Behavioural Processes 168 (2019) 103960

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Sexual dichromatisation and sexual differences in hunting behavior and dietary intake in a free-ranging small viperid snake, *Cerastes vipera*

Itay Tesler[a,b], Jaim Sivan[c,d], Avi Rosenstrauch[c], Sefi J.A. Horesh[b], A. Allan Degen[a], Michael Kam[a,*]

[a] Desert Animal Adaptations and Husbandry, Wyler Department of Dryland Agriculture, Institutes for Desert Research, Ben Gurion University of the Negev, Beer Sheva, 84105, Israel

[b] Negev Zoo, P. O. B. 4033, Beer Sheva, Israel

[c] Department of Life Sciences, Achva Academic College, M.P. Shikmim, 79800, Israel

[d] Department of Life Sciences, Ben Gurion University of the Negev, Beer Sheva, 84105, Israel

ARTICLE INFO

Keywords:
Hunting strategy
Caudal luring
Feeding mimicry
Sexual dichromatism
Sit-and-wait ambush
Cerastes vipera
Diet composition

ABSTRACT

The tip of the tail in female *Cerastes vipera*, a small viperid snake, is black and conspicuous, whereas that of the male is not. We tested the hypothesis, albeit indirectly, that this sexual dimorphic chromatisation is related to caudal luring, a feeding mimicry hunting strategy. *C. vipera* can hunt nocturnally-active lizards only via sit-and-wait ambush and, consequently, we predicted that females would use caudal luring more often than males and that the proportion of nocturnal prey items in the diet of females would be higher than in males. Our hypothesis was supported as: 1) only females demonstrated caudal luring towards nocturnally-active lizards and more than 85% did so, whereas none of the males demonstrated such behavior; and 2) females consumed a significantly higher proportion (15/40 vs 4/27) of nocturnally-active lizards than did males. We concluded that sexual dichromatisation in *C. vipera* is associated with hunting strategy that results in different hunting behavior and different dietary intake between sexes. These novel findings: 1) provide a functional explanation for the black tail of female *C. vipera*; and 2) suggest different evolutionary driving forces between sexes and, consequently, different ecological impacts of male and female *C. vipera* on lizard populations.

1. Introduction

On the continuum of hunting strategies employed by predators in capturing prey, sit-and-wait and active hunting are practiced at the two extremes (Schoener, 1971; Huey and Pianka, 1981; Scharf et al., 2006; Ross and Winterhalder, 2015). The predator can attract prey by using deceptive tactics categorized as “aggressive mimicry” or, functionally, as “feeding mimicry” (Schuett et al., 1984). Feeding mimicry was initially described in anglerfish, which use their first dorsal spine to simulate a ‘tiny creature’ to attract prey (Wilson, 1937; Pietsch and Grobecker, 1978), and alligator snapping turtles, which possess a vermiform-shaped appendage on the tip of their tongues to lure fish (Allen and Neill, 1950; Drummond and Gordon, 1979); however, it is quite common in viperid snakes that use sit-and-wait hunting by employing mainly caudal luring and, occasionally, lingual luring to deceive potential prey (Glaudas and Alexander, 2017). Such behavior in snakes is often accompanied by modifications at the end of the tail to mimic prey such as a worm to lure lizards (Reiserer, 2002; Reiserer and Schuett, 2008; Hagman et al., 2009) or frogs (Schuett et al., 1984; Reiserer, 2002) and as a spider to lure birds (Fathinia et al., 2015). Caudal luring is often associated with increased caudal segments for the effective imitation of invertebrate prey (Hampton, 2011), and with conspicuous tail coloration (Pough, 1988; Cooper and Greenberg, 1992; Rabatsky, 2008), although some studies in snake species reported caudal luring without conspicuous tail coloration (Leal and Thomas, 1994; Glaudas and Alexander, 2017). The hypothesis that tail wriggling is, in effect, caudal luring is difficult to test in free-ranging species. Studies of the function of caudal luring in snakes were done mainly on captive specimens and were divided, where some showed no effect (Burger and Smith, 1950; Greene and Campbell, 1972; Strimple, 1995), while others showed a positive effect on prey attraction (Wharton, 1960; Greene and Campbell, 1972; Pough, 1988; Chiszar et al., 1990; Rabatsky and Farrell, 1996; Reiserer and Schuett, 2008; Hagman et al., 2009; Nelson et al., 2010). Furthermore, the first study to quantify tail wriggling in free-ranging rattlesnakes raised doubts concerning its actual function (Clark et al., 2016).

* Corresponding author.
E-mail address: mkam@bgu.ac.il (M. Kam).

https://doi.org/10.1016/j.beproc.2019.103960
Received 6 May 2019; Received in revised form 8 September 2019; Accepted 8 September 2019
Available online 10 September 2019
0376-6357/

Many viperid species use caudal luring when young but not so when adults (Greene, 1992). In these species, the end of the tail is colored conspicuously at birth, but this coloring disappears when adulthood is reached. The end of the tail usually mimics a wriggling insect larva, typical prey for lizards (Pough, 1988; Hagman et al., 2009) and is termed 'vermiform' (Jackson and Cross, 2013). However, as adults, these snake species shift to a different diet (e.g., small mammals), where luring behavior is not effective and, therefore, not used (Greene, 1992). Only two viperid snake species, *Bothrops bilineatus* and *Cerastes vipera*, are reported to use caudal luring as adults and have conspicuous tail coloration throughout their whole ontogeny, with both species preying on lizards as young and as adults (Greene and Campbell, 1972; Heatwole and Davison, 1976; Sivan et al., 2013).

