Male mating success in a North American pitviper: influence of body size, testosterone, and spatial metrics

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Males with enhanced traits relative to conspecifics often show increased mating and reproductive success and thus have a fitness advantage. The opportunity or potential for sexual selection is predicted to occur under these conditions. Here, we investigated proximate determinants of mating success in male copperhead snakes (Agkistrodon contortrix), a medium-sized pitviper of North America. Specifically, we investigated the relationships of body size (snout-vent length, body mass), body condition index, spatial metrics (total distance moved, home range size), and plasma testosterone concentration on mating success in males. The single mating season lasts from August through September. We compared a set of candidate linear mixed models and selected the best-fitting one using the adjusted Akaike Information Criterion (AICc). The AICc-selected model (model 2), with testosterone, body condition index, and home range size as predictor variables, showed that male mating success was positively correlated with testosterone. To our knowledge, this is the first report to show the relationship of testosterone and individual mating success in any snake species. A parallel study conducted on male fitness in A. contortrix of the same population used microsatellite markers to assign parentage of fathers (known mothers). Unlike our study, they found that snout-vent length was positively correlated with reproductive success and that males were experiencing greater sexual selection. This relationship has been detected under natural conditions in other species of snakes. Although behavioural data are important in any mating system analysis, they should not stand alone to infer parentage, relationships or selection metrics (e.g. Bateman gradients). Long-term sperm storage by females, female cryptic choice, and other factors contribute to the complexity of mating success of males. Accordingly, we thus conclude that estimates of reproductive success and fitness in cryptic species, such as copperheads and other snakes, require robust molecular methods to draw accurate conclusions regarding proximate and evolutionary responses. © 2015 The Linnean Society of London, Biological Journal of the Linnean Society, 2015, 115, 185–194.


INTRODUCTION

Theoretical and empirical studies of animal mating systems have repeatedly demonstrated that males are the primary mate searching sex (Darwin, 1871; Bateman, 1948; Trivers, 1972; Emelen & Oring, 1977; Thornhill & Alcock, 1983; Kokko & Wong, 2007). Furthermore, male mating success is often correlated with visible phenotypic traits (e.g. horns, ornaments, body size) that increase priority-of-access to females. These traits are used in competitive fights with

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conspecifics, mate-searching tactics, and attracting females, hence mate choice (Thornhill & Alcock, 1983; Andersson, 1994; Emlen, 2001; Shuster & Wade, 2003; Smith et al., 2008; Klose, Welbergen & Kalko, 2009). However, mating success can also be influenced by non-visible traits such as performance ability (Arnold, 1983; Husak & Fox, 2008; Careau & Garland, 2012), personality (Dall et al., 2012; Wolf & Weissing, 2012), sexual and fighting experience (Riechert, Chastel & Becker, 2012), and concentrations of circulating sex hormones (Sinervo et al., 2000; Adkins-Regan, 2005; John-Alder et al., 2009; Neff & Knapp, 2009). In males, elevated levels of plasma testosterone (T) can increase aggression, vigilance at territories, quality of traits (e.g. colours of feathers and song type), courtship skills, and whole-body performance, including locomotor capacity during mate searching (Husak et al., 2006; Hau, 2007; Careau & Garland, 2012). Males with enhanced traits relative to conspecifics often show differential reproductive success (progeny) and thus a fitness advantage (Shuster & Wade, 2003). Under the aforementioned conditions, the opportunity is present for sexual selection to act on males (Darwin, 1871; Arnold & Duvall, 1994; Shuster & Wade, 2003; Jones, 2009).

Among terrestrial vertebrates, most research on mating systems and traits associated with mating success has concerned birds and mammals, with far fewer studies on amphibians and non-avian reptiles such as lizards and snakes. Taxon biases are even found within reptiles, with far less information available on snakes, for instance, than in other lineages (Bonnet, Shine & Lourdais, 2002; Shine, 2003). Secreciveness, cryptic habits, rarity, and small body size play a significant role in explaining this historic gap of information in snakes (Bonnet et al., 2002; Clark et al., 2014). Nonetheless, in recent years, radiotelemetry has circumvented many logistical problems in locating and observing wild individuals for extended periods (Reinert, 1992; Dorcas & Willson, 2009). Several lineages in particular, the vipers (Jellen et al., 2007; Glaudas & Rodríguez-Robles, 2011; Clark et al., 2014), several species of colubrids (Blouin-Demers, Gibbs & Weatherhead, 2005; Dubey et al., 2009), boids (Rivas & Burghardt, 2005) and pythonids (Slip & Shine, 1988) have proved particularly valuable in radiotelemetric studies of mating systems of snakes (Duvall, Arnold & Schuett, 1992; Aldridge & Duvall, 2002; Clark et al., 2014). This success is largely due to large body size, high visibility, spatial predictability, and high population densities (Duvall et al., 1992; Duvall, Schuett & Arnold, 1993), which have permitted the field study of their mating systems, reproductive success, and sexual selection (Duvall & Schuett, 1997; Coupe, 2002; Greene et al., 2002; Rivas & Burghardt, 2005; Jellen et al., 2007; Dugan, Figueroa & Hayes, 2008; Glaudas & Rodríguez-Robles, 2011; Schuett, Repp & Hoss, 2011; Schuett et al., 2013; Clark et al., 2014).

