

The feeding behavior and natural history of two Chilean snakes, *Philodryas chamissonis* and *Tachymenis chilensis* (Colubridae)

La conducta alimentaria e historia natural
de dos culebras chilenas, *Philodryas chamissonis* y
Tachymenis chilensis (Colubridae)

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ABSTRACT

Philodryas chamissonis, maximum length ca. 2.2 m, feeds on anurans, lizards, birds, rodents, and rabbits; constriction is used for killing endothermic prey. An ontogenetic dietary shift is demonstrated by smaller individuals eating only ectothermic prey. *Tachymenis chilensis*, maximum length ca. 0.7 m, feeds only on anurans and lizards and does not exhibit an ontogenetic dietary shift. Both species are diurnal hunters and typically swallow prey head-first. Prey/predator mass ratios are not especially large compared to other snakes. There is widespread sympatry and considerable overlap in diet, but *T. chilensis* eats more anurans and extends into cooler, moister habitats than does *P. chamissonis*. The low species richness of snakes in Chile appears to result from geographic isolation rather than ecological limits on inter-specific coexistence.

Key words: Diet, food habits, feeding behavior, Chile.

RESUMEN

Philodryas chamissonis, longitud máxima ca. 2,2 m, se alimenta de anuros, lagartijas, aves, roedores y conejos; usa constricción para matar las presas endotérmicas. Un cambio ontogenético en dieta se demuestra con los individuos pequeños predando sólo presas ectotérmicas. *Tachymenis chilensis*, longitud máxima ca. 0,7 m, se alimenta sólo de anuros y lagartijas y no muestra un cambio ontogenético en dieta. Ambas especies son cazadoras diurnas y típicamente ingieren sus presas con la cabeza por delante. Los cocientes de masa presa/predador no son particularmente grandes en comparación a otras culebras. Hay una extensa simpatria y sobreposición en dieta entre estas culebras, pero *T. chilensis* come más anuros y se extiende hacia hábitats más fríos y húmedos que *P. chamissonis*. La baja diversidad de culebras en Chile parece ser el producto de aislamiento geográfico antes que de límites impuestos por la coexistencia interespecífica.

Palabras claves: Dieta, hábitos alimentarios, conducta alimentaria, Chile.

INTRODUCTION

Lineages and faunas that have independently achieved similar characteristics provide natural experiments for examining questions about adaptation (e.g., Jaksic 1981; Donoghue 1989) and species richness gradients (e.g., Schall & Pianka 1978; Jaksic & Delibes 1987). Snakes possess several attributes that make them good candidates for such broader purposes (Arnold 1972; Vitt 1987), and detailed

case studies also are crucial for understanding the evolution of feeding in these highly unusual reptiles (Ananjeva & Orlov 1982; Greene 1983, 1989, in press; Savitzky 1983; Voris & Voris 1983). In the present paper we analyze the geographic distribution and diets of *Philodryas chamissonis* (Wiegmann) and *Tachymenis chilensis* (Schlegel), two poorly known and particularly interesting South American colubrids. We discussed elsewhere the roles of Chilean snakes as prey for and potential

competitors with other vertebrates (Jaksic *et al.* 1981a, 1982).

occidentalis from California) and laboratory mice.

METHODS

We reviewed the literature and collection tags for detailed information on geographic distribution and overlap, and on habitat preferences, of the two snakes. We examined the stomachs of *Philodryas chamissonis* and *Tachymenis chilensis* in the American Museum of Natural History; British Museum (Natural History); Field Museum of Natural History (FMNH); Museo Nacional de Historia Natural de Chile; Museum of Natural History, University of Kansas (KU); Museum of Comparative Zoology, Harvard University; Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); The Museum, Michigan State University; and Seckenberg Museum. Our data incorporate diet records in Walker (1945) and unpublished observations provided by J.E. Cadle, J.H. Carothers, and R.K. Colwell.

