Research

Sex differences in behavior associated with sex-biased mortality in an oviparous snake species

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Sex differences in behavior associated with reproduction often result in sex-biased mortality. Male-biased mortality appears to be the prevalent pattern for birds and mammals, but recent work suggests that higher female mortality may be the norm for snakes, at least for viviparous species. Here we used radio-telemetry to examine sex-biased mortality in Texas ratsnakes *Elaphe obsoleta*, an oviparous species, and test the hypothesis that differences in behavior are associated with higher rates of mortality. Female ratsnakes had lower survival than male ratsnakes. For both sexes decreased survival was associated with higher activity and increased basking. Male ratsnakes were most active and basked most during the spring when mating occurred, which was when almost all male mortality occurred. Although female ratsnakes also moved and basked most during the mating season, they maintained relatively high levels of movement and basking through the summer and fall, and female mortality occurred throughout that period. Thus, contrary to the expectation that the cost of reproduction should be highest prior to egg laying for females of oviparous snakes, the mortality pattern documented here suggests the cost of reproduction is greatest following egg laying, similar to what has been found for females of viviparous species. As capital breeders (whether oviparous or viviparous), female snakes must rebuild energy reserves following a bout of reproduction, and the associated increase in foraging and basking required to do so increases female susceptibility to predation. Further studies are required to determine if female-biased mortality is the norm in snakes and if so, to determine the demographic and life-history consequences.

Reproduction often entails increased risk of mortality for animals. When those risks differ between males and females, the resulting sex-biased mortality is likely to have important demographic, sexual selection and life-history consequences (Magnhagen 1991, Andersson 1994). Among birds and mammals, sex differences in longevity are common and most often females live longer than males (Promislow 1992, Promislow et al. 1992, Allman et al. 1998). Direct examination of sex ratios of prey taken by avian predators confirms that males of many prey species are often at greater risk (Christe et al. 2006, Costantini et al. 2007). Although sex-specific rates of mortality are not well documented for snakes, there is evidence that, unlike mammals and birds, costs of reproduction may make female-biased mortality the norm for snakes, at least among viviparous species (Madsen and Shine 1993). Here we use radio telemetry to estimate sex-specific rates of mortality in Texas ratsnakes *Elaphe obsoleta*, an oviparous species, and test the hypothesis that differences in behavior are associated with higher rates of mortality.

Proximately, the factors that could put one sex at greater risk of mortality include higher mortality costs associated with reproduction (Luiselli 1992, Luiselli et al. 1996), differences in conspicuousness associated with sexual dimorphism in size or color, (Christe et al. 2006), or sex differences in behavior (Magnhagen 1991, Andersson 1994). Snakes are well suited for testing hypotheses regarding the effects of behavior on mortality because many snake species (including the ratsnakes studied here) exhibit limited sexual dimorphism in size and no apparent sexual dimorphism in appearance, limiting any potential effect of these factors. At the same time, there are well-documented differences in behavior between male and female snakes that seem likely to put one sex at greater risk. Higher mobility of one sex can increase the risk of predation for individuals of that sex (Magnhagen 1991) and male snakes are known to move more than females when searching for mates (Gibbons and Semlitsch 1987, Gregory et al. 1987, Aldridge and Brown 1995, Bonnet et al. 1999). Although female ratsnakes also become more active during the mating season, overall they move less than males and have smaller home ranges (Blouin-Demers and Weatherhead 2002, Carfagno and Weatherhead 2008). Here we test the prediction that within sexes, the most mobile individuals should be at greatest risk of mortality. In addition, if mobility is the most important factor affecting survival and males move more than females, then we expect that overall mortality should be male-biased.

