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Fission-Fusion Dynamics in the Social Networks of a North American Pitviper

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away from dens—with different and fewer partners. Additionally, modules formed by individuals in the pairing network were frequently different from those in the parentage network, likely due to multiple mating, long-term sperm storage by females, and resultant multiple paternity. Further evidence for fission-fusion dynamics exhibited by this population—interactions were rare when snakes were dispersing to and traversing their spring-summer home ranges (to which individuals show high fidelity), despite ample opportunities to associate with numerous conspecifics that had highly overlapping ranges. Taken together, we show that long-term datasets incorporating SNA with spatial and genetic information provide robust and unique insights to understanding the social structure of cryptic taxa that are understudied.

Fission-Fusion Dynamics in the Social Networks of a North American Pitviper

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Abstract

Many animal species exist in fission-fusion societies, where the size and composition of

network structure and fission-fusion dynamics [28, 29, 35]. We asked three main questions: First, do group-level patterns emerge from distinct social interactions? Second, do individuals' traits influence their connectivity within social networks? Lastly, does genetic relatedness undergird social interactions in this system? We investigated three bipartite interactions (denning, sexual pairing, and parentage) and the drivers of individuals' centrality (Appendix). Specifically, we tested (a) whether these three bipartite networks presented non-random modular or nested structure (Appendix); (b) which attributes (body length, sex, and home range size) are associated with individuals' centrality in these three networks, and (c) whether interactions occurrence and or frequencies in the three social networks and home range overlap are significantly correlated with genetic relatedness among individuals (e.g., kin-based).

2 Materials and methods

2.1. Study system

A single population of western diamondback rattlesnakes in the Suizo Mountains (Pinal County, Arizona, USA) was studied for 15 consecutive years from 1 March 2001 to 31 December 2015 [28, 29, 33, 36]. The research site is 40 km SSE of the city of Florence, 8 km W of State Route 79. This region is designated as Sonoran Desert, Arizona Upland Desert-Scrub subdivision [33]. Data accumulated for this *C. atrox* population has contributed substantially to our understanding of the species' behavior, reproductive ecology, and life history in Arizona [28, 29, 37]. Key events of the annual cycle are summarized in Figure 1, but the typical phenology of this population is described for further clarity. Egress from communal dens is centered in late March to early April [28, 29, 33, 37]. In most cases egress lingers—from days to several weeks—and occurs in several phases, including basking at the den entrance (often in groups), making short-range movements, and returning to the den. The spring mating period (second mating season) occurs before migration movements to their spring home range areas. Courtship and coitus may occur at the den itself or in the general area. Male combat for priority-of-access to females also may occur but is rarely observed [28, 29]. Migration movements in March and April bring individuals to their spring and summer home ranges. Furthest straight-line distances traveled from communal dens to home ranges are from several dozen meters to over 2 km [28, 29, 33]; mating (first mating season), skin shedding, and hunting prey are the primary behavioral activities during this time [28, 29, 33], and except for the two distinct mating seasons, there is generally little contact observed among adults, especially males. In fall (late October through November) adult individuals initiate migration to return to their respective communal dens to re-establish long-term social groups (networks) lasting for up to five months (November through March). The most common social activity at the communal dens which can be observed in all winter months is termed "sun basking" and occurs at the entrance or alongside the den itself [28, 29, 37]. Females will sometimes alternate year-to-year from communal dens to overwintering singly in shelters such as rodent middens and small mammal burrows [28, 29]. Males show near absolute fidelity to communal dens but rarely overwinter privately in granitic rubble.

