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SYNCHRONY OF ECDYSIS IN SNAKES

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***Abstract*.—Observations of Florida Cottonmouth snakes (*Agkistrodon conanti*) at Seahorse Key, Florida, USA, provide strong evidence for synchrony of ecdysis among individuals of this insular population which live in relatively close social contact. Laboratory observations suggest that these and other snakes may also synchronize shedding cycles when individuals are kept in the same room but in separate cages. Current evidence suggests that synchronized ecdysis may well be a common phenomenon among squamate reptiles and is conceivably influenced either by external physical cues and/or by pheromones in both wild and laboratory populations. Further investigations of patterns of ecdysis might profitably advance our understanding of reproductive, behavioral, and physiological ecology of reptiles, particularly those that might exhibit close social associations characteristic of species or environmental circumstances. Such knowledge has application to the structuring of conservation strategies of snakes and other squamate reptiles.**

Key Words.—cottonmouth; behavior; island; ecdysis; skin-shedding; snakes

INTRODUCTION

One of the quasi-diagnostic features of snakes is their periodic, pan-body genesis of a new epidermal generation and the shedding of an older, outer epidermal generation that is sloughed (shed) from the body as one entire sheet of keratin (Lillywhite 2014). Periodic ecdysis is characteristic of all snakes, and the renewal and shedding of the epidermis are related to a cycle of cellular events that occur simultaneously over the entire body. Ecdysis in snakes results in the outer generation of epidermis separating from a new, inner generation. With rare exceptions, the shed skin is left behind in the environment of the snake as one single piece of material that is roughly the length of the individual that shed the item.

In general, the periodicity of ecdysis varies among species and individuals from once or twice per year in many terrestrial snakes to intervals of just several weeks in some species of sea snakes (Heatwole 1999). How often a snake sheds its skin is related to food consumption, growth, and metabolic rate, but other factors are important as well (Lillywhite 2014). These potentially include environmental influence related to temperature (Semlitsch 1978), exposure to dry air that increases cutaneous evaporative water loss (Lillywhite and Maderson 1982; Maderson 1984; Lillywhite 2006), wear and damage of the skin surfaces, attachment of ectoparasites (Loomis 1951; Heatwole 1999), hormones, and reproductive cycles (Kubie et al. 1978; Nilson 1980).

Comparatively little is known concerning the synchronization of ecdysis among individuals in wild populations, or the possible role of pheromones in producing such synchrony. Clearly, seasonal influence on the timing of ecdysis is evident from observations of shedding in snakes following emergence from overwintering dens, likely related to environmental influence on cyclic reproductive physiology (Kubie et al. 1978; Ford 1996; Parker and Anderson 2007; Lorioux et al. 2013). Ecdysis releases pheromones into the environment and informs other members of the local population about the reproductive status of the newly shed snake (Kubie et al. 1978). Individuals of *Vipera berus* and several closely related viperid species are reported to complete their first annual or spring ecdysis in synchrony that appears to trigger mating activities (Saint Girons 1980; Nilson 1980). Aspic Vipers (*Vipera aspis*) shed their skin prior to ovulation, and ecdysis provides a reliable index for the onset of gestation (Lorioux et al. 2013). Ecdysis also tends to be synchronous in neonates just prior to dispersal from parental attendance, or following hatching (Greene et al. 2002; Tu et al. 2002). Early postnatal shedding establishes the permeability barrier within the *stratum corneum* and is probably important for preventing excess cutaneous evaporative water loss in dispersing individuals that become active in open, arid, or semi-arid habitats (Tu et al. 2002; Lillywhite 2006).

