

# What do myrmecophagous geckos eat when ants are not available?: comparative diets of three Socotran species

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The diet of three populations of semaphore geckos (*Pristurus*) from Socotra archipelago is analysed based on 82 faecal pellets. *Pristurus samhaensis* from the small islands of Samha ( $n = 18$ ) and Darsa ( $n = 24$ ) and *P. sokotranus* from the main island of Socotra ( $n = 40$ ) were compared. Like other *Pristurus* species, *P. samhaensis* on Samha and *P. sokotranus* on Socotra were highly myrmecophagous (76.7% and 38.6% ants, respectively). However, ants were absent from the diet of *P. samhaensis* on Darsa. In contrast to the rich native ant fauna of the other islands, only one ant species was reported for Darsa, *Pheidole teneriffana*, likely a recently introduced species. *Pristurus samhaensis* seems to have overcome this scarcity in ant prey by consuming substitute prey, namely Coleoptera and Heteroptera, which are secondary for the other two populations studied. The two *P. samhaensis* populations inhabiting the small islands displayed less diverse diets compared to that of *P. sokotranus* from the main island where vegetation structure was more complex. Prey items of *P. samhaensis* from Darsa were also smaller than those of *P. sokotranus* from Socotra, those of *P. samhaensis* from Samha being intermediate. It remains unclear how ancient these differences are, but they are probably too recent to have promoted special morphological and ecological adaptations in these geckos.

**Key words:** trophic ecology, myrmecophagy, Gekkonidae, *Pristurus samhaensis*, *Pristurus sokotranus*, Socotra.

## INTRODUCTION

The Socotra archipelago is considered a biodiversity hotspot of global importance (Di Micco De Santo & Zandri 2004), characterized by a high degree of endemism in many groups of terrestrial flora and fauna, including reptiles. Among the latter, semaphore geckos of the genus *Pristurus* are represented by as many as seven species, all endemic to the archipelago (Rösler & Wranik 2006; Arnold 2009). Although some taxonomic and distributional information on these species is available (Rösler & Wranik 1999), studies on the ecology and life-history of this interesting group of diurnal geckos are largely lacking (Sindaco *et al.* 2008, 2009). Only limited information is available on the diet of these species. In a general review Arnold (1993) reported that 50% of the prey items found in stomach contents of *Pristurus sokotranus* were ants. This species, like other basal members of the genus, has been described as an active forager (Wranik 2003; Arnold 2009). Myrmecophagy is common among semaphore geckos, also in continental areas,

and can be considered a prominent trait in the feeding ecology of the genus (Arnold 1986, 2009).

In this paper, a quantitative analysis of the diet of *P. samhaensis* Rösler & Wranik, 1999 and *P. sokotranus* Parker, 1938 is presented. For the former, populations from two different islands (Darsa and Samha) are analysed. On the smaller island, Darsa, ants were never recorded during field sampling, whereas ants are common and widespread on the other islands of the archipelago. Although further work is needed to fully characterize Darsa's faunal assemblages, preliminary information suggests that only one ant species is present, which is likely the result of recent human-mediated colonization (Collingwood *et al.* 2004, see below). Therefore, of particular interest was the diet of this primarily myrmecophagous gecko when its usual prey is absent or rare. A population of the same gecko species from Samha island, where ants are abundant, was used for comparison. Furthermore, in order to evaluate possible phylogenetic influences, both populations were compared to *P. sokotranus*, a closely related (*S. Carranza*, unpubl. data), similarly sized species

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from Socotra, the main island, where ants are also abundant.

## MATERIALS & METHODS

### *Study species*

*Pristurus sokotranus* occurs exclusively on Socotra, whereas *P. samhaensis* is endemic to Samha and Darsa. Like other phylogenetically basal *Pristurus* species, these two species are mainly heliothermic climbers on rocky surfaces (Arnold 2009). Both seem to be relatively common throughout the islands, occupying a wide range of habitats, but especially rocky outcrops and stones used as basking sites. The geckos are active throughout the day and are constantly alert, taking quick refuge in the crevices when alarmed. According to Rösler & Wranik (2000), no significant differences in size (see Results) or external morphology exist between *P. samhaensis* individuals from Samha and Darsa.

