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The ecology of the Western Whip Snake, *Coluber viridiflavus* (LACÉPÈDE, 1789), in Mediterranean Central Italy
(Squamata: Serpentes: Colubridae)

Ökologie der Gelbgrünen Zornnatter, *Coluber viridiflavus* (LACÉPÈDE, 1789), im mediterranen Mittelitalien
(Squamata: Serpentes: Colubridae)

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KURZFASSUNG

Der englische Sammelbegriff "Whip Snakes" [Peitschennattern, Zornnattern] bezeichnet phylogenetisch nicht näher verwandte Schlangen (Colubridae und Elapidae), die durch bemerkenswerte Konvergenzen in verschiedenen morphologischen, ökologischen und ethologischen Merkmalsausprägungen einander ähnlich sind. Nach SHINE (1980), entwickelten sie diese Merkmalsausprägungen zur Ermöglichung einer erfolgreichen Jagd auf flinke, tagaktive Beutetiere, mehrheitlich Eidechsen.

Im mediterranen Mittelitalien (Tolfa Berge, Provinz Rom) untersuchten wir die Ökologie der Gelbgünen Zornnatter *Coluber viridiflavus* (LACÉPÈDE, 1789) im Hinblick auf Übereinstimmungen bzw. Widersprüche zu SHINEs Argumentationslinie. Wir machen Angaben über (jahres- und tageszeitliche) Aktivitätsmuster, Paarungsgeschehen, Fortpflanzung, Körpergröße, Geschlechterverhältnis, Biotopwahl, Jagdstrategie und Körpertemperatur. Im allgemeinen entsprachen unsere Befunde jenen Beobachtungen, auf deren Grundlage SHINE (1980) seine Ansichten über die morphologischen und ökologischen Ähnlichkeiten in dieser Schlangengruppe formulierte.

ABSTRACT

"Whip Snakes" are phylogenetically unrelated snakes (Colubridae and Elapidae) characterized by remarkable convergent evolution in several morphological, ecological and behavioural traits. According to SHINE (1980), these traits evolved to facilitate the chase and capture of fast-moving diurnal prey, usually lizards.

In a Mediterranean territory of Central Italy (Tolfa Mountains, province of Rome), we studied the ecology of the Western Whip Snake *Coluber viridiflavus* (LACÉPÈDE, 1789), to point out eventual congruences and differences with SHINE's line of arguments. We give data on activity patterns (seasonal and daily), mating activity, reproduction, body sizes and adult sex-ratio, habitat features, predatory strategies, and field body temperatures. On the whole the given data did mirror those by which SHINE (1980) generated his views on "Whip Snake" morphology and ecology.

KEY WORDS

Serpentes, Colubridae, *Coluber viridiflavus*, Whip Snakes; ecology, activity patterns, body size, life-history, convergent evolution, Mediterranean Italy

INTRODUCTION

The collective term "Whip Snakes" designates a variety of phylogenetically unrelated taxa that are very similar in morphology, behavior and ecology: they are characterized by slender bodies, long tails, large eyes, alertness, diurnality, saurophagy, oviparity, and great speed of movement (SHINE 1980). These snakes are conspicuous elements of the terrestrial snake fauna in most parts of the world: among others, obvious "Whip Snake" examples are the wide-ranging *Coluber* in Europe, Asia and North America, *Psammophis* in Africa, *Masticophis* in North America, *Liophis* in South America, and *Demansia* in Australia. Contrary to the former four colubrid genera, *Demansia* belongs to the Elapidae.

Ecological data on "Whip Snakes" are generally sketchy and anecdotal, apart for some detailed studies on Australian *Demansia* (SHINE 1980, 1991), African

Psammophis (BUTLER 1993), and North American *Masticophis* (e. g., cf. HAMMERSON 1979). By examining the literature available, SHINE (1980) suggested that the morphological and behavioral similarities between "Whip Snakes" are adaptations to facilitate the chase and capture of fast-moving diurnal prey, usually lizards. In fact, according to this author (1980, p. 388), "this hypothesis is consistent with the common saurophagy of Whip Snakes, and offers possible explanations for the other Whip Snake characteristics noted above: (i) diurnality and terrestriality clearly are related to this type of saurophagy, (ii) slender bodily form enables rapid movement, essential for capturing agile lizards; (iii) large eyes provide the visual acuity required for active chasing (in contrast to most other snakes, which rely heavily on chemoreception during foraging); and (iv) oviparity is advantageous because it minimizes the time period for which gravid females are physically burdened by eggs".

SHINE's (1980) arguments are plausible and extremely interesting to test on an evolutionary perspective. However to do this, much more field data on taxa other than *Demansia, Psammophis,* and *Masticophis* should be aquired. In this regard the problem is that detailed field studies on Whip Snake species are still rare in the scientific literature.

With regard to Italy, the Western Whip Snake *Coluber viridiflavus* (LACÉPÈDE, 1789), a large sized (up to 180 cm long), oviparous colubrid, is almost invariably the most abundant snake species of the Mediterranean environments (BRUNO & MAUGERI 1984). In recent years this species has been the subject of intense field studies, and now good quantitative scientific information is available on several aspects of its biology, including general ecology (FILIPPI 1995), homing (CIOFI & CHELAZZI 1991, 1994), reproduction and communal nesting (BONNET & NAULLEAU 1994, 1995, 1996a, 1996b; CAPULA & LUISELLI 1995; CAPULA & al. 1995), and dietary habits (CAPIZZI & al. 1995; RUGIERO & LUISELLI 1995; CAPIZZI & LUISELLI 1996).

Here we present detailed data on general ecology, activity patterns, phenology, foraging mode, habitat and activity temperature of Western Whip Snakes in a Mediterranean territory of Central Italy where they are widespread and very abundant (BRUNO 1977). We also compare our data with those on other Whip Snake species from elsewhere, in order to shed some further light on the reliability of SHINE's (1980) "adaptationist" hypotheses.

MATERIALS AND METHODS

Study area

All data given here were collected in the Tolfa Mountains (northern Latium, province of Rome). This region is characterized by a complex sedimentary basement crossed and overlied by eruptive rocks related to different volcanic cycles. Most data were collected in Rota, a hilly locality in the Tolfa Mountains situated about 60 km north-west of Rome (approximately 150 m a.s.l, 42°08' N, 12°00' E). The study area is characterized by a Mediterranean-temperate climate, with cool and rainy winters (without snow covering), wet springs and autumns, dry and hot summers (fig. 1).

