Social Snakes?

Non-random association patterns detected in

a population of Arizona black rattlesnakes (*Crotalus cerberus*)

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A Thesis Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

Approved November 2012 by the
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ARIZONA STATE UNIVERSITY

December 2012

ABSTRACT

Social structure affects many aspects of ecology including mating systems, dispersal, and movements. The quality and pattern of associations among individuals can define social structure, thus detailed behavioral observations are vital to understanding species social structure and many other aspects of their ecology. In squamate reptiles (lizards and snakes), detailed observations of associations among individuals have been primarily limited to several lineages of lizards and have revealed a variety of social structures, including polygynous family group-living and monogamous pair-living.

Here I describe the social structure of two communities within a population of Arizona black rattlesnakes (*Crotalus cerberus*) using association indices and social network analysis. I used remote timelapse cameras to semi-continuously sample rattlesnake behavior at communal basking sites during early April through mid-May in 2011 and 2012. I calculated an association index for each dyad (proportion of time they spent together) and used these indices to construct a weighted, undirected social network for each community.

I found that individual *C. cerberus* vary in their tendency to form associations and are selective about with whom they associate. Some individuals preferred to be alone or in small groups while others preferred to be in large groups. Overall, rattlesnakes exhibited non-random association patterns, and this result was mainly driven by association selection of adults. Adults had greater association strengths and were more likely to have limited and selected associates. I

identified eight subgroups within the two communities (five in one, three in the other), all of which contained adults and juveniles.

My study is the first to show selected associations among individual snakes, but to my knowledge it is also the first to use association indices and social network analysis to examine association patterns among snakes. When these methods are applied to other snake species that aggregate, I anticipate the 'discovery' of similar social structures.

This work is dedicated to my grandma, Lois Hayse, who instilled a love of nature in me when I was very young. Some of my earliest memories are watching *Nova* and *Nature* with her and learning how to identify the birds who visited her feeders. Unfortunately, she is no longer here to listen to my snake stories, but I feel her influence in everything I do.

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1. INTRODUCTION

Social structure can be defined as the pattern of relationships among individuals, which are defined by the quality and pattern of associations among individuals (Wilson 1975, Hinde 1976, Whitehead 2008). Social structure of organisms is important because it affects many aspects of population biology, including mating systems, dispersal, and movements (Wilson 1975, Couzin 2006, Whitehead 2008, Kelley et al. 2011). Dispersal capabilities are extremely limited in closed societies, such as those seen in Bechstein's bats (*Myotis bechsteinii*) and white-nosed coatis (*Nasua narica*), which can make range expansion difficult and reduce genetic diversity (Kerth and van Schaik 2012). And in the great desert skink (*Liopholis kintorei*), low juvenile dispersal is associated with the construction of burrows cooperatively built by closely related individuals to protect their offspring (McAlpin et al. 2011). Thus, detailed observations of individuals and associations among them are vital to understanding species social structure and many other aspects of their ecology (Wilson 1975, Croft et al. 2008, Whitehead 2008, Clutton-Brock 2012).

In squamate reptiles (lizards and snakes), detailed observations of associations among individuals have been primarily limited to several lineages of lizards. These studies have revealed a variety of social structures, including polygynous family group-living and monogamous pair-living (Chapple 2003, Davis et al. 2011, McAlpin et al. 2011). Most studies of snake behavior and ecology in the wild have been conducted using mark-recapture or radio-telemetry techniques (Fitch 1987, Brown et al. 2007, Dorcas and Willson 2009; Schuett et al. 2011; but

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see Clark 2006). In mark-recapture, a large proportion of the population

generally is sampled, but repeated observations of individuals are infrequent due

to the difficulty of locating individuals owing to their secretive nature (Dorcas and

Willson 2009). Alternatively, radio telemetry provides the opportunity for more

frequent, repeated observations, but is generally feasible for only a small

proportion of the population, because of the costly nature (both time and money)

of this technique (Dorcas and Willson 2009).

Here I used frequent, repeated observations on groups of wild rattlesnakes

(Arizona black rattlesnakes, *Crotalus cerberus*) to examine association patterns

and describe their social structure. Like many other snakes, groups of *C.

cerberus* will share a single shelter site (den) to escape cold winter temperatures,

and remain in aggregations on the surface near the den after emerging in the

spring (figure 1; Gillingham 1987, my unpubl. data). But unlike most spring

aggregations of snakes, no reproductive behavior (e.g., courtship or mating)

occurs in *C. cerberus* aggregations (unpubl. data). From early April through mid-

May, *C. cerberus* emerge each day from shelter sites adjacent to communal

basking sites, aggregate in relatively small areas, and return to the shelter at

night to avoid cool temperatures. I used remote timelapse cameras (Timelapse

PlantCam and TimelapseCam 8.0, Wingscapes, Inc., Alabaster, AL, USA) to

semi-continuously record behavioral observations at these communal basking

sites and applied two techniques novel to behavior research of snakes to analyze

my observations: association indices (Whitehead 2008, Ramos-Fernández et al.

2009, Kelley et al. 2011) and social network analysis (Croft et al. 2004, Croft et

al. 2008, Ramos-Fernández et al. 2009, Kelley et al. 2011).

Association indices (AI) estimate the proportion of time each dyad (pair of subjects) spends together, permitting comparison of relationship strength among dyads within a population (Cairns and Schwager 1987, Whitehead 2008). These indices have been used to distinguish between random (e.g., mutual attraction to a physical resource; Gillingham 1987, Graves and Duvall 1995) and non-random associations in lizards (Leu et al. 2010), primates (Ramos-Fernández et al. 2009), cetaceans (Gero et al. 2005, Lusseau et al. 2006), bats (Vonhof et al. 2004), and fish (Kelley et al. 2011). Additionally, AI can be used to construct weighted social networks (Croft et al. 2008, Whitehead 2008, Kelley et al. 2011).

A social network is a graphical representation of a population's (or smaller group's) social structure; it describes the population as a whole while accounting for the lack of independence among associating individuals within the population (Croft et al. 2008, Leu et al. 2010, Kelley et al. 2011). Social network analysis allows the identification of distinct groups, termed communities, wherein most individuals associate with each other and rarely with individuals from other communities (Whitehead 2008). Further, within communities we can delineate subgroups, which contain individuals that tend to associate more within than among other subgroups (Croft et al. 2008). One social network attribute, association strength, is particularly useful for investigating how demography affects social structure because it incorporates both the number and strength of associations for each individual (Croft et al. 2008, Whitehead 2008). In spotted hyenas (*Crocuta crocuta*), for example, association strength decreases with age (Holekamp et al. 2012). Social network analysis has been used to describe

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social structure of lizards (Leu et al. 2010) and a range of other vertebrates such as primates (Ramos-Fernández et al. 2009), cetaceans (Gero et al. 2005, Lusseau et al. 2006), bats (Vonhof et al. 2004), birds (Oh and Badyaev 2010), and fish (Croft et al. 2004, Kelley et al. 2011). To date, no study has investigated the social structure of snakes using these methods.

Here, I used AI and social network analysis to address the following questions in *C. cerberus*:

1. Does gregariousness (an individual's propensity to associate with conspecifics; Whitehead 2008) vary among individuals?

