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SHORT NOTE

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The Madeira lizard *Teira dugesii* may have the greatest population density of any terrestrial vertebrate

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Population density is a key demographic parameter that is fundamental to ecology, evolution, and conservation. All else being equal, denser animal populations should have lower extinction risk, higher intraspecific competition, greater genetic diversity, greater reproductive investment, and contribute more to energy flow through ecosystems, both by providing more resources to predators and by a tendency to be more generalist in their ecology than rarer species (Gaston & Kunin, 1997). Hence, understanding and documenting population densities of species gives important insight into their natural history beyond their population dynamics.

The Madeira lizard *Teira dugesii* is a lacertid species endemic to Madeira (both the Madeiran and the Selvagens archipelagos) and is the only native terrestrial reptile on those islands (Arnold & Ovenden, 2002). On Madeira, the species is typically very bold, allowing people to approach closely, and is found throughout the island from sea level to the top of the highest peaks at ~1850 m a.s.l. (Arnold & Ovenden, 2002). The Madeira lizard is found in a wide range of habitats including arid islands like Deserta Grande and rocky coasts within the spray zone (pers. obs.), and has a similarly broad diet (Sadek, 1981). Lizards occur almost everywhere on the island with sufficient cover for shelter, particularly holes in walls, tree bark, and other vegetation, including in the middle of the city of Funchal.

Perhaps as expected from the highly generalist habits of the species, it is frequently reported to be very abundant on the islands it inhabits. For instance, Arnold & Ovenden (2002) state it is “extremely common, sometimes with up to 4 individuals per square metre”, and Galán & Vicente (2003) refer to there being “very high densities over most of the island of Madeira”. Moreover, Koleska et al. (2017) published an observation of an aggregation of “>30 males and females on a single spot”, and added that “many more individuals (>100) were observed on cracked sun-exposed rocks in the surroundings”. While the latter authors provided a photo of the particular observation they document, showing many lizards using what appears to be a particularly good basking spot, there is no indication of the area over which the >100 other lizards were observed, or whether the photographed aggregation was typical or unusual. Indeed, with the exception of Arnold & Ovenden’s (2002) statement of “up to 4 individuals per square metre” we were unable to find quantitative statements or data on the population densities of Madeira lizards.

Figure 1. Illustration of high density of *Teira dugesii* on a representative wall with holes for shelter. This style of wall is common throughout the island and is a frequent lizard habitat.

Following a visit to Madeira on 15–22 April 2022, we were struck by the very high density of Madeira lizards throughout the island. We noticed comparably high abundances of lizards wherever there were suitable shelters (present over most of the island) such as rock outcrops, walls with holes, or vegetation, such that across the island we could readily find a great many individuals as soon as the sun shone on surfaces with nearby shelters (Fig. 1), as can also be seen in a video we recorded (BHS video, 2023). Consequently, we visited Madeira again on 23–30 May 2022 with the aim of estimating the density of Madeira lizards in a representative sample of suitable habitat within the gardens of the Quinta Jardins do Lago hotel.

Our primary estimate of density was based on surveys of walls containing holes which were in the sun at the time of survey, to ensure lizards would be active and hence visible. Such walls have several features which enable the most accurate estimates of density to be made. First, by using open walls (not covered by vegetation) our view was not obstructed and an accurate count of individuals could be made. Note that individuals could be identified due to substantial variation in colour-pattern, size, and location

Figure 2. Top of Galapagos tortoise shelter showing lizards basking on top and two in the foreground emerging from the gaps between bamboo that led to a tray under the roof

on the wall. Second, this is a representative habitat for the lizards, and similar walls (or analogous cliffs and outcrops) are found throughout the island, so such surveys should give meaningful natural history information. Third, the walls are easy to define and sample systematically to ensure representative surveys, such that we did not bias sampling towards disproportionately high-density areas. Finally, it is straightforward to calculate the surface area of walls and hence calculate density as number of lizards per m^2.

