

Is it better in the moonlight? Nocturnal activity of insular cottonmouth snakes increases with lunar light levels

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Abstract

Both theoretical and empirical investigations suggest that predation risk and availability of resources interact as trade-offs to produce patterns of predation-sensitive foraging. Such interactions have been explored intensely in terrestrial predator–prey systems where both nocturnal prey and predators adjust their activity and foraging behaviour to levels of moonlight. In the case of prey, higher levels of moonlight increase predation risks, and thus prey display lower levels of activity and/or shifts in their use of microhabitat during full moon nights. Predators also display parallel modifications of their activity rhythms during full moon nights – but why? Are predators also sensitive to increased predation, or do predators adjust their behaviour to that of their prey in order to optimize foraging success? Herein, we examined nocturnal predatory behaviour in a natural system where insular cottonmouth snakes, *Agkistrodon piscivorus conanti*, forage for fish carrion that is indifferent to levels of moonlight, thereby removing complexities linked to the behavioural patterns of prey. Our results demonstrated that insular cottonmouths increase their activity during full moon nights. Predation pressure on snakes foraging in the open does not seem to drive their nocturnal behaviour insofar as small-sized individuals – presumably more susceptible to predation – are equally abundant as adult snakes irrespective of levels of moonlight. These results suggest that variation in predator's activity in natural predator–prey systems during risky (full moon) nights might be attributable principally to the availability and detectability of prey rather than a foraging-safety trade-off specific to the predator.

Introduction

Consumption of requisite resources is essential to the survival of animals, which must locate resources and, in the case of predators, successfully capture prey in sufficient numbers to sustain a population relative to physical pressures, competition and predation by other species (Stephens & Krebs, 1986). Foraging tactics of a species are related to trade-offs among various benefits and costs. Benefits include increased quantity, quality and ease of capturing prey, while foraging costs include increased energy investment, risk of predation or injury and competition, among others (Krebs, Stephens & Sutherland, 1983; Stephens & Krebs, 1986; Berger-Tal *et al.*, 2009). The availability of resources and the risk of predation while foraging are two important factors that interact to influence both spatial and temporal patterns of foraging activity of animals (Lima & Dill, 1990; Ritchie, 1998). Empirical investigations with a variety of taxa suggest that foraging behaviours are generally sensitive to the conflicting fitness demands of food acquisition and the avoidance of predators (Longland & Price, 1991; Brown, Kotler & Bouskila, 2001; Brown & Kotler, 2004).

Numerous animals have been shown to alter their nocturnal activity and behaviour in relation to lunar cycle and lighting conditions in terrestrial habitats (e.g. Kotler, 1984*a,b,c*; Longland & Price, 1991; Kotler *et al.*, 1993, 2010; Clarke, Chopko & Mackessy, 1996). The influence of moonlight on behaviour has been documented to show that many nocturnal animals respond to bright moonlight by reducing foraging activity, restricting movements or changing movements from open to more concealed patches of habitat. In the majority of cases, the principal selective forces thought to explain these phenomena are changes either in predation risk of the forager or the availability of prey to the forager. In either case, the interplay of moonlight and nocturnal behaviour – for either forager or prey – involves a trade-off between activity and safety. The foraging behaviours of nocturnal animals related to changes in light conditions have provided an emergent model system for which a rich literature evaluates both theoretical and empirical aspects of foraging versus safety trade-offs (Bouskila, 2001; Brown *et al.*, 2001; Brown & Kotler, 2004; Kotler *et al.*, 2010).

Behavioural changes of prey species to avoid predation in open environments during full moonlight are supported by a

fairly robust literature, but the reactions of predators to nocturnal light conditions are less well studied (Brown & Alkon, 1990; Skutelsky, 1996; Mukherjee, Zelcer & Kotler, 2009). Do predators adjust their behaviour to that of the prey in order to optimize foraging success in relation to effort, or are predators susceptible to increased predation during full moon conditions as well? Teasing apart these two hypotheses is difficult in many natural predator–prey systems. Here, we examine the influence of moonlight on nocturnal foraging of a predator using a natural system where the predator (snake) forages for inert prey (fish carrion) that is indifferent to light levels, thereby eliminating the complexities that might be linked to the behaviour of the prey. We focus on a population of Florida cottonmouth snakes, *Agkistrodon piscivorus conanti*, that has been studied previously by Wharton (1969) and more recently by Lillywhite and co-workers (Lillywhite, Sheehy & McCue, 2002; Lillywhite & McCleary, 2008; Lillywhite, Sheehy & Zaidan, 2008; Young, Aguiar & Lillywhite, 2008). The population is unusual because these snakes are entirely terrestrial and live in close association with colonial-nesting water birds. They feed largely or exclusively on fish carrion that is dropped or regurgitated by the nesting birds during roughly three-fourths of the year. These snakes are largely nocturnal foragers when owls are the only potential predators. Greater predation pressures from raptors, herons and other bird species are present during daylight hours.

