



## Gastrointestinal responses to feeding in a frequently feeding colubrid snake (*Natrix maura*)

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### ABSTRACT

Ectotherm vertebrates show physiological mechanisms that reduce metabolic costs during prolonged fasting. Once feeding, these animals adopt a wide variety of metabolic responses such as changes in gastrointestinal organ masses. Up-regulatory responses after feeding have been widely explored in infrequently feeding snakes like pythons, whereas few studies have been devoted to frequently feeding snakes. In this study, we have considered the gastrointestinal responses after feeding in a frequent feeder, the viperine snake *Natrix maura*, in the Ebro Delta rice fields. In this habitat, viperine snakes are exposed to long periods of food deprivation due to the lack of available prey as a consequence of the man-induced rice cycle. We weighed prey items and full gut masses, and measured length of combined esophagus and stomach, and intestine of viperine snakes belonging to a wide range of sizes. Snakes concentrate foraging activity when rice fields were flooded. In this period, gut masses increased. Likewise, intestines increased in length during the feeding period, which suggests that viperine snakes probably experience a postfeeding hypertrophy of their small intestines that contributes to their larger length. Once the intestine length was corrected for the snake size, it was shown that adults present longer intestines than immature snakes, reflecting an increase in the posterior part of the body linked to the gonads development. This study contributes to explore the physiological responses to feeding in frequently feeding snakes modelled by abrupt shifts of food availability.

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### 1. Introduction

For many natural ecosystems, available food resources fluctuate seasonally. In such environments, animals exhibit behavioural and physiological responses to changes in food availability and feeding frequency (Starck, 2005; Wang et al., 2006). A recent interest in evolutionary physiology is the understanding of how some animals can endure long episodes of fasting and respond physiologically to refeeding (Piersma and Lindström, 1997; Wang et al., 2005; McCue, 2006). Extended periods of fasting for both ectotherms and endotherms are characterized by a reduction in basal rates of metabolism and atrophy of the gastrointestinal tract. With refeeding, the tract experiences rapid hypertrophy that results in restoration of digestive performance (Starck, 2005). Snake species that naturally feed infrequently on potentially large prey items have become popular models for studying the physiological and morphological responses to fasting and feeding (Secor and Diamond, 1998). Such snakes experience a large postfeeding increase in their metabolic rate (Andrade et al., 1997; Secor and Diamond, 1997; Ott and Secor, 2007), blood flow (Secor et al., 2000; Starck and Wimmer, 2005), and gastric and intestinal performance (Ott and Secor, 2007; Secor, 2003; Secor and Diamond, 2000), as well as an increase in the mass of

several organs (Andersen et al., 2005; Lignot et al., 2005; Ott and Secor, 2007; Secor and Diamond, 2000; Starck and Beese 2002).

There is a wide variation in dietary habits and foraging strategies between snake species (Greene, 1997; Mushinsky, 1987). These differences extend to correlated patterns of digestive physiology. For example, ambush foraging snakes that feed infrequently in the wild experience larger postfeeding changes in metabolism and gastrointestinal morphology and function compared to active foraging snakes that feed relatively frequently in the wild (Secor and Diamond, 2000). Although ambush foraging snakes mostly belong to the families Pythonidae, Boidae and Viperidae, and active-foraging behaviours characterize snakes within the families Elapidae and Colubridae, there are examples of boids that may feed relatively frequently (e.g., Amazon tree boa, *Corallus hortulanus*; Secor and Ott, 2007) and colubrid species that experience extended periods of fasting (e.g., African egg eating snakes, *Dasypteltis scabra*; Grossmann and Starck, 2006). The latter would fit the case of some fish-eating colubrid snakes that forage in temporary aquatic habitats where food availability varies dramatically throughout the year. One such example is the colubrid snake *N. maura*, which inhabits a variety of Mediterranean environments and feeds frequently on fish and anurans when available. The ecology of *N. maura* has been studied intensely in the Ebro Delta wetlands, a coastal Mediterranean locality of north-eastern Iberia, where the species is subjected to large periods of fasting during the dry season due to the absence of available food (Santos and Llorente, 1998; Santos et al., 2000). Our aim in the current

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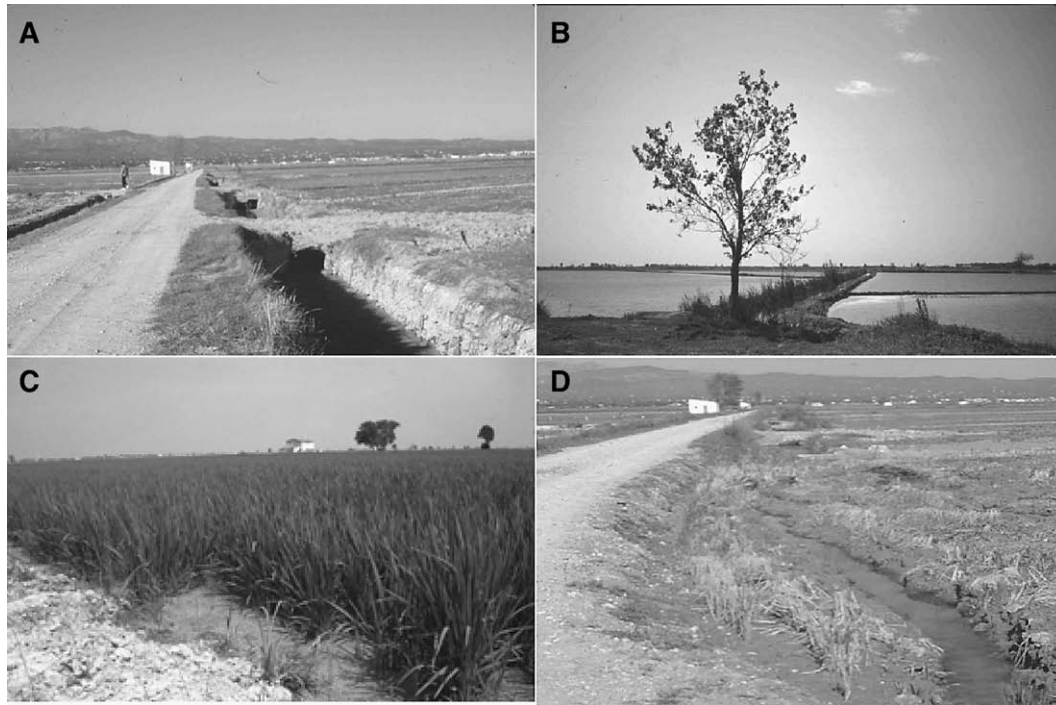