2. Are individuals selective about whom they associate with?

3. Do adults and juveniles differ in the strengths of their associations?

4. Do individuals form communities composed of meaningful subgroups?

If non-random association patterns are found this would suggest that individual *C. cerberus* aggregate for active benefits, possibly through cooperation (e.g., alloparenting, group defense, information transfer; Vonhof et al. 2004), rather than passive benefits (e.g. decreased predation risk, thermoregulation; Graves and Duvall 1995, Reiserer et al. 2008).

2. METHODS

(a) *Study system*

Arizona black rattlesnakes (*Crotalus cerberus*) are medium-sized pit vipers inhabiting mid to high elevations (900 – 3000 m) in Arizona and extreme western New Mexico (Campbell and Lamar 2004). I studied *C. cerberus* at a site with abundant isolated granite outcrops at the interface of Petran Montane Conifer Forest and Interior Chaparral (Brown 1994) at 1850 m in elevation. I located several basking sites used by *C. cerberus* after they emerge from their den in early April until mid-May (figure 2). These sites, with surface areas of 15 – 48 m^2, were adjacent to outcrops that presumably contained the den sites (figures 3 and 4). Five basking sites (MC; figure 3) were located within 20 m of each other on one side of a heavily used dirt road and multipurpose trail and two additional basking sites (ATR; figure 4) were located a few meters apart across the road and trail (ca. 350 m from MC),. Although the area between these two basking communities has additional rocky outcrops that appear capable of supporting *C. cerberus* aggregations, extensive searches (2009 – 2012) have failed to identify additional basking sites. Some pregnant females, their offspring, and the occasional male aggregate at the basking sites during the summer active season (Amarello et al. unpubl. data), but most aggregation behavior occurs during the spring, so I restricted analyses to this period.

(b) *Behavioral observations*

I set up 1 – 3 timelapse cameras at each basking site, depending on the size of the area used by the snakes (1 – 3 m^2), positioned to capture the majority of the

behavior at the site (based on my prior observations at these sites). At these sites, *C. cerberus* surface activity is diurnal, so I set cameras to take photographs every 30 s from ca. 0800 – 1800, depending on microclimate (e.g., west-facing sites started and ended later). During periods of inclement weather likely to inhibit snake activity, I increased photograph intervals to 60 s. I visited sites every 1 – 3 days to maintain cameras (e.g., download images, change batteries) and take high resolution photographs of aggregated rattlesnakes to assist with identification. Finally, I stitched timelapse photographs for each site into videos (Adobe After Effects CS4, Adobe Systems, Inc., San Jose, CA, USA) to facilitate data extraction; samples can be viewed online (http://vimeo.com/socialsnakes).

I primarily identified individual *C. cerberus* using natural variation in their dorsal patterns (Sheldon and Bradley 1989, Ramos-Fernández et al. 2009). When I captured rattlesnakes away from aggregation sites, I painted their rattles (Brown et al. 1984), which both assisted in identification and validated the pattern method. I assigned each snake to an age class (juvenile or adult) based on their size and the number of lifetime rattle segments. The only way to accurately sex rattlesnakes is by probing and because I did not capture all of the individuals, I was unable to assign sex to every individual in the study.

(c) *Definitions*

Dyad: A pair of individuals.

Associated: A dyad observed within a body length (≤1 m) of each other (Whitehead 2008, Ramos-Fernández et al. 2009).

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Association indices (AI): An estimate of the proportion of time each dyad spends together, permitting comparison of relationship strength among dyads within a population (Cairns and Schwager 1987, Whitehead 2008).

Gregariousness: An individual's propensity to associate with conspecifics (Whitehead 2008).

Selected associates: A dyad whose association index is more than twice the mean (excluding zero values) of randomized AI, (Gero et al. 2005, Whitehead 2008). This threshold value approximates twice the expected value if individuals were associating randomly (Whitehead 2008).

Limited associates: A dyad that was observed together at least once, but were not selected associates (*sensu* Gero et al. 2005).

Community: Group where most individuals associate with each other and rarely with individuals from other communities (Whitehead 2008).

Subgroup: A group within a community which contains individuals that tend to associate more within than among other subgroups (Croft et al. 2008).

Association strength: How well connected an individual is to other individuals in the social network; it incorporates both the number and strength of associations for each individual (Croft et al. 2008, Whitehead 2008).

Juvenile: Small individuals with ≤ 6 lifetime rattle segments (total number of

rattle segments acquired since birth), because that is the minimum at

reproduction in this population (unpubl. data).

(d) *Quantifying social associations*

I compiled observations for each site into daily sampling periods, which were

long enough to observe multiple associations but short enough to avoid

overestimating the frequency of associations between individuals that remained

at the basking site all day (Whitehead 2008, Ramos-Fernández et al. 2009).

Thus for individuals to be considered in association, I had to observe them

together at least once during a particular sampling period (day).

I calculated an association index (AI) in SOCPROG 2.4 (Whitehead 2009) to

estimate the amount of time each dyad spent together (Cairns and Schwager

1987, Whitehead 2008). The simplest AI divides the number of times a dyad was

observed together by the total number of times either individual was observed (0

= never associated; 1 = always associated). Because I was not always able to

identify every individual in a group, I used the half-weight AI, which is less biased

in these situations (Cairns and Schwager 1987, Whitehead 2008). The half-

weight AI is calculated for each dyad: $x / (x + y_{AB} + \frac{1}{2}(y_A + y_B))$, where x is the

number of sampling periods (in this case, days) that A and B were associated,

y_{AB} is the number of sampling periods where A and B were observed in different

groups, y_A is the number of sampling periods where only A was observed, and

y_B is the number of sampling periods where only B was observed.

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(e) *Analysis of gregariousness and association indices*

To examine individual differences in gregariousness I calculated the typical group size experienced by individuals (Jarman 1974): $(\Sigma Ng(i)^2) / (\Sigma Ng(i))$, where Ng is the size of each group (i). I included all unique groups in each sampling period (day). For example, if A associated with B and C, but B and C did not associate during that sampling period, then I included two groups for A (AB and AC). If all three associated together, I included one group (ABC). If gregariousness varies among individuals, then variation (sd: standard deviation) in typical group size will be greater for observed than random data. Alternatively, if all individuals prefer groups of similar sizes, then variation in typical group size will not differ between observed and random data (Whitehead 2008).

I examined association patterns by examining variation in AI. If subjects are selective about whom they associate with (i.e., there are individuals they avoid and/or individuals they select to associate with), then variation in AI (CV: coefficient of variation) will be greater for observed than random data (Whitehead 2008). If individuals are not selective about their associates, then variation in AI will not differ between observed and random data (Whitehead 2008). Other test statistics could be used here, but CV is the most intuitive, commonly used, and is usually highly correlated with other potential statistics (e.g., sd; Gero et al. 2005, Whitehead 2008, Ramos-Fernández et al. 2009, Kelley et al. 2011).

