

An analysis of courtship behaviour in the four-eyed spotted turtle, *Sacalia quadriocellata* (Reptilia: Testudines: Geoemydidae)

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Abstract. A total of 168 courtship sequences from 12 male and 18 female adult captive *Sacalia quadriocellata* were recorded on video. Thirty male and four female discrete motor patterns were defined and described. The behavioural sequences were summarized in an intra-individual dyadic transition matrix and analyzed using chi-square and kappa analyses. Courtship behaviour models and a flow diagram were constructed for this species. The male display patterns involved tactical and visual signals to induce female receptivity to mating. In response, females may emit olfactory signals for gender recognition. Female rejection of male suitors resulted in a male success rate of 4.17%. Only seven copulations were observed. Copulation only occurred when a female became quiescent and relaxed her tail for coition.

Keywords: chi-square test, cinematographic techniques, courtship behaviour, intraindividual dyadic transition matrix, kappa analysis.

Introduction

Captive breeding is a useful and important way to protect and conserve chelonians (Behler, 1997; IUCN, 1987). Because of illegal trade and habitat destruction, wild populations are decreasing rapidly (Debruin and Artner, 1987; Lau and Shi, 2000; Gong et al., 2003). Unfortunately, this decline in nature is also often accompanied by failure in captive breeding (Xia, 1983; Rodel, 1985; Zhou, 1997; Song and Yu, 2002).

The four-eyed spotted turtle, *Sacalia quadriocellata*, occupies natural ponds and streams in woodland habitats of southern China, northern Laos and northern Vietnam (Zhao, 1998; Stuart et al., 2002). They are found at elevations from approximately 170 to 470 m (Gong et al., 2006). The IUCN (2006) listed the species as being

threatened, and in China, it has been designated as endangered (Zhao, 1998). Research on this species has concentrated on field ecology (Shi et al., 2002), diet in captivity (Wang et al., 2005) and anatomy (Fu et al., 2004, 2006, 2007; Hong et al., 2004). The courtship behaviour of *S. quadriocellata* has not been documented.

The behavioural patterns of most turtles are still unknown (Carpenter and Ferguson, 1977). Most studies on courtship behaviour in chelonians have focused on emydids and testudinids in Europe and North America (Auffenberg, 1966, 1977; Mahmoud, 1967; Jackson and Davis, 1972; Davis and Jackson, 1973; Murphy and Lamoreaux, 1978; Hidalgo, 1982; Baker and Gillingham, 1983). Courtship behaviour has not been described in an Asian chelonian.

Herein we describe and quantify the courtship behaviour of captive *S. quadriocellata*. These data will be useful in captive breeding and could prove to be important characters for clarifying the taxonomy within *Sacalia*.

Materials and methods

Breeding

Thirty adult *S. quadriocellata* (12 males and 18 females) were collected from Qiongzong, Hainan Province, China

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and maintained in our laboratory for several years. The turtles were kept in two 130 × 80 cm indoor, cement pools, with males and females separated. Sex was determined by the eye spots on the top of the head. Eye spots are yellow in females and olive green in males (Shi et al., 2002). The depth of water in each pool was maintained at 20 to 25 cm. Turtles were fed ad libitum with standard food. A shelter with a diameter of 25 cm was provided. The photoperiod in the laboratory was the same as outside and UVB lamps were used to supply ultraviolet radiation during the daytime.

Luteinising hormone-releasing hormone (LHRH-A₃) and human chorionic gonadotropin (HCG) (Ningbo Second Hormone Factory, Ningbo, Zhejiang province) were injected into hind leg muscle of both males and females to stimulate courtship behaviour as follows: LHRH-A₃, males 4 µg/kg, females 8 µg/kg; HCG, males 800 IU/kg, females 1600 IU/kg. Protocols for hormonal injection followed the recommendations and oversight of Dr. Hua-cun Mi (Hainan Livestock Modification Centre, Haikou). Injections were made every 10 days for a total of 10 times. Courtship behaviour was observed from August through October. Once every five days, and always at least one day following hormonal injections, turtles were chosen randomly and placed in six 60 × 80 cm indoor cement pools fitted with a glass wall. Observation periods persisted for 24 hr. Each turtle could have been observed in a maximum of 18 trials. Two males and three females were placed in each pool. The water depth varied from 25 to 30 cm and food was provided. Three 40 × 25 cm cement slabs were used to form a culvert. The top slab formed a terrestrial area and was used to determine if any aspect of courtship behaviour occurred both in and out of water. Air and water temperatures and atmospheric relative humidity were recorded.

