

Mating and Male Combat in Australian Blacksnakes, *Pseudechis porphyriacus*

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ABSTRACT—We observed ritual combat and other agonistic behavior between male blacksnakes (*Pseudechis porphyriacus*) in a field population in central New South Wales. Combat bouts vary greatly in duration (2 to 30 minutes), and apparently function as male "strategies" to displace rival courting males. Direct attack and biting may serve to displace rival males *in copulo*. We briefly review published literature on male combat in snakes.

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INTRODUCTION

Ritualized "combat" behavior between rival males has been recorded in many snake species, including several Australian elapids (Fleay, 1937, 1951; Baker, 1968; Shine, 1977a; review in Shine, 1978a). However, few detailed observations on male combat have been made under field conditions. This dearth of information has led to differing interpretations of the adaptive significance of male combat in snakes (reviewed by Bogert and Roth, 1966). The present paper (i) describes field observations of mating and male combat in wild blacksnakes (*Pseudechis porphyriacus*), (ii) compares these observations to previous descriptions of male combat in snakes, and (iii) interprets the adaptive significance of *Pseudechis* male combat.

LOCATION, SPECIES AND METHODS

Our observations were made in the Macquarie Marshes, an extensive swamp in central northern New South Wales. The exact location was on a bypass channel running through "Sandy Camp" property, 20 km west of the town of Coonamble (147° 30'E, 30° 30'S). The channel runs north-south, is about 6 meters in width with fairly steep banks, and was full of slowly-flowing water at the time of our observations on 6 October 1979. The day was warm (maximum temperature about 25°C) with sunny periods, and followed several days of cooler weather.

The common or red-bellied blacksnake (*Pseudechis porphyriacus*) is a large, venomous elapid snake abundant in the Macquarie Marshes. The species is distributed widely in eastern Australia, usually in association with water (Cogger, 1978). Macquarie Marshes specimens typically attain large body sizes (adult males average 126 cm snout-vent length—Shine, 1978a). Mating occurs mainly in October and November (Shine, 1977a,b) and male combat in this species has been described by Fleay (1937, 1951) and Baker (1968).

The description below is based on notes taken at the time, plus analysis of 26 photographs taken during the observation period. We watched the snakes with binoculars from across the channel at a distance of 10 meters. Sexes of the snakes were determined by body size (males average much larger than females—Shine, 1978b) and by tail shape.

OBSERVATIONS

At 1230 hours, we noticed three blacksnakes coiled together on the eastern bank of the bypass channel. A male and a female were copulating, and another male was lying across the body of the female. The copulating snakes were in contact at their vents only—the female was lying loosely coiled in grass on the channel's bank, the male lying along the water's edge. The snakes were attached by a single hemipenis, which was stretched sufficiently to make it obvious in observations and photographs. Neither of the copulating snakes showed much movement. However, the "extra" male was constantly moving with abrupt, jerky motions. His mental area ("chin") was often adpressed to the female's dorsal surface, and his body was aligned with (and draped over) the female's body. This male's movements were so active that at one point the copulating male was "pushed" into the water, although copulation was not interrupted (see Fig. 1a).

An additional male blacksnake approached the above trio at 1235 hours. This snake was first seen 20 meters south of the trio, on the same (eastern) bank of the channel. He moved directly to the trio (Fig. 1b) but immediately upon contacting it, he took to the water rapidly and swam to the opposite (western) bank of the channel. This brought him into close proximity to the observers: he was then frightened away by our movements. At the time of contact between this male and the trio, the female blacksnake moved \approx 1 meter further up the bank, the *in copulo* male being dragged passively out of the water by his hemipenis.

A few minutes later, a fourth male was noticed approaching from the north along the eastern bank. He rapidly covered the 30 meters separating him from the trio, showing typical "searching" behavior similar to that seen in foraging blacksnakes (high frequency of tongue-flicks to substrate; side-to-side waving of head). This snake was identifiable by his very short tail, probably the result of some previous injury. As soon as "Short-tail" reached the trio of blacksnakes, his movements became more agitated. He bit the non-copulating male on the neck, and these two males then reared up, facing each other, with hoods spread (Fig. 1c). This posture was held only for a few seconds, and the two males then began writhing about and "plaiting" the foreparts of their bodies together (Fig. 1d). The form of combat in this species has been described and illustrated by Fleay (1951) and Baker (1968) and will be described here only briefly (see Fig. 1). The two snakes intertwined their bodies and engaged in "head-pushing" contests (c.f. Akester, 1979), where it appeared that each of the combatants attempted to push the other's head downwards with his own head. The combat behavior was vigorous, with the snakes moving about together rapidly. The combatants tumbled down the bank into the water soon after the commencement of the bout. Combat continued in the water (Fig. 1e), and as the snakes moved back onto the bank. The combat bout ended suddenly, with the original male (not Short-tail) taking to the water and swimming across to the eastern bank.

