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CARDIAC RESPONSES DURING COURTSHIP, MALE-MALE FIGHTING, AND OTHER ACTIVITIES IN RATTLESNAKES

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ABSTRACT--Heart rates associated with sexual behavior were recorded in an adult male northern Pacific rattlesnake (*Crotalus viridis oreganus*) via subdermal electrodes implanted adjacent to the heart. Cardiac rates were higher during male-male fighting than during courtship, indicating the more strenuous nature of fighting. Exhaustion may be an overlooked but important determinant of fighting success and duration. These comparisons and other studies of heart rates of snakes suggest that feeding, fighting, and defense require greater cardiac and metabolic support than courtship and exploratory behaviors, while behavioral sleep requires the least.

Previous electrocardiographic studies of snakes have focused on physiological responses to temperature (e.g., Jacob and McDonald, 1975; Jacob and Carroll, 1982) and diving (e.g., Pough, 1973; Jacob and McDonald, 1976; Heatwole, 1977; Baeyens et al., 1980), "fear" (Cowles and Phelan, 1958), death-feigning (McDonald, 1974), exploratory behavior (Chiszar et al., 1980), defensive escalation (Graves and Duvall, 1988), "sleep" (Peyrethon and Dusan-Peyrethon, 1969), and activity in general (Pough, 1973). However, the cardiac responses of snakes during courtship and male-male fighting have not been examined.

In male rattlesnakes, courtship consists largely of the three-act sequence of forward-jerking, tail-searching, and no-movement, which may be interrupted by episodes of female-chasing (Hayes, 1986; Schuett and Gillingham, 1988; Hayes et al., 1992). A prominent feature of male-male fighting is hooking, whereby a contestant with its anterior body in a vertical, swaying posture attempts to force a similarly postured opponent to the substrate (Schuett and Gillingham, 1989; Hersek et al., 1992; Madsen et al., 1993). These complex sexual activities presumably require various levels of cardiac and metabolic support. The purposes of the present study were to compare the cardiac responses of a northern Pacific rattlesnake (*Crotalus viridis oreganus*) during courtship and fighting and to provide comparisons of cardiac and metabolic support for various other activities.

MATERIALS AND METHODS

A large male *C. v. oreganus* (snake 05; 344 g, 84 cm snout-vent length) was housed with conspecifics in one of three lare pens (1.0 to 1.5 m^2 of floor space), each having paper floor coverings, several rocks, and a small container of water. The temperature was 24 to 30°C during a 12L:12D cycle. The snakes, collected from Walla Walla Co., Washington, were fed live laboratory mice on an irregular (two to four mice/month) basis.

Snake 05 was one of six subjects in a larger study of cardiac responses during feeding. Snake 05 was anesthetized, and subdermal electrodes were surgically implanted adjacent to the heart. Several weeks later, after the snakes resumed normal feeding, snake 05 was transferred to a feeding arena (91 cm long, 61 cm wide, and 46 cm in height) whereupon it struck and consumed a live mouse.

Shortly after consuming the mouse, two female (one gravid and one nongravid) conspecifics were placed into the feeding arena. Snake 05 quickly initiated courtship of the nongravid female. Two and a half hours later, a smaller male (snake 20; 202 g, 69 cm snout-vent length) was introduced, and a 10.5-min fighting bout ensued. Each male, kept in separate pens, had displayed previously to other noncontesting males when in the presence of females, but fighting was never observed. Electrocardiographic data were obtained from snake 05 during all of the feeding and courtship but only for 6 min of fighting, at which time the electrodes pulled out from under his skin. The interacting snakes appeared oblivious to the presence of the electrode cable attached to snake 05.

Sexual activities were captured on videotape (VHS format), and cardiac rates were determined from traces produced by a Gilson Polygraph (Model M5P). Discrete episodes of behavior (observed on a monitor) were simultaneously transcribed onto the polygraphic record to subsequently align finer details of the videotape with the cardiac record.

RESULTS

Most courtship activity by snake 05 consisted of forward-jerking bouts. Due to persistent and uncooperative coiling by the nongravid female, snake 05 was able to execute tail-searching only once (i.e., phase 1 courtship was primarily observed; see Hayes, 1986). Heart rates were typically 38 to 43 beats/min during forward-jerking bouts, 41 to 46 beats/min during the single tail-searching event, and 38 to 43 beats/min when not moving. Heart rate generally increased during and subsequent to female-chasing (43 to 50 beats/min). Courtship of the nongravid female by snake 05 was unsuccessful, as copulation was not achieved.