All observations used video cameras to preclude human disturbance. Four SUNMOON-820 video cameras, each with a 1/3 SONY Super HAD CCD DC12V video card (minimum contrast 0.005Lux/F1, made by PAL), were associated with one pool each. Video was shot at 12.5 frame/s. The video signal was transported to and stored in a computer. A multimedia digital surveillance system (WS: Vasion Electronic Scientific and Technical Corporation, Shenzhen, China) was used to the store and play the video data. Cinematographic analysis was used to identify unique motor patterns, and to evaluate the sequence, frequency and duration of all courtship behaviours.

Analyses

The percent of time occupied by each courtship pattern was calculated to construct a flow diagram with the frequency of transition to the next stage. An intraindividual dyadic transition matrix (Dawkins and Dawkins, 1976) was used to identify important motor pattern dependencies. In this matrix, all of the important motor patterns were permuted and combined into a single form that included all pattern sequences and their frequency of occurrence. Analysis of this matrix discovered which permutations and combinations had the highest probabilities. The highest probabilities were used to construct the behaviour sequence. Significant transitions were defined by using chi-square test and Kappa analysis

(Whitehurst et al., 1986). The Chi-square test was used evaluate whether the frequencies of all permutations and combinations were distributed randomly or not. A behaviour sequence was demonstrated to be invalid when one behaviour was followed by another randomly. When nonrandom, the kappa analysis was used to determine which pattern followed the preceding one, a courtship flow diagram (Baker and Gillingham, 1983; Bels and Crama, 1994) for males was constructed from these evaluations in order to visually summarize the behaviour sequences. All of the statistics were calculated in Excel 9.0.

Results

Environmental conditions

Air temperature ranged from 25 to 30°C, water temperature from 25 to 29°C, and relative humidity ranged from 85 to 95%. The environment conditions were similar to those in the field (Shi et al., 2002).

Motor patterns

One hundred sixty eight courtship sequences were recorded. Thirteen discrete motor patterns in males and four motor patterns in females were consistently identified and defined as follows:

Motor patterns of males

Approaching (AP). – This behaviour occurs at the beginning of every courtship interaction. When a male meets a quiescent female, he orients face-to-face with her. The male moves slowly (swimming or walking on the bottom of the pool) toward the female with his neck extended and head pointed at the female.

Chasing (CH). – This behaviour, also an initiative pattern in courtship, occurs when the female flees or moves. The male pursues her quickly, either swimming or walking on the bottom of the pool.

Cloacal sniffing and contacting (CS). – When behind the female, the male stands stably, fully extends his neck, and sniffs and contacts female's cloacal region.

Body side-sniffing and contacting (BS). – Male approaches or chases a female, stands sta-

bly and fully extends his neck to sniff and contact female's bridge region.

Head sniffing and contacting (HES). – When the male and female are face-to-face, the male stands stably and fully extends his neck to sniff and contact female's head.

Hind limb sniffing and contacting (HIS). – When the male is behind the female, he stands and fully extends his neck to sniff and contact female's hind limbs.

Standing by (SB). – The male stands still and looks around. This pattern can follow any behaviour.

Anterior turning movements (ATM). – The male adopts a face-to-face position, prior to beginning its next behaviour.

Posterior turning movements (PTM). – The male turns toward the female's side or posterior area, prior to begin its next behaviour.

Head-bobbing (HB). – When male and female are face-to-face, the male raises his forebody by extending his forelimbs. The male's neck fully extends upwards. Next the male lowers his fore-body until his chin touches female's forehead. This pattern is of short duration and repeated many times.

Mounting (MO). – The male climbs on the female's back from the front, rear or side with his claws grasping the female's marginal scutes. Simultaneously, the male fully extends his neck toward the female's head. In this position, the two bodies are parallel.

Adjusting on female's back (AO). – The male adjusts his angle and relative position to the female's body, especially moving backwards, in order to attain a copulatory posture.

Copulation (CO). – After the male has adjusted his body position to a copulation posture with his neck fully extended toward the female's head, he grasps the female's tail with his tail, then protrudes his penis and inserts it into the female's cloaca. In this position, their bodies form an angle of about 50 to 60 degrees.