Sexual dimorphism of tail coloration in viperid snakes is rare, and has been reported only for *C. vipera* and *Bothrops atrox* (Burger and Smith, 1950; Marx, 1958; Heatwole and Davison, 1976). However, conspicuous tail coloration and sexual dimorphism is absent in adult *B. atrox* (Burger and Smith, 1950) and there are no reports of caudal luring in adults (Pycraft, 1925; Burger and Smith, 1950). Thus, *C. vipera* is the only species demonstrating sexual dimorphic chromatisation (or dichromatisation) throughout ontogeny; the tip of the tail in the female is black and conspicuous over the light-colored background of the sandy dune habitat, whereas that of the male is brown colored and does not differ from the color of the rest of the body (Fig. 1). Male and female *C. vipera* employ mainly sit-and wait hunting (Horesh et al., 2017) and their diets are composed of nocturnally- and diurnally-active lizard species. Caudal luring by this nocturnal viperid could only be applied to entice a nocturnally-active prey species. At our study site, nocturnally-active lizards do not have distinct burrows, as is the case for skinks, nor do they seal their burrows when not active, as is the case for geckos (Bouskila, 1988) and, consequently, can only be captured by ambush, as *C. vipera* are too slow to chase prey.

Therefore, *C. vipera* is an excellent candidate to test the caudal luring hypothesis in free-living snakes. We hypothesized that sexual dichromatisation in this species is related to feeding mimicry via caudal luring and predicted that females would use caudal luring more intensively and would be more successful in sit-and-wait hunting than males and, thus, their dietary intake would include a higher proportion of nocturnally-active lizards than males. To test our hypothesis, we monitored hunting behavior and determined dietary intake in free-ranging male and female *C. vipera*.

2. Methods

2.1. Study species

The Saharan sand viper, *Cerastes vipera* (Linnaeus 1758) (previously *Aspis vipera* (Schnurrenberger, 1959), family Viperidae, is one of the smallest viperid species (Sivan et al., 2015), measuring up to 35 cm in length. This viper is nocturnally-active, moves by sidewinding and is limited to sand and dune systems (Sivan et al., 2013; Werner, 2016) across northern Africa's Saharan countries, the Sinai Peninsula and, in Israel, across the western Negev (Werner, 2016). This snake preys predominantly on lizards (Schnurrenberger, 1959; Subach et al., 2009; Sivan et al., 2013) and captures its prey mainly using sit-and-wait hunting (Horesh et al., 2017) by burying itself below sand level (Klemmer, 1970) and, occasionally, by active hunting (Subach et al., 2009; Horesh et al., 2017). *Cerastes vipera* is active from spring to autumn (April to late October) and inactive during winter (November to late March) (Sivan et al., 2013). Mating season is short, up to two weeks in early spring, from the end of April to the beginning of May, females are ovo-viparous and young appear in August. The female *C. vipera* is slightly, but significantly, larger than the male (Sivan et al., 2015), and the tip of its tail is black and conspicuously marked whereas that of the male is not (Fig. 1), resulting in a distinct sexual dichromatism that is apparent throughout ontogeny (Schnurrenberger, 1959; Kramer and Schnurrenberger, 1963; Heatwole and Davison, 1976; Sivan et al., 2015). At our study site, when individual *C. vipera* were checked for sex by inserting a probe into the cloaca, the probe was inserted 0–2 subcaudal scales in females (n = 50) and all had black tails; whereas, it was inserted 6–11 sub-caudal scales in males (n = 50) and none had black tails (JS unpubl. data). This tail coloration difference between sexes in *C. vipera* was first documented by Marx (1958) in 82 specimens; of 42 females, all but one had a black tail and of 40 males, 34 had tails with the same coloration of the body, while the other six had darker tails, but lighter than that of females (Marx, 1958). He also reported that the ratio of the tail length to the total body length was greater in males than in females (0.103–0.081), and that females had more 'number of ventrals' than males (117. 7–113.3).

2.2. Study area

The study was done in the desert sand dunes surrounding *Wadi* Seher in the western Negev, 15 km south of Beer-Sheva (31° 5.4′ N and 34° 48.6′ E), Israel, at 320–340 m above sea level. The area has an annual average rainfall of 150 mm, all occurring in winter, with 60% falling in December and January. The area is characterized by large annual variations in total rainfall and in its temporal and spatial distributions, and the dominant vegetation is of the Saharo–Arabian type (Sivan et al., 2013). Winters are mild - the coldest month, January, has mean minimum and maximum air temperatures of 7.6 and 18.1 °C, respectively. Summers are hot and dry, lasting from June to September. The hottest month, August, has mean minimum and maximum air temperatures of 20.2 and 33.5 °C, respectively. The study area was confined to a single dune, with low plant cover, and approximately 40,000 m^2 (100 m x 400 m) in size. Six species of lizards inhabited the area: the diurnal (1) Nidua fringe-fingered lizard (*Acanthodactylus scutellatus*), (2) Egyptian fringe-fingered lizard (*Acanthodactylus aegyptius*) and (3) sandfish (*Scincus scincus*), and the nocturnal (4) wedge snouted skink (*Sphenops sepsoides*), (5) Anderson's short-fingered gecko

Fig. 1. Sexual dichromatism in *C. vipera*: Female tail (right) is black and conspicuously marked whereas that of the male (left) is not.

