosmotic to full sea water (Parry, 1953; Wilson, 1970). This suggests that the body fluids of the isopods will have osmolarities of at least 1000-1100 m Osmoles kg⁻¹, some 2-3 times the likely plasma osmolarity (probably ca 350-400 m Osmoles kg⁻¹) of the lizards. Although the ready availability of Ligia will provide abundant food for intertidal P. dugesii, the lizards must incur a considerable salt load when exploiting this resource. Whether the lizards cope with this salt loading behaviourally by seeking out freshwater for drinking, or physiologically by extra-renal salt secretion is as yet unknown.

The melanic nature of the intertidal *P. dugesii* is undoubtedly cryptic, given the unrelieved black/grey colour of the rocks and stones of the Madeiran intertidal zone. The small body size of the species makes it unlikely that the black colour provides any thermoregulatory advantage; Crisp *et al.* (1979) have already provided good experimental evidence dismissing this possibility for the melanic *P. dugesii* living on the Desertas islands. The differences in size and proportions exhibited by the intertidal population of *P. dugesii* are more difficult to understand, although the Galapagos marine iguana (also melanic) has similarly well developed toes and claws for maintaining purchase on a slippery substratum (Bell, 1825; Trillmich & Trillmich, 1986).

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