Here, we tested hypotheses concerning the mating system of copperhead snakes (Agkistrodon contortrix), a medium-sized pitviper of North America (Fitch, 1960; Gloyd & Conant, 1990) using linear mixed models (Burnham & Anderson, 2004). Specifically, we asked the following questions: (1) Is body size (snout-vent length, body mass) and body condition index (BCI) in males correlated with their mating (copulation) success? This taxon exhibits male-biased sexual size dimorphism (Fitch, 1960). (2) Do males that move greater distances and have larger home ranges locate and copulate with more females? and (3) Are concentrations of plasma testosterone in males correlated with their mating success (which we define as the frequency of copulations with unique mates)?

MATERIAL AND METHODS

RESEARCH SITE

The study site was located in a 485 ha parcel of basalt trap rock ridge ecosystem situated 4.75 km NW of Meriden, Connecticut. Details of the topography and climate of this region are presented elsewhere (Smith, 2007; Smith et al., 2009).

SUBJECTS

After their initial capture in spring (April), subjects were transported to the laboratory for processing. Under Isoflurane anesthesia, body mass (± 0.5 g) was determined using a triple beam balance, and snout-vent length (SVL: cm ± 0.2) was measured using a non-stretchable cloth measuring tape. Ten adult males were surgically implanted with standard radiotransmitters (per Smith et al., 2009; Smith, Schuett & Schwenk, 2010). Using procedures of Wayne & Mason (2008), the BCI of each male we selected to radiotrack was calculated as the residual score from the general linear regression of ln-transformed mass against ln-transformed SVL.

Regardless of size, all copperheads encountered at the field site were permanently marked for future identification using passive integrated transponder (PIT) tags (125 kHz 12 mm, Biomark, Boise, Idaho, USA; Gibbons & Andrews, 2004). PIT tags were injected one-third of the body length anterior from the cloaca and the last three characters of the 10-character PIT code were used as an identification code for all records pertaining to an individual.

RADIO-TRACKING AND BEHAVIOURAL OBSERVATIONS

The ten male subjects implanted with radiotransmitters were located every 48–72 h in August.

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and September on foot using radio-tracking equipment described in Smith et al. (2009). Reproductive behaviours (i.e., bisexual pairings, courtship, and coitus) were determined by direct observation (Smith et al., 2009, 2010). Only observations involving coitus were used in the present analysis.

**SPATIAL MEASUREMENTS**

Subjects implanted with radio-transmitters were located and observed in the field on 17 occasions during August and 19 times during September (Smith et al., 2009). Movement distances and home range sizes for males were calculated using the Animal Movement Extension option in ArcView 3.2 (Hooge, Eichenlaub & Solomon, 1999). Home range size was estimated using 100% minimum convex polygon (MCP) and kernel 95% and 50% contour intervals as determined by ArcView. Because a single point lying outside the normal range of an animal can artificially inflate activity range size, range estimates were recalculated after removing 5% and 10% of outliers using the Animal Movement harmonic mean outlier removal procedure (Hooge et al., 1999). Comparisons of values prior to and following outlier removal showed no significant outlier effect; therefore, only values prior to outlier removal were used in the statistical analyses. For kernel estimates of home range size, smoothing values were determined using least-squares cross-validation (Seaman et al., 1999).

We were unable to monitor every movement made by each male; hence, we relied on analyzing their movements as straight-lines. Although straight-line estimates of movement can underestimate the actual distance moved by as much as 50% (Madsen, 1984; Tiebout & Carey, 1987; Secor, 1992), based on our tracking protocol we assumed underestimation of straight-line movement to be equivalent for all individuals (Secor, 1994; see Table 1 herein).