(*Stenodactylus petrii*), and (6) Lichtenstein's short-fingered gecko (*Stenodactylus sthenodactylus*) (Sivan et al., 2013; Werner, 2016).

Both *Acanthodactylus* and *Stenodactylus* dig burrows and remain within them during their non-active diel phase. However, only the burrows of *Acanthodactylus* stay open and, thus, allow active foraging by *C. vipera* (Werner, 2016; Horesh et al., 2017). When in their burrows during the non-active period, *Stenodactylus* seal and block the entrance from the inside and smooth the sand with the tip of the tail. In this way, the burrow is camouflaged (Bouskila, 1988; Werner, 2008, 2016). We have been studying *C. vipera* for over 20 years and have never observed *C. vipera* digging in the sand and entering a gecko burrow or impressions in the sand near a burrow indicating burrowing behavior. Furthermore, we are not aware of any report on such behavior.

2.3. Observations and data collection

Field research was done between spring (early April), when the snakes emerged from winter inactivity, and autumn (late October) 2017, when the snakes entered winter inactivity. The study area was searched for viper tracks for five to seven nights each month. Two researchers covered the entire area by walking length-wise twice on the plot at a distance of 20 m between them. When *C. vipera* tracks were observed, they were followed from their source to the point where active movement ended. Feces, along with characteristic sand impressions (Fig. 2) that indicated defecation behavior of *C. vipera*, were found occasionally on the trail of the snake usually within the first 15 m from the diurnal shelter. Sidewinding tracts continued after the fecal sample and these were followed until the individual snake was located. A snake was always located after observing a fecal sample and we are confident that the fecal sample was from that individual snake. The snake was observed submerged in the sand for up to 5 min before sexing the snake and taking measurements between 22:00 and 23:00. Each snake was weighed to 0.01 g (O'haus Balance, Model CT 200) and measured for SVL to 0.1 cm. Then, the abdominal area of each snake was palpated and fecal material, when present, was extracted by gently stroking its ventral side towards the cloaca. Handling of the snake was completed within 4 min, and then the snake was released at the point of capture. Fecal samples collected from the ground comprised 40% (38 of 95) and manually extracted fecal material (or regurgitated material) comprised 60% (57 of 95) of the samples analyzed for prey consumption. Individuals with a SVL ≤ 15 cm were classified as neonates (1–2 months old, August and October only) while those with a SVL > 15 cm were classified as adults (> 1 year old, and included subadults) (Sivan et al., 2015). All procedures on the snakes were approved by the Israel Nature and National Parks Protection Authority and the Ben-Gurion University Committee for the Ethical Care and Use of Animals in Experiments.

2.4. Fecal analysis

Nine *C. vipera* (body mass 14.5 ± 4.09 g, SVL 21.1 ± 2.54 cm, BCI 13.9 ± 2.39) were offered either *Acanthodactylus* spp. or *Stenodactylus* spp., in the laboratory and their feces were collected. Each fecal sample was air-dried and then was spread in a Petri dish over 1 mm grid paper. Scales, claws and teeth in the fecal samples were observed using a binocular microscope (Wild, model M7A, Heerbrugg, Switzerland); they allowed the identification of the lizard species and whether they were juveniles or adults (Supplementary Fig. 2; Supplementary Table 1)

Fecal samples collected from free-living *C. vipera* were treated in the same manner. Lizard plates, scales and claws were compared with these items *in-situ* and identified to the species/genus level based on their shape (Supplementary Fig. 2) and size (Supplementary Table 1). Most samples contained one prey item, however some contained two. Diet composition of *C. vipera* was determined from fecal samples, manually extracted fecal material and from regurgitation.

Fig. 2. An example of a fecal sample of *C. vipera* found along its trail, and specific sand impressions indicating defecation.

2.5. Body condition

Body condition, indicative of the nutritional status of the animal, could affect hunting behavior as well as dietary intake. Body condition index (BCI) is commonly calculated as a function of SVL and body mass, reflects fat reserves (Bonnet and Naulleau, 1996) and has been described as being "intimately related to an animal's health, quality or vigour and has been widely claimed to be an important determinant of fitness" (Peig and Green, 2010). The "scaled mass index" (Peig and Green, 2009), which is independent of body size, was used to estimate BCI in *C. vipera*, as has been done previously for this species from the same study site (Sivan et al., 2015).

2.6. Statistical methods

We did not scale-clip individuals for identification to minimize the effects of handling on hunting strategy and behavior of the snake. In previous studies at this site for over 20 years, re-capture of marked individuals was very low (Sivan et al., 2013; Horesh et al., 2017) and, consequently, each point was considered as an independent measurement. Chi square statistics were used to test whether age (neonates and adults) and sex of *C. vipera* affected prey captured and phi (Φ) was used for determining effect size (Cohen, 1988; Murphy and Myors 1998). Measurements are presented as means ± S.E., and differences are considered significant at $p < 0.05$.

3. Results

In total, 161 adult (83 males and 78 females) and 52 neonate (28 males and 24 females) *C. vipera* were observed year-round, and snout-vent length (SVL) as a measure of size did not differ between sexes (Table 1).

All *C. vipera* at sit-and-wait hunting were submerged in the sand. We

Table 1
Number of *C. vipera* with or without fecal samples (including regurgitated prey), and their mean (± SE) body masses, snout to vent lengths (SVL) and body condition indices (BCI). Body mass, SVL and BCI are not statistically different between sexes, within adults or neonates.