Fig. 1. Rice fields in the Ebro Delta Natural Park in April (A), May (B), July (C) and October (D) showing a contrasted landscape according to rice cycle and water flow.

study is to assess temporal changes in gut contents and gastrointestinal mass and length over an annual cycle of food availability.

## 2. Materials and methods

*N. maura* is a medium-sized oviparous snake inhabiting all kinds of continental waters and salt waters in several coastal populations in the western Mediterranean (Santos, 2004). In coastal localities, this aquatic snake inhabits wetland areas such as river deltas. The biggest delta in the Iberian Peninsula is the Ebro Delta, a wetland area (28,000 ha) where the natural vegetation has been partially substituted by rice fields and a dense network of water canals (40% of the Ebro Delta surface). This agro-ecosystem is a suitable habitat for *N. maura* because their potential prey (fish and frogs) are seasonally abundant (Santos et al., 2000). However, the rice cycle imposes big changes in the water flow: rice fields and canals remain dry up to the 15th of April (Fig. 1A) when they get flooded with water (Fig. 1B) and the area experiences highly dynamic changes in aquatic communities with a remarkable increase of fish abundance (González-Solís et al., 1996). Rice grows until October (Fig. 1C) and, after harvesting, fields become dry again (Fig. 1D). Several ecological traits of *N. maura* from the Ebro Delta are driven by the rice crop, such as trophic ecology (Santos et al., 2000), reproductive timing (Santos and Llorente, 2001, Santos et al., 2005), and lipid and protein dynamics (Santos et al., 2007; Santos and Llorente, 2004).

Snakes were located during sunny days in rice fields and canals, and collected by hand by two field-workers at monthly intervals in standardized transects during an annual cycle. Each monthly sampling lasted two days. In total, 50 adult males, 40 adult females and 53 juveniles were collected. Three adult males and three adult females were captured each month (with the exception of winter months) and so were the recently killed specimens found on the delta roads. Snakes collected from November to February were pooled in a winter category. Snakes were killed by cold torpor and later frozen with dry ice until lab procedures. In the laboratory, snakes were measured (snout-vent length, SVL) and weighed. The digestive tract was removed and weighed and then weighed again after removing all the detected food items. Following the removal and flushing, the

intestine length was measured by extending the tract after cautiously cutting the connective membranes. The mass of gut contents provides an estimate of food acquisition by snakes. The combined extended length of the esophagus and stomach and the combined extended length of the small and large intestine were separately measured, since the intestine experiences large variations after feeding in infrequently feeding snakes (Ott and Secor, 2007).

The variables analyzed in this study were: combined esophageal and stomach length, combined small and large intestine length, mass of the gastrointestinal tract, and mass of gut contents. Prior to statistical analyses, all variables were log transformed. To remove effects of snake size for each analysis, we calculated for each variable their residual value from a regression equation developed from plotting the measured variable against SVL. Monthly variation in the variables was tested by ANCOVAs using SVL as covariate. Furthermore, we calculated relative combined esophagus and stomach length and relative combined small and large intestine length by dividing these lengths by SVL to determine if these indexes of gut size vary ontogenetically. We similarly tested for sexual differences in intestinal length. Only adult snakes ( $n=90$ ) were examined for seasonal differences in intestinal length.

Table 1

Average monthly values of snout-vent length (SVL), intestine length (Intes, in mm), and intestine/SVL ratio in adult viperine snakes (*Natrix maura*) collected in the Ebro Delta rice fields

Month	Males				Females			
	n	SVL±SE	Intes±SE	Intes/SVL	n	SVL±SE	Intes±SE	Intes/SVL
M	6	319.0±20.9	294.5±24.6	0.918	4	363.8±29.3	363.3±44.0	0.990
A	7	361.9±21.9	312.7±23.0	0.860	3	465.0±67.2	440.7±71.8	0.942
M	9	331.2±17.9	317.0±12.9	0.963	5	448.6±36.5	400.6±26.1	0.899
J	7	341.6±20.0	332.9±20.0	0.980	6	378.8±31.2	413.3±40.5	1.0859
J	7	280.3±11.8	269.1±8.1	0.966	7	415.0±38.6	460.0±44.7	1.108
A	3	323.7±49.8	297.0±31.6	0.935	4	433.5±22.6	425.5±33.0	0.9798
S	3	334.7±42.9	301.3±48.7	0.891	5	409.0±35.2	407.0±43.2	0.989
O	5	317.6±13.7	302.6±17.7	0.954	2	296.0±16.0	278.5±46.5	0.9359
Winter	3	338.3±8.3	325.0±9.0	0.961	4	393.3±38.5	400.3±46.8	1.0129

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