Herein, we report data for 9 years of observations, which we have evaluated for correlations between lunar light level and foraging activity that was observed during counts of snakes that forage along a prescribed stretch of beach. If snakes are susceptible to increased predation during full moonlight conditions, then we predict that activity will decrease even if the prey is indifferent to light levels. Conversely, if snakes adjust their behaviours to that of the prey, then we would not detect any effect of moonlight on the foraging behaviours of the snakes. Furthermore, because smaller snakes are more secretive presumably due to higher susceptibility to predation (Bonnet, Naulleau & Shine, 1999; Krysko, 2002; Pike *et al.*, 2008), we expect to detect more variable activity in smaller individuals compared with larger conspecifics.

Materials and methods

Study site

Seahorse Key is a 67-ha island located 3.5 km offshore near Cedar Key on the Gulf coast of north-western peninsular Florida (Fig. 1). Biological communities on this island are diverse and include salt marsh, mangroves and a mixed hardwood hammock that covers much of the upland area of the island. The island is part of the Cedar Keys National Wildlife Refuge and supports a large rookery of colonial-nesting water birds. The rookery is concentrated largely at the western half of the island, and there is a white sand beach that extends in a large arc along its southern edge (Fig. 1). Cottonmouths feed largely on fish carrion and are most abundant in or near

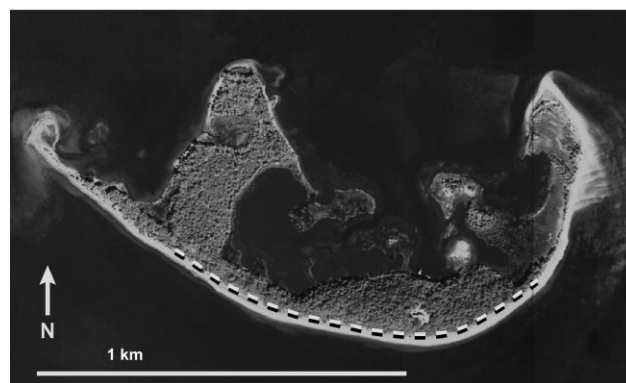


Figure 1 Aerial view of Seahorse Key. Sections in gray depict upland hardwood hammock, and the southern beach is seen as a white band along the island's perimeter. The transect used for assessing snake activity is indicated by the white and black heavy dashed line.

the hammock, which supports the colonial bird rookeries (Lillywhite & McCleary, 2008).

Snake activity

From June 2000 to September 2010, the activity of cottonmouths was monitored along a stretch of the south beach that extended from a midpoint on the island to a point 750 m to the west (Fig. 1). Beginning at dark, several persons (range 1–5, mean 2.5) walked over this area carefully searching each segment and proceeding once in each direction with respect to the length of the beach. We looked for snakes that were easily seen foraging in relatively open ground above the intertidal near the edge where beach transitioned to hammock. Rookery trees, largely supporting nests of Brown Pelicans, *Pelecanus occidentalis*, and Double-crested Cormorants, *Phalacrocorax auritus*, could be found at varying distances along this path. Snakes were encountered in larger numbers on relatively open ground beneath these trees, which were either rooted on the beach or had canopy extending over the beach. The observers walked with headlamps, and snakes were easily observed in artificial light either crawling, feeding or coiled. The snakes were not disturbed by a beam of light and moved away only when the observer came very close to the snake (typically within 1 m). Because inactive snakes are usually coiled in sheltered or concealed sites within the hammock and emerged at dark to move below rookeries, including open areas at the edge of the beach, we used the number of snakes sighted as an index of snake activity. Each survey lasted from 60 to 90 min, depending on time taken to photograph snakes or record other information. Surveys were conducted largely during the period from March to November when snakes were nocturnally active. Overall, during 77 searching transects, we sighted a total of 860 snakes (mean 11.17 snakes per night; range 0–44).