When courtship behaviour occurs, different sniffing patterns (*SI*) involving *HES*, *BS*, *CS* and *HIS* can lead to different sequences. The

sequences are divided into two classes: *HES*, or forward sniffing, and rearward sniffing (*RS*) including *BS*, *CS* and *HIS*.

Motor patterns of females

Alerting (AL). – In response to males exhibiting *HB* or *SI*, the female quickly approaches the male with her neck fully extended and with her head pointed at the male.

Biting (BI). – This pattern occurs when a male exhibits *HB* or *SI*. The female always bites when the male's head is slightly retracted.

Fleeing (FL). – This is the most common pattern when a male's courtship is rejected. It usually occurs in response to *HB* and *SI* patterns, and is the only pattern exhibited in response to *MO*.

Acceptance (AC). – The female remains still and relaxes her head, limbs and tail to accept a male's courtship.

Among these patterns, both of *AL* and *BI* were seldom observed. Therefore, in order to perform statistical analysis, these were combined into one pattern named "Rejection" (*RE*).

Courtship behaviour

In total, 168 courtship sequences were recorded. None occurred out of water. In all episodes, males always initiated courtship. Males used one of two patterns when approaching females. When the female was quiescent, *AP* was used. This behaviour lasted about 6 s (mean = 5.77 s, range = 2-27 s, SD = 2.61, $n = 332$) at a distance not exceeding 30 cm. Alternatively, when a female was moving, *CH* occurred. This behaviour lasted about 13 s (mean = 12.98 s, range = 4-56 s, SD = 12.21, $n = 134$). Both patterns rarely resulted in *RE* by a female: *AP* resulted in a *RE* rate of 1.72% and *CH* 2.17%.

When males and females were very close, *SI* occurred. The specific *SI* pattern corresponded to body positioning. *HES* occurred when a male and female were face-to-face. This pattern lasted about 9 s (mean = 8.89 s, range = 2-31 s, SD = 7.70, $n = 87$). *CS* and *HIS* occurred

when the male was behind the female. *CS* lasted about 11 s (mean = 10.84 s, range = 3-46 s, SD = 9.16, $n = 134$) and *HIS* about 8 s (mean = 8.29 s, range = 3-24 s, SD = 6.72, $n = 42$). Finally, *BS* was observed when the male approached from the side of the female. It lasted about 7 s (mean = 7.06 s, range = 3-17 s, SD = 3.94, $n = 51$). *SI* resulted in a female *RE* rate of 18.37%, which was much higher than that of other approach patterns (1.72% or 2.17%).

When observed, *HB* lasted about 41 s (mean = 40.96 s, range = 8-275 s, SD = 40.29, $n = 319$). *HB*, which often resulted in the female fleeing (*RE* = 48.63%), was often accompanied by sniffing and was always followed by *ATM*. *ATM* lasted about 6 s (mean = 6.07 s, range = 3-13 s, SD = 2.53, $n = 47$) and served as a transition pattern between *RS* and *HB*. In comparison, *HES* never lead to *ATM*. *HB* usually resulted in the female withdrawing her neck and retreating; sometimes she would stand still. Rarely, the female would extend her neck when the male's head was extended, but when this occurred she would sway her head following the male's movements, would withdraw her neck when the male's chin touched her forehead, and usually became quiescent.

PTM occurred when a female became quiet with her legs and neck drawn into her shell. The male moved to the side or posterior area with his head pointed at female's head; sometimes the male's head vibrated slightly. *PTM* lasted about 9 s (mean = 8.70 s, range = 3-25 s, SD = 4.34, $n = 133$).

MO, the longest occurring pattern, lasted about 120 s (mean = 120.33 s, range = 17-586 s, SD = 111.86, $n = 267$). It usually occurred when the female was quiet. The male grasped female's carapace very tightly with his claws to maintain his position on female's back. Occasionally a male attempted to mount a moving female, causing the female to flee vigorously; *MO* was never successful in this situation. Although *MO* was the most common of all male

motor patterns, it was accompanied by a *RE* of 57.00%.

