

Putative pair-bonding in *Agkistrodon contortrix* (Copperhead)

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Abstract - Pair-bonding between sexes is common in vertebrate taxa, yet it has been noted far less frequently in some groups such as reptiles, and snakes in particular. Evidence to date indicates that many snake mating-systems are polyandrous, with both males and females having multiple partners in a single breeding season, and thus unlikely to exhibit lengthy pair-bonds. Wittenberger and Tilson (1980) suggested that pair-bonding exists when pairs remain intact for a consecutive period equaling at least 25% of the breeding season. Using this criterion, we present evidence of pair-bond formation in a North American pitviper, *Agkistrodon contortrix* (Copperhead), a species with a polyandrous mating system.

Pair-bonding during all phases of reproduction (PBR) is common in birds (Lack 1968, Yezerinac et al. 1995), and in other vertebrate lineages, especially where biparental care is present (Black 1996, Mathews 2002). However, it has been documented much less often in other groups, such as reptiles (Harrison 2013, O'Connor and Shine 2003), and snakes in particular (Black 1996, Clutton-Brock 1989, Dobson et al. 2010, Fricke 1986), which may be due to difficulty with documenting PBR rather than to rarity. In animals that form PBRs, it was once assumed that male–female partners were parents to all offspring (Bull 2000, Bull et al. 1998), yet extra-pair copulations (EPCs) and multiple paternity have been documented in many bird species, even those showing life-long pair-bonding (Arden et al. 1997; Birkhead and Møller 1992, 1996; Lifjeld et al. 1993; Petrie et al. 1998; Westneat 1990; Yamagishi et al. 1992), as well as in mammals (Palombit 1994; Reichard 1995; Soulsbury 2010).

Evidence to date supports the view that many snakes are polyandrous (Clark et al. 2014, Duvall et al. 1992, Rivas and Burghardt 2005, Shuster and Wade 2003), and both males and females have multiple sex partners within a single breeding season. This mating-system type suggests that pair-bonding for the purpose of mating or mate guarding may not be common. However, in an insular population of *Agkistrodon piscivorus* Lacepede (Cottonmouth) on Sea Horse Key, FL, long-term (weeks-long) association of male–female pairs is common (H.B. Lillywhite, University of Florida, Gainesville, FL, pers. comm.; Wharton 1966). Continuous long-term male–female associations have also been documented in *Crotalus atrox* Baird & Girard (Western Diamond-backed Rattlesnake) (Clark et al. 2014) and *Crotalus molossus* Baird & Girard (Black-tailed Rattlesnake) (Persons et al., in press). In both species, pair-associations end after mating. Wittenberger and Tilson (1980) suggested prolonged male–female associations should be defined as those that persist for at least 25% of the breeding season. We suggest that this criterion for pair-bonding be applied to all species.

From 2001 to 2003, we radio-tracked 35 (20 males, 15 females) adult *Agkistrodon contortrix* (L.) (Copperhead), a medium-sized North American pitviper, on a 485-ha parcel of a basalt trap-rock ridge ecosystem located 4.75 km NW of Meriden, CT. Details on topography and climate of this region are presented in Smith (2007) and Smith et al. (2009). Although

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Copperhead populations in more southern and western localities show 2 mating seasons per annum (Aldridge and Duvall 2002, Fitch 1960, Schuett 1992, Schuett et al. 1996, 1997), only 1 mating season occurs in this population (Smith et al. 2009, 2010). Throughout the active season, males showed greater activity-range sizes and greater movement distances than females. This trend was most pronounced during the single mating season in late summer and early fall (late July–September; Smith et al. 2009, 2010, 2012). In spring, there was no evidence of copulations, bisexual pairing, or courtship (Smith et al. 2009, 2010).

During the July–September period, males showed a >17-fold increase in activity-range size and a 5-fold increase in movement distance compared to April and May. Females did not show similar large increases. Of the 42 copulations observed, 95.2% occurred during August and September (4.8% in July, 35.7% in August, 59.5% in September), concomitant with the expansion of activity ranges and increases in daily movements in males (Smith et al. 2009). Increased movement and activity-range size may represent a prolonged “scramble competition” among males to locate multiple female partners during the concentrated mating season (Duvall et al. 1992, 1993).

Males in our study often courted 2 different females on consecutive days, with the distance between females ≥ 100 m. Likewise, it was common for a female to be in the presence of a new male within 1–2 days following copulation with another male. As a result, the 42 copulations we recorded represent matings between 21 males and 16 females (2 matings were between marked and unmarked individuals) (Smith et al. 2009). The frequency of multiple mates was 63% in females and 59% in males (maximum mating success for females was 4 mates and for males was 5 mates). In all cases, pairings persisted for ≤ 48 hours.

Here, unlike most other observations we have documented (Levine et al. 2015; Smith et al. 2009, in press), we present observations of 1 pair of Copperheads that exhibited long-term association and hence, characteristics of pair-bonding based on the abovementioned criterion. Given a mating period spanning ~ 70 days (mid-July–September), a pair of Copperheads in our population would need to remain in close association for 14 consecutive days in a single breeding season for classification as pair-bonding; this pair met the criterion.

An adult male (male 740) and an adult female (female 960) Copperhead were located via radio-telemetry and found to be in physical contact with each other on 3 September 2001 (Fig. 1). We located the pair 11 times over a period of 26 days (3–28 September 2001). At each location, the male was either in contact with the female or within 1 m of her, although we never observed courtship or copulation. On ~ 28 September 2001, near the end of the breeding season, the pair separated after they had moved approximately 200 m in the preceding 26 days. Because movements by either individual were not directly observed during separation, it was unclear which individual initiated movement and hence separation of the pair.