We recorded the location and estimated the size of each snake that was sighted during visual surveys beginning at

dark. The observers were close enough to snakes to estimate the total length and to place each individual within a size category (young-of-the-year below 45 cm; juveniles 46–75 cm; and adults >75 cm). To ensure consistency on both the survey procedures and the field size estimations of the snakes, H. B. L. was present during all the observation sessions. During the course of other investigations, occasional snakes were captured, weighed and measured, which validated the field size estimations.

Environmental variables

Ambient air temperature was recorded (Fisher pen type Thermo-Hygrometer®, Waltham, MA, USA) at the beginning and at the end of each survey, and a mean was calculated to provide a single value per session. Cloud cover was visually estimated using simple categories (no cloud, light clouds, medium clouds, heavy clouds and very heavy clouds with rain).

To estimate nocturnal ambient light, we collated the dates of new moon, first quarter, full moon and last quarter between 2000 and 2010. We estimated the moonlight intensity for each of these phases, relative to the proportion of visible moon (0 for the new moon, 0.5 for both first and last quarters and 1 for the full moon). To provide relative moonlight estimates as continuous variables for all our surveys, we incremented the values between these moon phases by dividing the increase or decrease in relative moonlight intensity by the number of days separating the 'official' days of the successive moon phases. For analysis of covariance (ANCOVA) (see below), we used the moon phase (new moon, first quarter, full moon and last quarter) instead of relative moonlight intensities. In such cases, the week that centered on each moon phase (3 to 4 previous and following days) was coded under the corresponding moon phase to create a categorical variable.

Analyses

We explored the relationships between snake counts and temperature and relative moonlight intensities with single and multiple linear regressions. We used ANCOVA to analyse the effect of moon phase (new moon, first quarter, full moon and last quarter) on snake count independent of temperature. We used a similar design to analyse the effect of the snakes' size. We analysed the effect of cloud cover on the snake's activity using analysis of variance (ANOVA) and ANCOVA with both the temperature and the relative moonlight intensity as covariates. Prior to ANCOVAs, we performed homogeneity of slopes tests, and all P -values were ≥ 0.31 . Because the snake count might be related to the number of observers (ranging from 1 to 5), we explored the possible effects of searching effort with simple linear regressions.

Results

Effect of environmental variables

Regression analyses demonstrated that snake's activity (total number of snakes sighted per survey) was positively correlated

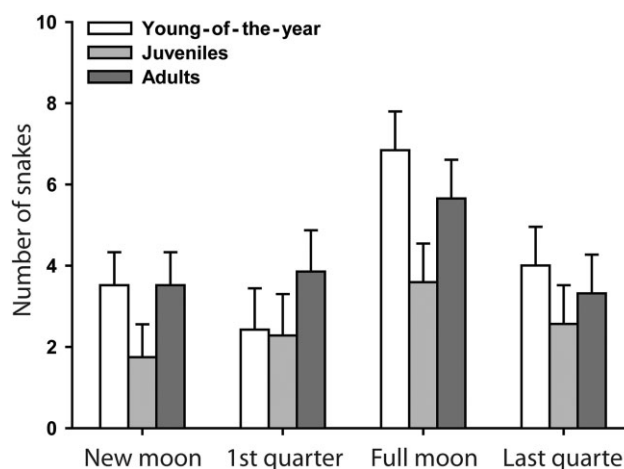


Figure 2 Number of active snakes (mean \pm SE, corrected for temperature; see text) of each size category observed during the four moon phases (including the week centered on each moon phase). Juveniles were generally less abundant than young-of-the-year and adult snakes. However, more snakes were active during full moon compared with the other moon phases. The total number of snakes = 801.

with temperature ($F_{1,67} = 9.76$, $P = 0.003$, $r^2 = 0.13$) and with relative moonlight intensity ($F_{1,75} = 7.98$, $P = 0.006$, $r^2 = 0.10$). Multiple regression analysis showed that both parameters positively influenced snake's activity ($F_{2,63} = 6.01$, $P = 0.004$, $r^2 = 0.16$; $\beta = 0.28$ for temperature and $\beta = 0.31$ for relative moonlight intensity).

An ANCOVA with the number of snakes sighted as the dependent variable, the moon phase (new moon, first quarter, full moon and last quarter) as the predictor and the temperature as the covariate showed that independent of temperature, snakes were more active on nights around full moon than during the remaining moon cycle ($F_{3,64} = 3.24$, $P = 0.02$; see also Fig. 2).