SB lasted about 16 s (mean = 16.32 s, range = 3-52 s, SD = 13.60, $n = 77$). It seemed occur randomly in that its appearance was not predictable. When a female became quiescent and receptive to a male's courtship, she would relax her tail. Here, the third transition pattern, *AO*, occurred. The male unclenched its claws and moved backwards, letting its hind limbs support its body. He used his forelimbs to grasp the female's marginal scutes in the middle of its carapace. This pattern lasted about 37 s (mean = 37.40 s, range = 9-112 s, SD = 35.78, $n = 35$). The male used its tail to search for and tightly intertwine with the female's tail. Next, the male would protrude his penis and insert it into female's cloaca (*CO*). This behaviour would last about 76 s (mean = 76.14 s, range = 37-242 s, SD = 74.27, $n = 26$). As this pattern ended, the courtship sequence of *S. quadriocellata* was completed. After copulation the female always moved vigorously to shake the male off her carapace, but the male always stayed on female's back for a short while before departing. In this courtship phase, the *RE* still occurred. Twice, females fled violently and dragged the males with only their tails in contact. Because copulation was rarely observed, it was not possible to calculate an accurate *RE*.

Seven successful courtship sequences were observed resulting in a success rate of about 4.17%. It took 350 s (mean = 353.57 s, range = 109-792 s, SD = 248.25, $n = 7$) to complete the courtship sequence. Male-male courtship was observed only five times. Once the pursuing male reached the *SI* pattern, it ended its amorous behaviour and retreated. When two males assumed the face-to-face position, *HB* occasionally occurred. However, *HB* never occurred more than three consecutive times during any contact, and the last *HB* always lasted less than 6 s. The other motor patterns were never observed during male-to-male contact.

Table 1. Intraindividual (male) dyadic transition matrix of courtship motor patterns in *Sacalia quadriocellata*. Numbers above are observed frequencies and parenthetical values are expected frequencies. See text for motor patterns coding.

Preceding behaviour	Following behaviour							Total
	SI	ATM	HB	PTM	MO	SB	AO	
AP	284 (130.931)	3 (19.85)	89 (99.56)	5 (58.58)	36 (106.60)	35 (27.85)	0 (9.23)	452
CH	97 (42.87)	0 (6.50)	7 (32.60)	0 (19.18)	28 (34.90)	15 (9.12)	0 (3.02)	147
HES	–	4 (10.36)	120 (51.98)	47 (30.59)	41 (55.66)	20 (14.54)	4 (4.82)	236
RS	–	48 (3.51)	11 (17.62)	8 (10.37)	9 (18.87)	4 (4.93)	0 (1.63)	80
ATM	0 (18.54)	–	65 (14.10)	0 (8.29)	0 (15.09)	0 (3.94)	0 (1.31)	65
HB	0 (40.55)	4 (6.15)	–	99 (18.14)	24 (33.02)	13 (8.63)	0 (2.86)	140
PTM	0 (48.66)	3 (7.38)	0 (37.00)	–	166 (39.62)	0 (10.35)	0 (3.43)	169
MO	0 (8.11)	0 (1.23)	3 (6.17)	0 (3.63)	–	0 (1.73)	25 (0.57)	28
SB	28 (27.81)	0 (4.22)	16 (21.14)	24 (12.44)	29 (22.64)	–	0 (1.96)	97
Total	409	62	311	183	333	87	29	1414

Sequence analysis

An intraindividual dyadic transition matrix (Dawkins and Dawkins, 1976) was constructed from 1414 motor patterns that were recorded (table 1). The behavioural sequences occurred in a significantly nonrandom pattern ($\chi^2 = 365.18$, $P < 0.001$, $df = 39$), which indicated the presence of specific sequences of display. Each motor pattern was observed to precede some patterns and follow others. Certain transitions occurred at a much higher frequency than others. Pairwise comparisons consisting of kappa values that exceed 0.3 and Z values (table 2) were calculated for all motor patterns. Transitions demonstrating 0.001 significance or better (i.e., $Z \geq 6.91$) were used to construct a flow diagram for courtship behaviours in male *S. quadriocellata* (fig. 1).

AP and *CH* always initiated the courtship sequence. *SI* closely followed the initial patterns. Following *SI*, males either shifted to *HB* either directly or by transitioning through *ATM*. Subsequently, there was a uniform linear sequence from *HB* to *PTM*, to *MO*, to *AO* and finally to *CO*. *RE* and *FL* had a relatively high probability

when males displayed *SI*, *HB* and *MO* patterns (fig. 2). Courtship success rates were very low and female *RE* rates were very high in all three male patterns (table 3). Consequently, *RE* was also denoted on the flow diagram (fig. 2). Transfer rates of motor patterns were not very high, and became very low during *SI*, *HB* and *MO* (table 3). Consequently, the probability of the completed sequence from *AP* to *CO* was only 0.0013.

