

NOTES ON THE FOOD HABITS OF *COLUBER HIPPOCREPIS NIGRESCENS* FROM PANTELLERIA ISLAND: A SNAKE THAT FEEDS ON BOTH CARRION AND LIVING PREY

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The food habits of *Coluber hippocrepis nigrescens*, a colubrid snake endemic to the island of Pantelleria in the southern Mediterranean Sea, were studied by means of both stomach contents and faecal analyses. Snakes preyed only on vertebrates, and most of the prey eaten were rodents (especially *Rattus norvegicus*). Ingested biomass per snake averaged 55.63±48.94 g (range: 8 - 131 g), i.e. about 28.5 % of the average snake mass (195.18 ±65.61 g; range: 39 -277 g). Log prey mass and log predator mass were positively correlated. The prey mass to predator mass ratio was not significantly correlated with log predator mass. 36.36% of the prey found in *C. hippocrepis* stomachs was eaten by snakes when it was already carrion, as demonstrated by the presence of abundant flesh-fly larvae in rats regurgitated by snakes. This is a very unusual foraging mode for snakes, which are known as active predators feeding on live organisms. We hypothesize that this unusual foraging mode is an adaptive strategy depending on (1) low level of food availability and (2) high abundance of dead prey, on this arid Mediterranean island.

INTRODUCTION

Coluber hippocrepis is a colubrid snake widespread in north Africa and western Europe, and has scattered populations on some islands of the Italian Mediterranean Sea, i.e. Sardinia and Pantelleria (Bruno & Maugeri, 1990). In the former island this snake is very rare and endangered (Bruno & Hotz, 1976; Puddu, Viarengo & Erminio, 1988), whereas on Pantelleria it is widespread and relatively common (Cattaneo, 1985). The Pantelleria population has recently been described as an endemic subspecies, *C. hippocrepis nigrescens*, characterized by a high tendency towards dark colouration and melanism (Cattaneo, 1985).

Detailed data on the food habits of *C. hippocrepis hippocrepis* are available from Spain (Garzon, 1974; Vericad & Escarré, 1976; Pleguezuelos & Moreno, 1990). On the other hand, practically nothing is known about the Pantelleria population (Cattaneo, 1985), which should deserve attention by herpetologists due to its endemic status. This lack of knowledge is also serious because island populations of snakes may be very interesting to study. They may reveal remarkable life-history traits that are not normally observable in mainland populations, due to the rapid adaptive shifts possible in island taxa with small and discrete populations (Pendlebury, 1974; Schwaner, 1985; Shine, 1987; Capula, Rugiero & Luiselli, 1994).

The aim of this paper is to present preliminary information on the dietary habits of *C. hippocrepis nigrescens* from Pantelleria, focusing our attention on a

very unusual foraging mode for snakes: feeding on prey corpses found in the field.

STUDY AREA AND METHODS

The field study was carried out in Pantelleria, an offshore volcanic island of the Mediterranean Sea (about 83 km² area) situated about 110 km SW of Sicily. The climate is Mediterranean-arid, with strong winds over much of the year. The vegetation is characterized by evergreen Mediterranean maquis, with very scarce arboreal cover. The snakes mainly inhabit grassy and bushy spots close to walls and stone piles. The surveyed area extended for about 95 ha. In the study area, *C. hippocrepis* is relatively widespread, although it cannot be considered common. Most of the adults encountered were about 110-140 cm long (total length), but larger individuals (all males) were occasionally found. The largest individual captured in the study area was 186 cm long (C. Bagnoli, personal communication), but there are records of specimens exceeding 190 cm (Cattaneo, 1985; A. Cattaneo, *in verbis* to C. Bagnoli). The melanistic condition was apparently more evident in large than in small individuals (Capula *et al.*, unpublished observations).

We collected field data during three surveys conducted in the island of Pantelleria: June 1995, October 1995 and April 1996. A total of 32 field days (each about ten hours long) were spent in the field. Moreover, additional data come from a survey by Mr Claudio Bagnoli (Rome), conducted in May, 1995.