Direction of ingestion (inferred from orientation in the gut), identification, and linear dimensions were recorded after exposing prey through a mid-ventral incision in specimens. Intact snakes and their prey (or a reference specimen of comparable size) were weighed after blotting and draining them briefly on paper towels. Abbreviations refer to snout-vent length (SVL), total length (TL), and prey/predator mass ratio (MR).

A shortcoming of using museum specimens for assessing field diet is that snake individuals may have been fed by the collector before being preserved. We did not detect any prey item exotic to Chile (e.g. house mouse), and thus we assume that this bias was negligible.

We observed feeding behavior by four *Philodryas chamissonis* in captivity, three from unknown localities and one from Santiago (Metropolitan Region) Chile (specimen now in the Academy of Sciences of Philadelphia). The snakes varied in TL from ca. 0.5-1.3 m, were housed in glass terraria, and were fed live iguanid lizards (*Liolaemus* sp. from Chile, *Sceloporus*

RESULTS

Distribution, sympatry, and habitats

Philodryas chamissonis and *Tachymenis chilensis* are broadly sympatric in Chile, from Copiapó (III Región) to Valdivia (X Región). *Tachymenis chilensis* ranges farther south, to Puerto Montt on the mainland and on Chiloé Island (X Región); a sibling species, *T. peruvianus* (sometimes considered conspecific with *T. chilensis*, see Ortiz 1973) occurs farther north than *P. chamissonis*, into Bolivia and Perú. *Philodryas chamissonis* is found from sea level to at least 1,730 m (KU 162039); *T. peruvianus* occurs at moderate to high elevations (to 4,000 m in the northern part of its range), whereas *T. chilensis* ranges down to sea level in the south (Walker 1945; Donoso-Barros 1966; Peters & Orejas-Miranda 1970; Thomas 1976; Cei 1986).

In Chile, *Philodryas chamissonis* and *Tachymenis chilensis* are reported as sympatric in several localities of Malleco (VIII Región) (Webb & Greer 1969); from Alto Vilches, Talca (VII Región) (Montecinos & Formas 1979); and from La Dehesa (Metropolitan Region) (Jaksic *et al.* 1981a). We have seen sympatric individuals from additional localities in Malleco and Santiago, as well as Coquimbo (IV Región), Aconcagua (V Región), Arauco (VIII Región) and Concepción (VIII Región). *Philodryas chamissonis* is reported from dry places in the lowlands, under rocks, near rock walls, and crossing roads (Donoso-Barros 1966; Webb & Greer 1969; notes with FMNH 23823; pers. obs.). *Tachymenis chilensis* has been found in bunch-grass meadows, under boards near pig pens, and foraging in open, short-grass pastures (Webb & Greer 1969). Withal, the evidence suggests that *P. chamissonis* and *T. chilensis* prefer warmer, drier habitats and cooler, moister sites, respectively.

Diet and feeding behavior of Philodryas chamissonis

Philodryas chamissonis is called "culebra de cola larga" (long-tailed snake) in Chile, and referred to the genera *Alsophis* or *Dromicus* in much of the literature (see Thomas 1976; Jaksic *et al.* 1981b). This oviparous species has a whipsnake-like habitus (cf. Shine 1980), and reaches a maximum length of ca. 2.2 m (Donoso-Barros & Candiani 1950; see Table 1). It has enlarged, or slightly grooved (Donoso-Barros 1966), or not grooved at all (Habit 1985) rear fangs and a well developed Duvernoy's gland. In our experience, this species is not especially prone to bite, but severe human envenomation is known (Schenone *et al.* 1954; Donoso-Barros & Cárdenas 1959; Donoso-Barros 1966).

Snakes of this species are diurnal hunters. John H. Carothers (pers. comm.) found four adults active in late afternoon at Lagunillas (Metropolitan Region) including a small adult eating a *Liolaemus lemniscatus*. Robert K. Colwell (pers. comm.) found a large adult constricting a rabbit (*Oryctolagus cuniculus*) during the day at Quebrada La Playa (Metropolitan Region) (Kodachromes on file in MVZ). Donoso-Barros & Candiani (1950) reported that *Philodryas chamissonis* swallows lizards quickly but kills rodents and birds with its venom and constriction.