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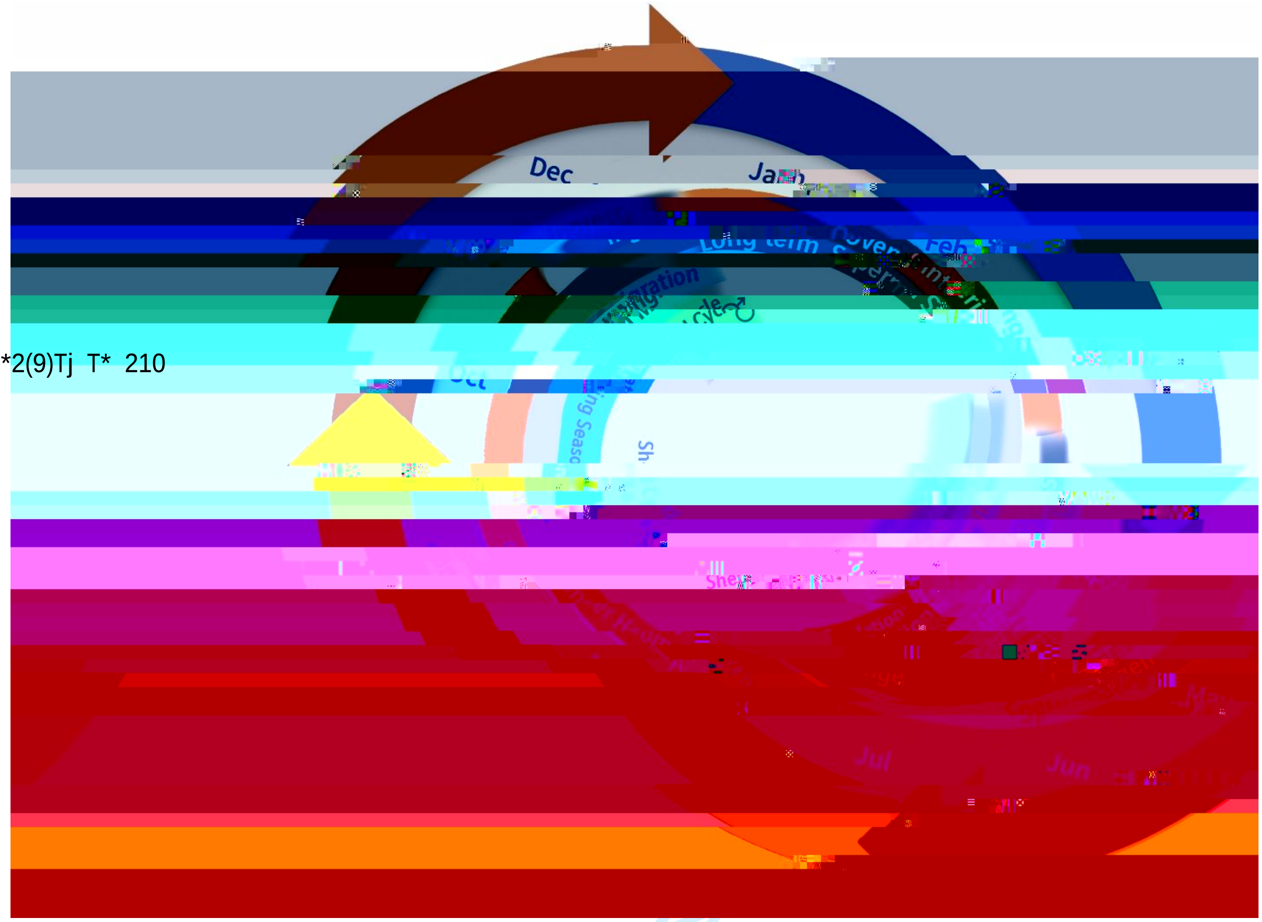

Figure 1. Annual cycle and phenology of behavioral, physiological, reproductive, and life history events for adult *Crotalus atrox* at Suizo Mountains (Pinal County, Arizona), and nearby areas, based on 15 consecutive years (2001–2015) of research [28, 29, 36–40]. Note: Shed Cycle refers to skin shedding (ecdysis).