When a snake was seen, it was captured by hand, sexed by analysing tail morphology, and body mass (to the nearest 0.1 g with an electronic balance) and SVL (snout-vent length, to the nearest 0.5 cm) were measured. Contrary to other studies (e.g. see Luiselli, Capula & Shine, 1996), we measured SVL rather than TL (total length) because several specimens had broken tails, possibly due to injuries caused by humans. Food items were collected by gentle pressing of the snake abdomen until regurgitation occurred, or by faecal analysis. Faeces were obtained only from snakes palpated in the field, and were not collected from the ground. Food items were identified to the lowest taxon possible. In the case of faeces, mammal hairs were easily recognized by medulla, cuticola and cross-section analyses, whereas saurian remains were identified by scale examination. Biomass of prey was measured only from stomach ingesta. In this case, we calculated the fresh mass of the prey as in Luiselli & Agrimi (1991). The snakes were also individually marked by "scale-clipping" to avoid multiple recounts of the same individuals. No snake was killed or injured during the course of this study.

RESULTS

Throughout the study period we captured a total of 36 snakes, including both captures (26 different specimens: 18 males and 8 females) and recaptures (10 recaptures of 9 individuals previously marked). The average capture rate was 1.12 snakes per day. The estimated population size (according to Lincoln's index in Seber, 1982, used as in Ineich, 1988) was 147.6 snakes, and the approximate density was 1.55 snakes per ha.

Handling of these snakes resulted in 28 prey samples, including those coming from both stomachs ($n = 11$) and faeces ($n = 17$). The summary of the dietary data is given in Table 1. The diet consisted only of vertebrates, and rodents constituted the main taxonomic category in the diet (71.43% of the total diet), followed

TABLE 1. Summary of the diet data obtained of *Coluber hippocrepis nigrescens* from the island of Pantelleria. Data come from analysis of both regurgitated ingesta and faecal pellets.

Prey type	<i>N</i> in faeces	<i>N</i> in stomachs	<i>N</i> total	%
Reptilia				
<i>Podarcis sicula</i>	4	3	7	25.0
Aves				
Passerine (unident.)	/	1	1	3.6
Mammalia				
<i>Rattus norvegicus</i>	6	5	11	39.3
<i>Mus domesticus</i>	1	2	3	10.7
Muridae (unident.)	6	/	6	21.4
Total	17	11	28	100.0

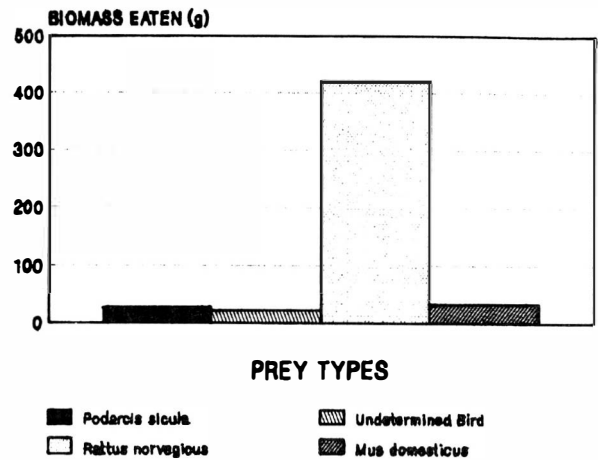


FIG. 1. Biomass (g) of the prey items regurgitated by *Coluber hippocrepis nigrescens* individuals from the island of Pantelleria. For each prey category, the biomasses of the various items obtained from snake stomachs are shown.

by lizards (25%) and passerine birds (3.57%). Contingency table analysis revealed that rodents were preyed upon significantly more often than birds ($\chi^2 = 8.59$, $df = 1$, $P = 0.0034$), but not significantly more often than lizards ($\chi^2 = 3.13$, $df = 1$, $P = 0.077$). *Rattus norvegicus* was the most predated taxon, followed by *Podarcis sicula* and by unidentified rodents. In terms of ingested biomass, *R. norvegicus* was still the most important prey source for *C. hippocrepis nigrescens* (Fig. 1).

Unfortunately, our sample of snakes containing prey remains included only two juveniles, both of them with a lizard in the stomach. Thus, we cannot fully evaluate eventual ontogenetic shifts in the diet of this snake population.