Other differences between males and females put female snakes at greater risk. Reproduction involves both behavioral and physiological changes for female snakes that can decrease survival (Madsen and Shine 1993, Bonnet et al. 2002). Gravid female reptiles often maintain higher body temperatures through behavioral modification, such as increased basking (Shine 1980, Schwarzkopf and Shine 1991, Blázquez 1995, Brown and Weatherhead 2000, Blouin-Demers and Weatherhead 2001a), which could increase vulnerability to predators. Carrying a developing clutch can also impair the ability of gravid females to escape from predators (Shine 1980, Seigel et al. 1987, Brown and Shine 2004, Winne and Hopkins 2006). Increased basking and impaired mobility should increase mortality of female snakes while they are gravid.

For viviparous snakes the cost of reproduction for females also extends beyond parturition and may in fact result in rates of mortality that are higher post- than pre-parturition (Madsen and Shine 1993). Gestation can take several months, during which female snakes eat little if at all (Shine 1980, Seigel et al. 1987, Madsen and Shine 1993, Gregory and Skebo 1998, Gregory et al. 1999). Prolonged starvation combined with heavy investment of stored reserves in their offspring leaves females in poor condition post parturition. In addition, protein catabolism during gestation can result in muscle loss that impairs mobility (Lourdais et al. 2004). Thus, after giving birth female snakes must actively forage to rebuild reserves (Madsen and Shine 1993) and do so with compromised locomotory ability. This can lead to pronounced female mortality immediately post parturition (Madsen and Shine 1993) and continuing for months thereafter (Bonnet et al. 2002).

For oviparous snakes, the mortality costs of reproduction up to the point that eggs are laid should be similar to pre-parturition costs of viviparous species. If these are the most substantial costs for oviparous snakes, we expect mortality of female ratsnakes to be highest in early summer when females are gravid. If increased basking associated with reproduction is the proximate cause of higher mortality, then among individuals survival should decline with basking frequency. Following egg laying the costs for oviparous females should be lower than the post-partum costs for viviparous females because oviparous females have not had to undergo an extended period of starvation (Qualls and Shine 1998). If those costs are low for ratsnakes we expect female mortality to decline after females have laid eggs. However, if the main cost of reproduction is associated with replacing energy reserves expended during reproduction (Madsen and Shine 1993), then mortality of female ratsnakes should be high following egg laying. For this study, our primary goals were to determine a) if Texas ratsnakes exhibit sex-biased mortality and b) if differential survival is associated with seasonal patterns of activity and behavior.

Methods

We conducted this study from 2004–2007 at Fort Hood, an 87 890 ha military installation in central Texas (30°10′N, 97°45′W). Snakes were caught opportunistically by hand throughout the field season. We measured mass and snout–vent length (SVL) and determined the sex of each snake. Snakes for which transmitters weighed <3% total body weight had a radio transmitter surgically implanted and were then released at their capture locations. Transmitters were implanted by veterinarians using Blouin-Demers and Weatherhead's (2001b) modification of Reinert and Cundall's (1982) method. Transmitters weighed 9 g or 13 g with batteries lasting 12 months and 24 months, respectively. Based on data from other ratsnake populations (Blouin-Demers et al. 2002), all the individuals in which transmitters were implanted were well above the minimum size of sexual maturity. We relocated snakes approximately every 48 h and recorded date, location (UTM coordinates) and whether or not the snake was basking. Snakes were considered basking if they were exposed and immobile.

Texas ratsnakes are primarily active nocturnally during the summer and are usually concealed during the day (Sperry unpubl.), which made it difficult to recapture females to determine which individuals were reproductive. In ratsnake populations at higher latitudes females generally reproduce in alternate years (Fitch 1999, Blouin-Demers and Weatherhead 2001b). In this population, however, observations of females known to be gravid and anecdotal observations of mating behavior suggest that other than in a drought year, most adult females reproduced every year (Sperry and Weatherhead 2008).