Aside from these circumstances, however, there is little information to indicate that members of a wild population of freely-ranging snakes exhibit synchronized ecdysis, and there seems little theoretical reason to assume so in populations where individuals are living apart and independently of one another. Common growth trajectories might synchronize ecdysis, although there is increasing evidence that shedding might be related to endogenous factors more so than to feeding or growth (e.g., Alexander and Brooks 1999; Lamonica et al. 2007). Physical insult to the skin attributable to

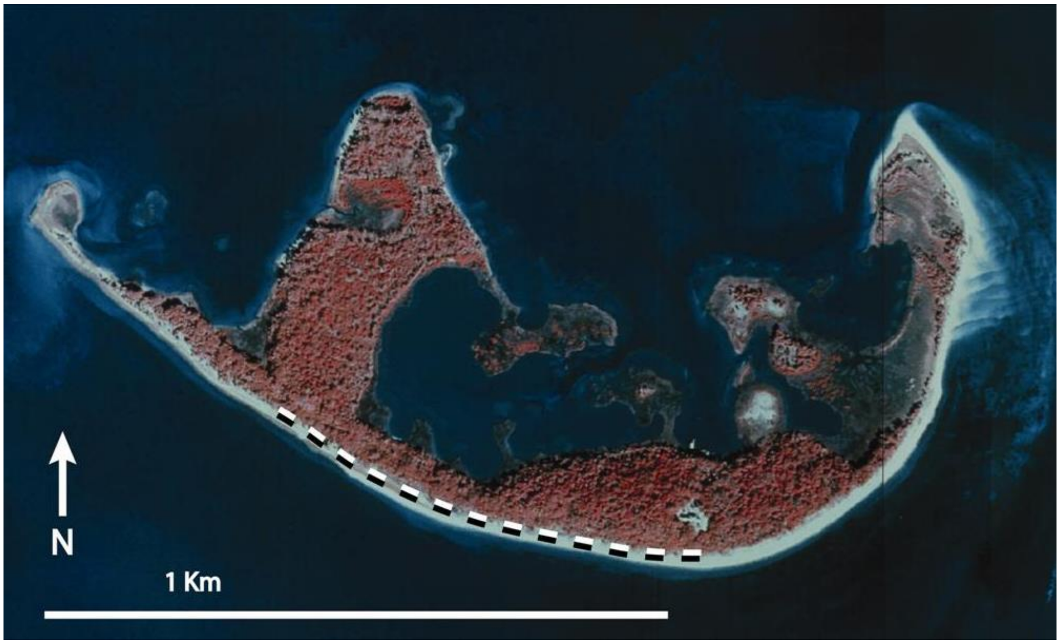

FIGURE 1. Aerial view of Seahorse Key, Florida, USA, where the study took place. Sections in red depict upland hardwood hammock, and the southern beach is seen as a white band along the perimeter of the island. The white dashed line represents the stretch of beach that was surveyed for snakes at the times reported herein.

wear, trauma, low humidity, temperature, etc. (Lillywhite 2006; 2014) could tend to synchronize ecdysis in a population of snakes, but does not necessarily influence individuals equally or simultaneously. Tavano et al. (2007) reported near simultaneous shedding among five Western Cottonmouths (*Agkistrodon piscivorus*) that were seen together on a root system of an overturned tree during August in the Missouri Ozarks, USA. Carlson et al. (2014) reported synchronous ecdysis in an aggregation of Eastern Ratsnakes (*Pantherophis alleghaniensis*), and these snakes were also in close social contact. We are not aware of other observations of this sort, and especially reports that might indicate this phenomenon is more widespread in natural populations.

Here we report observations of synchronous ecdysis in an insular population of Florida Cottonmouths (*Agkistrodon conanti*) having relatively close social contact throughout the year (Wharton 1969; Lillywhite and McCleary 2008). We consider synchronous ecdysis to reflect snakes shedding their epidermis around the same time, within a few days of one another, and thereafter being in similar Resting Stages of epidermis (Maderson 1965). These snakes associate closely with colonial nesting birds, and the droppings of guano produce white markings on snakes such that recently shed individuals can be distinguished visually from others (for several days, and sometimes weeks). Thus, based on impressions from earlier observations, we used this feature (natural contamination of skin) to test the hypothesis that insular cottonmouths are near-synchronous in skin shedding. Consideration of other species and data from captive snakes suggest that synchronized ecdysis among individuals of a population might be more prevalent than formerly supposed.

MATERIALS AND METHODS

We made observations of Florida Cottonmouths on the island of Seahorse Key, Levy County, Florida, USA. Seahorse Key is about 65 ha in area and is part of the Cedar Keys National Wildlife Refuge located on the northwest coast of peninsular Florida. Snakes in this population have been observed during numerous field activities since the authors began visiting the island in 1998. On various occasions, we observed that multiple snakes were in stages of ecdysis or had shed their epidermis very recently, further evidenced by finding freshly shed skins in the habitat. Here we report two occasions when careful notes were taken to better document this phenomenon.