Discussion

The courtship behaviour of nearly all terrestrial turtles was reviewed by Auffenberg (1977). Research on freshwater turtles has focused mainly on emydids (Taylor, 1933; Jackson and Davis, 1972; Davis and Jackson, 1973; Christensen, 1975; Shealy, 1976; Graham and Doyle, 1979; Baker and Gillingham, 1983), kinosternids (Mahmoud, 1967; Schmidt, 1970; Sachsse et al., 1976) and *Pleurodira* (Goode, 1967; Murphy and Lamoreaux, 1978). In contrast, courtship behaviours have been described in only one other species of batagurine turtle,

Table 2. Kappa and Z values for the sequence of courtship motor patterns in *Sacalia quadriocellata*. Numbers above are kappa values and Z values are given in parentheses. Abbreviations are defined in text.

Preceding behaviour	Following behaviour						
	SI	ATM	HB	PTM	MO	SB	AO
AP	0.55* (31.50)	-0.40 (-6.97)	-0.05 (-2.30)	-0.43 (-13.88)	-0.31 (-15.09)	0.12 (2.53)	-0.47 (-5.47)
CH	0.51* (14.96)	-0.12 (-3.09)	-0.22 (-7.00)	-0.15 (-5.75)	-0.06 (-1.88)	0.08 (2.38)	0.12 (-2.07)
HES	-	-0.12 (-2.67)	0.37* (15.46)	0.11 (4.25)	-0.08 (-3.33)	0.08 (1.96)	-0.03 (-0.50)
RS	-	0.76* (26.53)	-0.11 (-2.38)	-0.03 (-0.94)	-0.16 (-3.53)	-0.01 (-0.47)	-0.06 (-1.41)
ATM	-0.41 (-7.43)	-	1* (19.89)	-0.15 (-3.64)	-0.31 (-6.00)	-0.07 (-2.24)	-0.05 (-1.24)
HB	-0.41 (-11.47)	-0.04 (-1.04)	-	0.66* (24.83)	-0.08 (-2.52)	0.06 (1.80)	-0.11 (-1.99)
PTM	-0.41 (-12.77)	-0.08 (-2.00)	-0.28 (-9.60)	-	0.98* (32.71)	-0.14 (-4.03)	-0.13 (-2.26)
MO	-0.07 (-4.82)	-0.05 (-1.20)	-0.15 (-1.88)	-0.15 (-2.37)	-	-0.07 (-1.46)	0.89* (33.57)
SB	0.00 (0.06)	-0.07 (-2.34)	-0.07 (-1.70)	0.14 (4.20)	0.09 (2.10)	-	-0.07 (-1.57)

Rhinoclemmys pulcherrima incisa, by Hidalgo (1982).

Eight types of motor patterns have been described in *Rhinoclemmys pulcherrima incisa* (Hidalgo, 1982). Most of these patterns (i.e., approaching, sniffing, head and neck vibrating, and mounting) were very similar to those observed in *S. quadriocellata*. However, other patterns observed in *Rhinoclemmys pulcherrima incisa* were conspicuously absent in *S. quadriocellata*. For example, trailing was not observed in *S. quadriocellata*. Either *S. quadriocellata* did not have this behaviour or it only occurs in nature. Space was a limiting factor in our study and this might have precluded trailing behaviour. Another pattern not observed in our turtles was pumping. During copulation, male *Rhinoclemmys pulcherrima incisa* protrude and retract their heads slowly. In contrast, male *S. quadriocellata* fully extended their necks with no further actions. Hidalgo (1982) believed that pumping facilitated engorgement of the penis with blood. *Sacalia quadriocellata* had a fully engorged penis when its neck was fully extended. There is no unequivocal evidence to support the hypothesis that extension of the

neck is functionally associated with engorgement of the penis.

AP and *CH* occurred at the beginning of every courtship sequence (fig. 1). Visual signals, including body shape, were paramount. Indeed, male turtles are known to mount anything of similar shape to its own species (Murphy and Lamoreaux, 1978; Hidalgo, 1982; Baker and Gillingham, 1983; Bels and Crama, 1994).