Statistical analysis

We used the Kaplan–Meier product limit analysis and log-rank tests in program Systat (2004) to compare male and female snake survival over time. We lost radio signals for 11 transmitters. Lost signals could result from a snake traveling out of range or being carried out of range by a predator, transmitter failure or a mortality event that caused the transmitter to malfunction (e.g. crushed on roadway). Because lost signals can result from mortality of the snake, we ran two separate analyses, one with all snakes with lost signals assumed alive and one with all those individuals assumed dead (Pollock et al. 1989). In both cases, snakes that had their transmitters removed and those alive at the end of the study were considered to have survived (i.e. right censored). Two snakes that did not survive past a 7-day transmitter acclimation period were removed from analyses.

We used the distance snakes traveled between observations as our index of mobility because this measure is correlated with frequency of movement in our study population ($R^2 = 0.71$, $p < 0.001$). Distance moved between observations was calculated using Hawth's Analysis Tools (Beyer 2004) in ESRI ArcGIS ver. 9. We quantified basking as the percentage of relocations each snake was found basking. We compared distance traveled and basking percentage between sexes and months using ANOVA. We used linear regression to determine whether survival varied with seasonal activity and ANCOVA to determine if the slopes of regression lines differed between the sexes. Monthly survival was estimated as $1 - (M/D)$, where M = the number of snakes that died and D = the number of days in the month each tracked snake was known to be alive, summed across all snakes. To determine whether

individual snakes that died were more active immediately before their death, we used paired, two-tailed t-tests to compare the movement of each snake that died in the week prior to its death with the mean movement of snakes that did not die for which movement data were available for that week. Limiting data to one week prior to a snake dying controlled for seasonal variation in movement. We used the same approaches to examine how survival was associated with seasonal and individual variation in basking. For all analyses, alpha was set at 5%. Means are presented ± 1 SE.

Results

We implanted radio transmitters in 25 females and 38 males. Males were on average approximately 7% longer (120.91 ± 2.47 cm vs 112.55 ± 27.51; t $= 2.37$, p $= 0.02$) and 22% heavier (583.58 ± 29.99 g vs 477.88 ± 27.51; t $= 2.45$, p $= 0.02$) than females.

Over four years we tracked individual snakes for an average of 246.88 (± 36.30) days for females and 357.68 (± 45.88) days for males. Of the 38 male and 25 female snakes tracked, 13 males and 11 females were confirmed dead. Eleven of these snakes died of unknown causes (transmitter found with no associated carcass), 11 were probable predation events (e.g. researcher witnessed predation, talon marks, partially eaten) and two were killed by vehicles on roads. Kaplan–Meier survival analysis indicates that survival for females was lower than for males (Mantel log-rank test: $\chi^2 = 5.51$, p $= 0.02$, Fig. 1). For an additional 11 snakes (4 males, 7 females) we lost the signal from their transmitters. Difference in survival between sexes was even greater when these lost transmitters were considered mortalities (Mantel log-rank test: $\chi^2 = 12.70$, p < 0.001). We have included only snakes that were known mortalities in all subsequent analyses, providing a conservative estimate of female survival. For males, 12 of 13 recorded mortalities occurred in May, June and July, whereas female mortality occurred
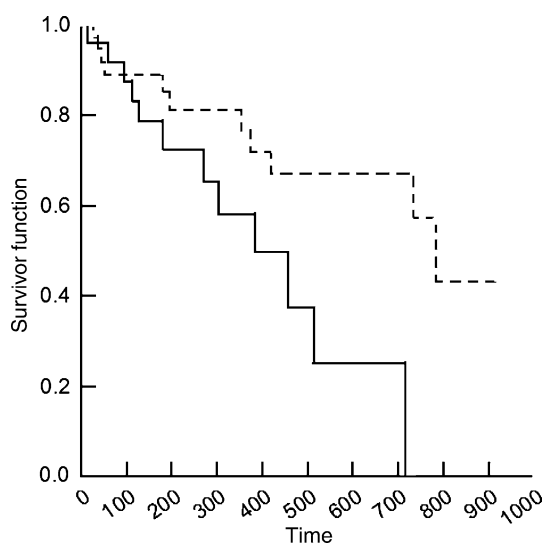

Figure 1. Survival function of male and female Texas ratsnakes using Kaplan–Meier survival estimates from Fort Hood, Texas 2004–2007. Dashed line indicates male snakes and solid line indicates female snakes.

in every month of the active season (April–November; Fig. 2).