### *Study areas*

Study sites were located on three islands of the Socotra Archipelago (Republic of Yemen), in the northwestern corner of the Western Indian Ocean, 250 km off the Somali coast. The main island, Socotra, covers an area of 3625 km<sup>2</sup> and reaches a maximum altitude of 1526 m a.s.l. (at Jabal Dryet Mount). Although *P. sokotranus* is widely distributed on the island, field sampling was carried out only at Wadi Da'arho (about 400 m a.s.l.), on the southeastern boundary of the Firmihin Mountains. A small, perennial stream runs through the otherwise dry riverbed (*wadi*), but most part of the bed is covered by stones and boulders. The vegetation is mainly represented by date palms (*Phoenix dactylifera*) along the edges and sparse succulent scrubland on the nearby rocky slopes, dominated by *Adenium obesum sokotranum*, *Jatropha unicostata*, *Croton sokotranus* and *Euphorbia arbuscula*. At Samha Island (41 km<sup>2</sup>, 779 m a.s.l., 40 km southwest of Socotra), the study area was the western coastal plain (10–20 m a.s.l.), characterized by sandy–rocky mixed substrate and covered by dwarf scrubland dominated by *Limonium sokotranum* and *Aizoon canariense*. At Darsa (12 km<sup>2</sup>, 350 m a.s.l., 50 km southwest off Socotra and 20 km west off Samha), the smaller and uninhabited island of the archipelago, field work was carried out on the northern slope (10–50 m a.s.l.) covered by chenopod shrubs, such as *Atriplex griffithii* and *Suaeda monoica*, and low herbaceous vegetation. The climate of the archipelago is typically arid, with a monsoon influence;

the limited downpours are concentrated in winter and increase with altitude (Mies & Beyhl 1998; Culek *et al.* 2006). According to the *Worldclim* database (<http://www.worldclim.org/bioclim>; Hijamns *et al.* 2005), the climatic differences between the three localities are minimal. Annual mean temperatures (minimum of the coldest month – maximum of the warmest month) and annual precipitation are 25.5°C (19.1–33.1), 9.5 mm for Socotra; 25.8°C (19.2–33.5), 8.0 mm for Samha; and 25.5°C (19.1–33.1), 9.5 mm for Darsa.

### *Sampling and laboratory methods*

Field sampling was carried out during the wet season, between February and March 2009. A total of 82 faecal pellets (18 of *P. samhaensis* from Samha, 24 of *P. samhaensis* from Darsa and 40 of *P. sokotranus* from Socotra) were obtained by gently handling collected geckos. All the specimens were measured (snout–vent length, SVL) to the nearest 0.1 mm using a digital calliper and released at the site of capture. The faecal contents were examined under a stereomicroscope ( $\times 10$ –40). Remains were sorted and identified to the order/family level. Item counting was based on cephalic capsules, wings and legs, following the minimum numbers criterion by sample. When possible, prey size was estimated by measuring fragments with a micrometer eyepiece and calculating length using regression equations (Hóðar 1997).