The next phase, *SI*, includes two important actions: sniffing and touching the female. Successful mating behaviour depends on sexual discrimination (Weaver, 1970). *SI* serves at least two possible functions. First, sniffing appears to be involved in recognition of its species and gender, including whether the female has ovulated or not. The vent and inguinal region of *S. quadriocellata* becomes aromatic during reproductive receptivity (Shi et al., 2002). Worrell (1963) and Goode (1967) found that all Indo-Australian chelids possess axillary and inguinal scent glands. *Chelodina longicollis* also releases a pungent odor (Murphy and Lamoreaux, 1978). The cloacal scent produced by a receptive female *Rhinoclemmys pulcherrima incisa* can elicit trailing in males (Hidalgo,

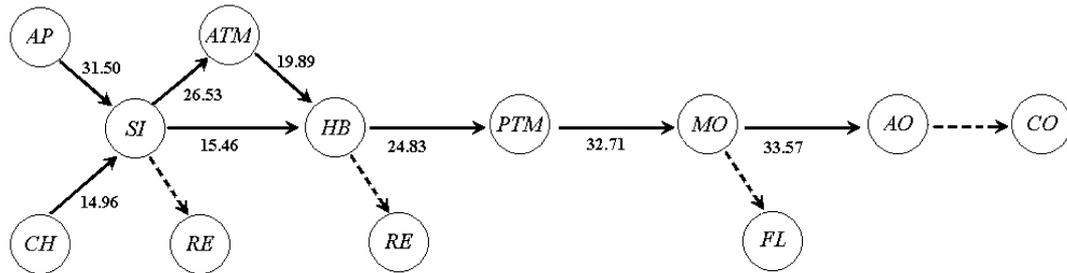


Figure 1. Flow diagram of the courtship motor patterns in *Sacalia quadriocellata*. See text for abbreviations. Numerical values are chi-square test and they represent transitions that are significant at $P \leq 0.01$.