Consistent with our assumption that size differences should not affect survival, we found no difference in size between individuals that died and individuals of the same sex that did not die (males: snout-vent length $= 123.15 \pm 2.62$ vs 125.08 ± 4.95, t $= -0.38$, p $= 0.71$; mass $= 554.31 \pm 35.06$ vs 628.62 ± 54.62, t $= -1.18$, p $= 0.24$, for live vs. dead, respectively; females: snout–vent length $= 118.10 \pm 3.10$ vs 111.07 ± 2.88, t $= 1.62$, p $= 0.12$; mass $= 439.64 \pm 45.28$ vs 437.73 ± 40.27, t $= 0.03$, p $= 0.98$, for live vs dead, respectively).

Four of five female snakes with known laying dates laid eggs between 11 June and 30 June and the fifth snake laid eggs in early August. Of these five snakes, three died soon after laying eggs (two at three days after and one at 17 days after). We recovered only a transmitter from one of those females, the carcass of another suggested hawk predation, and the third female was run over by a vehicle.

Activity differed by month ($F_{11, 481} = 26.14$, p < 0.001, Fig. 3) but overall was similar between male and female snakes (68.22 m ± 3.91 and 70.44 m ± 4.27, respectively; $F_{1,481} = 0.05$, p $= 0.83$). Males were more active than females in May and June but from July through December females were more active (Fig. 3). Monthly survival declined with movement when male and female monthly values are included in the same analysis ($R^2 = 0.42$, p $= 0.001$). Analyzed separately, survival declined with activity for both males ($R^2 = 0.64$, p $= 0.002$, Fig. 4) and females ($R^2 = 0.37$, p $= 0.04$, Fig. 4). ANCOVA analysis indicated that both activity ($F_{1,21} = 18.76$, p < 0.001) and sex ($F_{1,21} = 4.95$, p $= 0.04$) had a significant effect on survival. In the week prior to their death, females that died moved more females that lived (t $= 2.40$, p $= 0.03$) but the same was not true for males (t $= 0.13$, p $= 0.90$).

Percentage of time individuals spent basking differed by month ($F_{11,483} = 5.48$, p < 0.001) and by sex ($F_{1,483} = 5.48$, p < 0.01). Basking increased through the spring for both sexes but after May males steadily decreased their basking frequency whereas females continued to bask through December (Fig. 5). Monthly survival declined with increasing basking frequency when male and female monthly values are included in the same analysis ($R^2 = 0.50$, p < 0.001). Analyzing the sexes separately, survival declined with basking for both males ($R^2 = 0.69$, p < 0.001, Fig. 6) and females ($R^2 = 0.31$, p $= 0.06$, Fig. 6). ANCOVA analysis indicated that basking had a significant effect on survival ($F_{1,21} = 17.29$, p < 0.01) but the slopes of the regression lines were similar for males and females ($F_{1,21} = 0.43$, p $= 0.52$). However, in the week prior to death, female and male snakes that died did not bask significantly more than snakes that lived (females $= 12.8\%$ vs 5.0%, t $= 1.16$, p $= 0.27$; males $= 5.8\%$ vs 6.5%, t $= -0.18$, p $= 0.86$).