2.2 Collecting and processing subjects

Animals selected for this study were either collected at or near known communal dens during egress in spring (March–April) or found in their spring-summer home range. Animals were captured and processed as detailed in previous studies [28, 29, 36–39]. At capture, Global Positioning System (GPS) coordinates were obtained, and subjects were measured (snout-vent length, tail length, head dimensions to the nearest millimeter; body mass to the nearest 1.0 g) and sex confirmed (via probing) while under light anesthesia (isoflurane). Individuals were photographed, implanted with a unique passive integrated transponder (PIT) tag (AVID, Inc., Norco, California, U.S.A.), and their proximal rattle segments were colored via marker. A focal group of adult *C. atrox* collected from 2001–2010 were used in social network analyses (n = 50 focal animals: 22 males 28 females). Subjects were selected for radio-tracking based on size (700 mm SVL) and good state-of-health. Each animal had an appropriately sized (5% body mass) temperature-sensitive radio-transmitter (models SI-2T and AI-2T, 11-16 g; Holohil Inc., Carp, Ontario, Canada) surgically implanted within the coelom following general procedures used for snakes [46]. After processing, all subjects were released at their exact capture site.

2.3 Radio-tracking

Focal animals were radio-tracked minimally 2–4 times per month during winter. Tracking was increased substantially—sometimes daily or twice daily—from early August through mid-September, the period of birthing. During spring and fall, snakes were tracked weekly on average. For each animal location, UTM coordinates were recorded using along with behavioral data (particularly if associating with conspecifics), body and environment temperatures, feeding and ecdysis status, plant associations, subject location (above or below the ground surface), visible or not visible, and health status [28, 29, 36–39].

2.4 Spatial analyses

We estimated home range sizes by creating 100% minimum convex polygons (MCPs) around the outermost radiotelemetry locations for each snake in ArcGIS Pro 2.6.1. To produce a single value for the degree of overlap for each possible pair combination of telemetered snakes, we calculated the average overlap for the two individuals in each pair as (AB/A + AB/B)/2, where A is the home range size of individual A, B is the home range size of individual B, and AB is the area shared by both A and B. Using this method, we generated a pairwise matrix of average home range overlap values [33].

2.5 Genotype Data

All social network analyses performed in this study that incorporated DNA-based information was accomplished using previously published data [28, 29, 33]. See these studies for all procedures used in DNA sampling, extraction, genotyping, and parentage and relatedness analysis.

2.7 Social network analysis

We built an interaction matrix for each social interaction considered (denning, pairing, and parentage; Appendix). The denning network was a matrix of all male and female study subjects as rows and columns containing 1s and 0s indicating whether a given pair of all possible pair combinations of snakes from either sex were observed sharing the same den (Fig. 2a) or not, respectively. The pairing network was a matrix with females represented in columns and males represented in rows, containing a series of 1s and 0s indicating whether each possible male-female pair combination was observed engaging in any behavior associated with mating or not, respectively; examples of pairing behavior included male-female pairs in copulation (Fig. 2b) or whose bodies were in contact (e.g., males lying on females) or proximity during either mating season. The parentage network was a matrix with females represented in columns and males represented in rows, containing a series of 1s and 0s indicating whether each possible male-female pair combination produced offspring or not, respectively; relatedness among individuals was determined from tissues such as blood or shed skins from adults and neonates (Fig. 2c and 2d).


A)
B)

To investigate whether individual-specific variables were associated with individual's centrality in a network, we used generalized linear mixed models (GLMMs) where CC was the response variable and sex, snout-vent length (SVL), body mass, and MCP were predictors. Since we detected high correlation between SVL and body mass (Pearson's r = 0.87), we excluded body mass from our models, given lower variation in SVL measurements among individuals [22, 27]. For snakes tracked more than one year, we used mean MCP size as a predictor of CC; adults in this population have highly repeatable annual MCP sizes (R = 0.83, 95% CI: 0.69–0.90; unpublished data). For each of the three separate networks, CC was calculated independently, and used as the response variable in the models. In all models, we included the number of years an individual was detected as a random factor to control for sampling variation among individuals. Our analyses followed the general recommendations by Zuur and colleagues [48]. All predictor variables were scaled by mean centering and dividing by the standard deviation reproductive behaviors (Fig. 3c). Males largely overwintered in communal dens but would sometimes overwinter in isolation, including at sites far from communal shelters (Fig. 3b). Females often gave birth far from communal shelters and overwintered privately much more than males (Fig. 3d).