To test for nonrandom patterns of association (gregariousness and AI), I used a version of the permutation test developed by Bejder and colleagues (1998) and implemented in SOCPROG, which shuffles group membership within sampling

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periods (in this case, days) to generate a random distribution of data. This

procedure also identifies individuals with significantly larger ($p > 0.975$) or smaller

($p < 0.025$) typical group sizes and dyads that associated more ($p > 0.975$) or

less ($p < 0.025$) than if they were associating randomly (Whitehead 2008, Kelley

et al. 2011). Shuffling within versus among sampling periods accounts for

demographic effects including individuals entering and leaving sites throughout

the study (Gero et al. 2005, Whitehead 2008). I performed a sufficient number of

permutations to stabilize p-values within 0.01 (1000-30000; Whitehead 2008;

Kelley et al. 2011) with 1000 trials per permutation. For these permutation tests,

p-values indicate the proportion of permuted data that were less variable than the

observed data, thus at the 0.05 level, $p < 0.025$ and $p > 0.975$ are considered

significantly different than random expectation. I identified dyads that were

limited associates, selected associates, and never observed together (AI = 0).

(f) *Social network analysis*

I used AI to construct a weighted, undirected social network for each community

(MC and ATR; Croft et al. 2008, Whitehead 2008). In SOCPROG, I delineated

communities into subgroups using modularity: the difference between the

proportion of total associations observed within subgroups and the expected

proportion if they were associating randomly (Whitehead 2008). Modularity

varies between 0 (randomly assigned subgroups) and 1 (no associations

between members of different subgroups) and values ≥ 0.3 are considered

meaningful subdivisions (Croft et al. 2008, Whitehead 2008).

I calculated association strength, which incorporates both the number and strength of associations for each individual (Croft et al. 2008, Whitehead 2008). In a weighted social network, an individual's association strength is equal to the sum of their AI (Croft et al. 2008, Whitehead 2008). In UCINET (Borgatti et al. 2002), I tested whether association strength varied between adults and juveniles using a modified t-test that creates a permutation-based sampling distribution of the difference between the means (10,000 trials).

I drew social networks with NetDraw 2.121 (Borgatti 2002) and created all other graphics in the R statistical package (R Foundation for Statistical Computing 2011) with ggplot2 (Wickham 2009).

3. RESULTS

I recorded behavior within rattlesnake aggregations at 4 basking sites at MC and

2 basking sites at ATR 17 April – 13 May 2011 and 8 April – 22 May 2012. I was

unable to position cameras at one site at MC to identify individuals, but the

majority of those individuals also used the other basking sites at MC (unpubl.

data). Adults used more basking sites (mean ± sd = 1.7 ± 0.6) than juveniles (1.3

± 0.5). Of 578 rattlesnake observations, I was unable to identify an individual on

26 occasions at MC (5.8% of 451 observations) and 17 occasions at ATR (13.3%

of 127 observations). I excluded these unidentified snakes from all analyses. I

identified 64 individuals at MC (N = 33 adults and 31 juveniles) and 14 individuals

at ATR (N = 9 adults and 5 juveniles).

(a) *Gregariousness*

Gregariousness varied among individual rattlesnakes; some individuals tended to

select small groups, while others tended to select large groups (figure 5). At MC,

observed variation (sd) in typical group size was greater than random data (N =

64, observed sd = 1.07, random sd = 0.90, p = 0.993; figure 6). Four individuals

(2 adults, 2 juveniles) selected significantly small groups ($p < 0.025$) and three

individuals (2 adults, 1 juvenile) selected significantly large groups ($p > 0.975$).

Variation in typical group size was similar for observed and random data at ATR

(N = 14, observed sd = 0.74, random sd = 0.56, p = 0.816; figure 6).

(b) *Association patterns*

Some individuals were selective about whom they associated with. Observed variation in AI was significantly greater than random data at MC (N = 2016 possible dyads, observed CV = 3.80, random CV = 3.34, p = 0.99997; figure 7). Only juvenile-juvenile dyads were not selective about their associates (juvenile-juvenile N = 465, observed CV = 4.96, random CV = 4.98, p = 0.529; adult-adult N = 528, observed CV = 2.85, random CV = 2.41, p = 0.999; adult-juvenile N = 1023, observed CV = 4.18, random CV = 3.89, p = 0.996; figure 7). Adults were more likely to form selected associations with each other (1.7% of possible adult-adult dyads) and with juveniles (1.2% of possible adult-juvenile dyads) than juveniles were with each other (0.4% of possible juvenile-juvenile dyads; table 1). All significant dyads (6 adult-adult and 6 adult-juvenile) were cases of individuals selecting to associate with each other rather than avoidance (p > 0.975).

At ATR, observed variation in AI was significantly greater than random data among adult-adult dyads (N = 36, observed CV = 2.10, random CV = 1.68, p = 0.994; figure 7), but not adult-juvenile dyads (N = 45, observed CV = 2.06, random CV = 2.03, p = 0.757), juvenile-juvenile dyads (N = 10, observed CV = 3.08, random CV = 3.08, p = 0.488), or overall (N = 91, observed CV = 2.14, random CV = 2.04, p = 0.82). The only selected association at ATR was between two adults (table 1).

(c) *Social network analysis*

I constructed two social networks: one for MC (figure 8) and one for ATR (figure 9). At MC, I identified five subgroups (Q = 0.539, table 2, figure 8), excluding six

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individuals that were never observed with other snakes (2 adults and 4 juveniles).

I identified three subgroups at ATR (Q = 0.528, table 2, figure 9), excluding one

solitary juvenile. Subgroups ranged in size from 4 to 23 individuals (mean ± sd =

10.1 ± 7.8) and all contained adults and juveniles (mean proportion of adults =

0.59 ± 0.14, mean proportion of juveniles = 0.41 ± 0.14; table 2). Within each

subgroup, members were observed at 2.4 ± 0.7 basking sites (range = 2–4; table

2).

Adults had greater association strengths than juveniles at MC (adult: mean ± sd

= 1.52 ± 1.05, range = 0–3.55; juvenile: 0.95 ± 0.78, range = 0–3.22; two-tailed p

= 0.0173; figure 10). There was no difference between adult and juvenile

association strengths at ATR (adult: 0.62 ± 0.39, range = 0.12–1.23; juvenile:

0.50 ± 0.30, range = 0–0.83; two-tailed p = 0.5833; figure 10).

4. DISCUSSION

Arizona black rattlesnakes vary in their tendency to form associations and in their selectiveness of whom they associate with. While most individuals showed no significant preferences in group size, some individuals preferred to be alone or in small groups while others preferred to be in large groups. Overall, adult rattlesnakes exhibited non-random association patterns, although few individual dyads had significantly high or low association indices. Adults had greater association strengths and were more likely to have limited and selected associates. I identified eight subgroups within the two communities, all of which contained adults and juveniles and used multiple basking sites.

The social structure of this population of *C. cerberus* is characterized by a few strong associations, mostly among adults, and many null associations. Juveniles formed some limited and selected associations with adults, but very few with each other. One possible explanation for this result is that very few juveniles were observed in both years ($N = 6$, 16.7%). Some juveniles observed in 2012 were born after the 2011 field season and mortality is likely higher in juveniles than adults (Brown et al. 2007). While there is some evidence that neonate rattlesnakes follow their mother to her den (Cobb et al. 2005, Amarello et al. unpubl. data) and continue to use that site throughout their life (Brown et al. 2007), it may take years for juveniles to establish their home range, den site, and social group. Alternatively, if site fidelity for juveniles is higher than my data

suggest, selected associations may take years to develop and are thus only apparent in adults (but see Gero et al. 2005).