That entire combat bout took only three minutes (1242–1245 hours). The copulating pair of blacksnakes played no part in the bout, and appeared not to react to the fighting males in any way.

At the conclusion of the bout, the short-tailed male returned to the copulating snakes and began behaving in the same way as the male he had dispossessed (head on female's mid-dorsal surface, moving along female's body with abrupt jerky motions; body aligned with female's body, draped over female; tail pushed under female's tail in apparent attempt to insert hemipenis). Unlike the previous male, which had shown no interest in the copulating male, Short-tail bit the copulating male vigorously at mid-body on one occasion (1255 hours). The copulating male showed no reaction to this bite, and Short-tail continued to concentrate his attentions on the female.

At 1304 hours, yet another male blacksnake appeared, and moved towards the trio. This snake came from the north also, but along the western rather than the eastern bank; when it encountered the observers, it took to the water and we did not sight it again.

The short-tailed male persisted in his attentions to the copulating pair, with only brief periods of inactivity. His movements were often vigorous, with hood-spreading. At 1319 hours he again bit the copulating male at mid-body (Fig. 1f), and all three snakes fell from the bank into the water. The

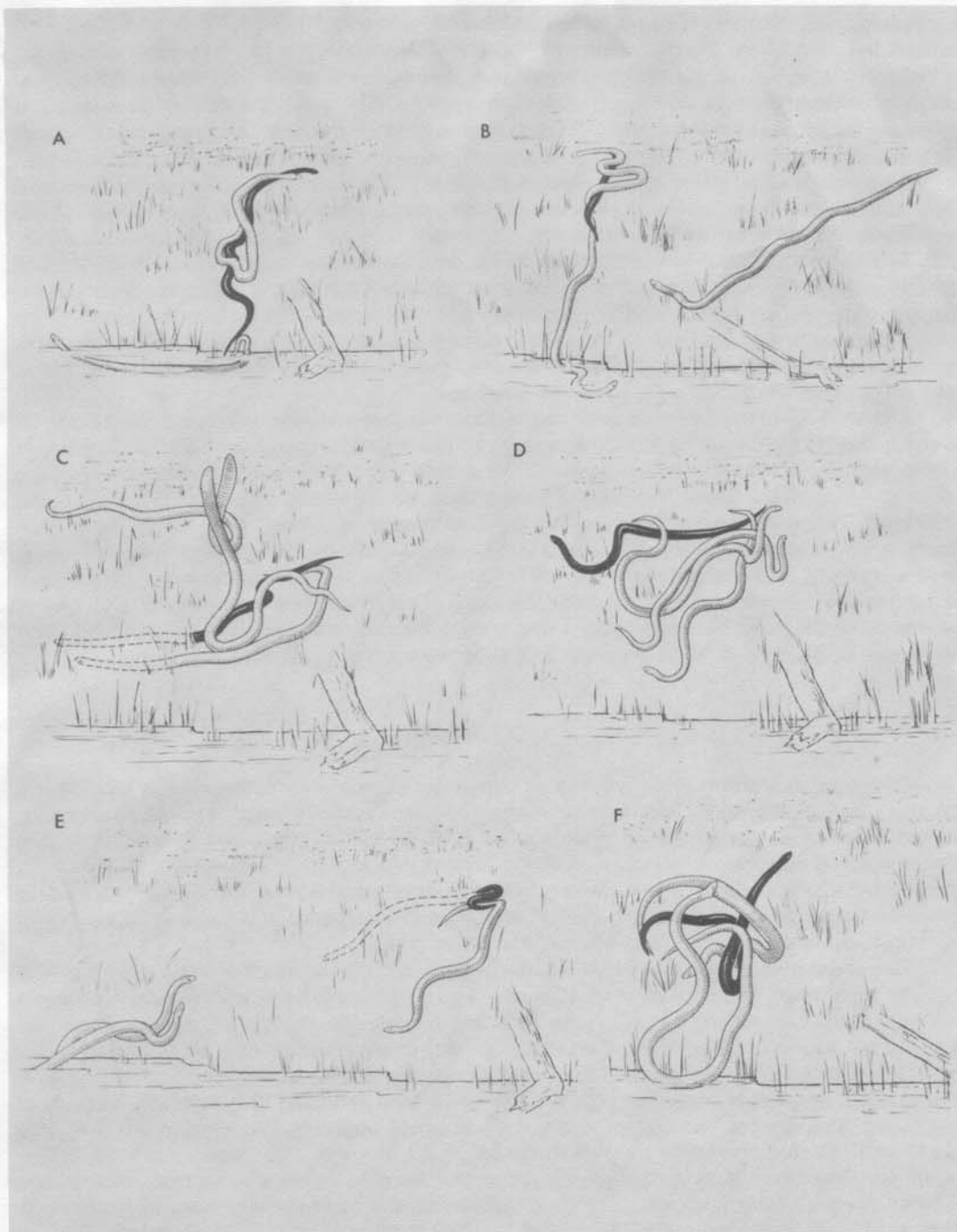


FIGURE 1. Mating and male combat in blacksnakes, as described in the text. Shaded snake is the female. Drawn from 35 mm colour slides. (a) Position of snakes when first sighted. Male lying in water is copulating with female (shaded). (b) Arrival of additional male snake to previous trio. (c) Commencement of ritual combat between male blacksnakes. Copulating pair lie beneath rival males. (d) Male blacksnakes in combat, with copulating pair beneath. (e) Male blacksnakes in combat, after having fallen into the bypass channel. (f) Disruption of copulating pair of blacksnakes by extra ("short-tailed") male. Photograph taken as all three snakes fell from the bank into the water.

short-tailed male immediately re-emerged and began "searching" behavior (tongue-flicking, etc.) around the area where the copulating pair had been. Meanwhile, the two copulating snakes, still attached by a hemipenis, floated downstream (north) along the channel. Both snakes attempted to swim, but often in different directions. The female finally swam across to the western bank, dragging the male tail first against the current. The two snakes reached the western bank about 30 meters downstream and across from their original position, and were still attached at that time. However, they had separated by the time they crawled 2 meters to the top of the western bank (1325 hrs). The male still had a hemipenis everted, and crawled about actively with "searching" behavior. The hemipenis was retracted within two minutes. The female coiled on the bank and remained still.