### *Statistical analysis*

Three diet descriptors were used: the percentage of pellets containing a specific prey category (%P), the percentage of numeric abundance of each prey category (%N), and the use index (IU) (Jover 1989). The latter is preferred because it combines %N and %P. The importance of a certain prey category in the diet was estimated by calculation of the homogeneity of its consumption throughout all the individual contents (Carretero 2004; Carretero *et al.* 2006). Brillouin's index was used to estimate the diet diversity according to Magurran (2004). For a given sample, the average individual diversity ( $H_i$ ) was obtained by averaging the diversity values of each pellet and the (asymptotic) population diversity ( $H_p$ ) was estimated through jack-knife pseudosampling (Jover 1989). Whereas  $H_i$  and  $H_p$  have standard errors and allow statistical comparisons, the total accumulated diversity ( $H_z$ ) of all pellets is a fixed value only provided to allow comparison with values in the literature (Ruiz & Jover 1981). Individual

**Table 1.** Taxonomic composition of the diet of three *Pristurus* populations. %P: percentage of presence; %N: percentage of numerical abundance; IP: probabilistic index; IU: resource use index: – not consumed; 0.00: consumed but index value close to zero. Hi: individual diversity; Hp: population diversity; Hz: total accumulated diversity; all using Brillouin's index. Numbers indicate mean  $\pm$  S.E.

Prey category	<i>Pristurus samhaensis</i> (Samha)				<i>Pristurus samhaensis</i> (Darsa)				<i>Pristurus sokotranus</i> (Socotra)			
	%P	%N	IP	IU	%P	%N	IP	IU	%P	%N	IP	IU
Isopoda	–	–	–	–	–	–	–	–	15.00	6.19	12.41	6.20
Araneae	11.11	3.45	3.69	1.31	–	–	–	–	17.50	7.22	9.84	7.86
Diptera	22.22	6.90	8.80	5.26	12.50	5.88	2.18	3.00	5.00	2.06	1.20	0.80
Orthoptera	5.56	1.72	0.46	0.00	4.17	1.96	5.15	0.00	5.00	2.06	3.35	0.80
Coleoptera	33.33	10.35	24.60	10.19	66.67	58.82	57.91	70.52	17.50	10.31	11.10	10.58
Hymenoptera	11.11	3.45	0.76	1.31	20.83	9.80	3.67	7.32	20.00	9.28	5.19	10.37
Formicidae	55.56	65.52	48.29	76.66	–	–	–	–	22.50	38.14	17.64	38.56
Homoptera	–	–	–	–	–	–	–	–	2.50	2.06	0.53	0.00
Heteroptera	22.22	6.90	12.93	5.26	33.33	19.61	28.52	17.89	20.00	8.25	15.85	9.60
Isoptera	–	–	–	–	–	–	–	–	2.50	2.06	1.47	0.00
Dermoptera	–	–	–	–	–	–	–	–	2.50	1.03	3.31	0.00
Arth unid.	5.56	1.72	0.46	0.00	8.33	3.92	2.57	1.26	27.50	11.34	18.11	15.22
N pellets, N items, items/pellet	18, 60, 2.13 $\pm$ 0.22				24, 51, 3.22 $\pm$ 0.48				40, 110, 2.45 $\pm$ 0.32			
Hi, Hp, Hz	0.10 $\pm$ 0.02, 1.78 $\pm$ 0.2, 1.57				0.07 $\pm$ 0.02, 1.77 $\pm$ 0.21, 1.57				0.07 $\pm$ 0.01, 0.07 $\pm$ 0.01, 2.63			

diversity and number of prey per pellet were compared using one-way ANOVA, whereas the population diversity was compared by *t*-tests corrected for multiple tests (Carretero & Llorente 1993), namely, using the False Discovery Rate (FDR) procedure (Benjamini & Hochberg 1995).

Similarity between diets was evaluated by means of Pianka's index of trophic overlap (Pianka 1973) applied on the IU values of prey categories and size classes (Carretero *et al.* 2006) using Ecosym software (Gotelli & Entsminger 2004). Hypotheses of non-random similarity (Gotelli & Graves 1996) were tested using the RA2 (niche breadth relaxed/zero states retained) and RA3 (niche breadth retained/zero states reshuffled) Monte Carlo randomization algorithms (Winemiller & Pianka 1990) generating 1000 pseudomatrices and considering each prey category equiprobable.