The total area surveyed, about 150 ha, is characterized by three macrohabitats: type (1), a riparian and wet forest phytocenosis (mainly *Ulmus campestris,* but also *Salix* spp., and *Populus* spp.) surrounding a stream called "Fosso Verginese" (about 10 ha surface); type (2), bushy pastures, i. e. open grassy fields interspersed with bushes (*Spartium, Cytisus, Pirus, Rubus,* and *Crataegus*) (about 95 ha surface); and type (3), a mesophilous forest of *Quercus cerris, Ostrya carpinifolia,* and *Qu. pubescens* (about 45 ha surface) (SPADA 1977).

Methods

The study was conducted from March 1991 to November 1994, but additional data were obtained in 1985 through 1990, and 1995. We walked along standardized routes in the study area between 07.00 and 15.30, but some visits were also made during late afternoon and night.

Snakes were captured by hand, sexed based on tail morphology, measured (snout-vent length - SVL and total length -

Table 1: Number of days (N) spent in the field in the months March through October and relative sampling effort index (E. I.) 1991-1994. E. I. is calculated following SEIGEL's (1992) procedure.

Tab. 1: Anzahl der Felduntersuchungstage (N) in den Monaten März bis Oktober und Index des relativen Sammelaufwandes (E. I.) der Jahre 1991 bis 1994. Die Berechnung von E. I. erfolgte nach SEIGEL (1992).

Month/Monat	M	A	M	J	J	A	S	O
N	7	16	22	20	12	7	18	2
E.I.	0.06	0.13	0.18	0.16	0.10	0.06	0.15	0.02

TL, both to the nearest ±0.5 cm), weighed, scale-clipped for future identification, paint-marked with a white number in the dorsal parts for visual identification at distance, and palpated to obtain ingested food. Dietary data are given elsewhere. No specimen was intentionally killed or damaged during the study, but twenty-six individuals found dead were collected. Date, hour and air temperature at each observation were recorded. Temperature was recorded in the shade, about 50 cm above ground. Cloacal temperatures of 27 adult individuals (ten females and seventeen males) were recorded with a Schultheis rapid recording thermometer, within one minute after capture. We did not measure cloacal temperature of inactive or basking individuals.

To study movements, site and date of oviposition, one of us (E. F.) radiotracked three gravid females from June 15 to July 20, 1995. Female 'a' was 115 cm TL, female 'b' was 116 cm TL, and female 'c' was 108.5 cm TL. Radiotransmitters were externally implanted following CIOFI & CHELAZZI's (1991) procedure. Three field trips per week were done, each lasting from 10.00 to 18.00; the position of the animals was usually determined every 60 minutes.

Snakes were considered "active" only when seen above-ground. Specimens found under stones were considered as "inactive". Because sampling intensity varied among months (the area was always visited by two researchers at the same time), we calculated a sampling effort index (SEIGEL 1992). The index was determined by dividing the numbers of days spent in the field each month by the total number of days in the field during the whole research period. We generated expected frequencies of snakes active each month by multiplying the total number of snakes observed during the study by the relative sampling effort index for each month. Finally, we compared the observed and the expected frequencies of snakes active in each month by χ^2 test (using Yates' correction factor), under the null hypothesis of an equal activity among months. The number of days in the field per month and the relative sampling effort index of each month are given in table 1.

Data were analysed with Statistica® (Windows® version 4.5, 1993) computer package, all tests being two-tailed and with alpha assessed at 5%.

RESULTS

Annual activity cycle, hibernacula characteristics and length of hibernation

In the study area *C. viridiflavus* is active from early March to late October (see below for details). The earliest observation of an active specimen was on 2 March (1992), and the latest was on 30 October (1995). The remaining months are spent in hibernation.

We discovered eight different hibernacula between October 1994 and March 1995. Two hibernacula were situated within large *Rubus ulmifolius* bushes, and six hibernacula were situated along a stony wall (more than 2 km long) transversing the study area. Access to the former two hibernacula was provided by holes in the ground (probably made by bank voles, *Clethrionomys glareolus*), while holes in the wall at a height from the ground of 0 to about 50 cm gave access to the latter six hibernacula. We do not know the depth at

Table 2: Approximate dates of ingress into hibernacula and spring emergence for eight adult *Coluber viridiflavus* between late autumn 1994 and spring 1995. Here we consider the latest date in which each animal has been observed in the year, while the emergence date given in the table indicates the third time in which each animal has been observed above-ground during spring. We have not considered our first spring observation of each animal because the Mediterranean snakes may occasionally be active above-ground also during wintertime (i.e. within their usual hibernation period in unusually hot days, see "first emergence" in the text); therefore their first spring observation may not represent the real emergence date after hibernation, but simply an occasional interruption of the latency phase. TL - Total length.

Tab. 2: Das ungefähre Datum der Einwinterung und Frühjahrs-Auswinterung bei acht adulten *Coluber viridiflavus* vom Spätherbst 1994 bis zum Frühling 1995. Als Einwinterungsdatum wird jeweils der späteste Termin im Jahr angegeben, zu dem das entsprechende Tier beobachtet wurde, als Auswinterungsdatum der dritte Tag im Frühjahr, an dem sich das entsprechende Tier an der Erdoberfläche aufhielt. Die jeweils erste Beobachtung im Frühling wurde nicht als Auswinterungstermin aufgefaßt, da mediterrane Schlangen ihre Winterruhe unterbrechen und gelegentlich (bes. an für die Jahreszeit ungewöhnlich warmen Tagen) auch im Winter an der Erdoberfläche aktiv sein können. GL - Gesamtlänge.

Sex Geschlecht	TL (cm) GL (cm)	Retreat (date) Einwinterungsdatum	Emergence (date) Auswinterungsdatum	Hibernation period (d) Überwinterungsdauer (d)	Hibernaculum Überwinterungsquartier
male/Männchen	125.5	22.X	06.III	135	wall / Mauer
male/Männchen	118.0	26.X	11.III	136	wall / Mauer
male/Männchen	97.3	27.X	16.III	140	wall / Mauer
male/Männchen	116.5	30.X	06.III	127	wall / Mauer
male/Männchen	120.8	26.X	06.III	131	bush / Busch
male/Männchen	105.5	26.X	11.III	136	bush / Busch
female/Weibchen	105.2	17.X	11.III	145	wall / Mauer
female/Weibchen	103.0	19.X	11.III	143	wall / Mauer

which these snakes hibernated, as we did not excavate any of the sites. However, in another locality of Tolfa Mountains (Oriolo Romano, approximately 450 m a.s.l), an adult male was excavated from a depth of about 35 cm on a south-west facing slope. All hibernacula discovered during this study were used by adult snakes. None of them was used by more than a single Whip Snake, but one of the hibernacula was also used by an adult male *Vipera aspis*. Both the viper and the Whip Snake were often seen basking together during early spring 1995 without any sign of interspecific aggressive behavior. In other areas of the Tolfa Mountains we often recorded juvenile Whip Snakes hibernating in small groups (2-3 individuals together).