Mean ingested biomass per snake was 55.63 ± 48.94 g (range: 8 - 131 g, $n = 11$), representing about 28.5% of the average snake mass (195.18 ± 65.61 g; range: 39 - 277 g, $n = 11$). The prey mass / predator mass ratio averaged 0.260 ± 0.184 (range: 0.050 - 0.560, $n = 11$).

There was a significant positive correlation between log prey mass (as dependent variable) and log predator mass ($r = 0.619$, adjusted $r^2 = 0.315$, $n = 11$, intercept = -3.087 , ANOVA: $F_{1,9} = 5.604$, $P < 0.04$; Fig. 2). However, the prey mass to predator mass ratio was not significantly correlated with log predator mass ($r = 0.244$, $n = 11$, intercept = -3.087 , ANOVA: $F_{1,9} = 0.570$, $P > 0.45$), which means that the larger snakes did not tend to feed upon larger prey (relative to their own size) than the smaller snakes.

Four out of eleven (36.36%) prey found in *C. hippocrepis* stomachs were ingested by snakes when they were already carrion, i.e. they were not captured alive by the snakes. This was true for one ingested *Podarcis sicula* and three ingested *R. norvegicus*, weighing 131, 116 and 103 g respectively. In fact, examination of these disgorged rats revealed that their bodies were (1) full of flesh-fly larvae and (2) so damaged that they had clearly been killed by humans before being eaten by snakes. Examination of the lizard corpse

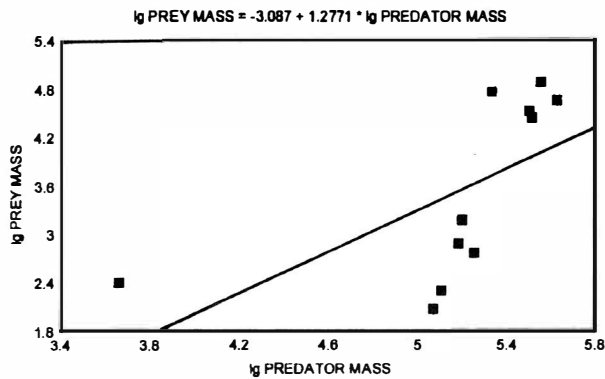


FIG. 2. Relationships between lg prey mass and lg predator mass in *Coluber hippocrepis nigrescens* from the island of Pantelleria. Regression statistics: $r = 0.619$, adjusted $r^2 = 0.315$, $n = 11$, intercept = -3.087 , ANOVA: $F_{1,9} = 5.604$, $P < 0.04$.

revealed that it had clearly been squashed by cars before being ingested by the snake.

The unexpected necrophagous foraging mode of *C. hippocrepis* from Pantelleria was also confirmed by experiments on captive animals: four adult snakes, housed in outdoor enclosures, immediately accepted dead and partially putrefied mice (*Mus domesticus*) only four days after their removal from the natural environment, thus showing they were familiar with this unusual type of prey.

Ten out of eleven prey found in snake stomachs were ingested head first (G test with $df = 1$, $P < 0.05$). In this regard, *C. hippocrepis* from Pantelleria mirror Spanish conspecifics (Pleguezuelos & Moreno, 1990).

DISCUSSION

Data given here, although preliminary, reveal remarkable foraging patterns for the endemic *C. hippocrepis nigrescens* from the island of Pantelleria.

To begin with, the taxonomic dietary composition of the Pantelleria snakes was rather similar to that of populations of *C. hippocrepis* from elsewhere, e.g. Spain (Pleguezuelos & Moreno, 1990). Adult diet consisted mainly of rodents and, to a lesser extent, lizards. However, in comparison to the Spanish populations studied by Pleguezuelos & Moreno (1990), the Pantelleria population preyed on larger prey (given that the body sizes of the two snake populations were quite similar). With regard to prey size in relation to predator size, *C. hippocrepis* from Pantelleria are unusual compared not only to Spanish conspecifics but also to most of the colubrid species studied until now. In fact, whilst the average prey mass to predator mass ratio averaged 0.260 ± 0.184 in the Pantelleria snakes studied here, this parameter averaged 0.18 in the various colubrid species from all over the world reviewed by Pough & Groves (1983), while the mean value for viperids was 0.36 (Pough & Groves, 1983). In this regard it is noteworthy that the prey mass: predator mass ratio of Pantelleria snakes is significantly higher (one-way ANOVA: $P = 0.0306$) than that of *Elaphe quatuorlineata* (mean = 0.125 ± 0.123 , see Capizzi & Luiselli, 1997), a large colubrid that suffocates prey before eating and that