Our captives often coiled under the edge of a rock shelter, with only the head and foreparts visible. On several occasions, snakes that had not eaten recently were seen with the head and anterior part of the body extended vertically, as if watching for prey. Lizards and mice were caught with a rapid forward movement of part or all of the body (rather than by striking with only the anterior part, from a retracted S-coil). Prey were always held in the jaws after seizure, and adult mice were constricted with an anterior, vertical coil that was wound such that there was no twist in the first loop. Those characteristics are typical of constricting coil application by many other genera of colubrids (Greene

& Burghardt 1978). In captivity, the rate of success in subduing *Liolaemus* lizards was 80.5% (n = 41), lower than that of the teiid *Callopistes palluma* (89.2%) and of the falconid *Falco sparverius* (100%) (Medel *et al.* 1988).

Of 23 prey items for which we could determine direction of ingestion, eight frogs, six lizards, two mammals, and two birds were swallowed head-first; three frogs and two lizards were swallowed tail-first ($P < 0.05$, Chi-square test). Lizards and mice were always swallowed head-first by captives.

Twenty-nine of 63 snakes examined contained a total of 38 prey items ($\bar{x} = 1.3/\text{snake}$). Our study confirms Donoso-Barros (1966) generalization that *Philodryas chamissonis* feeds mainly on lizards of the iguanid genus *Liolaemus*, that frogs are eaten occasionally, and that large adults also eat birds, rodents (including *Mus musculus* and *Octodon degus*, according to Donoso-Barros 1966), and rabbit kittens (*Oryctolagus cuniculus*). Of 17 lizards in our sample (Table 2), one was represented by eggs only and two by tails only. Only two snakes contained multiple items: two passerine birds, perhaps ingested as grouped nestlings; and eight *Pleurodema thaul*, from 14.0-32.1 mm SVL, and thus recently metamorphosed to adult size (cf. Cei 1962).

The data are not adequate for determining the extent to which endotherms occur in the diet of large individuals, but an ontogenetic dietary shift seems to occur, given that the smallest snake containing a bird or mammal had a SVL of 576 mm. This presumable ontogenetic shift may simply be associated to larger individuals being capable of handling larger prey. Records for *Oryctolagus* and *Oryzomys* show that even occasional ingestion of such relatively heavy items could contribute substantially to the annual energy budget of adult snakes (see Greene 1986; Bozinovic & Rosenmann 1988). MRs range from 0.05-0.60 ($\bar{x} = 0.15$, n = 7), the largest being a pregnant female *Oryzomys longicaudatus* (ca. 40 g) in a 67 g snake.

Diet of *Tachymenis chilensis*

Tachymenis chilensis is known as "culebra de cola corta" (short-tailed snake), has an apparently stockier habitus than *Philodryas chamissonis* and reaches a maximum TL of only ca. 0.7 m (Table 1). Snakes of this genus are live bearing; they have enlarged, grooved rear fangs and a well developed Duvernoy's gland. Bites from *T. chilensis* have produced severe symptoms in humans (Gajardo-Tobar 1947, 1958; Donoso-Barros 1966).

Walker (1945) surmised that snakes of the genus *Tachymenis* must be nocturnal, because they have vertical pupils, but Péfaur & Duellman (1980) listed *T. peruvianus* as diurnal. An observation of feeding in nature for this genus was of a *T. peruvianus* in the Department of Cuzco, Perú, that had apparently frozen while swallowing a *Liolaemus* sp. (J.E. Cadle, pers. comm.). The dead predator and prey were found early in the morning, so they must have succumbed as the result of a late afternoon encounter. Of 19 prey items for which we could determine direction of ingestion, eight frogs and nine lizards were taken head-first; one frog and one lizard were swallowed tail-first ($P < 0.05$, Chi-square test).