I did not detect significant differences in gregariousness or association patterns within the smaller community, ATR, which may be due to a limited number of observations or differences in behavior between the two communities. A poorly placed camera during the first couple weeks of my study may have resulted in missing many associations at the main basking site. Between my 2011 and 2012 sampling periods, several large trees sheltering the basking sites were removed, likely resulting in greater insolation and higher temperatures. This drastic change could have reduced the quality of the basking sites and thus the number of associations observed. In a highly differentiated society, approximately eight observed associations per individual are required to detect non-random association patterns (Whitehead 2008). On average, I only observed four associations per individual at ATR, compared to nine at MC. Alternatively, snakes at ATR may behave differently than snakes at MC and associate randomly.

My study is the first to show selected associations among individual snakes, but to my knowledge it is also the first to use association indices and social network analysis to examine association patterns among snakes. Thus, I cannot say this is a novel social structure. The closely related timber rattlesnake (*Crotalus horridus*) exhibits other complex social behavior, including preferentially associating with kin (Clark 2004, Clark et al. 2012) and using public information to locate den and foraging sites (Brown and MacLean 1983, Clark 2007).

Because many other snakes aggregate (e.g., Gillingham 1987, Graves and Duvall 1995), I anticipate the 'discovery' of similar social structures when these methods are applied to other species.

Even though my communities were located close to each other (ca. 350 m), I detected selected associations within, but not between them. This pattern of strong associations within communities in close proximity to each other suggests that active rather than passive benefits explain group formation in *C. cerberus* (Vonhof et al. 2004). Indeed, I have already observed several potential benefits of grouping in this population from June through September when some females gestate communally and alloparent (Amarello et al. unpubl. data). Whether rattlesnakes with stronger associations in the spring are more likely to exhibit cooperative behaviors (Vonhof et al. 2004) later in the year requires further investigation.

One potential limitation of my study is the assumption that my measure of association (proximity to conspecifics) accurately reflects a social interaction (Ramos-Fernández et al. 2009). Aside from reproductive behaviors (e.g., courtship, combat), at present I lack specific information on what a social interaction looks like in snakes, who primarily use chemical communication. However, proximity as a proxy for social interaction is often used in species whose social interactions would be difficult to describe (e.g., bats [Vonhof et al. 2004], guppies [Croft et al. 2004, Kelley et al. 2011], primates [Ramos-Fernández et al. 2009], cetaceans [Gero et al. 2005, Lusseau et al. 2006], lizards [Leu et al.

2010]). In the future, researchers should incorporate multiple behaviors in characterizing association patterns in snakes.

Finally, my findings have the potential to impact conservation of an entire group of misunderstood and often maligned organisms. Humans have an innate fascination with snakes (Burghardt et al. 2009), but unfortunately, this keen emotional response is often appropriated by fear. Although a relatively small proportion of snake species pose a significant health threat, fear of snakes is usually instilled at a young age by parents and/or peers and reinforced by pernicious myths and popular media that portray snakes as malicious villains (Murray and Foote 1979). This fear has led to widespread persecution and obstruction to snake conservation efforts (Seigel and Mullin 2009). In contrast to how snakes are usually seen in the media, recent research on rattlesnakes reveals the social nature of snakes. Some care for their young (Greene et al. 2002, Amarello et al. unpubl. data), exhibit cooperative behaviors (Amarello et al. unpubl. data), and aggregate with their relatives (Clark et al. 2012). These behaviors appeal to the general public and are starting to change their perception of snakes from "cold-blooded killers" to fascinating animals that can have social and even familial attributes. Such a change in the public attitude will have a positive impact on snake conservation efforts.

Table 1. Limited and selected associates by age and site as a percentage of possible dyads. *N* = number of possible dyads; na = never observed associated; la = limited associates (observed associated at least once, but not selected associates); sa = selected associates (association index at least twice the mean of non-zero indices); *p* = the proportion of permuted data that were less variable than the observed data; A-A = adult only dyads; A-J = dyads of adults and juveniles; J-J = juvenile only dyads.

	N	na	la	sa	*p*
ATR					
A-A	36	69.4%	27.8%	2.8%	0.994
A-J	45	77.8%	22.2%	0.0%	0.757
J-J	10	90.0%	10.0%	0.0%	0.488
all	91	75.8%	23.1%	1.1%	0.820
MC					
A-A	528	85.0%	13.3%	1.7%	0.999
A-J	1023	92.7%	6.2%	1.2%	0.996
J-J	465	95.3%	4.3%	0.4%	0.529
all	2016	91.3%	7.6%	1.1%	>0.999

Table 2. Size, composition, and number of basking sites used by *Crotalus cerberus* communities and subgroups. One individual at ATR (juvenile) and six at MC (2 adults and 4 juveniles) were never observed with other snakes and thus were not assigned to a subgroup. A = adults; J = juveniles; # sites used = the number of sites where by members of that subgroup were observed.

Group	N	A (N)	J (N)	A (%)	J (%)	# sites used
ATR						2
a	4	3	1	75.0	25.0	2
b	4	2	2	50.0	50.0	2
c	5	4	1	80.0	20.0	2
MC						4
d	15	7	8	46.7	53.3	4
e	16	8	8	50.0	50.0	2
f	23	14	9	60.9	39.1	3
g	2	2	0	100.0	0.0	2
h	2	0	2	0.0	100.0	2
overall	71	40	31	56.3	43.7	-
mean	8.9	5.0	3.9	57.8	42.2	2.4
sd	8.0	4.5	3.8	29.7	29.7	0.7

Figure 1. *In situ* group of Arizona black rattlesnakes (*Crotalus cerberus*; at least 3 adults and 4 juveniles) at an aggregation site near Prescott, AZ.