The short-tailed male remained close to the original site of copulation, with much tongue-flicking. About 30 minutes later, a male snake (possibly one of those observed earlier) swam up the bypass channel past this area. The short-tailed male immediately moved into the water, swam straight across to the other male, and a brief (2 minute) bout of combat occurred in midstream. This bout took the same form as the previous one, except that biting was not observed. At the conclusion of the bout, the "intruding" male swam away rapidly.

Another bout of male combat in *P. porphyriacus* had been observed and photographed by S. Cohn and party the preceding day, on a nearby part of the same property. Dr. Cohn kindly provided photographs and the following description: "The snakes were observed in the Southern Marshes along the Monkeygar Creek. We observed the snakes for at least 30 minutes between 1230 and 1300 hrs. The snakes were 'caught in the act' (i.e. already in combat) so they may have been carrying on for some time. No other snake was observed. They did not appear to bite each other; on the contrary, they seemed to the layman to rub each other almost affectionately . . . They really did not seem to cease their routine but only move out of our range. As the slides imply, they did this in and out of the water." His photographs clearly show the snakes intertwined; this posture, and the large size of the snakes, leave no doubt that these were males in combat.

DISCUSSION

In general, our observations are in good agreement with previous descriptions of reproductive behavior in *P. porphyriacus* and in other snakes. Firstly, the postures adopted by the fighting male blacksnakes were very similar to those figured by Fleay (1937, 1951) and Baker (1968). The "head-pushing" behavior of the snakes during combat is only slightly different from some of the manoeuvres seen in colubrid and viperid combat (e.g. Bogert and Roth, 1966; Akester, 1979). Also consistent with published records of combat are (i) the low frequency of biting, and (ii) the lack of response of the male *in copulo* to other males (Shaw, 1951).

The spasmodic movements of the courting males, and the adpression of the male's mental area to the female's mid-dorsum, seemed to one of us (R. Shine) to be almost identical to courtship sequences he has watched in the North American gartersnake *Thamnophis sirtalis*. These behaviors are known to be common in courtship of many colubrid snakes (e.g. Shaw, 1951).

However, our observations differ from previous reports in several respects. Most interesting is the *duration of combat bouts*: both bouts we watched were very brief (2-3 minutes). A review of published data on the duration of snake combat bouts suggests that most bouts are more prolonged (Table 1; \bar{X} duration = 34.5 mins, S.E. = 6.9, n = 24). This figure itself is an underestimate, since many bouts were already in progress when observations commenced (references in Table 1). Nevertheless, it is clear that *P. porphyriacus* combat bouts sometimes are protracted (e.g. Baker, 1968; observations by S. Cohn reported in present paper). Fleay (1937) described combat in captive blacksnakes as a series of minute-long "rounds," after each of which the snakes would disengage completely, separate, and immediately line up together again and repeat the "wrestling" behavior.

TABLE 1. Duration of combat "bouts" in snakes. Where data are available, mean and standard error of bout durations are calculated.