Between 1991 and 1995, the last five autumnal observations of active animals ranged from 18-29 October. The time of onset of hibernation (measured as the number of days elapsed since 15 October) was not correlated with snake TL in 8 adults monitored between autumn 1994 and spring 1995 (after log - normalization, $r = 0.27$, ANOVA with $df = 1.6$, $F = 0.481$, mean square = 0.046, $P = 0.51$), but males tended to retreat into hibernacula a few days (about 3-10 days) later than females (as judged by the fact that in every year 80-90% of the latest ten observations were relative to males). Thus, thermoperiods seem to be more important than photoperiods.

The midday air temperatures at the time of ingress into hibernacula averaged 14.5 ±6.6°C. The length of hibernation was rather accurately estimated for eight adults (six males and two females) monitored between October 1994 and March 1995 (table 2). They hibernated for an average of 136.6 ±6.0 days. There was a trend for length of hibernation to be inversely correlated with snake TL, but the significance level of this correlation fell short of statistical significance ($r = -0.67$, $n = 8$, ANOVA $F = 4.816$, $df = 1.6$, $P = 0.07$).

Both adult and juvenile Whip Snakes were occasionally seen basking 3-8 weeks before termination of hibernation. These temporary emergences always occurred on sunny and unusually warm days (air temperatures > 16°C). Emergences occurred after at least two to three days of mild weather. The movements of snakes during these occasional winter emergences were extremely limited (always < 10 m around the hibernaculum), and activity was restricted to basking. Winter activity in *C.*

Table 3: Date, time (in European Standard Time) and air temperature of five mating events of *Coluber viridiflavus* observed in "Rota" (Tolfa Mountains, province of Rome).

Tab. 3: Datum, Uhrzeit (Europäische Standardzeit) und Lufttemperatur bei fünf Paarungen von *Coluber viridiflavus* im Untersuchungsgebiet „Rota" (Tolfa Berge, Provinz Rom).

Date Datum	Time Uhrzeit	Air Temperature (°C) Lufttemperatur (°C)
11.IV.92	11.40	21
18.IV.92	16.15	21.5
18.IV.92	17.30	22
26.III.94	13.45	23.5
13.V.94	13.15	24

viridiflavus was similar to that already described for other temperate snakes, including e. g., *Crotalus horridus* (MARTIN 1992) and *Vipera aspis* (DUGUY 1963).

Spring general emergence (at least four individuals seen during the same research day) occurred at the very beginning of April in every study year, and at mid-April all the snakes in the population were active (FILIPPI 1995). Mean air temperature on days of general emergence was 17.5°C, and ranged between 15°C and 20°C. As a general rule, the snakes that hibernated in open areas and in south-east to south-west facing slopes emerged a few days (3-7 days) before snakes hibernating in north-oriented slopes and in sites with closed canopy structure.

Foraging may begin a few days after emergence: individuals (especially juveniles) with prey in the stomach were occasionally observed already in late March or in early April. Males started feeding shortly after spring general emergence (see also RUGIERO & LUISELLI 1995), contrary to other Mediterranean snakes which avoid feeding before and during the mating season (LUISELLI & AGRIMI 1991).

Females moulted three times and males twice per season; both sexes moulted in spring (April) and in early summer (late June), but the females also moulted shortly before hibernation (early to mid October). This pre-hibernation moulting was observed in females of other sympatric colubrids, including *Natrix tessellata, Elaphe quatuorlineata,* and *E. longissima* (FILIPPI 1995).

Aspects of reproductive biology

Five matings were observed in the field (table 3). However, 39 sexual combats between males were seen during the mating season. Spermatozoa were found in the cloacal mucus of females from mid March to mid May, with a maximum in the end of April (CAPULA & al. 1995), indicating a prolonged mating season, as observed in populations of *E. longissima* (CAPULA & al. 1995) and *N. natrix* (LUISELLI 1996) from the Tolfa Mountains.

Analysis of cloacal smears of 102 female Whip Snakes from Tolfa Mountains demonstrated that 95% of them copulated during the mating season, although some females were in a too poor condition to produce eggs (BONNET & NAULLEAU 1994; CAPULA & al. 1995).

Available literature data on female Whip Snakes from Tolfa Mountains indicate that these snakes lay eggs from late June to mid July, and hatching occurs from mid to late August (cf. CAPULA & LUISELLI 1995; CAPULA & al. 1995; FILIPPI 1995). Exact oviposition sites have not been determined. However, radiotracking of three gravid females during June-July 1995 have permitted some preliminary observations. Two of the females basked and moved along the same stone wall that they used as hibernaculum both before and after oviposition, suggesting that they laid eggs in the cavities of the stone wall. Both females oviposited in the end of June: female 'a' was seen still gravid in 23 June, but at the next visual record (26 June) was clearly emaciated. Female 'b' laid eggs, on the basis of our visual records, between 26 and 30 June. The third female was gravid on 23 June, but was not seen again until 16 July when not-gravid, although being radiotracked during this period. Thus, we cannot give any accurate data for oviposition of this female. Also the oviposition site of this female is unknown. However, as this female occupied a bushy habitat (*Cytisus scoparius*) with an area of 6000 m^2 throughout the whole pregnancy period, it most likely oviposited somewhere in this bushy area.

In June we examined 48 female Whip Snakes for their reproductive status, 37 out of which were gravid. The fact that 77% of the females were gravid could indicate an annual frequency of reproduction in Tolfa Mountains populations of this species, although one cannot exclude that gravid females are more easy to catch in the field than non-gravid females, thus influencing the proportion of occurrence of gravid animals in the sample (see BONNET & NAULLEAU 1996b). A total of 13 females was palpated for litter size; all were captured in Oriolo Romano (450 m a.s.l.), a locality of the Tolfa Mountains close to the study site. Litter size was positively correlated with female TL ($r = 0.82$, Y-intercept = -18.41, slope = 0.198, $F = 22.80$, $df = 1.11$, $P = 0.0005$).

Body size and sex-ratio

We obtained length (TL) measurements for 165 different adult Whip Snakes (immature individuals are characterized by a different livery from adults, see BRUNO & MAUGERI 1984).