Figure 2. Three basking sites used by aggregations of *Crotalus cerberus*.
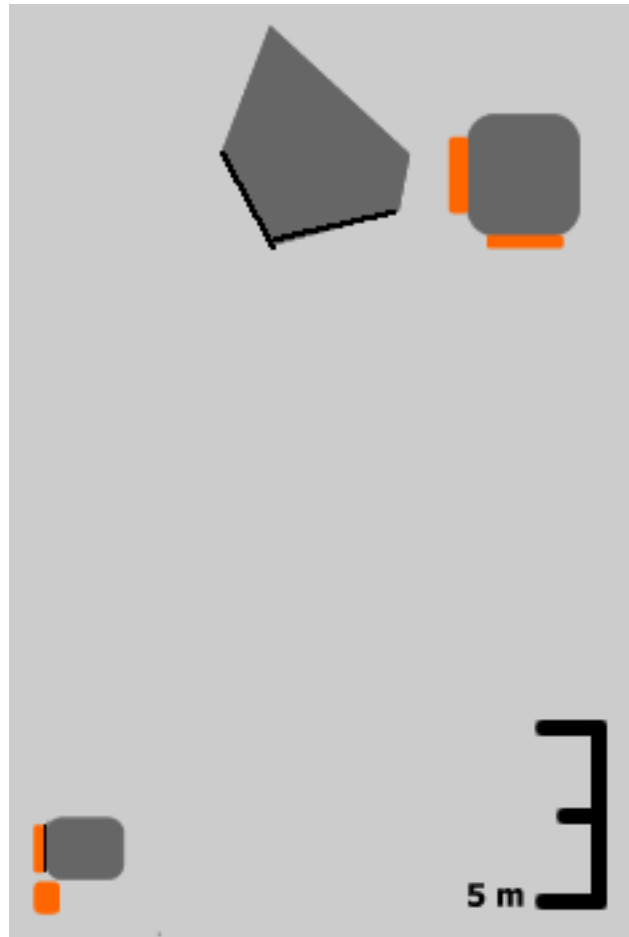
Figure 3. MC: dark gray polygons represent rock outcrops; orange polygons represent basking areas; black lines represent likely den entrances.
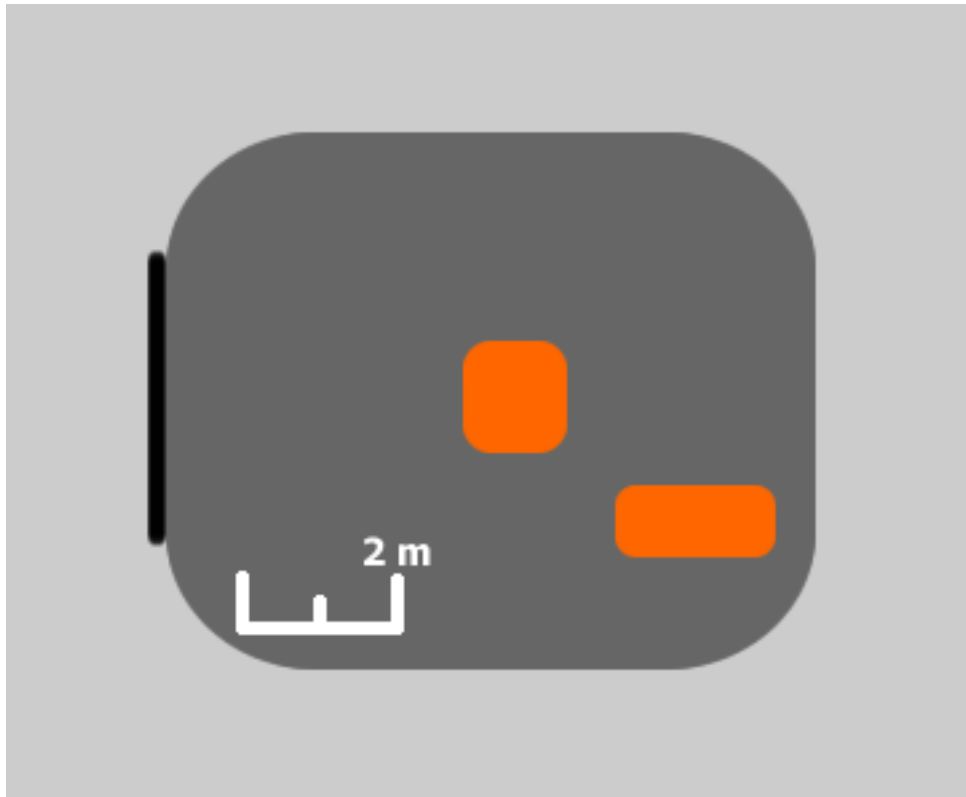
Figure 4. ATR: dark gray polygon represents rock outcrop; orange polygons represent basking areas; black line represents likely den entrance.
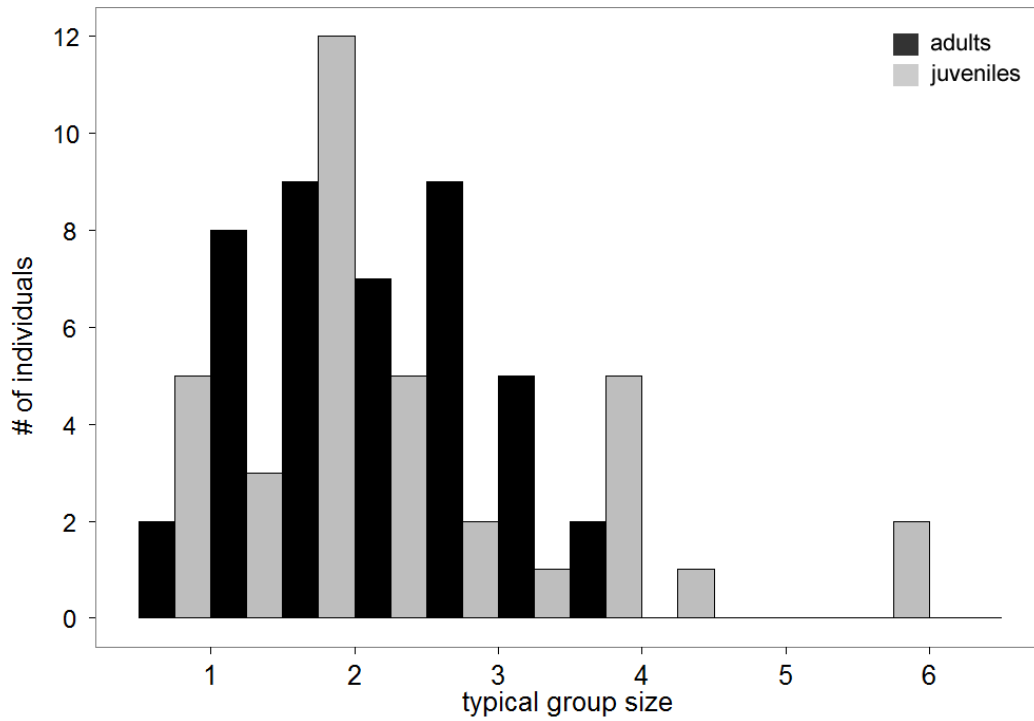
Figure 5. Distribution of gregariousness (typical group size experienced by individuals) for adult and juvenile rattlesnakes from both communities.
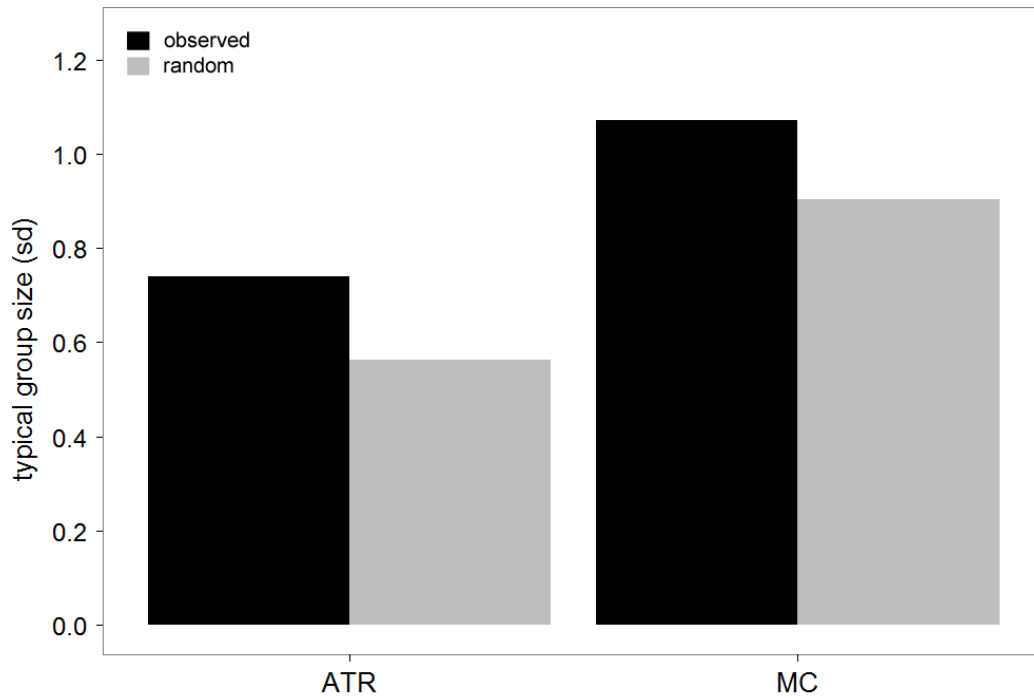
Figure 6. Gregariousness varied among individual rattlesnakes. At MC observed variation (sd) in typical group size was greater than random data (observed sd = 1.07, random sd = 0.90, p = 0.993). Variation in typical group size was similar for observed and random data at ATR (observed sd = 0.74, random sd = 0.56, p = 0.816).
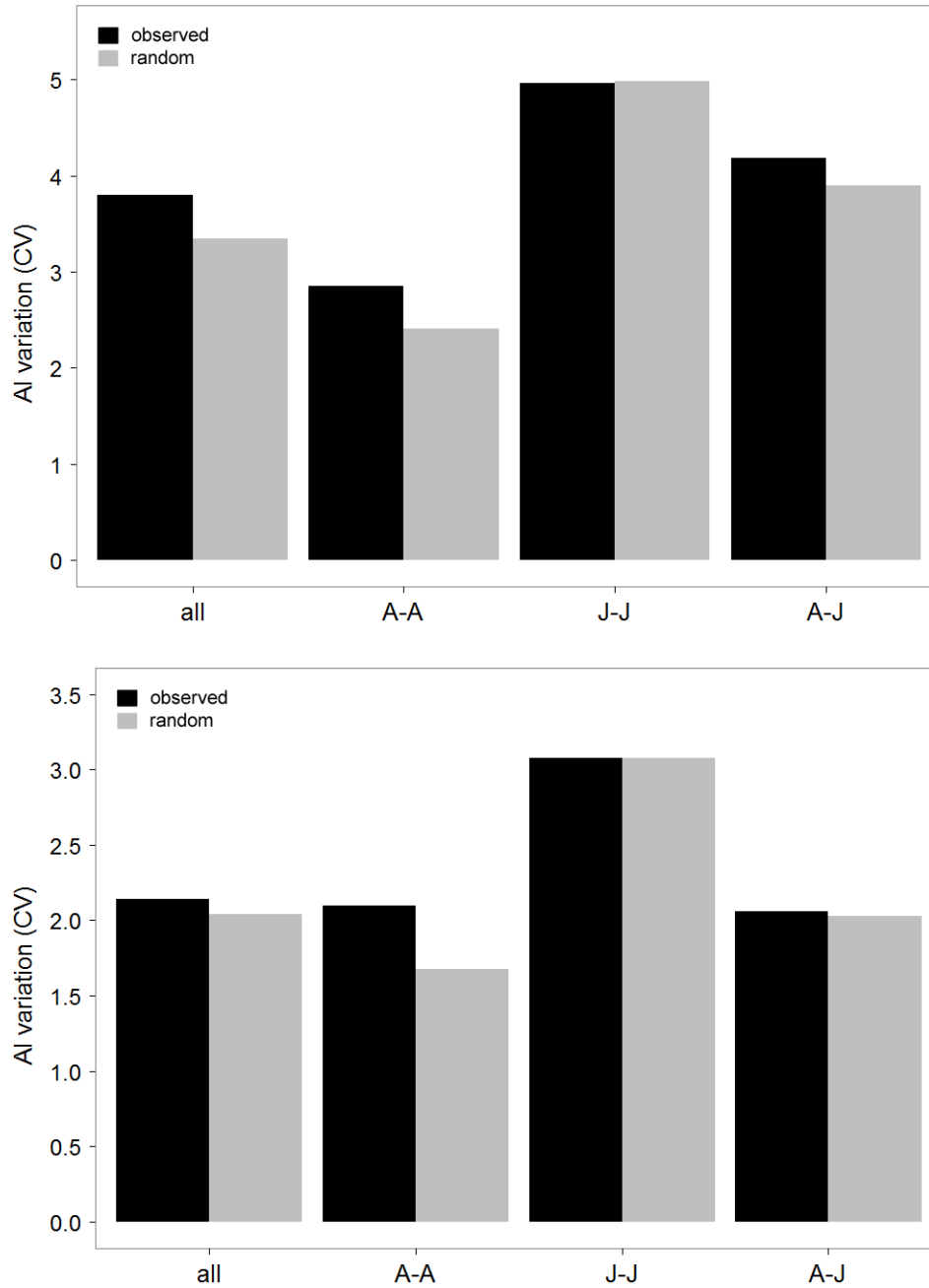