## RESULTS

*Pristurus samhaensis* from Samha (mean  $\pm$  S.E.: 42.58  $\pm$  0.60 mm; range: 38.50–49.40 mm;  $n = 18$ ), *P. samhaensis* from Darsa (mean  $\pm$  S.E.: 41.52  $\pm$  0.42 mm; range: 38.00–46.20 mm;  $n = 24$ ), and *P. sokotranus* from Socotra (mean  $\pm$  S.E.: 42.45  $\pm$  0.44 mm; range: 37.50–50.30 mm;  $n = 40$ ) did not differ significantly in body size (ANOVA  $F_{2,79} = 1.25$ ,  $P = 0.29$ ).

The number of prey items by pellet (Table 1) did not significantly differ between populations (ANOVA  $F_{2,79} = 2.04$ ,  $P = 0.14$ ). However, the three

populations displayed substantial differences in the prey taxa consumed (Table 1). The most obvious difference was the complete absence of ants in the diet of *P. samhaensis* from Darsa which constituted the most important prey for the same species on Samha and also for *P. sokotranus* on Socotra. In *P. samhaensis* from Darsa, Coleoptera and Heteroptera substituted ants as main prey; both OTUs were, in fact, the secondary prey of the other two populations/species. Diet diversity (Table 1) was similar between localities for individual pellets (ANOVA  $F_{2,79} = 0.52$ ,  $P = 0.60$ ). However, at population level, the diet of *P. sokotranus* was more diverse than those of the two *P. samhaensis* populations, which did not differ between them (*P. samhaensis* Samha–Darsa  $T_{40} = 0.03$ ,  $P = 0.48$ ,  $P_{FDR} = 0.48$ ; *P. samhaensis* Samha–*P. sokotranus* Socotra  $T_{56} = 2.94$ ,  $P = 0.002$ ,  $P_{FDR} = 0.004$ ; *P. samhaensis* Darsa–*P. sokotranus* Socotra  $T_{62} = 3.39$ ,  $P = 0.0006$ ,  $P_{FDR} = 0.002$ ).

Regarding the size of the items consumed (Table 2), differences were also marked. Mean prey size significantly varied between populations ( $F_{2,141} = 10.47$ ,  $P = 0.00006$ ), *P. sokotranus* from Socotra consuming larger prey items than the two populations of *P. samhaensis* (Scheffé tests,  $P < 0.05$ ), which were not distinguishable (Scheffé test,  $P = 0.29$ ). No significant correlations between predator (SVL) and prey sizes were detected within any of the species/populations (Scheffé tests,  $P > 0.05$ ).

**Table 2.** Prey size composition of the diet for the three *Pristurus* populations. %P: percentage of presence; %N: percentage of numerical abundance; IU: resource use index. 0.00: consumed but index value closet to zero.

Size class	<i>Pristurus samhaensis</i> (Samha)				<i>Pristurus samhaensis</i> (Darsa)				<i>Pristurus sokotranus</i> (Socotra)			
	%P	%N	IP	IU	%P	%N	IP	IU	%P	%N	IP	IU
0–3 mm	68.75	79.25	60.11	85.21	66.67	51.35	49.78	54.65	35.00	18.52	35.32	19.02
3–6 mm	31.25	9.43	10.36	7.40	55.56	43.24	48.32	45.35	45.00	72.22	44.45	75.23
6–9 mm	31.25	9.43	22.33	7.40	5.56	2.70	1.63	0.00	20.00	7.41	15.19	5.75
>9 mm	6.25	1.89	7.20	0.00	5.56	2.70	0.26	0.00	5.00	1.85	5.05	0.00
Total (mean $\pm$ S.E.)	53 (of 60) items measured 3.66 $\pm$ 0.24 mm				37 (of 51) items measured 3.53 $\pm$ 0.43 mm				54 (of 110) items measured 4.81 $\pm$ 0.48 mm			