On 24 May 2022 we sampled all walls around the gardens that met the a priori criteria of being free from vegetation, containing holes for shelter (i.e. not cemented), and in the sun at the time of sampling. These criteria were designed only to enable accurate counts in suitable habitat for the lizards, and resulted in ten surveys. Upon identifying each wall, we remained ~3 m away and observed the wall for five minutes, counting the number of individual lizards active on the wall surface. The distance was sufficient to avoid disturbance to the lizards and the timeframe was chosen since this was apparently sufficient for all or most lizards in the wall to become active (no new individuals were visible towards the end of the sampling period). We then measured the dimensions of the wall with a measuring tape and calculated its surface area in m^2. It is possible that some lizards remained sheltering in holes, such that our density estimates are underestimated, but our sampling strategy was optimised to provide as accurate a measure as possible.

Although our wall surveys are our primary estimates due to their relative accuracy, we also took two supplementary approaches to illustrate density measures with other methods and locations. We used a series of line transects along all paths in the gardens which were bordered with vegetation (providing shelter), and counted all lizards spotted basking or fleeing within 1 m of the path edge. There were 18 transects meeting the criteria of having vegetation along their borders, and we calculated density as number of lizards per m of path. These transects were surveyed on 29 May 2022, but as there

Table 1. Data from wall surveys including calculated density estimates in individuals per m^2, and conversions of these estimates to individuals per hectare and per km^2 to enable comparisons with previous studies of vertebrate population densities

Location	Observation start time	No. of lizards	Area of wall (m^2)	Density (per m^2)	Density (per hectare)	Density (per km^2)
1	11:30 h	17	1.548	10.982	10,982	10,982,000
2	11:45 h	7	4.305	1.626	1,626	1,626,000
3	12:02 h	18	1.872	9.615	9,615	9,615,000
4	12:22 h	9	3.1	2.903	2,903	2,903,000
5	12:35 h	2	0.425	4.706	4,706	4,706,000
6	12:45 h	13	0.624	20.833	20,833	20,833,000
7	12:54 h	8	0.86	9.302	9,302	9,302,000
8	13:07 h	16	1.578	10.139	10,139	10,139,000
9	14:12 h	10	2.675	3.738	3,738	3,738,000
10	14:28 h	16	2.981	5.367	5,367	5,367,000
			Mean:	7.921	7,921	7,921,000

was intermittent rather than full sun, basking conditions were varied. This factor, as well as the more limited visibility of lizards in path-side vegetation, will likely have resulted in substantial underestimation of density. We tried to estimate the effect of weather by resampling the two transects that were undertaken under the most cloud cover. Resampling was undertaken within one hour of the original samples to minimise the chances of lizards leaving or entering the area in substantial numbers.

Our final supplementary density measure made use of a bamboo shelter for a resident Galapagos tortoise. This structure enabled visibility both of lizards basking on top (analogous to wall surfaces) and also inside the roof of the structure, as this was visible from the side through gaps in the bamboo (Fig. 2). The roof had a relatively shallow gap of ~5 cm underneath which had a metal tray at its base, so we counted all lizards using this shelter at 14:38 h on 24 May 2022 and measured the surface area of the roof to calculate the density as the number of individual lizards per m^2.

Densities estimated from wall surveys were very high in all ten walls sampled, with a mean of almost eight lizards per m^2 and densities as high as >20 lizards per m^2; the lowest density recorded was still >1 lizard per m^2 (Table 1). Although prone to substantial underestimation, estimates of lizard densities from our line transects along pathways were still high, with a mean of ~1 lizard per m (Table 2). Notably, when the two transects that were surveyed under the most overcast conditions were repeated in sunny conditions the estimated densities increased ~twofold. This indicates the impact that the intermittent sun during the transects likely had in compounding the underestimation of density, and so reinforces the high densities of Madeira lizards reported here. Finally, we counted 31 lizards on and just under the 2.660 m^2 roof of the tortoise shelter, giving a density of

Table 2. Data from line transects along paths, including calculated density estimates in individuals per m and the two resampled transects