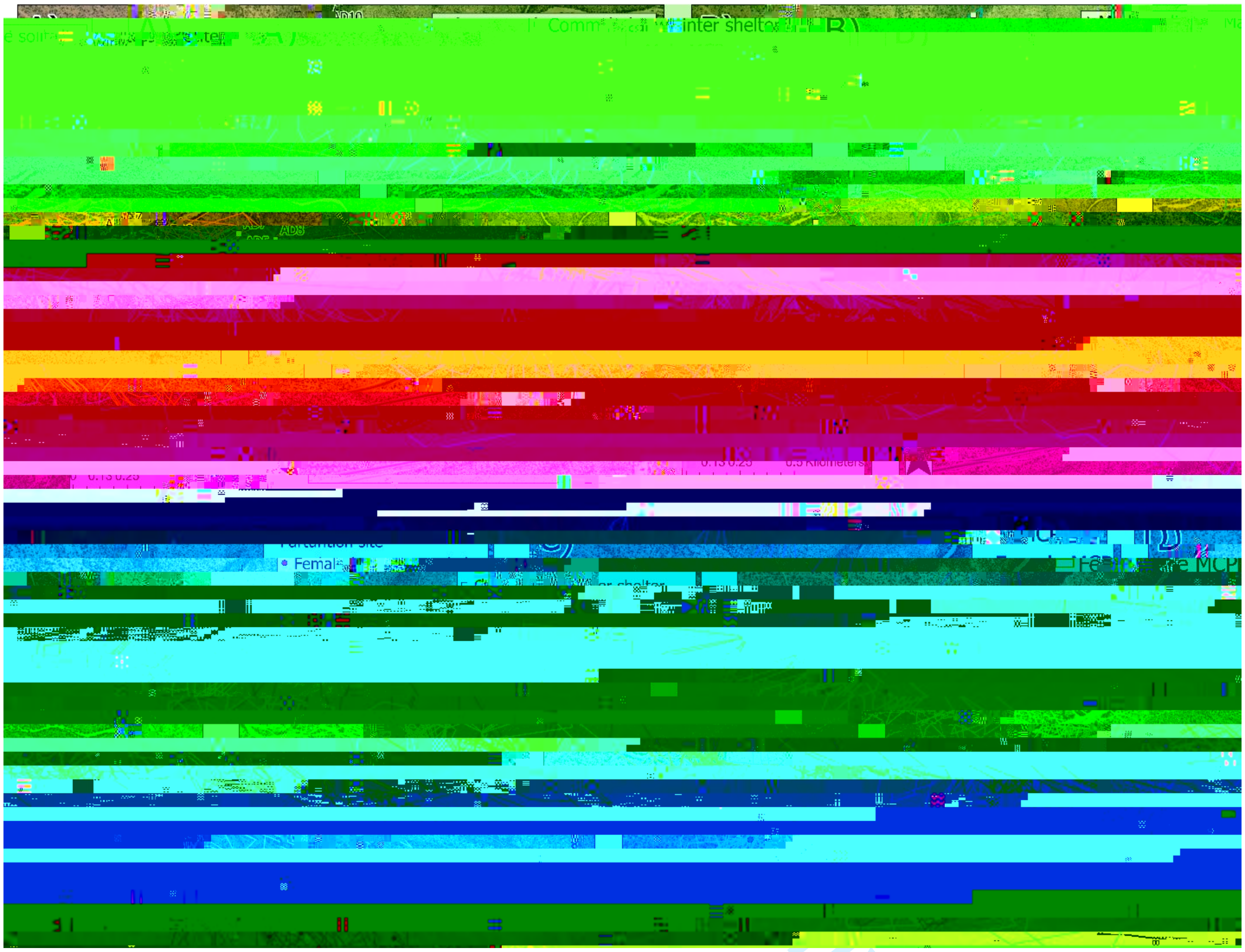

Figure 3. Spatial data on our focal group (22 males, 28 females) of adult *Crotalus atrox*. A) Annual home ranges (minimum convex polygons; MCP) of males (blue) and females (orange) that were observed overwintering in communal dens (AD = den ID). B) Sites where males overwintered in isolation (pink diamonds) or communal dens in relation to their annual home range; C) Home ranges of males and females that were observed engaging in reproductive behaviors. D) Sites where females gave birth (blue triangles) and overwintered privately (pink circles) or in communal dens (white squares) in relation to their home range.

b) Home range overlap and relatedness

Mantel tests comparing home range (MCP) overlap with relatedness revealed there was no correlation between the degree of pairwise home range overlap and relatedness (r = 0.004, *p* > 0.05).