**COLLECTION OF BLOOD FOR MEASURING HORMONES**

Blood for subsequent hormone analysis was sampled from all radio-tracked males at four equally spaced times; twice during August and twice during September. From these samples, radio-immunoassays (RIAs) were conducted for testosterone (T). Measurement of T in this copperhead population is detailed in Smith et al. (2010). Briefly, following their capture, blood was collected immediately in the field. Collection of blood samples to obtain plasma for sex steroid analysis was accomplished by gently restraining subjects in a clear acrylic tube. A small volume of blood (0.5-1 mL; less than 4% of total blood volume) was collected via heart-puncture (cardiocentesis) using a sterile-disposable 1 mL tuberculin syringe (coated with sodium heparin), fitted with a sterile-disposable 26-gauge needle. Sampling typically required <60 s from initial capture until the blood sample was obtained (Schuett et al., 2004a) and the subject released (or held for further processing). Blood was transported in individual 1.5 mL centrifuge tubes at ambient (~20 °C) temperature. Steroid levels are unaffected when blood is maintained at ambient temperatures for short (<24 h) periods (Taylor & Schuett, 2004).

In the laboratory, the blood samples were placed in disposable microcentrifuge tubes (1 mL) and centrifuged at 13 000 g at room temperature (21–23 °C) for 5 min to separate plasma. Plasma was collected using a micropipette fitted with a sterile-disposable tip and transferred to another microcentrifuge tube that was

<table>
<thead>
<tr>
<th>ID</th>
<th>SVL</th>
<th>BM</th>
<th>BCI</th>
<th>T (ng mL⁻¹)</th>
<th>TDM</th>
<th>HRS</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>15a</td>
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<tr>
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<td>0.4340</td>
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<td>1985.69</td>
<td>2.92</td>
<td>5</td>
</tr>
<tr>
<td>9c</td>
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<td>160.2</td>
<td>-0.1351</td>
<td>32.31</td>
<td>2068.30</td>
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</tr>
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<td>35.92</td>
<td>1438.27</td>
<td>1.97</td>
<td>2</td>
</tr>
</tbody>
</table>

ID = male subject; SVL = snout-vent length (cm); BM = body mass (g); BCI = body condition index; T = mean plasma testosterone (ng mL⁻¹) level for the mating season; TDM = total distance moved (m); HRS = home range size (minimum convex polygon, hectare); MS = frequency of male mating success (coitus) with unique females for the mating season.
permanently labeled with the specimen identification code and date. Plasma samples were placed in an ultra-low freezer (−80 °C) until RIAs could be performed.

**Radio-immunoassay of testosterone**

Procedures for conducting radio-immunoassays (RIAs) of testosterone (T) followed Schuett et al. (1997, 2004a, b, 2005, 2006). Briefly, in quantifying T, we used commercial RIA kits but with several appropriate modifications (e.g. use of snake plasma rather than rat plasma for validation procedures) to measure steroid concentrations from the collected plasma of subjects. Validation included both quantitative recovery and parallelism. All values for plasma T concentrations are in ng mL⁻¹. Two different RIAs were performed for T and all samples were run in duplicate (duplicate reactions from a single extraction). The intra-assay coefficients of variation (CVs) were 9.1% and 11.1%, and the inter-assay CV was 11.9%. Testosterone data (Table 1) represent the arithmetic means of four samples for each of the ten males during the mating season (August and September).

**Variables of male mating success**

The influence of body length (SVL), BCI, testosterone (T), total distance moved (TDM), and home range size (HRS) on male mating success (number of unique copulated females) were compared with five linear mixed models using the R statistical program (R Core Team, 2014) and packages lme4 (Bates et al., 2014), lmerTest (Kuznetsova, Brockhoff & Christensen, 2014), and MuMIn (Barton, 2014). We included month (to account for serial autocorrelation) and ID (to account for non-independence of multiple records of individuals) as random variables, male mating success as a response variable, and SVL, BCI, TDM, HRS, and T as predictor variables. To select the best-fitting, most parsimonious model from among the five candidate models, we used Akaike’s Information Criterion adjusted for small sample sizes (AICc) (Burnham & Anderson, 2004; Bolker, 2008).

**Results**

**Subjects**

Variables (SVL, BCI, TDM, HRS and T) analyzed in this study are presented in Table 1. Snout-vent length (SVL) and body mass (BM) were highly correlated \( F = 15.47, P = 0.004, R^2 = 0.66, N = 10 \); therefore, owing to the stability of SVL (e.g. mass can change instantaneously with food or water consumption), it was used as the metric of male body size in all subsequent analyses. The SVLs of the ten radio-tracked males ranged from 62.1–85.2 cm (SVL mean = 74.87 cm, ± 3.21 SE, \( N = 10 \)). Mean SVL of the radio-tracked males was not significantly different from mean SVL of all other adult males we measured (SVL mean = 75.20 cm ± 1.58 SE, \( N = 47, P = 0.46 \)).