Observations were made on two separate occasions when the activity of cottonmouths was monitored along a stretch of the south beach which extended from a midpoint on the island to a point 750 m to the west (Fig. 1). Beginning at dark, we carefully searched this area while proceeding once in each direction with respect to the length of the beach. We observed snakes that were easily seen foraging in relatively open ground above the intertidal zone and including edge habitat where the

FIGURE 2. Florida Cottonmouths (*Agkistrodon conanti*) in various stages of shedding cycle and photographed at Seahorse Key, Florida, USA. (A) Recently shed snake with some spotting of avian guano. (B) Snake with considerable spotting of guano and in pre-shed condition indicated by bluing of the eyes. (C) Snake with avian guano covering most of its body. (D) Snake that has shed very recently as evidenced by the clean, iridescent condition of its skin. (Photographed by Harvey Lillywhite).

beach transitioned to hammock. Rookery trees supporting nests of Brown Pelicans (*Pelecanus occidentalis*) and Double-crested Cormorants (*Phalacrocorax auritus*) occurred at varying distances along this path. We encountered snakes on relatively open ground beneath these trees, which were either rooted on the beach or had canopy that extended over the beach. The observers walked with headlamps, and snakes were easily observed in artificial light while they were crawling, feeding, or resting while coiled in the open. The snakes were seldom disturbed by a beam of light and moved away only when the observer came very close to the snake (typically within 1–3 m). Characteristically, diurnally inactive snakes were usually coiled in sheltered or concealed sites within the hammock from which they emerged at dark to forage beneath rookeries, including open areas at the edge of the beach (Lillywhite et al. 2002; Lillywhite and McCleary 2008; Lillywhite and Brischoux 2012). Each survey, involving observation and sometimes capture of snakes, lasted about 90 min.

Snakes with home ranges beneath the rookeries become spotted with excrement that falls from nesting birds above them (Lillywhite et al. 2002). The extent of such spotting with excrement increases with time since shedding, and some individuals become almost white in appearance before the next ecdysis (Fig. 2). Thus, snakes in this population might be unique insofar as the amount of guano on the skin increases with time following ecdysis, and rainfall does not seem to remove it (although the white coloration might become somewhat duller in appearance). Such marking is most intense during the nesting season of various colonial water birds, which extends from roughly March through October or November (Lillywhite and McCleary 2008). The presence of Brown Pelicans (*Pelecanus occidentalis*) extends the nesting season well into autumn. Notwithstanding the variability of guano spotting among individual snakes (Fig. 2), the absence of such marking and the sleek appearance of skin appear to be very reliable indicators of recent ecdysis.