	Adults		Neonates	
	Males	Females	Males	Females
Number	83	78	28	24
With sample	27 (32.5%)	34 (43.6%)	14 (50.0%)	15 (62.5%)
Body mass (g)	17.8 ± 0.94	22.3 ± 1.78	4.6 ± 0.47	4.5 ± 0.56
SVL (mm)	219 ± 4.7	226 ± 4.0	130 ± 5.1	134 ± 3.8
BCI	15.2 ± 0.52	16.4 ± 0.76	19.7 ± 1.24	16.7 ± 0.99
Without sample	56 (67.5%)	44 (56.4%)	14 (50.0%)	9 (37.5%)
Body mass (g)	17.9 ± 0.74	21.8 ± 1.61	4.1 ± 0.60	5.8 ± 0.61
SVL (mm)	212 ± 6.2	211 ± 8.9	130 ± 7.2	154 ± 6.0
BCI	16.6 ± 0.84	16.9 ± 0.66	16.3 ± 1.13	14.6 ± 0.88

Fig. 3. Sit-and-wait ambush at night of an adult female *C. vipera* while caudal luring. *C. vipera* eyes at surface level (A) near fresh *Stenodactylus* spp. feces (B). When the *Stenodactylus* spp. appeared near the snake (foot prints C1), the blackened tip (D) of *C. vipera* tail wriggled, leaving impressions on the sandy surface (E), then, the lizard left the area, leaving deep foot prints (C2).

detected sand impressions near the tail of 69 of the 78 adult females (> 85%), which indicated tail wriggling (Supplementary Fig. 1). In six of these females, we observed nocturnal tail wriggling in front of *Stenodactylus* spp. (Fig. 3), which fits in well with the behavior of caudal luring. Neither tail wriggling nor sand impressions near the tail were observed in any of the 83 adult males, which provided further evidence to support our hypothesis. In fact, in most cases, we were able to predict the sex of the snake before examination by the presence of or lack of sand impressions near the tail.

Fecal samples for prey identification were obtained from 33% and 44% of adult males and females and from 50% and 63% of neonate males and females, respectively (Table 1). Overall, 47 *Acanthodactylus* spp. 15 *S. sepsoides*, 4 *Stenodactylus* spp. and 1 *S. scincus* were identified in adult samples, and 27 *Acanthodactylus* spp., 1 *S. sepsoides* and 1 *Stenodactylus* spp. were identified in neonate samples (Table 2). Adults consumed a significantly higher proportion of nocturnally-active lizard species than neonates (31.1% vs 7.1%, $Chi^2_{(1)} = 5.45$, $p = 0.02$). Only adults were tested for sexual differences in feeding habits as neonates occurred only between August and October, and the sample size was too small for analysis. Within adults, females consumed a higher proportion of nocturnally-active lizards (37.5% vs 14.8%) than males ($Chi^2_{(1)} = 4.08$, $p = 0.043$), and effect size indicated a large magnitude ($\Phi = 0.50$). Hence, our prediction was supported. In addition, SVL and body condition index (BCI) of females that consumed nocturnally-active lizards did not differ from females that consumed diurnally-active lizards and, also, not from males, although body mass of females was larger than that of males ($p < 0.05$) (Table 1).

4. Discussion

Our hypothesis was supported as: 1) only females demonstrated caudal luring towards nocturnally-active lizards and more than 85% did so, whereas none of the males demonstrated such behavior; and 2) females consumed a significantly higher proportion of nocturnally-active lizards than did males, which could be captured only by sit-and-wait hunting.

Table 2
Diet composition of free-ranging *C. vipera*, based on fecal analyses.

Prey	Activity	Adults		Neonates	
		Males	Females	Males	Females
Acanthodactylus spp.	Diurnal	23	24	13	14
Scincus scincus	Diurnal	0	1	0	0
Sphenops sepsoides	Nocturnal	2	13	1	0
Stenodactylus spp.	Nocturnal	2	2	0	1

We are aware that the hypothesis was tested indirectly, as the study was observational, and that there may have been other differences between sexes, such as size, and temporal or spatial preferences that affected dietary intake. However, although *C. vipera* females are larger than males, sexual size dimorphism is very low (Sivan et al., 2015) and, in this study, was non-significant. Furthermore, both sexes are nocturnal (Sivan et al., 2013; Werner, 2016) and were observed in the same habitat. Therefore, we rejected size and spatial and temporal differences between sexes as plausible reasons for dietary differences. We are also aware that feeding habits could be linked to mate-searching activities in males. Such activity for males is an intensive two week period after emerging from winter inactivity in April (Sivan et al., 2012). During this time, *C. vipera* often do not eat and, in this study, dietary intake was recorded for only two females and four males and none consumed nocturnally-active lizards. This eliminated the premise that the difference between sexes was due to mate-searching activities in males and, consequently, our hypothesis had a sound basis. Among the questions that emerged from this study included: (1) what are the possible costs and benefits for the morphological and behavioral differences between sexes; and (2) what might be the short-term and/or the evolutionary forces driving these differences.

4.1. Sexual dietary differences and size dimorphism

It has been stated that, "sexual differences in diet are almost inevitable if the sexes differ greatly in body size" (Shine, 1989) and this was evident in several snake species (Shine, 1991; Manjarrez et al., 2014; Loebens et al., 2019). In reptiles, sexual size dimorphism (SSD) could evolve from sexual selection (usually males are larger), fecundity selection (favoring larger females) and/or natural selection for resource partitioning (Cox et al., 2007), the latter based on environmental forces (ecological causation) (Shine and Madsen, 1994). Furthermore, intraspecific differences in nutritional demands could lead to sexual dimorphism via competition of a limited resource (Bonnet et al., 1998) and, therefore, our findings on differences in feeding habits between males and females could be a mechanism to decrease intraspecific competition.