We did not detect any effect of cloud cover on the snakes' activity (ANOVA with the number of snakes as the dependent variable and the cloud cover categories as the predictor; $F_{4,48} = 1.34$, $P = 0.27$). Taking into account both temperature and relative moonlight intensity did not change the result (ANCOVA with temperature and relative moonlight intensity added as covariates to the above design; $F_{4,45} = 2.02$, $P = 0.11$).

Searching effort

We did not detect any effect of the searching effort on the number of snakes sighted ($F_{1,60} = 1.37$, $P = 0.24$, $r^2 = 0.02$), thereby suggesting that our ability to detect snakes was not related to the number of persons involved. We did not expect the level of moonlight to affect our abilities to detect snakes owing to our search efforts being aided by artificial lights. However, because ambient light levels (moonlight) theoretically might affect our ability to detect snakes, and because snake counts were higher during full moon (see above), we repeated the same analysis but with data restricted to nights

with higher ambient light levels (e.g. around full moon). There was no effect of the searching effort on the snake count under conditions of full moon ($F_{1,13} = 0.16$, $P = 0.69$, $r^2 = 0.01$).

Size-specific activity and moonlight

An ANCOVA with the number of snakes sighted as the dependent variable, both the moon phase (new moon, first quarter, full moon and last quarter) and the size categories as the predictors, and the temperature as the covariate showed that both snake size and moon phase had an impact on the snake's activity. Juvenile snakes were less abundant than both young-of-the-year and adult snakes [$F_{2,191} = 3.88$, $P = 0.02$; Fisher's least significant difference (LSD) having juveniles significantly different from young-of-the-year and adults; Fig. 2]. However, all size categories were more abundant on full moon nights ($F_{3,191} = 4.74$, $P = 0.003$; Fisher's LSD having full moon different from all other moon phases; Fig. 2). More importantly, there were no significant interactions between size categories and moon phases ($F_{6,191} = 0.56$, $P = 0.76$; Fig. 2).

Discussion

There is a robust literature demonstrating that prey species affected by visually orienting predators adopt more cryptic behaviours during bright moon phases presumably to avoid predation (e.g. Kotler, 1984b; Longland & Price, 1991; Kotler *et al.*, 1993, 2010; Clarke *et al.*, 1996; Bouskila, 2001; Brown *et al.*, 2001; Leaver & Daly, 2003; Brown & Kotler, 2004). These and other studies also suggest that predators might adjust their activity to match that of the prey, either to economize foraging or to avoid predation risks themselves (Bouskila, 2001; Lang *et al.*, 2006). Accordingly, anecdotal accounts, together with published observations and experimental data, have generally supported the view that both snakes and their prey tend to avoid bright moonlight and will increase nocturnal activity with diminishing moonlight intensity (Klauber, 1939, 1972; Kotler, 1984a,b,c; Price, Waser & Bass, 1984; Gibbons & Semlitsch, 1987; Kotler, Brown & Hasson, 1991; Clarke *et al.*, 1996; Brown & Shine, 2002).

As in other systems, the accepted explanation for these patterns is that snakes avoiding bright moonlight increase encounters with nocturnal prey – which are more active under darker conditions – while simultaneously diminishing potential exposure to nocturnal predators themselves. Overall, what had remained unclear is which of these two factors (prey availability or avoidance of predators) is the primary driver of the lunar-phobic foraging behaviour of a predator. Our results allow disentangling, at least in part, these two alternative hypotheses. In the insular system where prey is insensitive to predation risks, predators do not decrease their foraging activity under potentially risky conditions. On the contrary, our results indicate that insular cottonmouths increase foraging/scavenging activity during nocturnal periods of high moonlight (Fig. 2), which is a novel situation compared with those previously studied.

Why would scavenging cottonmouth snakes increase foraging activity during bright nights? The principal reason is likely

related to the detection of, and orientation to, fish carrion. Olfaction is important to foraging behaviour of cottonmouths (Young *et al.*, 2008), but they are also known to have comparatively good visual acuity among snakes (Gloyd & Conant, 1990). Responses of snakes to prey items (i.e. head movements as well as tongue-flicking; Young *et al.*, 2008) suggest that vision is important to the foraging behaviour of these snakes (Brischoux, Pizzatto & Shine, 2010). Additionally, fallen fish are likely to glisten when exposed to bright moonlight, thereby enhancing the visual detection of carrion by snakes. Moreover, scavenging cottonmouths converging on prey items interact with each other, and larger individuals repel subordinate conspecifics by elevated head displays (Lillywhite & McCleary, 2008). These interactions are clearly visual and suggest that increased visibility of moonlight might facilitate scavenging harvest due to successful competition as well as improved detection of prey. In circumstances such as Seahorse Key, improved visibility might enhance the organization and success of foraging where numerous individuals interact in close vicinity to each other. Finally, we do not know if nesting diurnal birds tend to drop more fish during periods of bright moonlight, but we can think of no reason why this should be so. Most dead fish tend to be dropped during parental feeding of chicks in daylight and remain on the ground for prolonged periods, which would tend to dampen the temporal heterogeneity of resource availability attributable to pulses of fish fall.