3.3 Social network analyses

a) Communal den occupants

With few exceptions, all telemetered individuals that used communal dens exhibited absolute fidelity to these sites over the 10-year period where snakes were consistently radio-tracked (Table 1). For example, CA-1, the longest tracked snake in this study, showed fidelity to den AD1 for the seven winters it was tracked. Conversely, females CA-2 and CA-77 used a communal shelter for only one winter and were otherwise observed overwintering privately. Similarly, male CA-55 used a communal shelter twice in three winters (Table 1).

Table 1. Data on the use of eight communal dens by a subset (11 adult females, 20 adult males) of the focal group (subjects fitted with radio-transmitters) of adult *Crotalus atrox* studied in the Suizo Mountains, Arizona (2001–2010). The focal group (N = 50) consisted of 22 adult males

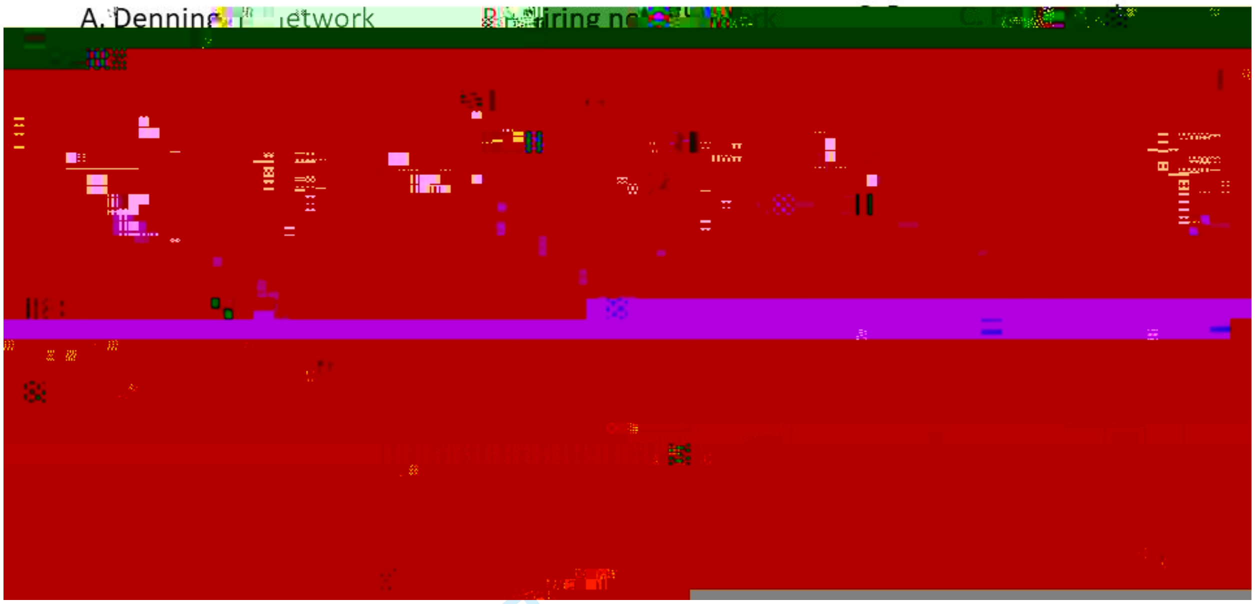

Figure 4. Modularity of individuals' A) denning network, B) pairing network, and C) parentage network of *Crotalus atrox* subjects in this study. Inner boxes indicate subsets of individuals interacting preferentially with each other (i.e., modules). In A), individuals of both sexes can be at the x and y axis since multiple males and females may share a communal den. In C) color intensity indicates the number of offspring sired. In C), UM indicates "unidentified male" (sampled but not radio-tracked; see text). Nine unidentified males were genotyped in the analysis: UM 1–4, 7–9, and 10, 13. See [46].