Shine (1991) reasoned that sexual size differences are due to differences in reproductive biology and, consequently, most snake species exhibit female-biased SSD (Cox et al., 2007; King et al., 1999). Viperidae are exceptional within snake lineages where SSD is generally male-biased (Cox et al., 2007), suggesting selective pressures via sexual selection and/or natural selection. However, the female-biased SSD in *C. vipera* suggests selective pressure via fecundity selection which fits in well with the advanced reproductive strategy of *C. vipera* being ovo-viviparous (Sivan et al., 2015).

However, although *C. vipera* females are larger than males, the sexual size dimorphism index in *C. vipera* is very low (0.0476; Sivan et al., 2015), and, in this study, snout-vent length (SVL) did not differ between sexes (Table 1). In addition, BCI did not differ between sexes or within females that consumed nocturnally- and diurnally-active lizards. Therefore, although these parameters could have been driving forces for the sexual differences in hunting behavior, they could not explain our main finding that females consumed more nocturnally-active lizards than males.

4.2. Caudal luring and risk of predation

It has been suggested that caudal luring, and specifically as a 'vermiform' (Jackson and Cross, 2013), is strongly related with a diet comprising of amphibians or reptiles. This is the case in *C. vipera*, where dietary intake of both young and adults consists solely of reptiles.

Theoretically, sit-and-wait hunting reduces the risk of predation compared to active foraging and caudal luring increases the opportunity for prey encounter. Both behaviors are advantageous to the hunter. However, tail wriggling attracts not only potential prey but also potential predators and, consequently, bears additional costs by increasing predation risk (Rowe et al., 2002; Rabatsky and Waterman, 2005). Snakes of various species were observed with damaged tails as a result of predation escape (e.g., Shine et al., 1999; Costa et al., 2014), which lends support to this premise. In the area inhabited by *C. vipera*, the Eurasian stone curlew, *Burhinus oedicnemus*, a nocturnally foraging predator that feeds on both invertebrates and vertebrates (Paz, 1986; Green et al., 2000), is commonly observed; sand impressions at our research site (IT and JS, unpublished data) indicated predation of *C. vipera* by this curlew. Also, the red fox, *Vulpes vulpes*, and the black desert cobra, *Walterinnesia aegyptia* (Elapidae), a sauropagous snake (Mendelssohn, 1977), were seen preying on *C. vipera* at night on several occasions (IT and JS, unpublished data). Other potential nocturnal predators which share the same sandy habitat with *C. vipera* include the little owl, *Athene noctua*, which preys on reptiles (Paz, 1986), and a larger viperid, *Cerastes cerastes*, which preys on rodents and reptiles (Mendelssohn, 1977). The overall effect of such costs on the longevity of female *C. vipera* is unknown, but we cannot rule out the scenario described by Reiserer (2016) for *Crotalus cerastes* where there is a difference in longevity between the sexes. In this species, females are also larger than males and, although size confers some advantage, males live longer (Reiserer, 2016). Reiserer (2016) suggested that costs imposed upon adult females, mainly due to reproduction, are “far greater than those on males, despite males presumably being more vulnerable to predation owing to a more mobile life style”. We were not able to distinguish age classes in adult *C. vipera*, but a similar scenario might occur where reproductive costs require additional energy and nutritional demands that affect survival. Indeed, reproduction strategy of ovo-viviparity in *C. vipera* suggests increased reproductive efforts compared with other Vipiridae. In support of this reasoning, we found that shortly after reproduction, in August, the body condition of female *C. vipera* was significantly lower than that of the male (Sivan et al., 2015). The improved prey catch at night employing caudal luring by females could possibly have been among the evolutionary driving factors for determining sexual differences in predation behavior.

Our findings suggest that caudal luring in female *C. vipera* at night allow them to be more efficient in hunting nocturnally-active lizards than males. Consequently, males are expected to increase chances of hunting diurnally-active lizards using two alternative strategies: 1) they may shift into a more risky and energetically demanding active hunting at night (via entering burrows of diurnally-active lizards; Subach et al., 2009; Horesh et al., 2017); and/or 2) expand sit-and-wait activity into crepuscular hours when diurnally-active lizards start their activity, but with higher costs of predation for this small and cryptic predator. Although *C. vipera* is considered a nocturnal hunter (Schnurrenberger, 1959; Sivan et al., 2013; Werner, 2016), crepuscular activity has been suggested for this species (Schnurrenberger, 1959; Heatwole and Davison, 1976). However, to date, there is no supportive data for this option.

4.3. Sexual dichromatisation

Sexual dichromatisation in viperids has been stated as “not important” (Klauber 1956) and conspicuous tail coloration does not necessarily reflect the use of caudal luring; of 66 viperid snake species reported to possess conspicuous tail colors, only 21 species employed caudal luring (Rabatsky, 2008). Also, tail coloration did not affect foraging success in neonate pigmy rattlesnakes (Farrell et al., 2011). Sexual dichromatism is common among vipers where mainly adult females have more cryptic colors than adult males (Shine and Madsen 1994), a difference generally attributed to mate selection and sexual behavior (Shine and Madsen, 1994).