Assuming an equal catchability between sexes, adult sex-ratio was significantly skewed towards males (1.43:1, $\chi^2 = 10.33$, $df = 1$, $P < 0.001$). Males ($n = 97$) were significantly longer than females ($n = 68$) ($\bar{x} = 119.5 \pm 8.9$ cm versus 106.7 ± 7.8 cm, differences between two samples at KRUSKAL-WALLIS one-way ANOVA: $P < 0.00001$).

Habitat features

From 1991 to 1994, 328 Whip Snake observations were recorded (including both captures and the recaptures of marked individuals). Although observations were done in all three habitat types (fig. 2), a significant excess of observations was made in bushy pastures (i. e. habitat type '2'; 83.5% of the total number of observations, χ^2 test, $P < 0.0001$ in all pairwise comparisons), while there were no significant differences between habitats '1' and '3' (Yates' χ^2 test, $df = 1$, $P > 0.5$). When the frequency of observations was corrected for different areas of the three habitats, the excess of observations in habitat type '2' still remained statistically significant (χ^2 test, $P < 0.01$ in all pairwise comparisons). Most observations (70%) of snakes within habitat type '2' were done in stony walls and rocky zones surrounded by spiny shrubs (mainly *Crataegus* and *Rubus*). However, snakes were also frequently observed while climbing trees (15%), and / or when basking in branches well exposed to the sun (often more than two meters above ground).

There were no significant differences in recapture rates between seasons (considering March to May as springtime, June to August as summertime, and September to November as autumn) within each habitat type (χ^2 test, $P > 0.2$, $df = 2$). This suggests that no seasonal variation in habitat use occur in the studied *C. viridiflavus* population.

Foraging mode

Whip Snakes of Mediterranean Central Italy are well known for preying lizards when juveniles, and lizards and rodents when adults (cf. CAPIZZI & al. 1995; RUGIERO & LUISELLI 1995; CAPIZZI & LUISELLI 1996).

During our field work (1985-1995) we observed the predatory behavior of free-ranging *C. viridiflavus* in 23 different occasions. Five times we were unable to distinguish whether the snakes used (i) ambush or (ii) quick pursuit as predatory strategy. In 16 out of 18 remaining cases, the snakes used strategy (ii). The frequency of utilization of these two different predatory strategies differed significantly (Yates' $\chi^2 = 4.71$, $df = 1$, Fisher exact $P = 0.015$), which suggests quick pursuit is the usual foraging strategy adopted by *C. viridiflavus.* The success rate of predatory attempts was 26.1% ($n = 23$).

Field body temperatures

Body temperatures of 17 males and 10 females were recorded. Body temperature was highly correlated with air temperature in both males ($r = 0.79$, ANOVA $F = 24.29$, $df = 1.15$, $P = 0.0001$) and females ($r = 0.81$, ANOVA $F = 15.36$, $df = 1.8$, $P < 0.005$) (fig. 3). The high positive correlation between body and air temperatures suggests some thermoconformity in this species. However, most of the individuals were able to maintain a higher body temperature than that of the air (fig. 3), the mean difference between body and

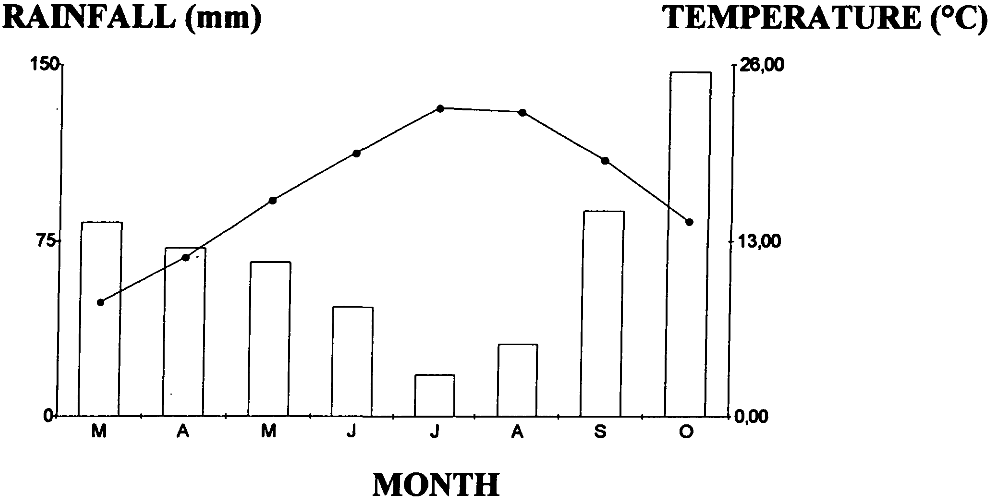

Figure 1: Mean monthly rainfall (bars) and mean monthly ambient temperatures (lines) of the study area.

Abb. 1: Mittlere monatlicheNiederschlagsmengen (Balken), und mittlere monatliche Umgebungstemperaturen (Linien) im Untersuchungsgebiet.

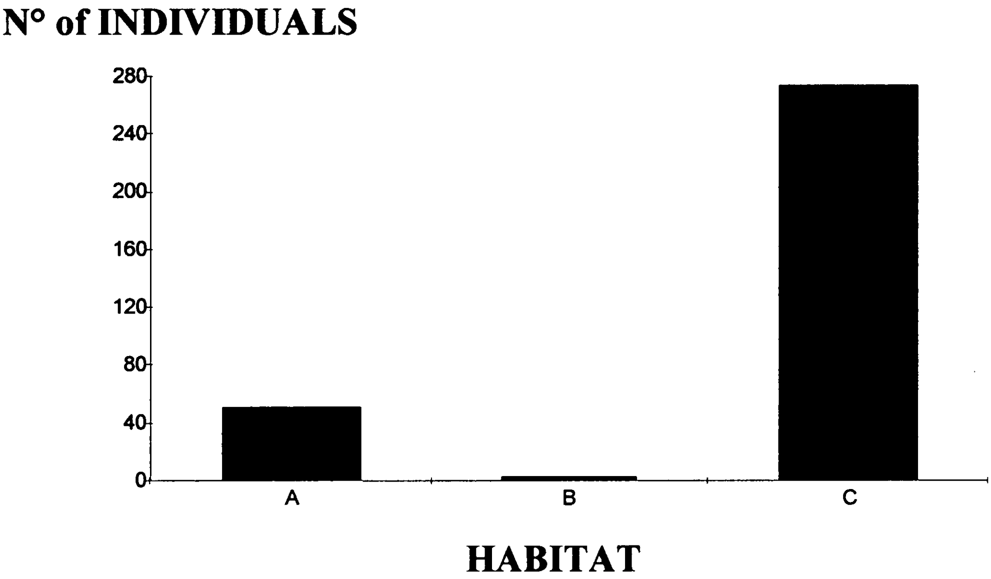

Figure 2: Distribution of the observations of *Coluber viridiflavus* in three habitat types of the study area. Type (1): riparian and wet forest; type (2): bushy pastures; type (3): mesophilous forest. For more details, see text.