Tachymenis chilensis reportedly feeds on frogs, including *Batrachyla taeniata* (Donoso-Barros 1966). Thirty-four of 65 snakes we examined contained a total of 47 prey items ($\bar{x} = 1.4/\text{snake}$). We found exclusively frogs and lizards in stomachs (Table 2), and noted no ontogenetic differences in the frequencies of those two prey types. Multiple prey items in five snakes included one gravid *Liolaemus pictus* and the tail of another lizard; one *L. tenuis* and a frog; two frogs; at least seven frogs, including one with a resorbing tail; and four *Batrachyla taeniata*, ca. 32-36 mm SVL and thus adults (cf. Cei 1962). MRs ranged from 0.04-0.18 ($\bar{x} = 0.10$, $n = 8$).

Characteristics of potential and actual prey

The three identified species of frogs eaten by Chilean snakes are common terrestrial taxa with extended breeding seasons (Cei 1962). *Bufo chilensis* (Bufonidae), thus far found only in *Philodryas chamissonis*, occurs in fairly xeric parts of central Chile (Cei 1962), and in open grassy areas farther south (Webb & Greer 1969). *Batrachyla taeniata* (Leptodactylidae) thus far found only in *Tachymenis chilensis*, oc-

TABLE 1
Measurements of Chilean snakes and their corresponding prey.
Medidas de culebras chilenas y sus correspondientes presas.

Characters	<i>P. chamissonis</i>		<i>T. chilensis</i>		t	P
	$\bar{x} \pm \text{SD}$	(n)	$\bar{x} \pm \text{SD}$	(n)		
SNAKES						
Snout-Vent length (mm)	532.6 \pm 197.6	(63)	312.2 \pm 105.9	(60)	7.66	< 0.001
Tail length (mm)	208.8 \pm 77.3	(59)	60.9 \pm 22.2	(60)	12.31	< 0.001
Head width (mm)	11.3 \pm 3.7	(53)	8.0 \pm 1.8	(53)	5.76	< 0.001
Head length (mm)	23.2 \pm 7.0	(62)	15.2 \pm 3.1	(59)	8.11	< 0.001
Mid-body diameter (mm)	15.3 \pm 5.2	(37)	9.4 \pm 3.4	(40)	6.06	< 0.001
Weight (g)	96.3 \pm 86.2	(50)	22.4 \pm 16.4	(56)	6.29	< 0.001
PREY						
Snout-Vent length (mm)	33.1 \pm 19.9	(12)	34.4 \pm 14.7	(16)	0.20	> 0.84
Mid-body diameter (mm)	8.7 \pm 2.7	(13)	8.4 \pm 1.9	(14)	0.38	> 0.70
Weight (g)	1.9 \pm 2.6	(13)	1.8 \pm 1.7	(15)	0.14	> 0.89
Prey/predator mass ratio (%)	7.7 \pm 3.1	(6)	10.1 \pm 5.7	(8)	0.84*	> 0.41

* Using the angular transformation to normalize proportions.

TABLE 2

Prey of Chilean snakes. Subtotals in parentheses.
Presas de culebras chilenas. Subtotales entre paréntesis.

Prey	<i>Philodryas chamissonis</i>				<i>Tachymenis chilensis</i>			
	n	%	Freq. in stomachs	%	n	%	Freq. in stomachs	%
ANURANS	(14)	36.8	(6)	20.7	(30)	63.8	(20)	58.8
<i>Bufo chilensis</i>	1		1		—		—	
<i>Batrachyla taeniata</i>	—		—		5		2	
<i>Pleurodema thaul</i>	11		3		6		6	
Unidentified*	2		2		19		12	
LIZARDS	(17)	44.8	(17)	58.6	(17)	36.2	(15)	44.1
<i>Liolaemus chiliensis</i>	1		1		—		—	
<i>Liolaemus cyanogaster</i>	—		—		1		1	
<i>Liolaemus fuscus</i>	1		1		—		—	
<i>Liolaemus pictus</i>	1		1		3		3	
<i>Liolaemus tenuis</i>	—		—		2		2	
<i>Liolaemus</i> sp.	13		13		10		10	
Eggs	1**		1		1***		1	
LAGOMORPHS	(1)	2.6	(1)	3.4	(0)	0.0	(0)	0.0
<i>Oryctolagus cuniculus</i>	1		1		—		—	
RODENTS	(3)	7.9	(3)	10.3	(0)	0.0	(0)	0.0
<i>Akodon olivaceus</i>	1		1		—		—	
Unidentified	2		2		—		—	
PASSERIFORMS	(3)	7.9	(2)	7.0	(0)	0.0	(0)	0.0
Unidentified	3		2		—		—	
TOTAL PREY	38	100.0	—	—	47	100.0	—	—
STOMACHS WITH PREY	29	—	—	100.0	34	—	—	102.9****
TOTAL STOMACHS	63		—		65		—	

