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Short communication

Courtship and mating behaviour in the diadem snake, *Spalerosophis diadema cliffordi* (Colubridae)

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Courtship signals which vary among related species, often serve in species identification; whereas differences among individuals within a species may allow for the assessment of individual quality (Ryan & Rand 1993). Additionally, for some species reproductive behaviour co-ordinates the production of gametes by the two sexes. The behavioural acts involved in mating that are species specific may be useful taxonomic characters in systematic problems (Brooks & McLennan 1991; Secor 1987). Although there are over 2000 species of snakes, the courtship of only a few have been described in sufficient detail to be helpful in evolutionary comparisons. Most of the recorded descriptions of reproductive behaviour are for North American snakes of the family Colubridae (i.e., *Thamnophis*, *Pituophis*, *Lampropeltis* and *Elaphe*) and so detailed accounts for Old World species are especially needed.

The diadem snake, *Spalerosophis diadema*, is a diurnal, terrestrial colubrid in the subfamily colubrinae, found in desert and semi-desert regions of northern Africa through Arabia into central Asia (Latifi 1991; Schleich *et al.* 1996). This paper describes the courtship and mating behaviour of Clifford's diadem snake, *Spalerosophis diadema cliffordi*, utilising the behavioural categories of Gillingham (1977) and sequence analyses developed by Schuett & Gillingham (1988, 1989). A comparison to the courtship and mating behaviours described for other colubrids is also made.

Diadem snakes imported from Egypt were obtained from a commercial dealer and maintained in the Ophidian Research Colony at the University of Texas at Tyler (www.uttyler.edu/sciencemath/biology/Ophidian.html). Animals were housed individually in a facility kept at 28 °C with a 14L:10D light cycle. They were provided with water *ad libitum* and fed mice each week. Animal care protocols established for the University of Texas at Tyler were followed.

Courtship trials were conducted by placing one male and one female together in a glass aquarium measuring 92 x 46 x 43 cm (122 L) and containing a layer of aspen bedding. Trials were videotaped and observational notes were made. If no courtship was observed within four hours, the animals were returned to their home cages. Observations were initiated in March 1996 and continued on an occasional basis until May 1997.

In Israel, courtship in the diadem snake has been observed during June (Dmi'el 1967). Our laboratory conditions seemed to produce similar timing of reproduction, as females and males exhibited little interest in each other during March, April and May of 1996. During this time animals coiled at opposite ends of the arena, whereas, in trials conducted during June of 1996, males actively pursued females. These females were initially unreceptive and reacted by elevating the anterior fourth of their bodies and aggressively biting the males.

[2]Deceased

Males responded by terminating chases for several minutes and then typically resumed courtship attempts. Animals were separated when it was evident the female was unreceptive. During these spring months it was also noted that males exhibited combat behavior with other males. The successful reproductive activity in 1996 was first recorded in July. During 1997, snakes were artificially hibernated at 15 °C for four months and returned to the facility in late March. Mating occurred in May of that year. This suggests that the healthier condition of the animals after a year of captivity and the cold period stimulated more rapid cycling of the females. Obviously, data on timing of breeding in captivity should not be extrapolated to animals in the wild. However, courtship behaviors seen in the laboratory may be very similar to what occurs in free-living snakes if the restricted conditions in cages are taken into account.

Sixteen trials using various pairings of three males and three females in the two years resulted in a total of six complete courtship and mating sequences as well as a number of other behavioral interactions. In the mating observations a total of three females and two different males were involved. Six complete sequences, which involved two males with three females, were analysed. (We recognise these are not independent trials but felt because we were interested in the overall courtship pattern, not individual variation that the use of all the data would generate a more accurate picture of the species typical acts.)

Table 1. Relative frequency of male motor patterns in Phases 1 and 2 of courtship of *Spalerosophis d. cliffordi*. See text for explanation of abbreviations of behavioral acts.