Adult males were significantly larger (SVL, BM) than females (SVL: \( F = 18.8677, P < 0.0001 \); body mass: \( F = 3.9757, P = 0.0256 \), a phenomenon termed male-biased sexual size dimorphism (SSD). This relationship has been reported in copperheads (Fitch, 1960, 1981) and many other snake species (Shine, 1994; Amarello et al., 2010).

**Radio-tracking and Behavioural Observations**

During August and September, mating was recorded in the ten males with radio-transmitters on 33 occasions involving 18 females (14 females fitted with radio-transmitters for a related concurrent study and 4 ‘incidental’ females that were not fitted with radio-transmitters) (Table 1). Highly significant correlations were detected among the three parameters used to estimate male HRS (MCP, 95% kernel, 50% kernel home range, \( R^2 > 0.63, P < 0.006 \), but for reasons discussed by others (Row & Blouin-Demers, 2006), MCP was selected for all statistical comparisons. Total distance moved (TDM) and HRS were also highly correlated (\( R^2 = 0.96, P = 0.0001 \)).

**Male mating success variables**

The AICc-selected model (model 2) included HRS, T, and BCI as predictor variables (Fig. 1, Table 2). The frequency of male mating success was significantly correlated with T (\( \beta = 0.051 ± 0.02, t = 2.99, P = 0.013 \)), but not BCI (\( \beta = 0.588 ± 0.94, t = 0.63, P = 0.552 \)) or HRS (\( \beta = 0.125 ± 0.06, t = 2.03, P = 0.079 \)). None of the other candidate models were equally parsimonious (\( \Delta \text{AIC} < 4 \)), but model 1, which included HRS, T, and SVL as predictor variables, was close based on \( \Delta \text{AIC} (\text{AIC} = 5) \). In model 1, male mating success was significantly correlated with HRS (\( \beta = 0.137 ± 0.06, t = 2.45, P = 0.026 \)) and T (\( \beta = 0.054 ± 0.02, t = 3.35, P = 0.0004 \)), but not SVL (\( \beta = 0.045 ± 0.03, t = 1.75, P = 0.10 \). Unlike model 2, HRS was significant in model 1, and in both models T was significant.

**Discussion**

The AICc-selected model (model 2), with T, BCI, and HRS as predictor variables, showed that the frequency of male mating success was positively correlated only with T. Of our three hypotheses, we did not anticipate rejecting large body size (SVL) and BCI.

Schuett (1997), for example, reported that large body size in male copperheads was important in winning fights and obtaining priority-of-access to mates under laboratory conditions. Other studies concerning snakes support these results (Madsen et al., 1993; Madsen & Shine, 1994; Shine, 2003; Jellen et al., 2007; Dubey et al., 2009; Ursenbacher, Erny & Fumagalli, 2009).

We also predicted that total distance moved (TDM) and HRS would be positively correlated with male mating success, but under model 2 TDM was not selected and HRS was rejected though approached significance ($P = 0.079$). In model 1, however, HRS was significant ($P = 0.026$). Other studies of snakes have shown a positive relationship with movements, HRS and mating (coitus) success in males (Duvall & Schuett, 1997; Prosser et al., 2002; Weatherhead et al., 2002; Jellen et al., 2007; Glaudas & Rodriguez-Robles, 2011).

In model 2 we found support for our hypothesis that plasma testosterone levels of males would be significantly correlated with frequency of mating success (the number of copulations with unique mates). Studies investigating the relationship of $T$ and mating success in wild snakes are essentially nonexistent, but studies of other vertebrates show that males with high levels of circulating androgens (e.g. $T$) often secure more mates and have greater mating success through displays and colour patterns influencing female choice, successfully holding territories, or by winning fights, challenges and guarding mates (Wingfield, 1984; Alatalo et al., 1996; Kettersson & Nolan, 1999; Westneat & Stewart, 2003; Hau, 2007; Ouyang et al., 2011). Furthermore, males with higher $T$ levels show greater locomotor and whole-body performance (Irschick et al., 2008; Higham & Irschick, 2013), which can lead to increased encounters with females (Garamszegi et al., 2005) and greater reproductive success (Sinervo et al., 2000; Gowan, McBrayer & Rostal, 2010). Importantly, Garland, Bennett & Daniels (1990) showed that locomotor performance in garter snakes ($Thamnophis s. fitchi$) is heritable and thus a target of selection (Husak et al., 2006, 2009; Irschick et al., 2008). In general, high levels of activity coupled with mate searching and interactions with females, a sort of endurance rivalry, can often predict male mating and reproductive success (Keogh et al., 2012).