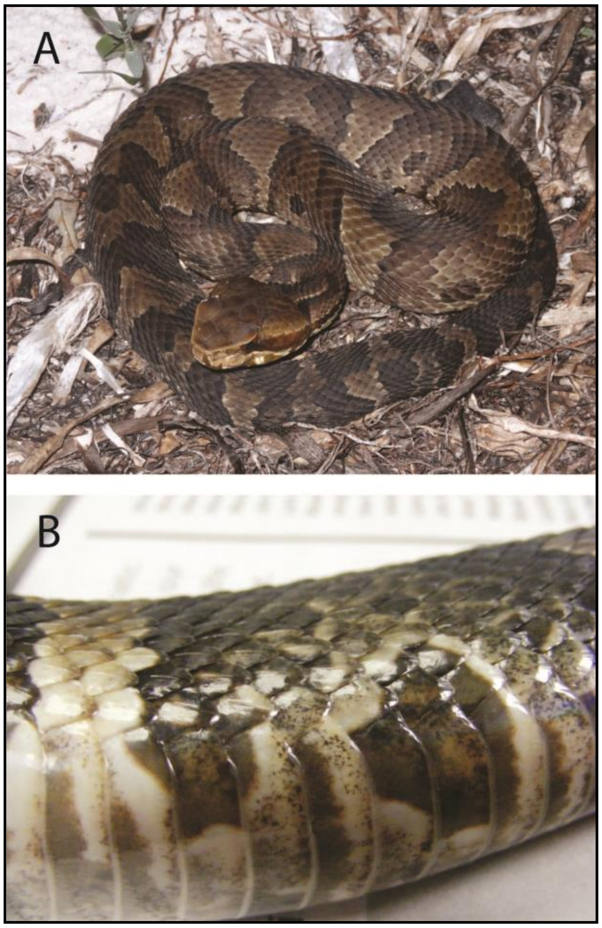

FIGURE 3. (A) Photograph of a juvenile Florida Cottonmouth (*Agkistrodon conanti*) photographed at Seahorse Key, Florida, USA, 13 November 2008. The appearance and refractive properties of the skin, as well as a lack of white spots from bird guano, indicate this snake has recently shed its skin. (B) Examination of new skin on a cottonmouth from Seahorse Key confirms it has recently undergone ecdysis. Both snakes were photographed within two days of each other. (Photographed by Harvey Lillywhite).

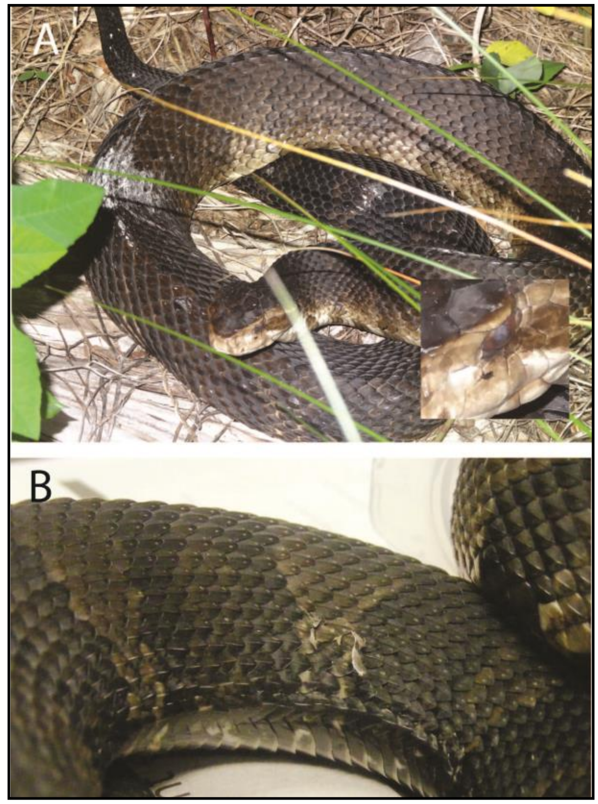

FIGURE 4. (A) Photograph of an adult Florida Cottonmouth (*Agkistrodon conanti*) at Seahorse Key, Florida, USA, 28 August 2013, with clouded eyes (see inset) indicating the animal was in a pre-shedding condition. (B) Photograph of another cottonmouth from Seahorse Key and examined in the laboratory. A small piece of the older outer generation of epidermis has been peeled off (center of photo) to confirm this animal was in a pre-shedding condition also. (Photographed by Harvey Lillywhite).

RESULTS

During a survey of snakes at Seahorse Key on 13 November 2008, we observed 48 snakes of various sizes. Nine snakes were young of the year, 15 were juveniles, 11 were of moderate size (estimated at 45–75 cm), and 13 were adults, > 75 cm total length (Lillywhite and Brischoux 2012). We were able to observe 44 of the snakes carefully; we noted they had shed very recently, and their skin was clean and shiny (Fig. 3). We captured two juveniles and a medium-size snake that we returned to the laboratory where we confirmed by closer inspection the recently shed condition of the skin (Fig. 3). We saw four other snakes moving at a distance that we did not observe close-up. However, these were not noticeably spotted with guano (see below) and appeared uniformly black. We found a freshly shed skin during these observations.

During another survey at Seahorse Key on 28 August 2013, we observed 14 snakes. One individual had clouded eyes characteristic of a pre-shedding condition. All of the other snakes showed very clean skin, with only one individual having a white spot from bird droppings where the snake was found at a rookery. We returned this snake to the laboratory where clouded eyes and condition of the skin indicated it was in a pre-shed condition (Fig. 4).