Discussion

Overall survival was lower for female than for male Texas ratsnakes. The difference in survival was associated with differences in both how much males and females moved and seasonal differences in basking activity. Although males
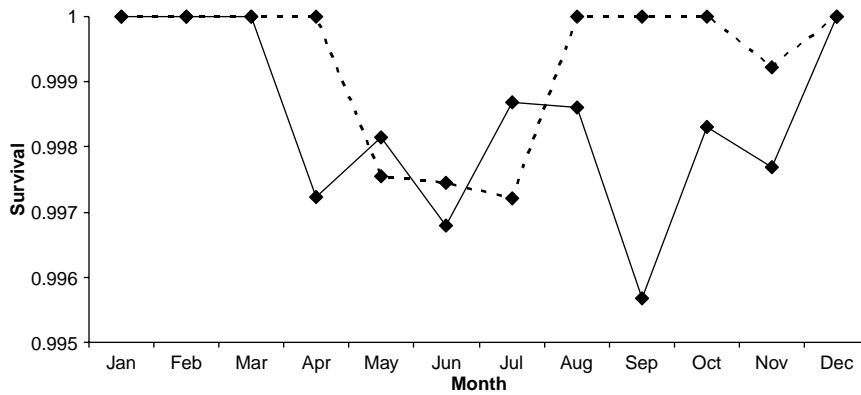
Figure 2. Survival estimates by month for male and female Texas ratsnakes at Fort Hood, Texas 2004–2007. Dashed line indicates male snakes and solid line indicates female snakes.

moved more than females in the spring, females moved more thereafter and suffered higher mortality. Differences in basking were more pronounced, with females basking more than males from mid-summer through the fall. Taken together, the seasonal patterns of mortality and seasonal patterns of behavior suggest that differences in both movement and basking contributed to the higher mortality of females.

In addition to differences in how males and females behave, sex differences in appearance and physiology have been proposed to contribute to sex-biased mortality (Magnhagen 1991, Andersson 1994, Moore and Wilson 2002, Christe et al. 2006). Male and female ratsnakes do not differ in appearance and although males grow slightly larger than females, we found no evidence that size affected survival. Thus, intrinsic differences in appearance between males and females are unlikely to have affected sex-specific rates of mortality. Moore and Wilson (2002) proposed that higher testosterone levels in male animals could compromise their immune system, with the resulting higher parasite loads making males less able to escape predators. Males have been shown to have higher parasite loads in some snake species (*Python regius*, Aubret et al. 2005), although it is not clear if this is a consequence of

testosterone differences or of divergent habitat use between the sexes (Luiselli 2006). Not only did male ratsnakes have higher survival than females, elsewhere we show male and female ratsnakes did not differ in a variety of hematological characteristics (i.e. hematocrit, white blood cell concentrations, total corticosterone concentrations) or in the prevalence of either internal (haemogregarine) or external (chigger) parasites (Sperry et al. unpubl.). Therefore, physiological differences associated with immune function and parasite loads seem unlikely to have contributed to sex differences in survival.

For many animals male reproductive success is contingent on finding receptive females. Mate searching requires increased mobility, which is widely assumed to increase mortality risks for males (Magnhagen 1991). Based on the laying dates of females, mating in our study population of ratsnakes probably begins in May, which was when males moved the most, consistent with a previous study that found that male ratsnakes moved most during the mating season (Blouin-Demers and Weatherhead 2001c). We also found that males basked more in spring and that mortality was associated with basking. It is possible, however, that males recorded as basking may actually have been searching for mates. Brown and Shine (2004) found
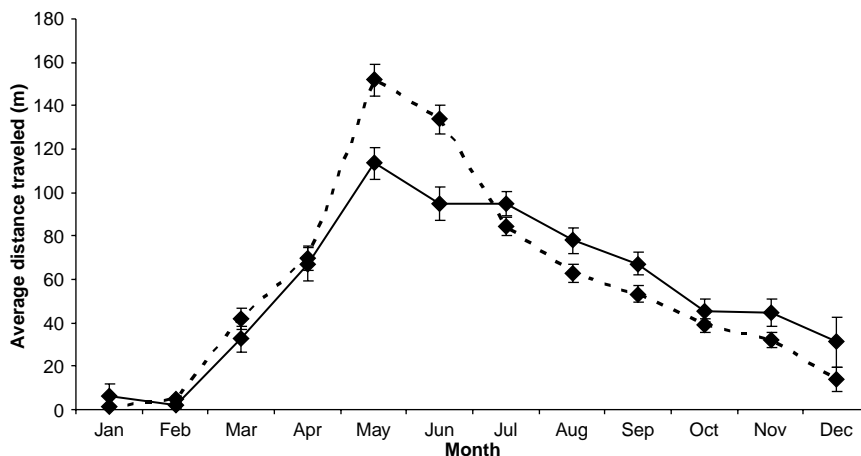