Abb. 2: Verteilung der *Coluber viridiflavus* - Beobachtungen in drei Habitattypen im Untersuchungsgebiet. Typ (1): Flußbegleitende und feuchte Wälder; Typ (2): bebuschte Weiden; Typ (3): mesophile Wälder.

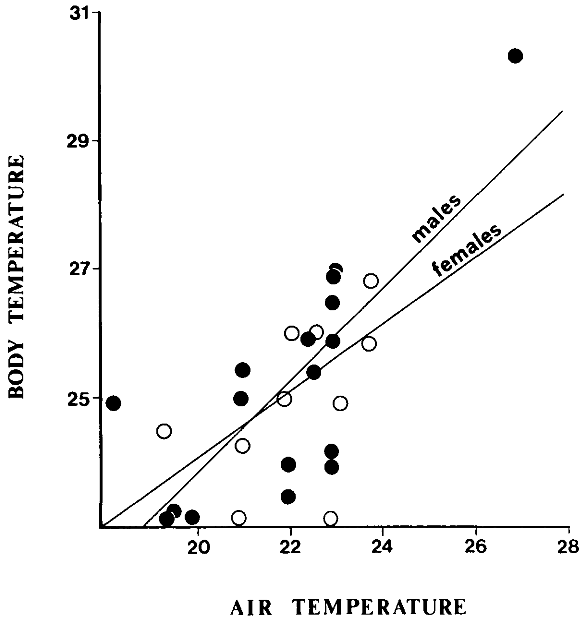

Figure 3: Correlation between body temperature (°C) and air temperature (°C) in *Coluber viridiflavus* from the study area. ● - Males; ○ - Females.

Abb. 3: Die Beziehung zwischen Körpertemperatur (°C) und Lufttemperatur (°C) bei *Coluber viridiflavus* im Untersuchungsgebiet. ● - Männchen; ○ - Weibchen.

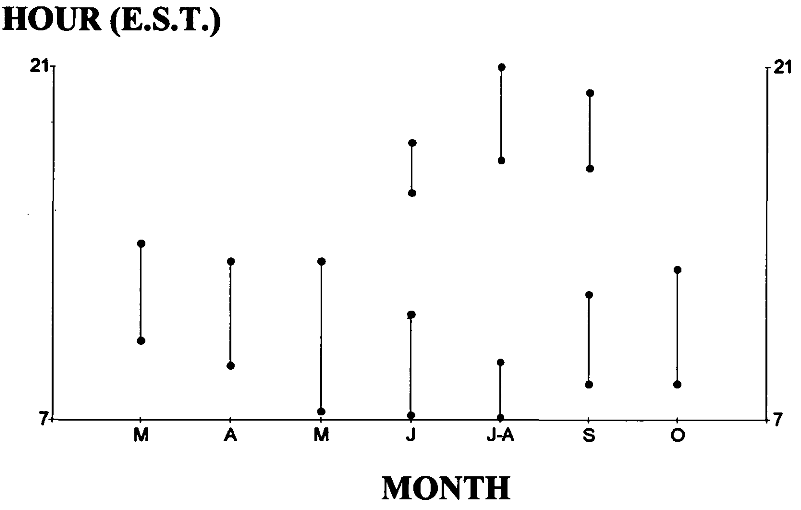

Figure 4: Daily activity pattern of *Coluber viridiflavus* at the study area. July and August are pooled together due to the too little amount of findings done in August. Note the shift from an activity in the middle of the day (springtime and late autumn) to an activity in the earliest daylight hours and in the late afternoon hours (summertime).

Abb. 4: Tagesaktivitätsmuster von *Coluber viridiflavus* im Untersuchungsgebiet. Juli- und August-Daten sind aufgrund zu geringen Funderfolges im August gepoolt. Man beachte die Verlagerung des Aktivitätsmaximums von der Tagesmitte (im Frühjahr und Herbst) in die Morgen- bzw. späten Nachmittagsstunden (im Sommer)..

Table 4: Average annual air temperature of activity (AAT, in °C, ± S.D.) for *Coluber viridiflavus* and three sympatric snakes from the study area. For statistical comparisons, see text.

Tab. 4: Die mittleren Lufttemperaturen bei denen die im Jahreslauf beobachteten *Coluber viridiflavus* und drei weitere Schlangenarten im Untersuchungsgebiet aktiv waren (AAT, in °C, ± Standardabweichung).

Species / Art	AAT	n
Coluber viridiflavus	20.6 ± 4.1	111
Elaphe longissima	20.8 ± 3.0	62
Elaphe quatuorlineata	20.8 ± 3.5	90
Vipera aspis	21.4 ± 2.8	78

air temperatures being positive in either males ($\bar{x}$ = 3.5 ±1.5°C) or females ($\bar{x}$ = 3.0 ±1.5°C; differences between sexes: P = 0.41 at KRUSKAL-WALLIS one-way ANOVA). The average body temperature of males in our study area ($\bar{x}$ = 25.3 ±2.1°C) was similar to that recorded by SCALI & ZUFFI (1994) in *Coluber viridiflavus* from northern Italy ($\bar{x}$ = 26.6 ± 0.7°C, n = 15, P = 0.29, Student t test with df = 30), while the average body temperature of the females ($\bar{x}$ = 25.1 ±1.5°C) was significantly lower than that reported by SCALI & ZUFFI (1994) (P = 0.026, Student t test with df = 23). Intersexual differences in mean body temperatures were not significant (P = 0.79, KRUSKAL-WALLIS one-way ANOVA).

Daily activity pattern

The daily activity pattern of *C. viridiflavus* is summarized in figure 4. Daily activity changed seasonally from a unimodal pattern in spring and late autumn (activity peak in the midday hours) to a bimodal pattern in late spring and summer (activity peak in early morning and late afternoon). This pattern is likely a result of the drastic monthly variations in air temperature, which frequently exceeded 30°C during the hottest months (July and August, fig. 1).