The heart rate of snake 05 (the larger contestant) was high when fighting first began ($\leq$57 beats/min), declined as the bout progressed while both contestants were in vertical, swaying posture (43 to 55 beats/min), and reached a sustained maximal level (55 to 60 beats/min) during

the period of three hooking attempts (at 4.25, 5.35, and 5.68 min) by snake 05 and the only hooking attempt by snake 20 (at 4.30 min). The electrodes pulled out shortly after the third hooking by snake 05, which won the contest after his eighth hooking attempt at 10.50 min.

The heart rates of snake 05 during several activites are given in Table 1. Heart rates were clearly greater during defensiveness ("after handling;" 50 to 54 beats/min), feeding (especially during swallowing; 53 to 60 beats/min), and fighting (43 to 60 beats/min) than during courtship (38 to 50 beats/min). A literature review of heart rates exhibited by rattlesnakes also is included in Table 1. When comparing studies, there is a consistent pattern wherein heart rate "after handling" is greater than that after "strike" which is greater than the heart rate while "resting" (quiet wakefulness). The range of heart rates reported for rattlesnakes is considerable; in our work with *C. v. oreganus*, we observed heart rates as low as eight beats/min during behavioral sleep and 71 beats/min when very defensive immediately after handling.

DISCUSSION

Heart rates observed during the sexual activities of rattlesnakes suggest that male-male fighting is more strenuous than male courtship of a female. Pough (1983) proposed that exhaustion may be an important determinant of fighting success and duration in anurans. The sustained tachycardia associated with hooking attempts during fighting suggests that exhaustion may be an overlooked but important determinant of fighting success and duration in snakes. Pough (1983) showed that endurance in snakes generally increases with age. Since larger male snakes tend to win in agonistic encounters, greater stamina, among other factors (see Schuett and Gillingham, 1989; Hersek et al., 1992; Madsen et al., 1993), could contribute to their success.

The heart rates we observed generally were within the range of values reported for other activities of rattlesnakes (Table 1). Since differences among taxa and circadian, temperature, emotional, and other factors presumably contribute to variation in heart rates, comparisons among studies should be made with caution. Nevertheless, cardiac responses of snake 05 are meaningful because he served as his own control and because the different studies reveal a consistent pattern for the various activities. Because heart rate is a general correlate of metabolic activity, the ranges in Table 1 suggest that feeding and fighting require substantial cardiac and metabolic support and may even approach the support needed for defensive behavior. By comparison, courtship and exploratory behavior appear to be less energetically expensive, while behavioral sleep seems to be least expensive.

TABLE 1. Summary of behavior and associated heart rates (beats per minute) for rattlesnakes (*Crotalus*). Values are ranges unless otherwise indicated. Defensive behavior corresponds to "after handling," and "resting" is equivalent to "relaxed wakefulness."

Behavior	Heart rate
Fear[1]	
Resting	34-46
After "control" odor	32-46
After "fear" odor	41-60
Defensiveness and provoked strike[2]	
Resting	16-20
After handling	54
After strike	46
Defensive escalation[3]	
Resting	25.6 ± 0.7
Procrypsis	24.6 ± 0.8
Rattling	37.6 ± 1.1
After strike	41.4 ± 1.4
After handling	47.3 ± 1.1
Exploration, wakefulness, and sleep[4]	
After handling	57-71
Exploratory behavior	26-55
Relaxed wakefulness	20-35
Behavioral sleep	8-27
Feeding[5]	
After handling	50-54
Before mouse	34-44
Before strike	39-50
After strike	44-52
Chemosensory searching	32-55
Swallowing	53-60
After swallowing	46-60
Male courtship[5]	
Forward-jerking	38-43
No-movement	38-43
Chase female	43-50
Male-male fighting[5]	43-60

[1]*Crotalus viridis*, *C. atrox*, *C. ruber*, *C. scutulatus* (Cowles and Phelan, 1958).

[2]*Crotalus r. ruber*, $n = 1$ (Clark and Marx, 1960).

[3]*Crotalus v. viridis*, $n = 14$, $\bar{X} \pm SE$ (Graves and Duvall, 1988).

[4]*Crotalus v. oreganus*, $n = 4$ (W. K. Hayes, pers. obser.).

[5]*Crotalus v. oreganus*, snake 05 male (present study), 7-8 May 1986; feeding, 2300-0004 h; courtship, 0006-0240 h; fighting, 0240-0300 h.

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