King and colleagues (King, 2002; King, Cline & Hubbard, 2004; King & Bowden, 2013) provide groundbreaking research on the inheritance of testosterone ($T$) levels in North American natricine snakes (genus $Thamnophis$). Importantly, significant effects were detected with respect to heritability estimates ($h^2$) and family differences. However, whether greater $T$ levels in adult male $Thamnophis$ translates to increased reproductive success remains for future studies (King & Bowden, 2013). Though not known in non-avian reptiles, selection can act on testosterone production in wild birds (McGlothin et al., 2010).

**Figure 1.** Relationship of plasma testosterone and mating success (frequency of copulation involving new females) in ten male copperheads (Agkistrodon contortrix). Gray circles denote August, and black circles denote September. See Table 1.

**Table 2.** Model selection criteria (Akaike’s Information Criterion, AIC) and fitted parameters. Each model included month to account for serial autocorrelation and ID to account for non-independence of multiple records of individuals as random variables, and male mating success as a response variable. AICc = Akaike’s Information Criterion adjusted for small sample sizes, $\Delta$AICc = difference between AICc and most parsimonious model’s AICc. HRS = home range size; $T$ = testosterone; BCI = body condition index; TDM = total distance moved; and SVL = snout-vent length. See Table 1. For further details see Methods.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>Predictor variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>91</td>
<td>0</td>
<td>HRS, T, BCI</td>
</tr>
<tr>
<td>1</td>
<td>96</td>
<td>5</td>
<td>HRS, T, SVL</td>
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<tr>
<td>0</td>
<td>116</td>
<td>24</td>
<td>HRS, T, SVL, TDM</td>
</tr>
</tbody>
</table>

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Heritability, family differences, and selection on T levels and production have not been studied in copperheads or other snakes and is thus a rich area for future research.

Finally, with few exceptions (Schuett & Grober, 2000), most studies concerning steroid levels in snakes report only means and standard errors rather than individual values for individuals (Taylor & DeNardo, 2011). Our previous work on copperheads from the population we report here, for example, only provided means and standard errors (Smith et al., 2010). Accordingly, we support the view that a full understanding of variance in reproductive success and endocrinological metrics will need to incorporate the shifting paradigm of individual differences and animal personalities (Kempenaers, Peters & Foerster, 2007; Zera, Harshman & Williams, 2007; Dall et al., 2012; Wolf & Weissing, 2012). Instead of abandoning altogether the ‘tyranny of the Golden Mean’ (Bennett, 1987; Williams, 2008), we suggest also presenting data on individuals.

MEASURING SEXUAL SELECTION

In other species of snakes, including vipers, standard variances on mating frequencies (\( IS = \sigma^2/\mu^2 \), Wade, 1979; Wade & Arnold, 1980) have been used as estimates of the potential for sexual selection (Madsen & Shine, 1994; Duvall & Schuett, 1997; Prosser et al., 2002). For example, based on our mating data in Table 1, we found that \( IS \) for copperheads showed no sex differences (Kolmogorov–Smirnov two-sample test, \( \sigma^2 = 0.45 \), \( \mu = 0.40 \), \( P = 0.61 \); Zar, 1999). However, based on Arnold & Duvall (1994) and Shuster & Wade (2003), mating success and the potential for sexual selection is best expressed as a function of the number of progeny produced by an individual in a given reproductive season. Furthermore, methods have been generated to overcome statistical biases associated with analyzing sexual selection gradients in open populations (Mobley & Jones, 2012).

Our research group (Levine et al., 2014) conducted a parallel study on male fitness in A. contortrix from the population discussed herein, but analyzed mating success per Arnold & Duvall (1994) using 22 microsatellite markers to assign the paternity of fathers (all mothers were known) and the methods outlined in Mobley & Jones (2012) for open populations. Unlike the results of this study, Levine et al. (2014) found that SVL was positively correlated with male reproductive success (progeny) and males were experiencing greater sexual selection than females. With a range of alternative reproductive tactics operating in copperheads and other snakes, such as long-term sperm storage, cryptic female choice, sneaky males, and mate mimicry (Schuett, 1992; Zamudio & Sinervo, 2000; Booth & Schuett, 2011; Jellen & Aldridge, 2011; Clark et al., 2014; Levine et al., 2014), the relationship of male body size, copulation success and production of progeny to individual fitness is complex and requires further investigation.

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