DISCUSSION

Florida Cottonmouths at Seahorse Key appear to engage in sexual and mating behaviors during two times of the year, once in the spring and once again during the fall (Wharton 1966; pers. obs.). Because of the role of cutaneous pheromones in reproductive behaviors (Kubie et al. 1978; Parker and Mason 2011), it seems likely that

FIGURE 5. A male (m) and female (f) Florida Cottonmouth (*Agkistrodon conanti*) found together and photographed 28 September 2006 at Seahorse Key, Florida, USA. Note the female is in the act of shedding (ecdysis). (Photographed by Harvey Lillywhite).

ecdysis might coincide with spring and fall mating periods. Indeed, we have observed ecdysis to be common during such periods of reproductive behavior (Fig. 5). It should also be noted, however, that the insular cottonmouths at Seahorse Key form male-female pairs during all times of the year, males exhibit year-round fertility, and mating might occur at times other than spring or fall (Wharton 1966; 1969). Importantly, observations of male-female pairing during all times of the year reflect the close communal associations of snakes in this dense and largely isolated population (Wharton 1969; unpubl. obs.).

Data reported here confirm the impression that ecdysis is frequently synchronized among individuals over the course of a year at Seahorse Key. Particularly noteworthy are observations of shedding synchrony among a large sample of snakes during very late fall (mid-November) that is beyond the earlier periods of known reproductive behaviors, including male combat. We and our associates visiting Seahorse Key at other times of the year have also noted that many of the snakes observed on particular occasions appeared to have shed recently, evidenced by sleek skin that is free of avian guano and increased presence of freshly-shed epidermal skins in the environment. We have also noted what appears to be highly synchronous ecdysis in snakes that are maintained in the laboratory, including Florida Cottonmouths. However, we have not kept records that might provide quantitative support for these latter observations.

Tavano et al. (2007) reported near synchrony of shedding among Western Cottonmouths during August. We surmise this time was after mating and before females in the population gave birth. Moreover, shedding aggregations of adult Midget Faded Rattlesnakes (*Crotalus oreganus* [formerly *viridis*] *concolor*) are reported to occur independently from communal hibernacula and unrelated to mating behavior (Ashton 1999). Thus, synchrony of ecdysis in wild populations of pit vipers is conceivably a more general phenomenon.

More data are required to confirm the generality of synchronized ecdysis in wild populations. However, the available data and observations suggest the very interesting possibility that airborne (or substrate-mediated) pheromones might have a role in synchronizing ecdysis in populations of snakes. Alternatively, other physical features of the environment (ingestion of meals, temperature and humidity fluctuations, etc.), as well as endogenous cycles, might influence the timing of ecdysis and lead to its synchrony in populations from time to time. However, variability of the activity, seclusion, and microhabitats of individual snakes within a population, as well as observations in the laboratory, suggest that pheromone-mediated synchrony of ecdysis is a hypothesis that merits future investigation. For example, sensory deprivation experiments involving snakes kept in controlled environments might prove to be informative. We do not believe that deposition of avian guano on the exterior of snakes induces the synchrony of ecdysis we have observed because the amount of such contamination is highly variable among snakes. The stimulus of ecdysis by guano contamination could, however, be tested in the laboratory.

Insofar as synchronized ecdysis has implications for the structuring of reproductive and other social behaviors of snakes, it is also relevant to conservation strategies and habitat protection. Observed synchrony of ecdysis might help to identify those habitats or areas where the density and social behaviors of snakes merit high priority for protection relative to the dynamics of metapopulations of a species. For example, synchrony of ecdysis might signal the timing of reproductive events that merit the application of special protective measures such as road closures or other actions that mitigate human impacts. It seems clear that pheromones are associated with the skin of snakes and are used to communicate cues involved in the recognition of sex, initiation of courtship, and engagement in combat behavior (Parker and Mason 2011). Synchronization of spring ecdysis and its correlation with the onset of mating has also been documented in lizards (Bauwens et al. 1989). Ecdysis is a significant event in the lives of snakes and other squamates, and it may often signal the timing of phenomena that are critical to the resilience and survival of a species or community (Sala et al. 2000).

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