In general, sexual dichromatisation is most common in avian species where males are more colorful. Furthermore, some colors have been shown to be related with nutritional status and immune function of the individual, and were suggested as evolutionary driving forces in honestly reflecting body condition (Badyaev and Hill, 2000; Siefferman et al., 2007).

Vipera berus demonstrates sexual dichromatisation where males are brighter-colored with more distinct black dorsal zigzag lines than females, which are “generally duller in overall color and apparently well-camouflaged in the natural habitat” (Shine and Madsen, 1994). In testing alternative hypotheses for this sexual dichromatisation, sexual selection was declined and the “flicker fusion” hypothesis, based on natural selection, was suggested as a plausible explanation for male distinct coloration (Shine and Madsen, 1994). In this species, sexes did not differ in their dietary habits (Prestt, 1971). In the boomslang (*Dispholidus typus*), one of the most dichromatic snake species in which females are much darker than males, neither diet composition nor niche differed between sexes (Smith et al., 2019). In the present study, we demonstrated that sexual dichromatisation should be tested functionally. *C. vipera* represented a unique case where sexual dichromatisation of a specific organ (tail) and sexual differences in hunting behavior and in dietary intake are all linked. As this is also the smallest known viperid and a cryptic predator, we cannot rule out that these characteristics have evolved due to the small size of the snake.

5. Conclusions

The costs and benefits accompanying the *C. vipera* hunting strategy and the life history of this snake species are among the evolutionary driving forces shaping sexual, morphological and behavioral differences. The sexual dietary differences suggest eco-physiological causation for the sexual dichromatism, but this does not explain why males have not developed similar characteristics. This is puzzling and in contrast with the general trend of viperid males that are considered more efficient in caudal luring than females (Rabatsky and Waterman, 2005). Results of this study are novel in that they link differences between sexes in tail dichromatiation, behaviorial hunting strategy and dietary intake. It is also the first study demonstrating different dietary habits between sexes and, hence, might have different ecological impacts on lizard populations.

Authors’ contributions

All authors contributed critically to the drafts and gave final approval for publication. I.T., S.J.A.H. and J.S. collected the data, I.T. and M.K. analyzed the data, I.T., J.S., A.R., A.A.D. and M.K. wrote the manuscript text and I.T. prepared the figures.

The authors declare no competing financial or non-financial interests.

Acknowledgements

We thank Shlomo Hadad for helpful suggestions on the manuscript. We thank two anonymous reviewers for their constructive review and most helpful suggestions on an earlier version of the manuscript. Permission for the study was granted by the Israel Nature and National Parks Protection Authority. The authors declare that they do not have conflict of interest related to this publication.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2019.103960.

References

Allen, E.R., Neill, W.T., 1950. The Alligator Snapping Turtle, *Macrochelys Temminckii* 4. Ross Allen’s Reptile Institute Special Publication, pp. 1–15.
Badyaev, A.V., HILL, G.E., 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. Biol. J. Linn. Soc. 69, 153–172.

Bonnet, X., Naulleau, G., 1996. Are body reserves important for reproduction in male dark green snakes (Colubridae: *coluber viridiflavus*)? Herpetologica 52, 137–146.

Bonnet, X., Shine, R., Naulleau, G., Vacher-Vallas, M., 1998. Sexual dimorphism in snakes: different reproductive roles favour different body plans. Proc. R. Soc. London 265, 179–183 B.

Bouskila, A., 1988. Use of the tail in blocking the burrow: a new explanation for the low frequency of tail loss in two desert geckos. Isr. J. Zool. 35, 100–101.

Burger, W.L., Smith, P.W., 1950. The coloration of the tail tip of young fer-de-lance: sexual dimorphism rather than adaptive coloration. Science 112, 431–433.

Chiszar, D., Boyer, D., Lee, R., Murphy, J.B., Charles, W., 1990. Caudal luring in the southern death adder, *Acanthophis antarcticus*. J. Herpetol. 24, 253–260.

Clark, R.W., Dorr, S.W., Whitford, M.D., Freymiller, G.A., Putman, B.J., 2016. Activity cycles and foraging behaviors of free-ranging sidewinder rattlesnakes (*Crotalus cerastes*): the ontogeny of hunting in a precocial vertebrate. Zoology 119, 196–206.

Cohen, J., 1988. Statistical Power and Analysis for the Behavioral Sciences, 2nd ed. Lawrence Erlbaum Associates, Inc, Hillsdale, N.J.

Cooper Jr., W.E., Greenberg, N., 1992. Hormones, brain, and behavior. In: Gans, C., Crews, D. (Eds.), Biology of the Reptilia Volume 18, Physiology E. University of Chicago Press, Chicago, IL, pp. 298–422.

Costa, H.C., Moura, M.R., Feio, R.N., 2014. A tale of lost tails: pseudoautotomy in the neotropical snake genus *Drymoluber* (Serpentes: Colubridae). Can. J. Zool. 92, 811–816.

Cox, R.M., Butler, M.A., John-Alder, H.B., 2007. The evolution of sexual size dimorphism in reptiles. In: Fairbairn, D.J., Blanckenhorn, W.U., Székely, T. (Eds.), Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford, pp. 38–49.

Drummond, H., Gordon, E.R., 1979. Luring in the neonate alligator snapping turtle (*Macroclemys temminckii*): description and experimental analysis. Z. Tierpsychol. 50, 136–152.

Farrell, T.M., May, P.G., Andreadis, P.T., 2011. Experimental manipulation of tail color does not affect foraging success in a caudal luring rattlesnake. J. Herpetol. 45, 291–293.