Seasonal activity pattern

The monthly distributions of observation frequencies are shown in figure 5. In every year the observation frequency peaked in both spring and autumn, but most of the animals (60.37%) were seen during the spring mating season. The numbers of expected (taking into account the sampling effort) and observed animals in each month are shown in figure 6. The observed sample significantly exceeded the expected one in April and May (peak of the mating activity: April, χ^2 = 6.67, P = 0.009; May, χ^2 = 38.15, P = 0.000001), but it was significantly lower than the expected in March (χ^2 = 7.54, P = 0.006), July (χ^2 = 8.10, P = 0.004), August (χ^2 = 16.80, P = 0.00001), and November (χ^2 = 5.60, P = 0.018). The two samples did not differ significantly in June (χ^2 = 2.30, P = 0.13), September (χ^2 = 0.15, P = 0.69), and October (χ^2 = 0.01, $P > 0.9$).

The minimal air temperature of activity (in the shade) for Whip Snakes was 8°C (h 08.25, 22 October 1991), and the maximum air temperature of activity was 28°C (h 10.10, 2 September 1991). Mean air temperature of activity was 20.6 ±4.1°C (n = 111). A one factor ANOVA with year as the factor showed that there were no statistically significant annual variations in the air temperatures of activity of snakes (1991: $\bar{x}$ = 20.8 ±5.2°C, n = 36; 1992: $\bar{x}$ = 21.2 ±3.4°C, n = 46; 1993: $\bar{x}$ = 19.3 ± 3.8°C, n = 21; 1994: $\bar{x}$ = 20.1 ±2.0°C, n = 8). Comparisons between air temperatures of activity of *C. viridiflavus* and three sympatric snakes are given in table 4. The air temperature when Whip Snakes were active did not differ significantly from that recorded for *Vipera aspis* (KRUSKAL-WALLIS one-way ANOVA: P = 0.09), *Elaphe longissima* (KRUSKAL-WALLIS one-way ANOVA: P = 0.70), and *E. quatuorlineata* (KRUSKAL-WALLIS one-way ANOVA: P = 0.64), and also the interspecific differences between these latter three species fell well short of statistical significance (KRUSKAL-WALLIS one-way ANOVA, P values ranging from 0.22 to 0.99). The monthly distribution of mean air temperature (in the shade) of the sites where active snakes were observed is shown in figure 7. Activity temperature was significantly higher (KRUSKAL-WALLIS one-way ANOVA: P < 0.02) in June than in every other month (see fig. 7). This depended on the thermal behavior of the gravid females, that probably selected higher ambient temperatures to meet their increased heat necessities due to pregnancy (see SLIP & SHINE 1988; GRAVES & DUVALL 1993; CHARLAND 1991, 1995; LUISELLI & ZIMMERMANN 1997).

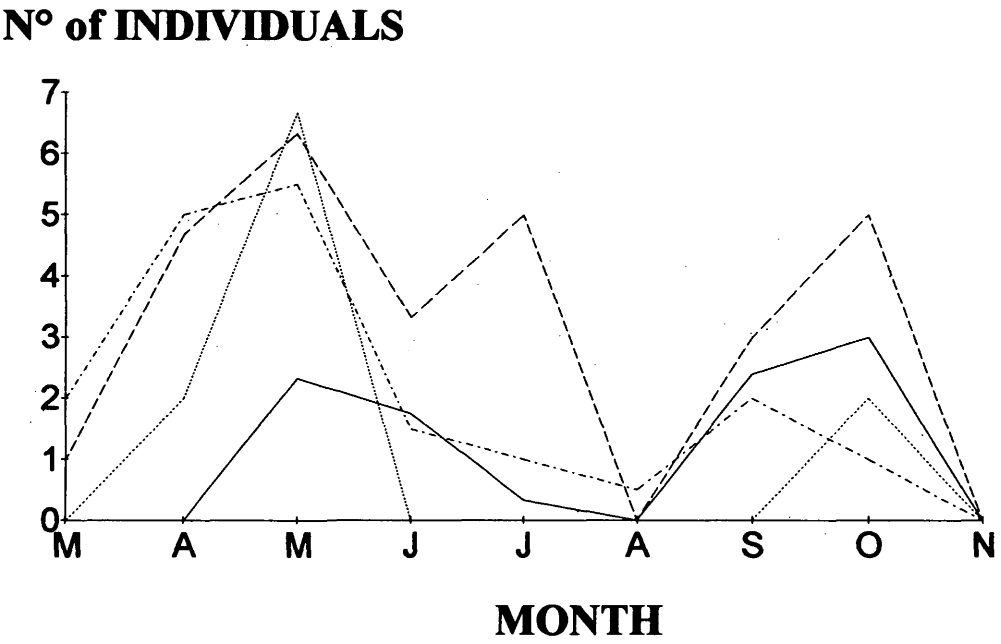

Figure 5: Monthly frequencies of *Coluber viridiflavus* observations in the field during four study years. —— 1991; —— 1992; ········ 1993; - · - · 1994. Note the bimodal distribution of observations in all years.

Abb. 5: Monatliche Häufigkeiten der Feldbeobachtungen von *Coluber viridiflavus* im Untersuchungsgebiet. —— 1991; —— 1992; ········ 1993; - · - · 1994. Man beachte die bimodale Beobachtungsverteilung in allen Jahren.

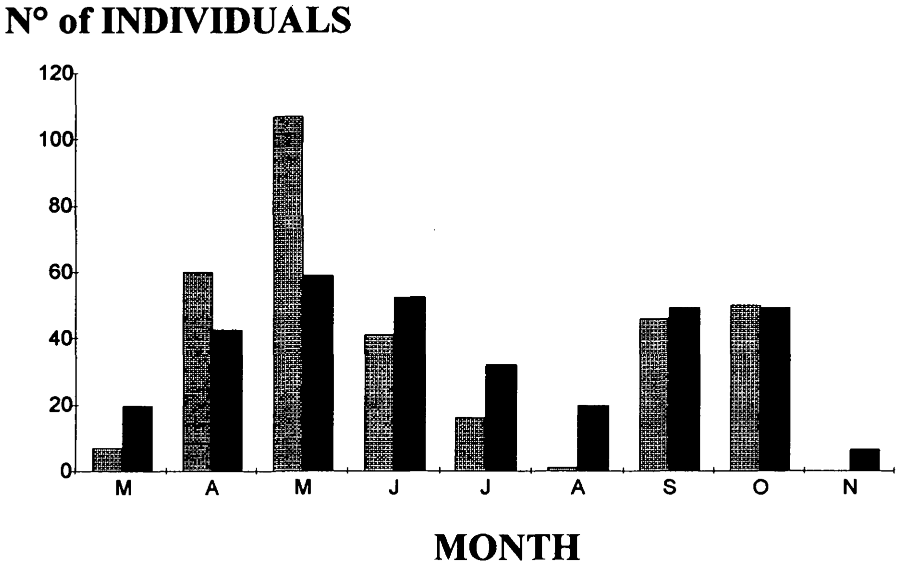

Figure 6: Observed (grey columns) and expected (taking into account the sampling effort, black columns) frequency of observations of *Coluber viridiflavus* individuals in the period 1991-1994. For statistical details, see text.