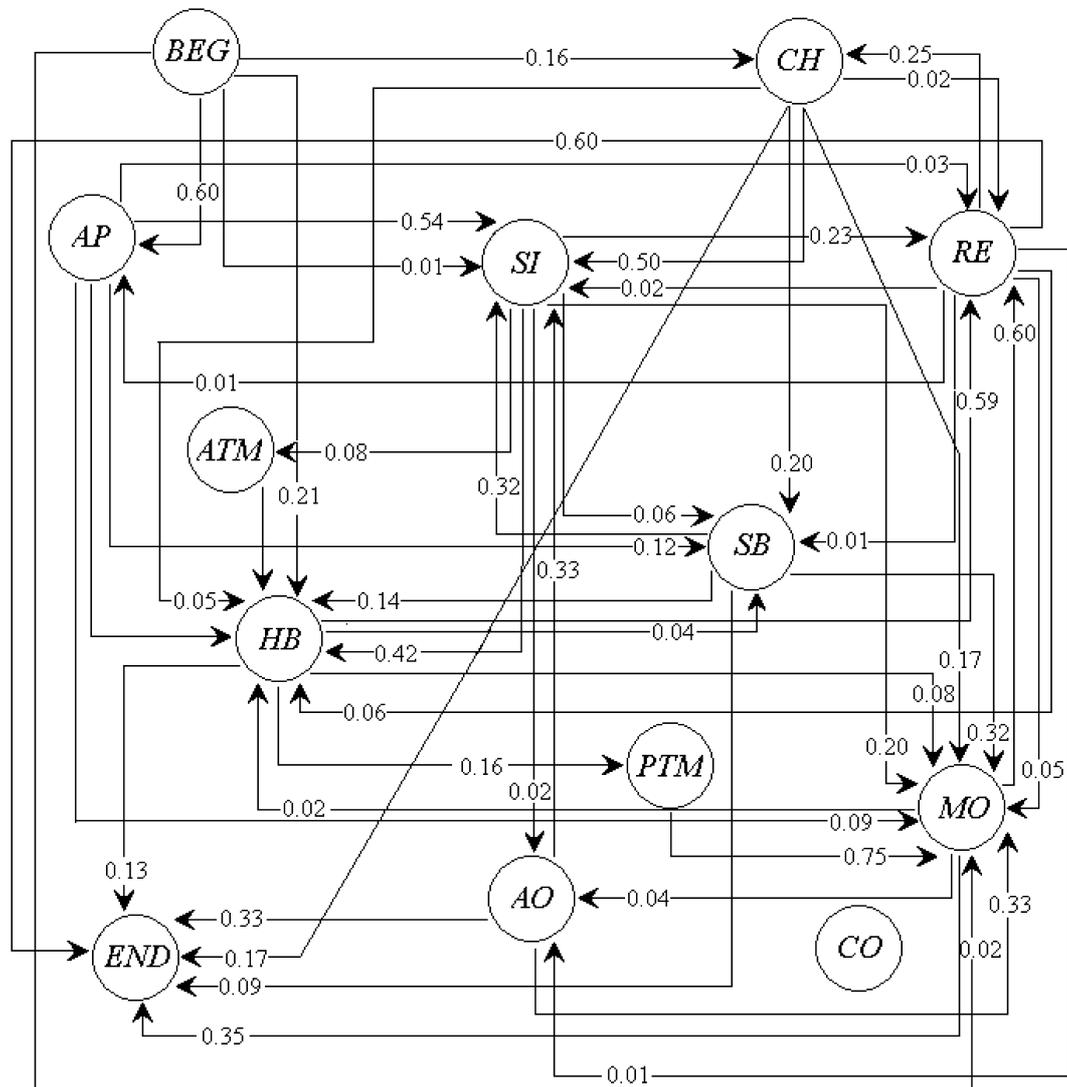


Figure 2. Flow diagram of the transition probabilities between the courtship motor patterns in *Sacalia quadriocellata*. BEG = beginning of episodes; END = end of episodes. See text for other abbreviations.

Table 3. The rejection rate, success rate and accumulative success rate of male courtship motor patterns in *Sacalia quadriocellata*. Abbreviations are defined in text.

	AP	CH	SI	HB	TM	SB	MO	AO
Rejection rate	1.72%	2.17%	18.37%	48.63%	4.69%	0.00%	57.00%	22.22%
Success rate	61.62%	52.18%	46.94%	22.02%	64.06%	100.00%	6.00%	55.56%
Accumulative success rate	56.70%		26.61%	5.86%	3.75%	3.75%	0.23%	0.13%

1982). Mahmoud (1967) discovered that olfactory releasers may be involved in certain ritualised movements, as did Sachsse et al. (1976) and Schmidt (1970). Indeed, the cloacal scent serves a discriminatory function in many turtles, such as *Geochelone travancorica* (Auffenberg, 1964), *Geochelone carbonaria* and *Geochelone denticulata* (Auffenberg, 1965), *Gopherus polyphemus* (Auffenberg, 1966), probably *Rhinoclemmys funerea* (Iverson, 1975). When male-male courtship was observed in *S. quadriocellata*, most advances terminated after *SI*. Although *SI* appears to have a discriminatory function in *S. quadriocellata*, further investigations involving male and female secretions are required to demonstrate it. Second, touching by the male appears to stimulate the female. Hidalgo (1982) observed touching in the first phase of courtship in *Rhinoclemmys pulcherrima incisa*. In *Emydura macquarii* and *Elseya latisternum*, the touching of a female's vent would result in her turning 180° to face the male (Murphy and Lamoreaux, 1978). This was also observed in *S. quadriocellata*.

The third phase, *HB*, involves visual signals. This behaviour is common in turtles (Mahmoud, 1967; Jackson and Davis, 1972; Davis and Jackson, 1973; Christensen, 1975; Murphy and Lamoreaux, 1978; Hidalgo, 1982; Bels and Crama, 1994), but serves different functions in different species. *Geochelone carbonaria* and *Geochelone denticulata* use head-bobbing to identify conspecific males (Auffenberg, 1965). *HB* serves as a dominance indicator in male *Gopherus berlandieri* and *Gopherus polyphemus* (Weaver, 1970). In *Rhinoclemmys funerea* (Iverson, 1975), *Rhinoclemmys pulcherrima incisa* (Hidalgo, 1982), *Graptemys pulchra* (Shealy, 1976), and *Graptemys versa* (Ernst et al., 1972),

the head vibration serves as a titillation device to trigger the next phase of courtship. In some tortoises (Auffenberg, 1966), *HB* might spread scent from the male's chin glands, which acts as a chemical stimulus to the female. *HB* in *Rhinoclemmys pulcherrima incisa* serves this function via their rostral pores (Winokur and Legler, 1974; Hidalgo, 1982) and mental glands (Winokur and Legler, 1975; Hidalgo, 1982). *Emydoidea blandingi* releases air bubbles when its "frantic head-bobbing" occurs (Graham and Doyle, 1979). Typically, males vibrate their heads without involving other body parts. However, male *S. quadriocellata* raise their forebody with their neck fully extended upwards, and then lower its forebody with its chin touching the female's forehead. Color might also be involved in *S. quadriocellata*. Shi et al. (2002) discovered conspicuous red strips on the ventral side of the neck that might function as visual signals. *HB* ends with the male touching the female's head with his chin. This contact might serve to calm the female. *HB* serves as a titillation device in some emydid turtles (Hidalgo, 1982), and might have evolved to supersede biting as a means of stopping females from moving away (Jackson and Davis, 1972).