Fathinia, B., Rastegar-Pouyani, N., Rastegar-Pouyani, E., Todehdehghan, F., Amiri, F., 2015. Avian deception using an elaborate caudal lure in *Pseudocerastes urarachnoides* (Serpentes: viperidae). Amphib. Reptil. 36, 223–231.

Glaudas, X., Alexander, G.J., 2017. A lure at both ends: aggressive visual mimicry signals and prey-specific luring behaviour in an ambush-foraging snake. Behav. Ecol. Sociobiol. 71 (2).

Green, R.E., Tyler, G.A., Bowden, C.G.R., 2000. Habitat selection, ranging behaviour and diet of the stone curlew (*Burhinus oedicnemus*) in southern England. J. Zool. 250, 161–183.

Greene, H.W., Campbell, J.A., 1972. Notes on the use of caudal lures by arboreal green pit vipers. Herpetologica 28, 32–34.

Greene, H.W., 1992. The ecological and behavioral context for pitviper evolution. In: Campbell, J.A., Brodie Jr.E.D. (Eds.), Biology of the Pitvipers. Tyler, Texas. Selva Press, U.S.A, pp. 107–118.

Hagman, M., Phillips, B.L., Shine, R., 2009. Tails of enticement: caudal luring by an ambush foraging snake (*Acanthophis praelongus*, Elapidae). Funct. Ecol. 22, 1134–1139.

Hampton, P.M., 2011. Ventral and sub-caudal scale counts are associated with macrohabitat use and tail specialization in viperid snakes. Evol. Ecol. 25, 531–546.

Heatwole, H., Davison, E., 1976. A review of caudal luring in snakes with notes on its occurrence in the Saharan sand viper, *Cerastes vipera*. Herpetologica 32, 332–336.

Horesh, S.J.A., Sivan, H., Rosenstrauch, A., Tesler, I., Degen, A.A., Kam, M., 2017. Seasonal biotic and abiotic factors affecting hunting strategy in free-living Saharan sand vipers, *Cerastes vipera*. Behav. Processes 135, 40–44.

Huey, R.B., Pianka, E.R., 1981. Ecological consequences of foraging mode. Ecology 62, 991–999.

Jackson, R.R., Cross, F.R., 2013. A cognitive perspective on aggressive mimicry. J. Zool. 290, 161–171.

King, R.B., Bittner, T.D., Queral-Regil, A., Cline, J.H., 1999. Sexual dimorphism in neonate and adult snakes. J. Zool. 247, 19–28.

Klemmer, K., 1970. Uber die avicenna-viper *Cerastes vipera*. Nat. Mus. 100, 454–459.

Kramer, E., Schnurrenberger, H., 1963. Systematik, verbreitung und ökologie der Libyschen schlangen. Rev. Suisse Zool. 70, 453–568.

Leal, M., Thomas, R., 1994. Notes on the feeding behavior and caudal luring by juvenile *Alsophis portoricensis* (Serpentes: colubridae). J. Herpetol. 28, 126–128.

Loebens, L., Hendges, C.D., Almeida-Santos, S.M., Cechin, S.Z., 2019. Morphological variation and sexual dimorphism in two sympatric dipsadine snakes from Southern Brazil. Zool. Anz. 280, 42–51.

Manjarrez, J., Contreras-Garduño, J., Janczur, M.K., 2014. Sexual size dimorphism, diet, and reproduction in the Mexican garter snake, *Thamnophis eques*. Herpetol. Conserv. Biol. 9, 163–169.

Marx, H., 1958. Sexual dimorphism in coloration in the viper *Cerastes vipera* L. Natural History Miscellanea. CAS. 164, 1–2.

Mendelssohn, H., 1977. On the biology of the venomous snakes in Israel. The Family Physician 7, 29–59 In Hebrew with an English Abstract.

Murphy, K.R., Myors, B., 1998. Statistical Power Analysis: A Simple and General Model for Traditional and Modern Hypothesis Tests. Lawrence Erlbaum Associates, Inc, Mahwah, N.J.

Nelson, X.J., Garnett, D.T., Evans, C.S., 2010. Receiver psychology and the design of the deceptive caudal luring signal of the death adder. Anim. Behav. 79, 555–561.

Paz, U., 1986. Birds. In: Alon, A. (Ed.), Plants and Animals of the Land of Israel, Volume 6, Birds. Ministry of Defence/The publishing House and Society for Protection of Nature, Israel.

Peig, J., Green, A.J., 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118, 1883–1891.

Peig, J., Green, A.J., 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Funct. Ecol. 24, 1323–1332.

Pietsch, T.W., Grobecker, D.B., 1978. The complete angler: aggressive mimicry in an antennariid anglerfish. Science 201, 369–370.

Pough, F.H., 1988. Mimicry and related phenomena. In: Gans, C., Huey, R.B. (Eds.), Biology of the Reptilian, Vol 16, Defence and Life History 2. Ann Arbor, MI. Branta Books, USA, pp. 153–234.

Prestt, I., 1971. An ecological study of the viper, *Vipera berus*, in southern Britain. J. Zool. 164, 373–418.

Pycraft, W.P., 1925. Camouflage in Nature. Hutchinson and Co., London.

Rabatsky, A.M., Farrell, T.M., 1996. Reptiles: the effects of age and light level on foraging posture and frequency of caudal luring in the rattlesnake, *Sistrurus miliarius barbouri*. J. Herpetol. 30, 558–561.