Abb. 6: Beobachtete (graue Säulen) und (unter Berücksichtigung des Sammelaufwandes) erwartete (schwarze Säulen) Beobachtungshäufigkeit von *Coluber viridiflavus* - Individuen in der Zeit von 1991 bis 1994.

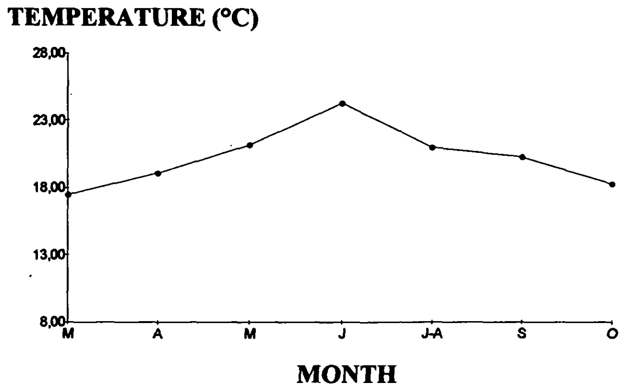

Figure 7: Monthly distribution of the mean air temperatures of the sites where active *Coluber viridiflavus* were observed. All the four study years are pooled together.

Abb. 7: Die Monatliche Verteilung der mittleren Lufttemperaturen an Stellen, an denen aktive *Coluber viridiflavus* beobachtet wurden, gepoolt aus den Daten aller vier Untersuchungsjahre

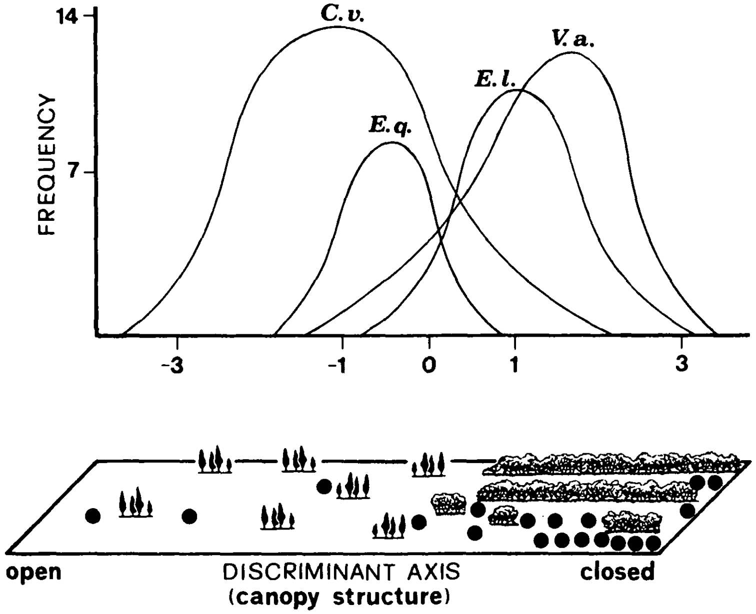

Figure 8: Habitat relationships of snakes in the territory of Tolfa Mountains on the basis of unpublished data collected during 1995. Illustrated are the frequency curves of discriminant scores (above) and the first two discriminant axes (below; canopy structure was superimposed) based upon twelve structural variables sampled in all populations. Detailed description of methods and results are given elsewhere (FILIPPI & CAPULA & LUISELLI, submitted). The picture of canopy structure is inspired by REINERT (1993).
C.v. = *Coluber viridiflavus;* E.l. = *Elaphe longissima,* E.q. = *Elaphe quatuorlineata;* V.a. = *Vipera aspis.*

Abb. 8: Die Habitatbeziehungen der Schlangen aus dem Gebiet der Tolfa Berge nach unpublizierter Daten des Jahres 1995. Wiedergegeben sind die Häufigkeitskurven der 'discriminant scores' und eine bildliche Darstellung der Achsen der ersten beiden Diskriminanzfunktionen auf Grundlage von zwölf in allen Populationen untersuchten Strukturvariablen. Eine genaue Beschreibung der Methoden und Ergebnisse findet sich an anderer Stelle (FILIPPI & CAPULA & LUISELLI, eingereicht). Die Darstellung der Struktur des Blätterdaches erfolgte in Anlehnung an REINERT (1993).
C.v. = *Coluber viridiflavus;* E.l. = *Elaphe longissima,* E.q. = *Elaphe quatuorlineata;* V.a. = *Vipera aspis.*

DISCUSSION

Our study provides some relatively detailed information of the ecology and activity of *C. viridiflavus* in the Tolfa Mountains. This account could be usefully compared with available data on Whip Snakes from other geographic regions (e. g., see PARKER 1974; SHINE 1980). In this regard, the comparisons with the phylogenetically unrelated taxa (e. g., the Elapid snakes of the genus *Demansia*) are particularly interesting, as they suggest convergent evolution.

To begin with, European *C. viridiflavus* mirrors Australian *Demansia* in terms of sexual size dimorphism, the males of both genera attaining larger body sizes than females. Given this sexual size dimorphism and the fact that in both *C. viridiflavus* and several *Demansia* (e. g., *D. olivacea, D. psammophis,* and *D. torquata*) the existence of male-male combats has been confirmed (this study; SHINE 1980, 1994), it may well be that also the mating strategies of these phylogenetically unrelated Whip Snakes are similar. More data on these issues should be supplied to confirm this suggestion. In any case, to consider the occurrence of reversed sexual size dimorphism in both *Coluber* and *Demansia* as a per se proof of convergent evolution is possibly hazardous, as the same pattern is shown by most large viperids (cf. SHINE 1994).