Finally, diet similarities estimated through Pianka's index provided a summary of the overall differences. At the taxonomic level, the two *P. samhaensis* populations were the most dissimilar (0.15), *P. samhaensis* from Samha and *P. sokotranus* the most similar (0.92); and *P. samhaensis* from Darsa and *P. sokotranus* intermediate (0.31). In contrast, *P. samhaensis* from Samha and *P. sokotranus* displayed the lowest prey size similarity (0.33), the overlaps between the two populations of *P. samhaensis* (0.82) and between *P. samhaensis* from Darsa and *P. sokotranus* being higher (0.81). Pseudocommunity analysis revealed that taxonomic similarity attained a similar mean but higher variance ( $P = 10^{-5}$ ) than simulated in the RA2 matrix (zero states retained) whereas the mean was higher ( $P = 0.03$ ) and variance was similar than simulated in the RA3 matrix (niche breadth retained). No significant differences were detected for the size similarity for any of the algorithms.

## DISCUSSION

Our finding that the diet of *Pristurus samhaensis* from Darsa did not include ants, previously identified as the most important prey item of semaphore geckos (Arnold 1986, 2009), may suggest that the presence of ants may not be a limiting factor in the distribution of these geckos. On the other hand, the absence of native ants on Darsa may be a recent, man-induced phenomenon, the impact of which may not yet be fully apparent in the local gecko population.

As previously stated, Darsa seems to harbour an extremely impoverished ant fauna. The only ant species reported for this island is *Pheidole teneriffana*, a species native from North Africa (Wilson 2003) and which has widely colonized the Middle East, Arabia and the Mediterranean countries. A number of collecting surveys have been

undertaken on Darsa during recent years (see e.g. Wranik 2003; Taiti & Ferrara 2004) and it is unlikely that other ant species have remained undetected. Alien ants are frequently introduced by man on islands (McGlynn 1999), as seems to be the case for *P. teneriffana* on Darsa (Collingwood *et al.* 2004). Since it may displace native species (Collingwood *et al.* 1997), its occurrence could possibly explain the unexpected lack of native ant species, although its invasive potential is often low (Snelling 1992; Espadaler & Bernal 2003; Gómez & Espadaler 2006; Wetterer *et al.* 2007). It must be taken into account that even strictly myrmecophagous lizards do not indiscriminately consume ants but usually select certain species and avoid others (Newbold & MacMahon 2009). Thus, an abrupt change in the ant fauna on Darsa may have severely altered the prey consumption by *P. samhaensis*.

*Pristurus samhaensis* seems to have overcome the restriction in its preferred prey by consuming more of other prey categories within the usual prey spectrum of *Pristurus* (Arnold 1983). This has kept trophic diversity fairly similar between the two small islands of Samha and Darsa. Only *P. sokotranus* from the bigger and entomologically richer Socotra displayed a more diverse diet. Thus, the diet of semaphore geckos on the three islands varied from *P. samhaensis* feeding almost exclusively on small Coleoptera and Heteroptera on Darsa, to also incorporating ants on Samha, to adding other big prey such as Isopoda and Araneae on Socotra.

It remains unclear how ancient these trophic patterns are, but they are probably too recent to have promoted special morphological and ecological adaptations in the semaphore geckos. Apart from the probable contemporary introduction of *P. teneriffana*, it must also be taken into account that the isolation of *P. samhaensis* on Darsa only dates back to the last eustatic sea event (about 18 000 y



B.P.), the island being connected to Samha and Socotra during the Last Glacial Maximum (Fleitmann *et al.* 2004; Van Damme 2006). To what extent the population of *P. samhaensis* on Darsa is stable under these conditions is also unknown and would require proper monitoring. Further research should also explore seasonal variation in diet, as well as trophic behaviour of the three populations. A phylogenetic assessment of all Socotran *Pristurus*, including biogeographic scenarios and calibrations, is also needed (Arnold 2009).

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