Motor pattern	Phase 1 (rel. freq.)	Phase 2 (rel. freq.)
TOMT	1.97	8.40
DM	5.43	21.23
CHMT	3.47	12.60
WR	5.68	17.53
TSCA	1.73	20.99
TOTAL	18.28	80.75

For colubrid snakes, courtship and mating can be subdivided into three distinct phases: phase 1, tactile-chase; phase 2, tactile alignment; and phase 3, intromission (Gillingham 1977, 1979). Most of the species-typical behaviors for male colubrids occur during phase 2 when the male is positioned on the female's back. The terminology used to describe these acts follows Gillingham (1979). Modification for the diadem snake is as follows:

1 Touch Mount (TOMT): the male contacts the female with the snout, head and neck placed on the female's dorsum.

Table 2. Transition matrix for courtship acts of male *Spalerosophis d. cliffordi* (pooled data from 2 males). Structural zeros were placed in the diagonals because patterns can not be accurately determined for behaviours directly following themselves. See text for abbreviations of the behavioral acts.

	Following					
	TOMT	DM	CHMT	TSCA	WR	TOTAL
Preceding						
TOMT	-	38	8	0	0	46
DM	3	-	10	38	57	108
CHMT	4	32	-	12	17	65
TSCA	3	36	20	-	33	92
WR	0	32	15	47	-	94
TOTAL	10	138	53	97	107	405

2 Dorsal Advance Movement (DM): a mounted male moves in an anterior direction with the chin pressed against the dorsum of the female.
3 Chase Mount (CHMT): the male follows the fleeing (crawling) female and maintains chin and/or trunk contact with the female's dorsum.
4 Tail Search Copulatory Attempt (TSCA): movements of the tail as the male attempts to insert his hemipenes into the female's cloaca.
5 Writhe (WR): sliding and twisting of the male when the male is mounted on the female.

The relative frequency of the individual motor pattern within each phase was determined by dividing the observed frequency of each act by the frequency of occurrence of all motor patterns (Walker & Ford 1996; Table 1). Six complete courtship sequences, which involved three each from the two males, resulted in 405 two-event transitions (Table 2). A transition matrix of preceding and succeeding pairs of male behavioural acts was produced and tested for independence (Bishop *et al.* 1975) using Systat (Systat Inc.). A model of quasi-independence was used to generate expected values. A state transition diagram was constructed from the matrix (Bakeman & Gottman 1986). A *G*-test of independence indicated that the male snakes did not perform these behaviours in a random fashion ($G_I = 471.73$, $P = 0.001$). The state transition diagram is shown in Figure 1.

The courtship pattern of *S. diadema* is basically similar in sequence to the courtship behaviour of other colubrids that have been studied (Gillingham 1987; Secor 1987; Walker & Ford 1996). Phase 1, from the male's first touch of the female to his first tail search copulatory attempt (TSCA), was comparable to that in other colubrid snakes with the male diadem contacting the female and attempting to mount her dorsum. During the early part of this period the female sometimes moved away with the male chasing her. When the male managed to get on the female's back, he aligned his body with loops that slid back and forth across the female (Writhe). This positioned his cloaca near her's and he began tail-search copulatory attempts (TSCAs). If the female shifted position, the male once again aligned his body and repeated TSCAs. Male *Elaphe*, *Pituophis* and *Lampropeltis* occasionally bite and hold the female during this phase but in *Spalerosophis*, males did not bite the female. However, it was common for apparently nonreceptive females to bite the male repeatedly. These females would also lift the anterior portion of the body, forming body loops and/or bridges, and rapidly crawl away. Receptive female diadems on the other hand seem to calmly accept the male with little inclination to flee. This reduced activity in receptive animals allowed males to rapidly mount the females and probably caused the short duration of phase 1 (mean = 165 s, range: 82.8-256.8 s). However, this difference should be interpreted cautiously as the limited size of the aquarium (122 L) may have constrained the females' actions.

Once aligned on the female's dorsum the male diadems began multiple repetitions of behaviours that encompass phase 2. These involved

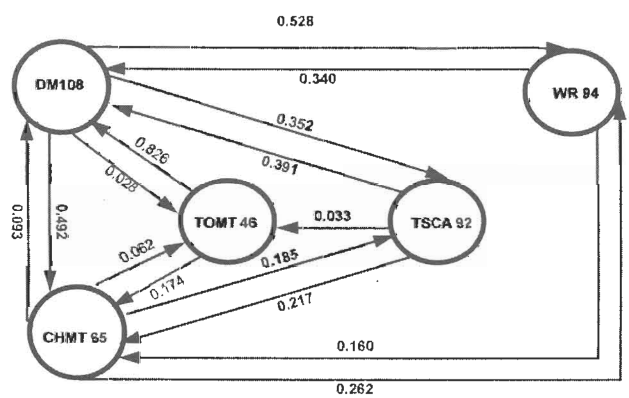

Figure 1. State transition diagram for the courtship acts of male *S. d. cliffordi* (six pooled trails with different males). Values in circles represent observed frequencies of individual behaviours while the values next to arrows represent the transitional probabilities. See text abbreviations used to describe behaviours.