Figure 7. At MC (top panel), association indices (AI) were more variable in observed than random data among all snakes (observed CV = 3.80, random CV = 3.34, p = 0.99997), adult dyads (observed CV = 2.85, random CV = 2.41, p = 0.999), and adult-juvenile dyads (observed CV = 4.18, random CV = 3.89, p = 0.996). At ATR (bottom panel) association indices (AI) were more variable in observed than random data among adult dyads (observed CV = 2.10, random CV = 1.68, p = 0.994). Variation in AI is represented by coefficient of variation (CV); p-values indicate the proportion of permuted data that were less variable than the observed data.
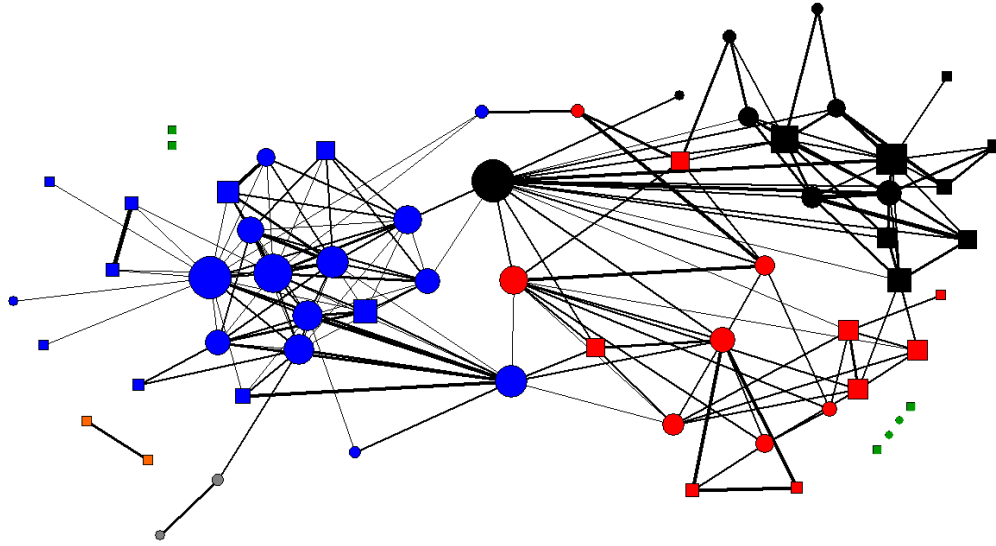
Figure 8. Visualization of the rattlesnake social network at MC using spring-embedding layout. Associations are represented by lines between nodes (individuals), weighted so that stronger associations are heavier lines. Node color indicates to which subgroup that individual belongs (6 groups; *Q* = 0.539) and node shape and size depicts individual attributes: shape indicates age (circles = adults; squares = juveniles) and size indicates association strength.