Vigorous *HB* patterns were observed in *S. quadriocellata* but it is unlikely that this behaviour involves chemical signals. All cases of *HB* involving chemical signals occurred in terrestrial chelonians (Auffenberg, 1966; Graham and Doyle, 1979). In comparison, courtship behaviour in *S. quadriocellata* was never observed on land. Regardless, there is a need for further study into the function of male neck glands in *S. quadriocellata*.

HB is a common recognition behaviour of chelonian courtship (Murphy and Lamoreaux,

1978), including *S. quadriocellata*. Courtship will be aborted when one male displays in front of another male. In contrast, a receptive female will either keep quiet or just slightly vibrate her neck. When encountered, this response by females will initiate a male's *MO* pattern. Consequently, *HB* serves the function of sexual discrimination and quieting females.

MO may be the most important of all patterns in the courtship sequence because it is required for copulation. The mount position of *S. quadriocellata* is very similar to that of other chelonians (Auffenberg, 1966, 1977; Mahmoud, 1967; Jackson and Davis, 1972; Davis and Jackson, 1973; Murphy and Lamoreaux, 1978; Hidalgo, 1982; Baker and Gillingham, 1983). The male stays on the carapace of the female with his neck fully extended and head pointed at the female's head. Sometimes the male's chin will contact female's neck. Chin-rubbing, which occurs in many emydine turtles, seems to calm females (Mahmoud, 1967; Baker and Gillingham, 1983). The action in *S. quadriocellata* may serve the same function as chin-rubbing in emydine turtles. A female's receptivity is essential for copulation. Often, a female's movements cause the male to lose his mounted position, which leads to failure (Auffenberg, 1966, 1977; Mahmoud, 1967; Jackson and Davis, 1972; Murphy and Lamoreaux, 1978; Hidalgo, 1982; Baker and Gillingham, 1983).

For copulation, the male moves backwards and down the female's carapace. His hind legs support his body. This position also occurs in some tortoises (Auffenberg, 1966). Typical of some other turtles, the male's tail searches for and intertwines tightly with female's tail (Legler, 1955; Hendrickson, 1958; Mahmoud, 1967; Shealy, 1976).

The completion of courtship from initiation through copulation is uncommon. The female's *RE* rate is very high, especially in *SI*, *HB*, *AO* and *MO* (table 2). A high *RE* rate is also normal in some other turtles (Auffenberg, 1966; Mahmoud, 1967; Murphy and Lamoreaux, 1978; Hidalgo, 1982). Taylor (1933) and Jackson and

Davis (1972) agree that females appear to be indifferent toward males. The high *RE* rate could owe to the circumstances of captivity where encounters are frequent. We have no data for *S. quadriocellata* with respect to *RE* in the field.

Bels and Crama (1994) defined types of courtship sequence: premounting-courtship, mounting-courtship and intermediate-type. Premounting-courtship is typical of *S. quadriocellata* because most patterns occurred before *MO*; it has six premounting patterns but only one pattern after *MO*. In comparison, mounting-courtship was reported in turtles such as *Emydoidea blandingi* (Baker and Gillingham, 1983), and the intermediate-type was typified by *Sternotherus minor* (Bels and Crama, 1994). Alternatively, Berry and Shine (1980) divided turtles into two groups based on their mating strategies: (1) aquatic swimmers, females larger than males and they always use premounting-courtship; (2) semiaquatic and bottom-walking species with similar body size in both sexes and they always use the mounting-courtship. In their system, *S. quadriocellata* would be assigned to the bottom-walking species that use the mounting-courtship. However, this system does not adequately account for variation in courtship behaviours. In aquatic species where females are much larger than the males, premounting-courtship may be commonplace because males cannot display their courtship behaviour when mounted on a female's carapace. The classification system of Berry and Shine (1980) does not account for bottom-walking species where females and males have nearly identical body sizes and must use the mounting-courtship approach. Consequently, the classification system of Bels and Crama (1994) better encompasses the observed variation in courtship behaviour.

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