Given this association during the peak of the breeding season, we postulate that the pair association we describe is indicative of pair-bonding. Although the selective factors promoting the formation of pair-bonding in this population are unknown, we hypothesize that limited mating opportunities, particularly among smaller males, may be a factor.

Under conditions where operational sex ratios are male-biased due to biennial or longer female reproductive cycles (as in the present study), strong competition for mates is expected between males (Emlen and Oring 1977). Previous research on male combat (competition) in Copperheads (Schuett 1997) and *Sistrurus catenatus* Rafinesque (Massasauga Rattlesnake) (Jellen et al. 2007) has shown that body size (snout–vent length [SVL], body mass) is important to win fights and secure mates. Additionally, in this population, SVL was correlated with reproductive success (number of offspring produced), with larger males

siring more offspring (Levine et al. 2015). Therefore, smaller males are not as likely to sire offspring under conditions where they must compete with larger males for access to females. Perhaps significantly, the male presented here was smaller (67.3 cm SVL) than the average for the population (75.2 cm SVL \pm 1.58 SE, $n = 47$; Smith et al. 2009).

Females in this population were highly dispersed during the mating season (Smith et al. 2009), and multiple paternity has been documented, with evidence of more than 1 sire found in 45% of litters tested (Levine et al. 2015). As a result, smaller males may realize greater reproductive success by forming short-term pair-bonds with unaccompanied females once located rather than by searching for additional females for which they may have to directly compete with larger males (Schuett 1997).

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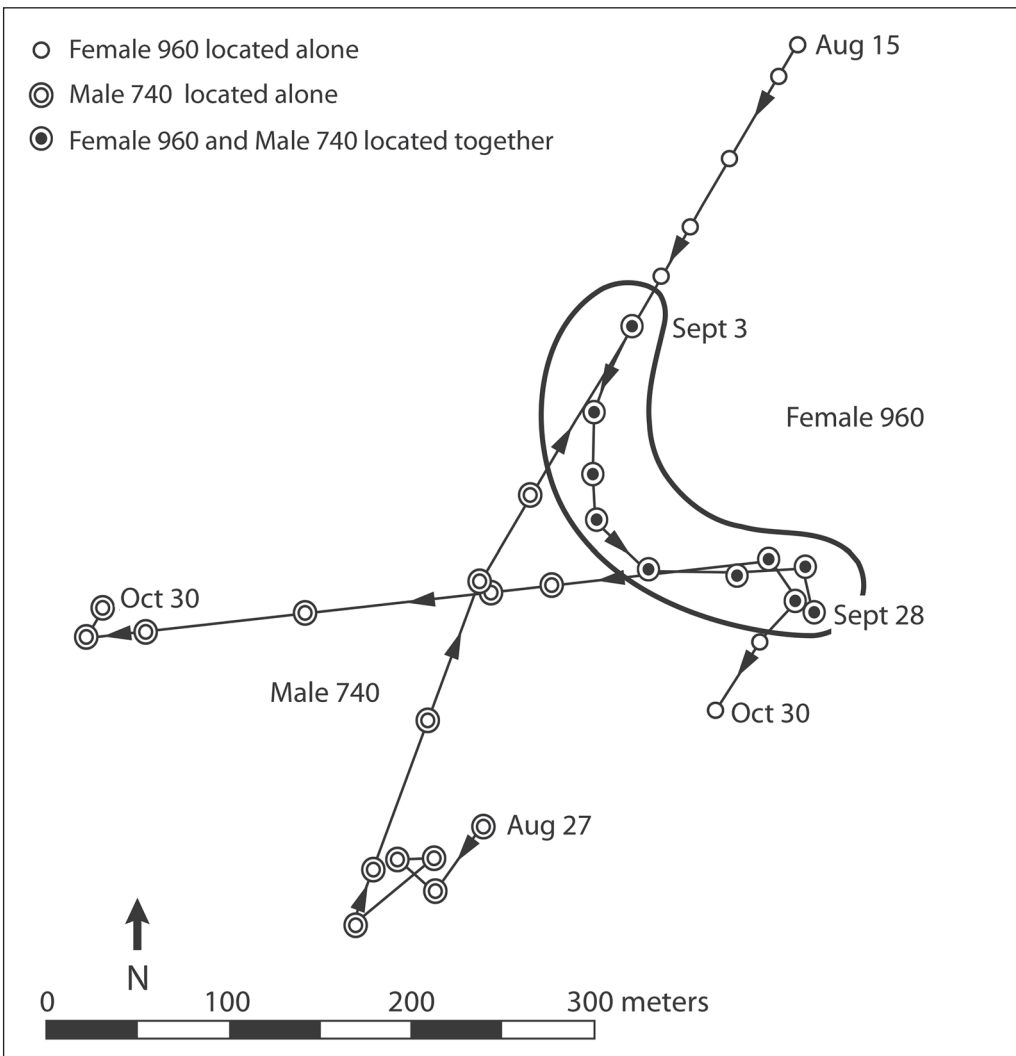


Figure 1. Putative pair-bonding in *Agkistrodon contortrix* (Copperhead). Male 740 and Female 960 were located together 11 times in succession for 26 days, from 3 to 28 September 2001.

pair-bonding in insular Cottonmouth. The American Wildlife Research Foundation, The University of Connecticut Department of Ecology and Evolutionary Biology Wetzel Fund, the Connecticut Department of Environmental Protection Non-game Fund, Sigma Xi, Georgia State University (Biology Department), Zoo Atlanta, and a National Science Foundation Predoctoral Fellowship (CFS) provided funding. Outside reviewers made helpful comments during manuscript review. This research was conducted under the supervision of the University of Connecticut Institutional Animal Care and Use Committee, protocol number S211 1201.

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