Figure 3. Mean (±SE) daily distance male and female Texas ratsnakes traveled each month at Fort Hood, Texas 2004–2007. Dashed line indicates male snakes and solid line indicates female snakes.
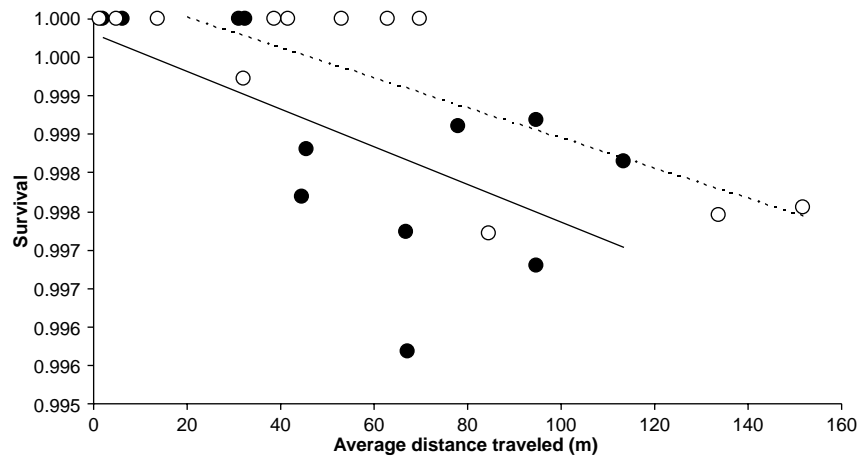
Figure 4. Relationship between mean daily distance male and female Texas ratsnakes traveled each month and monthly survival at Fort Hood, Texas 2004–2007. Open circles and dashed regression line indicates male snakes, closed circles and solid regression line indicates female snakes.

that male keelback snakes *Tropidonophis mairii* allowed human observers to approach them more closely during the breeding season. We recorded a snake as basking if it was in the open and stationary. Therefore, it is possible that at least some of these observations could have been males engaged in mate searching that simply stopped moving when they detected our approach. In any case, it was clear that males moved more and were out in the open more during spring, and that was when male mortality was high.

We expected that the costs of reproduction for female ratsnakes should be greatest in the spring when eggs were developing, because unlike the viviparous European adders *Vipera berus* studied by Madsen and Shine (1993), female ratsnakes do not have to undergo a prolonged period of starvation associated with gestation. Female snakes bask more when developing eggs or young (Shine 1980, Blázquez 1995, Brown and Weatherhead 2000, Blouin-Demers and Weatherhead 2001a) and carrying eggs impairs mobility (Shine 1980, Seigel et al. 1987, Brown and Shine 2004, Winne and Hopkins 2006), both of which should put females at risk prior to egg laying. Some female ratsnakes did die in the spring, but unlike males, females