* : likely *Eupsophus* sp. (Velošo, pers. comm).

** : one set of 4.

*** : one set of 2.

**** : one stomach contained both a lizard and a anuran.

curs in central Chile in humid, litter-covered soils in relict forests (Cei 1962); to the south this frog is syntopic with *Pleurodema thaul* (Leptodactylidae) which prefers open riparian and marshy areas with tall grass or moist, short forests (Webb & Greer 1969).

This latter species is shared as prey by the two snakes. Both *B. taeniata* and *P. thaul* were found under rocks and logs in dry woods in Malleco (Webb & Greer 1969).

Given their species richness and abundance (Fuentes & Jaksic 1979), it is not surprising that all of the lizards in the diet of Chilean snakes are diurnal members of the iguanid genus *Liolaemus*. We are unable to discern the predominance of any particular species or of taxa with particular characteristics in the snake diets. Both *L. chiliensis* and *L. cyanogaster* are ground dwellers that prefer open, grassy areas (Webb & Greer 1969). *Liolaemus fuscus* is a saxicolous lizard of open, rocky patches

(Jaksic *et al.* 1980), but is also abundant in the *Puya*-cactus formations (Donoso-Barros 1966). *Liolaemus pictus* is a forest species, usually found on, under, or near fallen logs (Webb & Greer 1969). *Liolaemus tenuis* is the only tree-dwelling species in central Chile (Jaksic *et al.* 1980), but it sometimes occurs in rocky, treeless areas (Donoso-Barros 1966) as well as on fence posts and stumps in open pastures (Webb & Greer 1969).

Of mammalian prey taken by *Philodryas chamissonis*, *Oryctolagus cuniculus* is an introduced (European) rabbit now abundant in open areas in chaparral vegetation (Jaksic *et al.* 1979). The olivaceous mouse, *Akodon olivaceus*, inhabits shrublands and open forests (Iriarte *et al.* 1989).

It is surprising that *Philodryas chamissonis* evidently does not take *Callopistes palluma*, a sympatric, fast moving, diurnal teiid lizard that is sometimes moderately common and no heavier than the mammals that *P. chamissonis* eats (Jaksic *et al.* 1982). Moreover, *Masticophis flagellum*, a nonvenomous, fast moving colubrid of western North America that resembles *P. chamissonis* in size, behavior, and general habitus commonly eats *Cnemidophorus tigris* (H.W. Greene, unpubl. data), a teiid that is morphologically and ecologically similar to *C. palluma* (Fuentes 1976). However, adult *C. palluma* weigh at least 60 g, more than twice as much as *C. tigris*, and the former can deliver a powerful bite (pers. obs.). Our impression is that lizards of the genus *Liolaemus* are relatively more abundant than equivalently slow moving, alternative prey (e.g., iguanids of the genera *Sceloporus* and *Uta*) in western North America within the range of *M. flagellum*. Perhaps *P. chamissonis* ignores *C. palluma* because that big lizard is not worth the risk (cf. Jaksic *et al.* 1982; Greene 1988a).