The predatory strategy ("quick pursuit") adopted by *C. viridiflavus* suggests a behavioural specialization for capturing ground-dwelling agile prey, including terrestrial lizards. The same is true also for the other Whip Snakes studied to date (e.g., see SHINE, 1980). In this regard it is interesting to note that *C. viridiflavus* is the sole diurnal Mediterranean snake that, at the adult age, continues to use lizards as primary prey (CAPIZZI & al. 1995; CAPIZZI & LUISELLI 1996; RUGIERO & LUISELLI 1995). However, adult Whip Snakes prey frequently also upon small rodents (CAPIZZI & LUISELLI 1996; T. MADSEN, in lit.). Lizards are preyed by several other diurnal snakes (e. g., *V. aspis, E. longissima, E. quatuorlineata*), but usually when the snakes are juveniles (e. g., see LUISELLI & AGRIMI 1991). Conversely, lizards are primary prey for the semi-fossorial, semi-nocturnal, and small sized snakes of the genus *Coronella* (AGRIMI & LUISELLI 1994). The same trend is also found in Australian snakes: *Demansia* Whip Snakes are the sole diurnal taxa to be saurophagous, while the other Elapids that definitely feed primarily on lizards are small, fossorial and nocturnal (SHINE 1977, 1991). All these data also argue in favour of the hypothesis of convergent evolution between phylogenetically unrelated Whip Snakes.

Apart from diurnality, it is more difficult to find life-history convergency between *C. viridiflavus* and the other Whip Snake species as far as the activity pattern is concerned. In fact, *C. viridiflavus* is nearly identical to all the other snake species inhabiting the territory of Tolfa Mountains in terms of fundamental activity timing (FILIPPI 1995). So, it seems quite difficult to separate the genetically-coded effects on the activity patterns from the effects which are due to the proximate environmental conditions (e. g., ambient temperatures, rainfall, etc). At any rate, the change in daily activity rhythm (from an unimodal to a bimodal pattern when the hot season comes on) observed in Western Whip Snakes is a widespread pattern in Mediterranean snake populations whose daily activity patterns are strongly related to fluctuations in external temperatures (AGRIMI & LUISELLI 1994).

In terms of reproduction biology, *C. viridiflavus* mirrors other Whip Snakes in reproductive mode (oviparity) but not in fecundity rates. For instance, compared with *Demansia,* the Western Whip Snake has a lower fecundity relative to body size (only 4-7 eggs produced by a snake 110 to 140 cm long), so that no obvious convergent evolution could be detected in this character.

As far as the habitat feature is concerned, our data (i) largely confirm the wide ecological distribution already described for this species (as Western Whip Snakes were found in every habitat type available at the study area, see BRUNO 1977); and (ii) suggest a clear-cut preference for hot and dry spots (bushes interspaced with open-grassy fields). We believe that the choice of hot and dry spots could be explained on grounds of the peculiar thermal requirements of this taxon, which has usually higher body temperatures than *N. natrix* and other sympatric snakes (SCALI & ZUFFI 1994). In this regard it is interesting to note that the other Whip Snakes studied to date have all shown high preferred body temperatures (BRATTSTROM 1965; HEATWOLE 1976; HAMMERSON 1979), thus indicating a further convergency with *C. viridiflavus.* With regard to habitat preferences, a detailed study by radiotracking is needed before stressing firm conclusions, as the excess of observations in a given habitat type could be an artefact of different probabilities in observing snakes in open and/or closed habitats.

Our data also confirm that Western Whip Snakes may be active at relatively high air temperature, especially in June when most of the adult females are gravid. Although the mean annual air temperature of activity for *C. viridiflavus* was not significantly higher than that recorded for the other sympatric species (see table 4), the mean air temperature of activity during June was significantly higher for *C. viridiflavus* than for any of the other sympatric species, including both oviparous and livebearing taxa (all differences between samples differ at least at $p < 0.01$ level, KRUSKAL-WALLIS one-way ANOVA; CAPULA & al., unpublished data). Moreover, the mean annual air temperature of activity recorded in this study was very similar (Student *t*-test with 146 *df*, $p = 0.14$) to that ($\bar{x} = 19.6 \pm 0.5$ °C, $n = 37$) recorded by SCALI & ZUFFI (1994) in northern Italy.

Compared with the other sympatric snakes, the strong preference of *C. viridiflavus* for dry habitats emerges clearly (fig. 8); a discriminant function analysis of twelve structural variables sampled in all the populations (for detailed description of methods and results, see FILIPPI & al., submitted) revealed that the frequency curves of discriminant scores along the major habitat gradient showed the preference of *C. viridiflavus* and *E. quatuorlineata* for open canopy structures, while *E. longissima* and *V. aspis* clearly preferred forested areas with closed canopy structure (fig. 8). These interspecific differences were consistent among six different study areas in Tolfa Mountains (differences between sites: $p > 0.3$, KRUSKAL-WALLIS one-way ANOVA; FILIPPI & al., submitted), thus demonstrating that the above pattern is widespread in Mediterranean Central Italy.

The bimodal seasonal activity pattern of *C. viridiflavus* (with a major peak in spring and a minor peak in autumn) is similar to that shown by other Whip Snakes in different geographic regions (e. g., *C. constrictor* (LINNAEUS, 1758): OLIVER 1955). However, since bipeaked seasonal activity patterns were also noted in sympatric snakes from Tolfa Mountains (*V. aspis, N. natrix, E. quatuorlineata* and *E. longissima:* FILIPPI 1995) as well as in several non-European snakes from temperate regions (e. g., see JACKSON & FRANZ 1981, but also MOORE 1978; SEMLITSCH & al. 1981; FUKADA 1993), it seems reasonable to hypothesize that these global similarities reflect adaptations to local bioclimate rather than convergent evolution between Whip Snakes. The "global" effect of the strong air temperature fluctuations on snake behaviour at the study area is indicated by the congruence between data from *C. viridiflavus* and sympatric *Elaphe* and *Vipera* species: during summertime all these snakes not only avoid to be active during the central daylight hours (fig. 4), but also reduce their activity intensity in the open (figs. 5 and 6) and their feeding frequency (LUISELLI & AGRIMI 1991).

In most of the species with bipeaked seasonal activity studied to date, the spring activity peak is determined by the occurrence of a spring mating season. This is just the case in *C. viridiflavus.* The duration of the mating season of snake populations from high altitudes or latitudes is much shorter (normally about 2-4 weeks long) and the onset of copulation activity is also better synchronized (see MADSEN & al. 1992; HOGGREN 1995; LUISELLI 1995). As a result, while in mountainous areas it is very easy to find female snakes (e. g., *V. berus*) accompanied by males during the peak of the mating season, in Mediterranean areas the meetings with Whip Snake pairs are rare events, also when mating activity peaks (April). The autumnal activity peak may also depend on a second, less intense mating period as it is the case of some populations of *V. aspis* (SAINT GIRONS 1952, 1957, 1994), and *N. natrix* (LUISELLI 1996), but this is not true in *C. viridiflavus*, that has not an autumnal mating period.

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