Rabatsky, A.M., Waterman, J.M., 2005. Ontogenetic shifts and sex differences in caudal luring in the dusky pygmy rattlesnake, *Sistrurus miliarius barbouri*. Herpetologica 61, 87–91.

Rabatsky, A.M., 2008. Caudal luring as a precursor in the evolution of the rattle: a test using an ancestral rattlesnake, *Sistrurus miliarius barbouri*. In: Hayes, W.K., Beaman, K.R., Cardwell, M.D., Bush, S.P. (Eds.), The Biology of Rattlesnakes. Loma Linda University Press, pp. 143–154.

Reiserer, R.S., 2002. Stimulus control of caudal luring and other feeding responses: a program for research on visual perception in vipers. In: Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H.W. (Eds.), Biology of the Vipers. Eagle Mountain Publishing, Utah, pp. 361–383.

Reiserer, R.S., 2016. The rattle: a window on rattlesnake life history. In: Schuett, G.W., Feldner, M.J., Smith, C.F., Reiserer, R.S. (Eds.), The Rattlesnakes of Arizona. ECO Publishing, pp. 301–342.

Reiserer, R.S., Schuett, G.W., 2008. Aggressive mimicry in neonates of the sidewinder rattlesnake, *Crotalus cerastes* (Serpentes: Viperidae): stimulus control and visual perception of prey luring. Biol. J. Linn. Soc. 95, 81–91.

Ross, C.T., Winterhalder, B., 2015. Sit-and-wait versus active-search hunting: a behavioral ecological model of optimal search mode. J. Theor. Biol. 387, 76–87.

Rowe, M.P., Farrell, T.M., May, P.G., 2002. Rattle loss in pygmy rattlesnakes (*Sisturus miliarius*): causes, consquences, and implications for rattle function and evolution. In: Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H.W. (Eds.), Biology of the Vipers. Eagle Mountain Publishing, Utah, pp. 385–404.

Smith, C.C.D., Layloo, I., Maritz, R.A., Maritz, B., 2019. Sexual dichromatism does not translate into sex-based difference in morphology or diet for the African boomslang. J. Zool. https://doi.org/10.1111/jzo.12670. in press.

Scharf, I., Nulman, E., Ovadia, O., Bouskila, A., 2006. Efficiency evaluation of two competing foraging modes under different conditions. Am. Nat. 168, 350–357.

Schoener, T.W., 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2, 369–404.

Schnurrenberger, H., 1959. Observations on behavior in two Libyan species of viperine snakes. Herpetologica 15, 70–72.

Schuett, G.W., Clark, D.L., Kraus, F., 1984. Feeding mimicry in the rattlesnake *Sistrurus catenatus*, with comments on the evolution of the rattle. Anim. Behav. 32, 625–626.

Shine, R., 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. 64, 419–461.

Shine, R., 1991. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. Am. Nat. 138, 103–122.

Shine, R., Madsen, T., 1994. Sexual dichromatism in snakes of the genus Vipera: a review and a new evolutionary hypothesis. J. Herpetol. 28, 114–117.

Shine, R., Olsson, M.M., Moore, I.T., LeMaster, M.P., Mason, R.T., 1999. Why do male snakes have longer tails than females? Proceedings of the Royal Society 266, 2147–2151.

Siefferman, L., Wang, Y.J., Wang, Y.P., Yuan, H.W., 2007. Sexual dichromatism, dimorphism, and condition-dependent coloration in blue-tailed bee-eaters. Condor 109, 577–584.

Sivan, J., Kam, M., Hadad, S., Degen, A.A., Rozenboim, I., Rosenstrauch, A., 2012. Reproductive cycle of free-living male Saharan sand vipers, *Cerastes vipera*, (Viperidae), in the Negev Desert, Israel. Gen. Comp. Endocrinol. 179, 241–247.

Sivan, J., Kam, M., Hadad, S., Degen, A.A., Rozenboim, I., Rosenstrauch, A., 2013. Temporal activity and dietary selection in two coexisting desert snakes, the Saharan sand viper (*Cerastes vipera*) and the crowned leafnose (*Lytorhynchus diadema*). Zoology 116, 113–117.

Sivan, J., Kam, M., Hadad, S., Degen, A.A., Rosenstrauch, A., 2015. Body size and seasonal body condition in two small coexisting desert snake species, the Saharan sand viper (*Cerastes vipera*) and the crowned leafnose (*Lytorhynchus diadema*). J. Arid Environ. 114, 8–13.

Strimple, P., 1995. Comments on caudal luring in snakes with observations on this behaviour in two subspecies of cantils, *Agkistrodon bilineatus* ssp. Liueratura Serpentium 15, 74–77.

Subach, A., Scharf, I., Ovadia, O., 2009. Foraging behavior and predation success of the sand viper (*Cerates vipera*). Can. J. Zool. 87, 520–528.

Wharton, C.H., 1960. Birth and behavior of a brood of cottonmouths, *Agkistrodon piscivorus piscivorus* with notes on tail-luring. Herpetologica 16, 125–129.

Werner, Y.L., 2008. Tales of tails. Gekko 5, 6–18.

Werner, Y.L., 2016. Reptile Life in the Land of Israel. Chimaira, Frankfurt, Germany.

Wilson, D.P., 1937. The Habits of the Angler-Fish, *Lophius piscatorius* L., in the Plymouth Aquarium 21. Marine Biological Association of the United Kingdom, pp. 477–497.