DISCUSSION

Our data are sufficient to suggest that both species of Chilean snakes are rather generalized diurnal, terrestrial predators on small ectothermic vertebrates, with the

larger *Philodryas chamissonis* adding several species of endotherms to the diet as it reaches maximum size. The diets of *P. chamissonis* and *Tachymenis chilensis* thus resemble those of many other species of colubrids, including other members of the South American xenodontine clade (Cadle 1988) to which *Philodryas* and *Tachymenis* belong (see Walker 1945 for other *Tachymenis*; Thomas 1976 and Vitt 1980, for other *Philodryas*; Henderson *et al.* 1988 for Antillean snakes; Greene & Reynolds, in press, for Galápagos snakes) as well as more distantly related taxa (e.g., Seib 1984, 1985). Prey are typically swallowed head-first by the two Chilean species, as in many other snakes (Greene 1976, 1983, 1984, 1989, in press; Ananjeva & Orlov 1982; Voris & Voris 1983; Seib 1984, 1985), and MRs are not especially large (cf. Voris & Moffett 1981; Greene 1983, 1984, 1989, in press; Seib 1984, 1985; Jayne *et al.* 1988).

The geographic ranges of *Philodryas chamissonis* and *Tachymenis chilensis* overlap broadly (see above) as do perhaps their diets (Jaksic *et al.* 1981a). Both species feed frequently on leptodactylid frogs and iguanid lizards of the genus *Liolaemus*, and we encountered two instances of shared prey in sympatry: *L. pictus* in one *P. chamissonis* and in two *T. chilensis* at Nahuelbuta Range (IX Region), and *Pleurodema thaul* in one *P. chamissonis* and in two *T. chilensis* from La Dehesa (Metropolitan Region).

Nevertheless, frogs are clearly more important in the overall diet of *T. chilensis* than they are for *P. chamissonis* of equivalent sizes ($P < 0.01$, Chi-square test for frogs versus lizards in snakes with SVL < 500 mm).

Globally, the number of sympatric snake species varies from one (e.g., on some islands) to more than 50 at some neotropical localities (Arnold 1972; Vitt 1987; Greene 1988b). *Philodryas chamissonis* and *Tachymenis chilensis* are the only snakes in most of Chile, and the only snakes west of the Andes from approximately 19°S to 43°S. Presumably the paucity of snakes on the west coast of

South America is due largely to isolation by the uplifted cordillera (Donoso-Barros 1960; Duellman 1979), rather than to ecological limits on interspecific coexistence (see Vitt 1987 for a general discussion of factors limiting species richness in snakes). Indeed, despite extensive convergence in many ecosystem components (e.g., Mooney 1977), snake faunas in similar mediterranean habitats of California and Spain contain three or more times as many snake species (Fitch 1949; Valverde 1967; Jaksic *et al.* 1982). Some sites at comparable latitudes east of the Andes in Argentina probably contain at least 10 species of snakes (Cei 1986). More importantly, other mediterranean snake faunas and those in Argentina contain several genera in two to four families.

A survey of more than 500 species in four families of advanced snakes (the Caenophidia) found that only *Philodryas chamissonis* exhibited the primitive state for all 50 characters examined (Marx & Rabb 1972; Rabb & Marx 1973). Because of the method used to assess character polarities in that study (primarily in-group comparisons and commonality, rather than out-group comparisons, see Arnold 1981), that finding might simply mean that *P. chamissonis* best represents a generalized colubrid. In any case, although *P. chamissonis* has a reasonably broad diet, it is no more so than many species of snakes in other genera with much more derived morphologies (e.g., some Australian elapids, Shine 1980; a neotropical viperid, *Bothriechis schlegelii*, Greene & Solorzano, unpubl. data).

We expect that ecological comparisons of *Philodryas chamissonis* and *Tachymenis chilensis* with other taxa in more complex assemblages eventually will shed light on broader issues, such as ecological release in depauperate faunas and the lower limits on phenotypic specialization required for handling particular prey types. Additional details on individual, local, and geographic variation (Greene 1989, in press) in the diets of Chilean snakes would be especially valuable for assessing these questions.

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