What about predation pressures on insular cottonmouths? There are numerous species of birds present at Seahorse Key that potentially prey on cottonmouth snakes, including raptors, frigate birds, egrets and several species of herons. The majority of these birds are day-active predators, with the notable exception of owls that are more active and effective nocturnal predators during high levels of moonlight (Dice, 1945; Clarke, 1983; Kotler *et al.*, 1988). Seahorse Key cottonmouths are occasionally observed foraging/scavenging during daylight (Lillywhite *et al.*, 2002), but the predominance of nocturnal activity should eliminate dangers of detection and attack from diurnally active predatory birds. In the few circumstances where we have observed diurnal feeding by Seahorse Key cottonmouths, the snakes were beneath relatively dense canopy that would impede penetration or sighting by diurnal avian predators. Seahorse Key cottonmouths tend to be darker than their mainland counterparts, and we suggest that nocturnal foraging behaviours generally decrease avian predation risks in this population (Wharton, 1969; unpublished observations).

Five species of owls have been recorded from Seahorse Key (*Otus asio*, *Athene cunicularia*, *Asio flammeus*, *Bubo virginianus* and *Strix varia*), but we have only noticed the latter two species during our nocturnal activities related to counting snakes. The other species might be occasional visitors to the island without nesting there. Although we cannot discount the predation risk entirely, avian predation pressure on insular cottonmouths might be low. Scars, damaged tails, and other evidence of predation attempts are rarely observed in the cottonmouths that have been captured over many years. Additionally, although it is generally known that smaller snakes are more reclusive in behaviour than are larger individuals, pre-

sumably to avoid predation (Clarke *et al.*, 1996; Bonnet *et al.*, 1999; Krysko, 2002; Pike *et al.*, 2008), smaller cottonmouths on Seahorse Key were as abundant as adult snakes irrespective of the levels of moonlight (Fig. 2). Indeed, the relatively high numbers of smaller foraging snakes strengthen the case for selective foraging behaviours being related to resource acquisition rather than adjustment to predation risks. Clearly, much of the nocturnal activity of insular cottonmouths involves exposure in relatively open terrain (see the Material and methods section), and the occurrence of snakes in open habitat might simply reflect movement among patches where fear or risk of predation is not especially high (Mukherjee *et al.*, 2009).

To summarize predation risks in Seahorse Key cottonmouths, it appears that avian predation on snakes is potentially high at Seahorse Key but largely avoided by activity of snakes being largely nocturnal, thereby avoiding exposure to the numerous diurnal predatory birds. Predation by owls poses some risk at night, but the number of owls on the island is low and there are no mammalian predators present in the system.

In conclusion, the salient points of our study are (1) insular cottonmouth snakes of all age classes increase foraging/scavenging activity during nocturnal periods of high moonlight; (2) prey are indifferent to moonlight, which is a novel attribute of our system; (3) selective foraging behaviours appear to be more related to resource detection and acquisition than to any influence of possible predation risks for the foraging snakes. We suggest that the foraging behaviour we observed in these insular snakes favors a fitness benefit from food acquisition in a habitat where conflicting fitness demands of predator avoidance appears to be largely absent. Unless other unknown factors are at play, it appears that activity of snakes reflects decisions based on the sensory perception of light levels within a range of nocturnal choices. Such behavioural decisions might be different on the mainland where both avian and mammalian predators are present. Future studies might investigate whether optimal patch use theory has useful application to understanding the foraging behaviours of insular cottonmouths in the contexts of scavenging versus risk trade-offs (Brown, 1988; Mukherjee *et al.*, 2009). As foraging decisions of both prey and predator can have important consequences for stability of the trophic system (Brown *et al.*, 1999, 2001; Mchich, Auger & Lett, 2006), we further suggest that understanding trophic interactions should benefit from further investigations of complex systems in which predators are also prospective prey and foraging decisions involve trade-offs between successful acquisition of food resources and being safe (Brown & Kotler, 2004).

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