Family	Species	Conditions	Duration of bout (min)	Authority
Boidae	<i>Morelia spilotes</i>	Field	> 60	Covacevich, 1975
	<i>Sanzinia madagascariensis</i>	Captive	7.5 (2.1)	Carpenter <i>et al.</i> , 1978
Colubridae	<i>Drymarchon corais</i>	Captive	20	Tinkle, 1951
	<i>Elaphe longissima</i>	Field	> 60	Stemmler-Morath, 1935
	<i>E. obsoleta</i>	Field	> 18	Rigley, 1971
	<i>Lampropeltis calligaster</i>	Field	> 30	Moehn, 1967
	<i>L. mexicana</i>	Captive	5	Murphy <i>et al.</i> , 1978
	<i>Masticophis taeniatus</i>	Field	8	Bennion and Parker, 1976
	<i>Pituophis melanoleucus</i>	Field	> 15	Woodbury, 1941
	<i>P. melanoleucus</i>	Field	> 60	Bogert and Roth, 1966
	<i>Sonora episcopa</i>	Captive	5.7 (2.3)	Kroll, 1971
	Elapidae	<i>Austrelaps superbus</i>	Field	> 30
<i>Oxyuranus scutellatus</i>		Field	> 8	Hosmer, 1953
<i>Pseudechis porphyriacus</i>		Field	> 5	Fleay, 1937
<i>P. porphyriacus</i>		Field	> 10	Baker, 1968
Viperidae	<i>P. porphyriacus</i>	Field	2, 3, > 30	Present study
	<i>Agkistrodon contortrix</i>	Field	> 20	Gloyd, 1947
	<i>A. piscivorus</i>	Field	> 30	Perry, 1978
	<i>Bothrops moojeni</i>	Captive	> 120	Leloup, 1975
	<i>Crotalus sp.</i>	Field	> 30	Klauber, 1956
	<i>C. cerastes</i>	Captive	> 90	Lowe and Norris, 1950
	<i>C. horridus</i>	Field	> 30	Klauber, 1956
	<i>C. ruber</i>	Captive	> 15	Klauber, 1956
	<i>C. viridis</i>	Field	> 30	Gloyd, 1947
	<i>Sistrurus miliarius</i>	Captive	> 120	Palmer and Williamson, 1971

The long duration of combat bouts reported in the literature could be interpreted as an artefact of captivity, since under these conditions the snakes are forced to remain in close proximity to each other. At first sight, this hypothesis is supported by data in Table 1: mean combat duration is much greater in captive bouts ($\bar{X} = 47.9$ min., S.E. = 18.6, $n = 8$) than in field bouts ($\bar{X} = 27.8$ min., S.E. = 4.6, $n = 16$). However, these two means are not significantly different from each other (using Wilcoxon's rank-sum test, $p > > .1$); the difference is entirely due to three prolonged captive bouts in vipers (Table 1). More importantly, some of the longest bouts have been observed in the field. Hence, protracted combat cannot be a laboratory artefact. Instead, the data in Table 1 indicate the great range of combat durations observed both in the field and in the laboratory. Our observations on *Pseudechis porphyriacus* include the briefest combats recorded (2-3 minutes), but it seems likely that many such brief combats could escape attention. The longer a bout persists, the greater the probability of its being observed.

We believe that our observations on blacksnake behavior shed some light on the adaptive significance of male combat in this species. Combat in snakes has been interpreted as a male "strategy" for (i) forcing rival males to flee from the vicinity of a receptive female (e.g. Prior, 1933), (ii) physically "carrying" rival males away from a female (Leloup, 1964), (iii) defending against homosexual courtship (Shaw, 1951), and (iv) gaining access to food items (Shaw, 1951). Our observations support the first of these hypotheses: in both of the combat bouts we observed, the short-tailed male (initiator of both bouts) displaced other males.

Of equal interest is the behavior of male *P. porphyriacus* in relation to the copulating pair. Two different males, at different times, engaged in active courtship of the female while she was *in copulo*. In both cases, the actions of the courting males were so vigorous that the copulating snakes were pushed about. In the second episode, where the "extra" male bit the copulating male

as well as jostling the pair, the "extra" male's movements were sufficient to throw all three snakes into the bypass channel. This ultimately separated the mating pair, an event which should tend to increase the mating opportunities of the displacing male. We interpret our observations to mean that the adaptive significance of agonistic behavior in male blacksnakes may be (i) to displace copulating or courting males through direct attack and biting, and (ii) to displace rival courting males through ritual combat.

Tests of these hypotheses will come only from detailed field studies on male reproductive behavior in relation to mating success. The lack of quantitative data on this topic for any snake species is a serious gap in our understanding of snake ecology.

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