continued to die through the summer and fall. Madsen and Shine (1993) found a similar pattern for adders which suggests that, analogous to what has been found in lizards (Qualls and Shine 1998), the costs of reproduction are similar for oviparous and viviparous snakes. Snakes are capital breeders (Bonnet et al. 1998) and therefore females must begin accumulating the resources required for the next bout of reproduction as soon as the current bout is finished. The relative clutch mass (clutch or litter mass divided by post-partum maternal mass) is similar for ratsnakes and adders (Madsen and Shine 1993, Blouin-Demers and Weatherhead 2007), indicating that females of both species invest similarly in a reproductive bout. Thus, regardless of the mode of reproduction, females must forage extensively as soon as they have laid eggs or given birth. Increased foraging also requires more basking to promote digestive efficiency (Blouin-Demers and Weatherhead 2001a). We found that female ratsnake mortality was associated with both movement and basking. In this instance ratsnakes appear to differ from adders, however, because Madsen and Shine (1993) did not find that basking increased the risk of predation for adders.
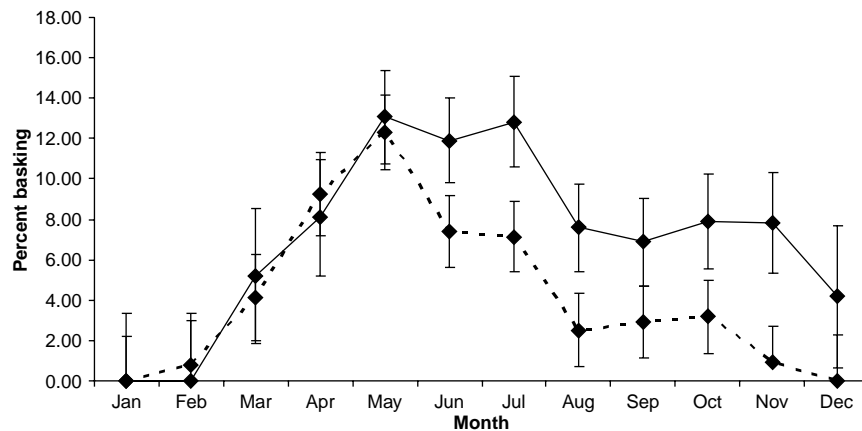

Figure 5. Mean (±SE) percent of relocations male and female Texas ratsnakes were found basking each month at Fort Hood, Texas 2004–2007. Dashed bar indicates male snakes and solid line indicates female snakes.
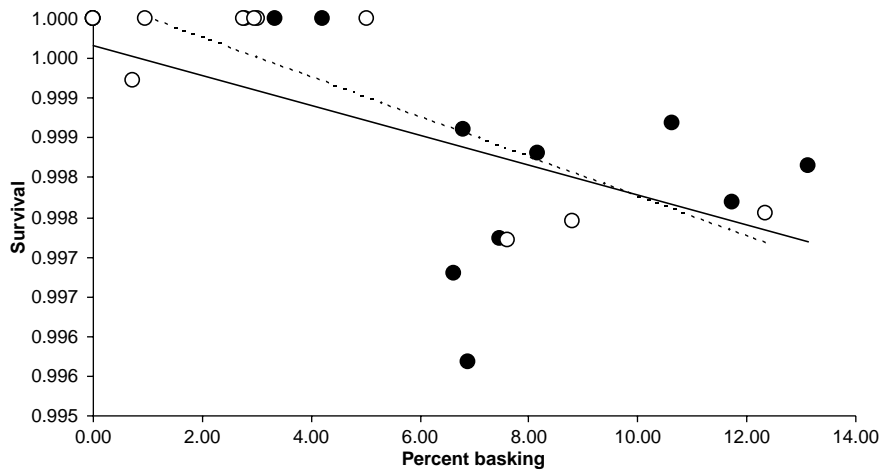
Figure 6. Relationship between percent of relocations male and female Texas ratsnakes were found basking each month and monthly survival at Fort Hood, Texas 2004–2007. Open circles and dashed regression line indicates male snakes, closed circles and solid regression line indicates female snakes.

More studies of sex-specific mortality rates in snakes are required to determine the generality of the patterns discussed here. It seems likely that the abundance of both predators and prey will affect mortality rates among populations, but it is not clear that either factor would affect relative rates of male and female mortality within populations. If female-biased mortality proves to be the norm, snakes would be different from other taxa (Magnhagen 1991), and as such would provide an opportunity to explore the demographic and life-history consequences (Sæther et al. 2003, Dyson and Hurst 2004, Christe et al. 2006) of that difference.

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