advancing up the female with the chin pressed on her back and after looping his body over both sides of the female, the male writhed his body back and forth. These motions were different from the ripples or waves that other colubrids like *Thamnophis* and *Elaphe* exhibit, in that the loops did not move up or down the body but across the female's back. The TSCAs, however, were typical for a colubrid and involved the male wrapping his tail around the female's and attempting to lift her tail while shaking it.

The duration of phase 2 (from the male's first TSCA to intromission with the female) was longer than phase 1 but its duration was quite variable among trials (mean = 830.4 s; range = 174-1273.8). Walker and Ford (1996) noted similar variation in the duration of phase 2 in the African house snake, *Lamprophis fuliginosis* (120-7320 s). However, the longest duration for phase 2 in the diadem snake was much shorter than the longest phase 2 in the house snake. Walker and Ford (1996) suggested that either the females varied in receptivity or males varied in their performance of the phase 2 behaviours. Because house snakes do not engage in combat behavior, they suggested that the latter was more likely and the motor activities of phase 2 were being used by the female to evaluate male quality. The shorter phase 2 duration of *Spalerosophis d. cliffordi* may therefore relate to the occurrence of combat in the diadem snake. Females may already have information concerning male quality, if only males that win combat bouts exhibit courtship as has been suggested for other species of snake that engage in combat (Ford & Burghardt 1993). The phase 2 period in diadem snakes may only be required to evaluate species identity and not male quality, although our data do not preclude that the latter is evaluated in some other way.

Phase 3 (intromission) was of extremely long duration for a colubrid (mean = 23232 s, range: 16500-30000 s, $N = 5$). Gillingham and Chambers (1980) reported a long coital time for the eastern indigo snake, *Drymarchon corais couperi*. In addition, long coital periods have been recorded in several viperids (Gillingham *et al.* 1983; Schuett & Gillingham 1988). Whether the long intromission occurs to prevent the female from mating again quickly or to physiologically change her behavior is unknown. Cloacal swelling was very evident in the females for several hours after mating, suggesting cloacal plugs were present. However, females were receptive again just a few days later and would mate a second or third time. Male-male combat and long coitus, coupled with delays of several days between successive matings, does suggests that mating with the first successful male (highest quality?) should result in fertilisation of most, if not all of the female's eggs.

The involvement of specific snake courtship behaviours in species recognition or in evaluating individual quality will most likely be elucidated by comparative research. This study on an Egyptian snake, *Spalerosophis d. cliffordi,* adds an Old World species to the literature on snake courtship. As most sequence analyses of snake mating activity are of North American species, these data contribute to our understanding of the role of particular acts in communicating information between the sexes.

The behavioral acts that occur early in snake courtship likely are involved in coupling the opposite sexes. Most snake species exhibit some form of anti-predator response when the male first touches a female. Female diadem snakes showed head and body elevation, tail lashing, and biting, during the early part of courtship. Females of other species have reportedly displayed body jerking along with fleeing (Gillingham 1977, 1979; Perry-Richardson 1987; Secor 1987; Schuett & Gillingham 1988; Walker & Ford 1996). Males must behaviourally indicate that they are not a threat. We believe that for most species this involves mounting the female's dorsum and performing species typical tactile movements. Repetition of these movements may be required to convey reproductive information and convince the female to cease resisting. Male colubrid snakes begin tail search copulatory attempts at this point, and females may accept intromission quickly or else these tactile activities may have to be repeated extensively. The length of this phase may depend on her receptivity (Ford & Cobb 1992) and whether or not she uses these acts to evaluate the male's quality (Perry-Richardson 1987). At this point we can not overgeneralise from our data, but we suggest that species that engage in combat may have shorter phase 2 periods because male quality is not evaluated by his ability to keep up with a moving female, but by the prior combat event. In species that do not engage in combat, repetition of the components of the male's behavior on the female's dorsum could also allow her to evaluate tactile information that might indicate male quality.

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