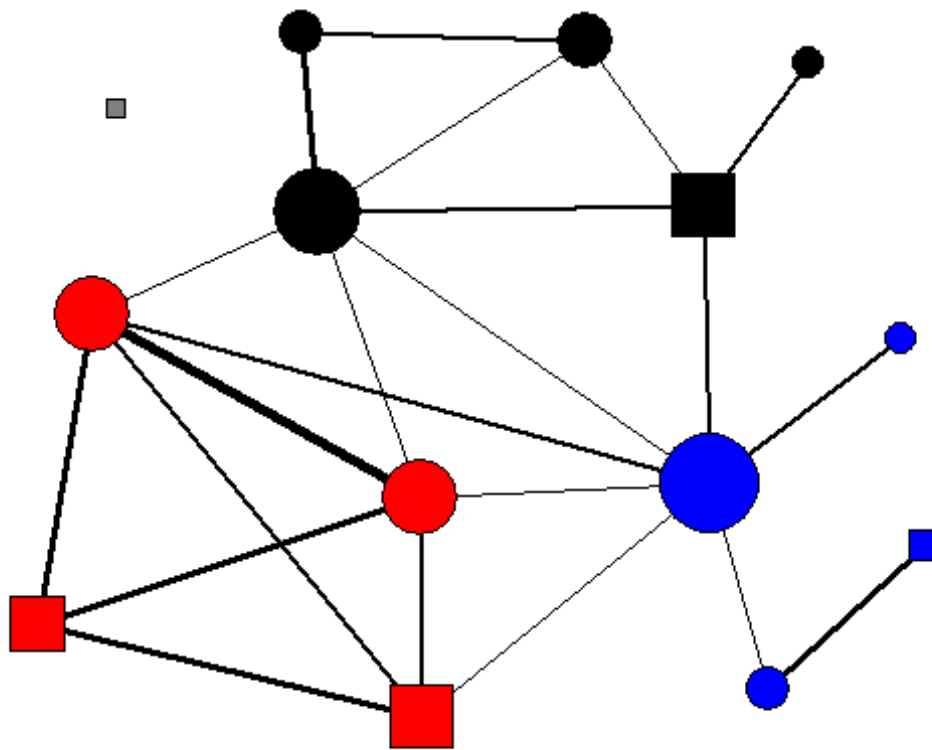
Figure 9. Visualization of the rattlesnake social network at ATR using spring-embedding layout; associations are represented by lines between nodes (individuals), weighted so that stronger associations are heavier lines. Node color indicates which subgroup that individual belongs (4 groups; Q = 0.528) and node shape and size depicts individual attributes: shape indicates age (circles = adults; squares = juveniles) and size indicates association strength.
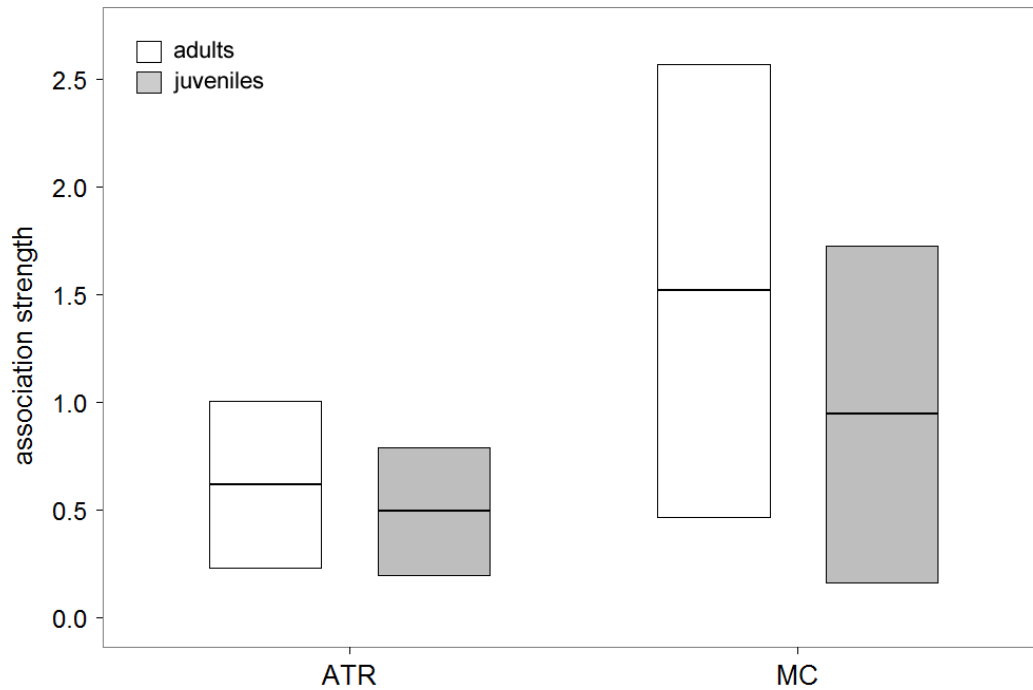
Figure 10. Adult rattlesnakes had higher association strengths than juveniles at MC (MC; adult: mean ± sd = 1.52 ± 1.05, range = 0–3.55; juvenile: mean ± sd = 0.95 ± 0.78, range = 0–3.22; two-tailed p = 0.0173), but there was no difference in association strengths between adults and juveniles at ATR (adult: mean ± sd = 0.62 ± 0.39, range = 0.12–1.23; juvenile: mean ± sd = 0.50 ± 0.30, range = 0–0.83; two-tailed p = 0.5833). Boxes = upper and lower standard deviation; midline = mean clustering coefficient.