could probably feed upon organisms larger (relatively to its own body size) than those normally available to non-venomous colubrids that eat live prey (e.g. *Coluber* species). Moreover, the mean prey mass: predator mass ratio of Pantelleria snakes was significantly higher (one-way ANOVA: $P = 0.0023$) than that (mean = 0.076 ± 0.053 , $n = 13$) of mainland *Coluber viridiflavus* (see Rugiero & Luiselli, 1995), a congeneric species characterized by similar (or even larger) body size. The same was true also for the mean size of the prey eaten, which was significantly larger (one-way ANOVA: $P = 0.0059$) in our island population of *C. hippocrepis* than in the mainland population of *C. viridiflavus* studied by Rugiero & Luiselli (1995) (mean = 13.09 ± 11.67 g, $n = 13$).

Why did *C. hippocrepis* from Pantelleria feed upon such unusually large prey? And, why did these snakes feed also upon carrion instead of having a "typical" snake diet based on living prey? We suggest that both questions could be answered with the argument that Pantelleria snakes developed such unusual traits in response to low level of live prey availability and high abundance of dead prey (chiefly rats killed by humans, cars and dogs), in this Mediterranean-arid island.

Indeed, it is in fact well-known that snakes inhabiting areas with low levels of food availability frequently try to capture and to ingest disproportionately larger prey (e.g. see Stergulc, 1983). On the other hand, foraging on carrion, although being an exceptionally rare event for free-living snakes, is a possible alternative strategy for these organisms, as demonstrated by the fact that many species (e.g. those belonging to the genera *Vipera*, *Elaphe*, *Coluber*, *Coronella*, *Natrix*, etc.) do easily accept dead prey when housed in captivity (Trutnau, 1981, 1982, and personal observations). Moreover, although rare, findings of free-ranging snakes scavenging on carcasses (also of large mammals such as wild pigs) have already been reported (e.g. see Heinrich & Studenroth, 1996; Torr & Richards, 1996). It is arguable that snakes consuming dead prey should probably be opportunistic predators that use chemical cues for foraging.

Foraging on corpses could also be important for permitting the Pantelleria snakes to feed upon disproportionately large organisms in an island ecosystem with low levels of food availability. In fact, these "necrophagous" snakes could benefit from the fact that they have no difficulty associated with subduing large and vigorous prey. Moreover, it is likely that the advanced state of putrefaction of the ingested dead prey speed up digestion, thus reducing the digestive problems usually associated with eating prey of large volume. If this hypothesis is right, it is possible to conclude that foraging upon corpses might achieve for Pantelleria *C. hippocrepis* the same effect of speeding up digestion as the venom (with digestive properties) injected by vipers into the body cavity of their prey (e.g. cf. Bdolah, 1977).

Therefore, it is hypothesized that the alternative strategy of foraging on corpses could be widely found

in snakes, but that only in peculiar conditions do these predators adopt this alternative strategy. These peculiar conditions could thus be present on the island of Pantelleria.

Our study documents at least a partial shift in feeding habits of island *C. hippocrepis* in terms of (1) average prey size and (2) status of the prey (carrion versus living organisms). Previous studies on island populations of snakes also documented shifts in feeding habits, although the type of prey rather than the foraging mode was the trait subjected to shift. For instance, island *Notechis* prey more frequently on endothermic prey than those of the mainland (Shine, 1987), and similar shifts have also been observed in boids (Pendlebury, 1974) and pitvipers (Wharton, 1969). In all these cases the shifts were probably responses to differences in prey availability, the same being true in the case of *C. hippocrepis* of the island of Pantelleria.

As rightly pointed out by Shine (1987), it is, however very difficult to determine whether these shifts in feeding habits and foraging modes reflect genetically-based adaptations or direct phenotypic responses to different food supplies.

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