M. Vences, J. Köhler, T. Ziegler, W. Böhme (eds): Herpetologia Bonnensis II.
Proceedings of the 13th Congress of the Societas Europaea Herpetologica. pp. 51-54 (2006)

Experimental examination of the combat behaviour of the snake *Lampropeltis mexicana* (Garman, 1884)

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Abstract. This paper examines the combat behaviour of the mexican kingsnake *Lampropeltis mexicana.* The results base on 149 experiments, for which in each case two males were put together in an experimental arena. The test animal group existed of 13 males. A description of the combat behaviour with its most important motor patterns is given and a classification in three phases is made. Three different variations of combat behaviour are described. The mean duration of combat is for the typical combat 16 minutes and 33 seconds and for escalated battles 85 minutes and 53 seconds. The existence of escalated combats is described, from which one would have a lethal ending without engagement from outside. A significant positive correlation of body-size and body-weight with the number of the won combats is established. There is no significant difference of the quantity of biting between the winner and the looser of the combat. Agonistic behaviour for food between males is described.

Introduction

Combat behaviour exists in many animal species. The reasons for the combats can be territories, food sources or breeding mates. Two different kinds of combat behaviour exist, the ritualised combat and the escalated combat (Franck, 1979). In the escalated combat the participants try to harm or even kill the rival, while the ritualised combat prevents severe damage. The ritualised combat is very common in animals with dangerous "weapons" like ungulates with horns, and venomous snakes. Combat behaviour occurs between young, females and animals of both sexes for different resources, but in most cases it is a ritualised combat of sexual mature males for receptive females. Because of a strong relation between the fighting strength and the body size and body weight, in many species with an intensive combat behaviour a sexual dimorphism in body size and body weight between males and females exists (Alcock, 1996), males being larger than females. Combat behaviour is common in many snake species (Gillingham, 1980; Shine et al., 1981; Gillingham et al., 1983; Osborne, 1984; Hammond, 1988; Hersek et al., 1992; Aldridge, 1993; Drobny, 1993; Heimes, 1995; Firmage & Shine, 1996). For many species and subspecies of the genus *Lampropeltis* combat behaviour has been described (Shaw, 1951; Mohen, 1967; Carpenter & Gillingham, 1977; Murphy et al., 1978; Clark et al., 1983; Secor, 1990).

Lampropeltis mexicana was described in 1884 by Garman (Garman, 1884). It is a moderately sized colubrid snake of about one metre in length. The males are larger and heavier than the females. *L. mexicana* lives in the mountains south of the Saladan Region of the Chihuahua Desert in Mexico (Garstka, 1982). Three subspecies have been described: *L. mexicana mexicana* (Garman, 1884), *L. m. greeri* (Webb, 1961) and *L. m. thayeri* (Loveridge, 1924). *L. mexicana* has a strictly seasonal breeding phenology. After a hibernation of four to five months (Trutnau, 2002) the breeding season takes place from early March to the end of May (Hilken & Schlepper, 1998). The combats of the males for receptive females occur during this breeding period.

In this study, I describe the combat behaviour of the males of *Lampropeltis mexicana*. The goal was to address the following questions: (1) How long is the duration of the combats? (2) Does an escalation of combat behaviour exist and can damage be a consequence of these escalations? (3) Do larger or heavier males always win the combat? (4) Does the frequency of biting differ between the winner and the loser of the combat? (5) Do battles among males for food occur?

Material and methods

The test animal group consisted of 13 adult males of *Lampropeltis mexicana*. For each experiment two males of *L. mexicana* were put together in an experimental arena and the interactions were recorded by videocameras. The examination took place during the natural breeding season of *L. mexicana* in the years 1998, 2000, 2001 and 2002.

Results

The results are based on 192 experiments, in 149 of which a combat behaviour could be recorded. The motor patterns of the combat behaviour of *Lampropeltis mexicana* were as follows, following the terminology described by Gillingham (1980) for *Pantherophis obsoletus*:

(a) Touch (TO): an act of initial contact where one male

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Combat variation	Number of experiments	% of experiments
0	43	22
1	73	38
2	65	34
3	11	6
total	192	100
1, 2 and 3	149	78

Table 1. Combat variations observed in the experiments performed.

Combat duration	Number of experiments	% of experiments
-10 min	36	55
10-20 min	8	12
20-30 min	9	14
30-60 min	9	14
More than 60 min	3	5
Total	65	100

Table 2. Duration of typical combats (combat variation 2).

Combat duration	Number of experiments	% of experiments
-60 min	3	27
60-120 min	5	45
More than 120 min	3	27
Total	11	100

Table 3. Duration of escalated combats (combat variation 3).

physically touches the second with the snout or body. (b) Mount (MT): one male crawls on the opponents back from the rear. (c) Dorsal Pin (DP): the initiator creates a short U-shaped loop with the anterior one third of his body, elevates this above the opponent and uses it to forcefully push his head region down to the substrate. (d) Hover (HV):
one male forms a rigid S-shaped loop with the anterior one third of his body and holds this posture above the same region of the opponent. (e) Push-Bridge (PB): an upward body-bridging movement of one male in order to get rid of the mounted opponent or a bite of him. (f) Biting (BT): one male bites the other into his body, head, tail or neck. (g) Twist (TW): the rear one-third of the body of both males get twisted in each other like a cork-screw. (h) Avoid (AV):an anteriorly, posteriorly or laterally directed gliding movement to avoid further aggressive interactions. (i) No Response (NR): one male shows no response on the behaviour of the opponent.
Phases of the combat behaviour were as follows: (1) Phase: Phase of contact: The initial phase with the first contact between the males in form of the motor pattern Touch. (2) Phase: Phase of the real combat: Starts with a first agonistic motor pattern like Mount, Dorsal Pin or Biting. (3) Phase: Phase of ending: In this phase one male takes to flight to Avoid further aggressions of the opponent and gets pursued by him, or both males show No Response.
Variations of the combat behaviour observed were as follows: (1) Variation 1: Short aggression: After the first agonistic motor pattern like Mount, Dorsal Pin or Biting of one male the opponent takes to flight. (2) Variation 2:

	Short aggressions	Typical combats	Escalated combats
Number of observations	73	65	11
Mean duration	few seconds	16 min 33 sec	85 min 53 sec
Maximal duration	few seconds	1 Std 28 min	2 Std 37 min
Maximal quantity of bites of the winner	12	20	68
Maximal quantity of bites of the looser	0	19	105
Maximal duration of bites	4 sec	5 sec	112 sec

Table 4. Comparison of different combat variations

Table 5. Combat balance, body size and body weight of ten males in the experiments.

Specimen	Body length (cm)	Body weight (g)	Total experiments	Experiments with agonistic behaviour	Combats won	% of combats won
M 1	106	245	9	8	6	75
M 2	110	370	9	9	9	100
M 3	102	390	9	3	0	0
M 4	84	200	9	7	5	71
M 5	79	105	9	7	3	42
M 6	80	180	9	8	5	63
M 7	75	115	9	6	1	17
M 8	64	90	9	7	1	14
M 9	64	75	9	5	0	0
M 10	61	75	9	6	0	0

Typical combat: The real combat of *L. mexicana* with the aggressive motor patterns Mount, Dorsal Pin, Hover and Biting and the defensive motor pattern Push-Bridge. Often the rear one third of the bodies of the opponents get twisted. (3) Variation 3: Escalated combat: It shows the same motor patterns like the typical combat. More Biting occurs and the combat is more intensive and damages take place.

The duration of the combats varied from a few seconds up to more than two and a half hours. Combat Variation 1 (short aggressions) had a durations of a few seconds. Combat Variation 2 (typical combats) varied from 34 sec to 88 min (middle duration: 16 min 33 sec). Combat Variation 3 (escalated combats) varied from 36 min to 157 min (middle duration: 85 min 53 sec).

In 11 experiments an escalated combat was observed. Typical attributes of the escalated combat are a distinct longer duration, a higher quantity of bites and a longer duration of biting than in the other combat variations. In one case an escalated combat, without engagement from outside, came to a lethal ending. Such an occurrence is also described by Perry-Richardson (1991) for *Morelia viridis*. Until now no description of a combat of snakes with a lethal ending in nature exists. Escalated combats do not only occur among similarly sized males.

Relationship between the body length and the body weight and won combats are shown in Table 5. The calculation of the Spearman-Rank-Correlation-Coefficient (r_s) shows a significant positive correlation between the body length of the males and the combats won ($r_s = 0{,}7214$, $N = 10$, $p < 0{,}05$), and a significant positive correlation between the body weight of the males and the combats won ($r_s = 0{,}5326$, $N = 10$, $p < 0{,}2$). Hence, larger and heavier males are more successful in combats.

In 71 of 149 combats biting of the opponents was observed. The Wilcoxon-Test shows no significant difference of the quantity of biting between the winner and the looser of the combat ($T = 623{,}5$, $N = 65$, $z = 0{,}299$, $p > 0{,}1$).

Outside the breeding season the males competed for food items. Not only short aggressions (combat

Combat variation	Quantity of experiments	Quantity of experiments with biting	Percentage of experiments with biting
0	43	0	0
1	73	23	32
2	65	37	57
3	11	11	100
total	192	71	37
1, 2 and 3 (experiments with agonistic behaviour)	149	71	48

Table 6. Occurrence of biting in different combat variations.

variation 1) but also typical combats (combat variation 2) with the typical motor patterns Mount, Dorsal Pin, Push-Bridge and Twist occurred. In no case the motor pattern Biting was observed. Also no escalated combats (combat variation 3) for food items could be seen.

Discussion

The combat behaviour of *Lampropeltis mexicana* with its typical motor patterns is very similar to that of many other colubrid species (Gillingham, 1980; Drobny, 1993; Heimes, 1995) especially of other species in the genus *Lampropeltis* (Carpenter & Gillingham, 1977; Murphy et al. 1978; Clark et al. 1983).

The combat duration of up to 157 min is very long for snakes. Most descriptions of combats in literature give a duration of some minutes to one hour (Carpenter & Gillingham, 1977; Gillingham, 1980; Shine et al., 1981; Clark et al., 1983; Hammond, 1988; Hersek et al., 1992; Drobny, 1993; Firmage & Shine, 1996). Only Murphy et al. (1978) described a combat with a duration longer than one hour. This combat had a duration of 305 min and was observed in of *Lampropeltis alterna,* a species closely related to *L. mexicana*.

No occurrence of escalated combats of snakes in nature has been described until now indicating that escalated combats may be an artifact of captivity.

The significant positive correlation between the body length and body weight of the males and the combats won possibly explains the reason for the sexual dimorphism in length and weight, with larger and heavier males, in *L. mexicana*.

Food induced combat behaviour has been described for a few snake species (Kelleway, 1982; Firmage & Shine, 1996). The food induced combats of *L. mexicana* occur only between two males or between two females but never between one male and one female.

Acknowledgements. I am grateful to Prof. Dr. W. Böhme (Bonn), Dr. R. Schlepper (Quickborn), W. Kloebe (Hamburg), A. & G. Kölpin (Norderstedt), M. Döring-Hochet & G. Döring (Celle), G. Schüßler (Quickborn), O. Samuels (Heist).

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