REFERENCES

Bejder L, Fletcher D, Bräger S. 1998. A method for testing association patterns of social animals. Animal Behaviour 56:719–725.

Borgatti SP, Everett MG, Freeman LC. 2002. Ucinet for Windows: Software for Social Network Analysis. Available from: https://sites.google.com/site/ucinetsoftware/home

Borgatti SP. 2002. NetDraw: Graph Visualization Software. Available from: https://sites.google.com/site/netdrawsoftware

Brown DE. 1994. Biotic communities of the southwestern United States and northwestern Mexico. Salt Lake City, Utah: University of Utah Press.

Brown WS, Gannon VPJ, Secoy DM. 1984. Paint-marking the rattle of rattlesnakes. Herpetological Review 15:75–76.

Brown WS, Kery M, Hines JE. 2007. Survival of timber rattlesnakes (*Crotalus horridus*) estimated by capture-recapture models in relation to age, sex, color morph, time, and birthplace. Copeia 2007:656–671.

Brown WS, MacLean FM. 1983. Conspecific scent-trailing by newborn timber rattlesnakes, *Crotalus horridus*. Herpetologica 39:430–436.

Burghardt G, Murphy J, Chiszar D, Hutchins M. 2009. Combating ophiophobia: origins, treatment, education and conservation tools. In: Mullin SJ, Seigel RA, editors. Snakes: ecology and conservation. Ithaca, NY, USA: Cornell University Press. p. 262–280.

Cairns SJ, Schwager SJ. 1987. A comparison of association indices. Animal Behaviour 35:1454–1469.

Campbell JA, Lamar WW. 2004. The Venomous Reptiles of the Western Hemisphere. Ithaca, NY: Cornell University Press.

Chapple DG. 2003. Ecology, life-history, and behavior in the Australian Scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. Herpetological Monographs 17:145–180.

Clark RW, Brown WS, Stechert R, Greene HW. 2012. Cryptic sociality in rattlesnakes (*Crotalus horridus*) detected by kinship analysis. Biology Letters 8: 523–525.

Clark RW. 2004. Kin recognition in rattlesnakes. Proceedings of the Royal Society of London Series B: Biological Sciences 271:S243–S245.

Clark RW. 2006. Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus.* Copeia 2006:181–187.

Clark RW. 2007. Public information for solitary foragers: timber rattlesnakes use conspecific chemical cues to select ambush sites. Behavioral Ecology 18:487–490.

Clutton-Brock TH. 2012. Long-term, individual-based field studies. In: Kappeler PM, Watts DP, editors. Long- Term Field Studies of Primates. Springer Berlin / Heidelberg. p. 437–449.

Cobb VA, Green JJ, Worrall T, Pruett J, Glorioso B. 2005. Initial den location behavior in a litter of neonate *Crotalus horridus* (Timber Rattlesnakes). Southeastern Naturalist 4:723–730.

Couzin ID. 2006. Behavioral ecology: social organization in fission–fusion societies. Current Biology 16:R169–R171.

Croft DP, James R, Krause J. 2008. Exploring Animal Social Networks. Princeton, NJ, USA: Princeton University Press.

Croft DP, Krause J, James R. 2004. Social networks in the guppy (*Poecilia reticulata*). Proceedings of the Royal Society of London Series B (Suppl.) 271:S516–S519.

Davis AR, Corl A, Surget-Groba Y, Sinervo B. 2011. Convergent evolution of kin-based sociality in a lizard. Proceedings of the Royal Society of London Series B 278:1507–1514.

Dorcas ME, Willson JD. 2009. Innovative methods for studies of snake ecology and conservation. In: Snakes: Ecology and Conservation. In: Mullin SJ, Seigel RA, editors. Snakes: ecology and conservation. Ithaca, NY, USA: Cornell University Press. p. 5–37.

Fitch HS. 1987. Collecting and life-history techniques. In: Seigel RA, Collins JT, Novak SS, editors. Snakes: ecology and evolutionary biology. New York, NY, USA: Macmillan Publishing Co. p. 143–164.

Gero S, Bejder L, Whitehead H, Mann J, Connor RC. 2005. Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp. Canadian Journal of Zoology 83:1566–1573.

Gillingham JC. 1987. Social Behavior. In: Seigel RA, Collins JT, Novak SS, editors. Snakes: ecology and evolutionary biology. New York, NY, USA: Macmillan Publishing Co. p. 184–209.

Graves BM, Duvall D. 1995. Aggregation of squamate reptiles associated with gestation, oviposition, and parturition. Herpetological Monographs 9:102–119.

Greene HW, May P, Hardy Sr. DL, Sciturro JM, Farrell T. 2002. Parental behavior by vipers. In: Schuett GW, Höggren M, Douglas ME, Greene Harry W., editors. Biology of the vipers. Eagle Mountain, Utah. USA: Eagle Mountain Publishing. p. 179–205.

Hinde RA. 1976. Interactions, relationships and social structure. Man 11:1-17.

Holekamp KE, Smith JE, Strelioff CC, van Horn RC, Watts HE. 2012. Society, demography and genetic structure in the spotted hyena. Molecular Ecology 21:613–632.

Jarman PJ. 1974. The social organisation of antelope in relation to their ecology. Behaviour 48:215–267.

Kelley JL, Morrell LJ, Inskip C, Krause J, Croft DP. 2011. Predation risk shapes social networks in fission-fusion populations. PLoS ONE 6:e24280.

Kerth G, van Schaik J. 2012. Causes and consequences of living in closed societies: lessons from a long-term socio-genetic study on Bechstein's bats. Molecular Ecology 21:633–646.

Leu ST, Bashford J, Kappeler PM, Bull CM. 2010. Association networks reveal social organization in the sleepy lizard. Animal Behaviour 79:217–225.

Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM. 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. Journal of Animal Ecology 75:14–24.

McAlpin S, Duckett P, Stow A. 2011. Lizards cooperatively tunnel to construct a long-term home for family members. PLoS ONE 6:e19041.

Murray EJ, Foote F. 1979. The origins of fear of snakes. Behaviour Research and Therapy 17:489–493.

Oh KP, Badyaev AV. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. The American Naturalist 176:E80–9.

R Foundation for Statistical Computing. 2011. R: A language and environment for statistical computing. Available from: http://www.r-project.org

Ramos-Fernández G, Boyer D, Aureli F, Vick L. 2009. Association networks in spider monkeys (*Ateles geoffroyi*). Behavioral Ecology and Sociobiology 63:999–1013.

Reiserer RS, Schuett GW, Earley RL. 2008. Dynamic aggregations of newborn sibling rattlesnakes exhibit stable thermoregulatory properties. Journal of Zoology 274:277–283.

Schuett GW, Repp RA, Hoss SK. 2011. Frequency of reproduction in western diamond-backed rattlesnakes (*Crotalus atrox*) from the Sonoran Desert in south-central Arizona is variable within individuals: potential role of rainfall and prey densities. Journal of Zoology 284:105–113.

Seigel RA, Mullin SJ. 2009. Snake conservation, present and future. In: Mullin SJ, Seigel RA, editors. Snakes: ecology and conservation. Ithaca, NY, USA: Cornell University Press. p. 281–290.

Sheldon S, Bradley C. 1989. Identification of individual adders (*Vipera berus*) by their head markings. Herpetological Journal 1:392–396.

Vonhof MJ, Whitehead H, Fenton MB. 2004. Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. Animal Behaviour 68:507–521.

Whitehead H. 2008. Analyzing Animal Societies. Chicago: University of Chicago.

Whitehead H. 2009. SOCPROG programs: analysing animal social structures. Behavioral Ecology and Sociobiology 63:765–778.

Wickham H. 2009. ggplot2: elegant graphics for data analysis. Available from: http://had.co.nz/ggplot2/book

Wilson EO. 1975. Sociobiology: the new synthesis. Cambridge, MA, USA: Harvard University Press.