Transect	Observation start time	Number of lizards	Transect length (m)	Density (lizards/m)
1	12:46 h	8	26	0.308
2	12:48 h	7	14	0.5
3	12:52 h	6	5	1.2
4	12:55 h	16	13	1.231
5	12:57 h	29	20	1.45
6	13:00 h	3	5	0.6
7	13:04 h	16	12	1.333
8	13:07 h	6	9	0.667
9	13:09 h	7	17	0.412
10	13:10 h	8	23	0.348
11	13:13 h	11	18	0.611
12	13:15 h	20	14	1.429
13	13:19 h	15	21	0.714
14	13:23 h	27	24	1.125
15	13:25 h	15	14	1.071
16	13:26 h	17	9	1.889
17	13:29 h	14	25	0.56
18	13:32 h	9	16	0.563
Resample				
1	13:37 h	19	26	0.731
5	13:41 h	69	20	3.45
			Mean of original samples:	0.89
			Mean of resamples only:	2.09
			Mean using resamples for transects 1 and 5:	1.02

11.654 lizards per m^2. Notably, this is within the range of the wall surveys but slightly higher than the estimates from most walls, perhaps reflecting the fact that we could also view lizards which may have stayed hidden inside the shelter rather than just those which were active on the surface.

Taking the mean density calculated from the wall surveys as the most accurate estimate, our data suggest population densities of Madeira lizards as almost twice the value stated by Arnold & Ovenden (2002), though it is unclear what (if any) data the latter is based on. The estimated density of Madeira lizards in our study is higher than the highest values reported for birds or mammals, and is towards the high end of estimates from reptile and amphibian populations compiled by Santini et al. (2018a). Importantly, those authors caution that the values reported in their compilation are not means, and extreme values may be unrepresentative; in this vein we note that 40 % of our individual wall samples had higher densities than the maximum in that compilation. Indeed, Rodda et al. (2001) reported that many population density estimates make little attempt to be representative and in fact target specific areas for their disproportionately high-density populations. In contrast, we aimed to choose a representative location based on our casual observations of Madeira lizards across the island and took repeated samples from conditions specified a priori to estimate a mean.

Rodda et al. (2001) report that the highest density terrestrial vertebrate population is their estimates of 13,400 and 52,800 *Sphaerodactylus macrolepis* geckos per hectare. Our mean estimate of 7,921 *T. dugesii* per hectare therefore appears to fall short of this record in number of individuals. However, since most vertebrates living in high densities are small, Rodda et al. (2001) argue that biomass density may be a better comparison across species than number of individuals, for which their estimates of *S. macrolepis* density is 3.60–15.26 kg per hectare. Since *T. dugesii* are much larger than those geckos, we estimate their biomass density using our mean individual density multiplied by a mean body size of 4.84 g (Galán & Vicente, 2003) as 38.34 kg per hectare, over twice the previous record density for terrestrial vertebrates.

Many factors have been found to influence population density (Santini et al., 2018b), but an important promoter of high population density is low predation rate (Salo et al., 2010). Although no direct data on total predation rates exist for Madeira lizards, these may be expected to be low compared to many other lizards. Despite many individuals having regenerated tails (pers. obs.), which may be from predation or intraspecific aggression, and occasional records of predation from species that don't usually prey upon vertebrates (Rocha et al., 2010), potential predators of lizards are few in number on Madeira. The native fauna of the island contains no snakes, larger lizards, terrestrial mammals, or corvids, and while some other birds such as shrikes, hoopoes, and starlings may occasionally eat lizards, they are all relatively rare on Madeira (Bowler, 2018). Only diurnal raptors are likely notable predators but the rate at which they feed on *T. dugesii* is unknown. Even more indirectly, low predation rate is known to favour slower life histories (Promislow & Harvey, 1990; Sparkman et al., 2013), and consistent with this, Madeira lizards tend to have higher longevity and larger eggs than other lacertid species (Galán & Vicente, 2003; Jesus, 2012), even compared to insular species which also tend to have slower life histories (Novosolov et al., 2013).

Although achieving comparable estimates of population density across species is challenging, we here report that the Madeira lizard has a very high population density, indeed one of the highest amongst terrestrial vertebrate species in terms of number of individuals. If biomass is incorporated, this species may in fact have the highest biomass density of any terrestrial vertebrate so far recorded. We suspect this is a consequence of unusually low predation pressure on Madeira lizards from the paucity of predators on Madeira, and encourage more detailed studies into the natural history of this species.

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