GLMMs indicated that individuals' CC in the denning, pairing, and parentage networks were not associated with individuals' morphology (SVL) and home range (MCP) (Table A1–A6). Sex was a significant predictor only in the parentage network, with females having slightly higher CC than males `y = - 0.016, 95% CI: -0.034, -0.002; Table A6).

Overall CC was low, varying from 0 to 0.14 in the denning network, 0 to 0.11 in the pairing network, and 0 to 0.08 in the parentage network (Table A7). Because many individuals were not observed interacting, it was common to have individuals whose CC = 0 (Table A7).

Mantel tests revealed no significant correlations between genetic relatedness and denning (*r* = -0.138, p = 0.938), pairing (*r* = 0.135, p = 0.297), or parentage (*r* = -0.150, p = 0.775) networks, which suggests that individuals interacting in modules were unlikely to be closely related.

4 Discussion

interact with more socially connected individuals [42, 43]. Our results mirror, to some extent, those of the first and only other study to incorporate social network analysis for a wild snake, the Arizona black rattlesnake, *Crotalus cerberus* [29, 38]. Adult male and female *C. cerberus* exhibited non-random association and formed multiple subgroups at communal dens and shelters, yet few dyads had strong associations. More studies are needed to understand the structure of social networks of snakes in general, but we suspect most would not show nested structure. In sharp contrast, the social networks (particularly related to mating) of other terrestrial vertebrates including African lions [55], equids and other ungulates [56], great apes and other primates [57] and several squamates [31, 58, 59], are characterized by one or several males that dominate a group of females and likely are the only ones to interact with most or all partners in a group [21].

The low CC values obtained reinforces the lack of nestedness and existence of modularity, indicating that each focal subject interacted only with a few other individuals in the three social networks examined. Furthermore, centrality was not significantly predicted by body size, home range, sex, or genetic relatedness. In this social environment, individuals with large bodies or large home ranges do not den, pair with more sexual partners, or produce more offspring than smaller and/or spatially restricted individuals [46, 58]. Nonetheless, we found females had greater centrality than males in the parentage network—meaning that they produce more offspring with a greater number of partners than males—yet this effect, though statistically significant, is not robust [39].

Genetic relatedness of our focal group was not correlated with denning, pairing, or parentage. Spatial analyses revealed that home range overlap also was not significantly correlated with relatedness; thus, social structure between pairs of individuals during the active season was not based on kin associations [29, 33; Supplemental Material]. Increasingly, studies of other terrestrial vertebrates demonstrate that group living and stable paired associations, for example, are not necessarily kin-biased or correlated with genetic relatedness [42, 60; but see 31, 61]. In network studies involving lizards, for example, relatedness and group living varies depending on the species (system) being investigated. Group living involves close relatives in some cases [8, 58, 62], yet in others, even in strongly connected individuals, social interactions are not defined by relatedness [30; but see 61]. As we discuss later, however, when a larger sample of subjects included unmarked adults (e.g., no radio-transmitters) was analyzed, the relationship of communal denning and relatedness of *C. atrox* showed mixed results, with multiple communal dens containing related occupants [29, pp. 196-198. See Supplemental Information, Tables S1–S8].

Communal denning is a type of clumped spacing behavior often defined as “aggregation” [29]. However, with respect to *C. atrox* in this study, and likely other rattlesnake species, we abandon use of the term “aggregation” and alter the lexicon by defining communal denning as *the formation of social groups or colonies by individual preference*. We suggest that these groups form and evolve through mutual attraction of individuals (regardless of members’ relatedness) for cooperative benefits to survival and reproduction [6, 71, 75]. These social groups we observed, whether kin- or non-kin-based, occur seasonally in a predictable manner. Importantly, these social groups involve only a subset of adult individuals, occurring in microhabitats that are not limited in the local population. These traits indicate that social groups are not just a result of attraction to particular microhabitats. It is likely that communal denning behavior, such as in *C. atrox* and other snakes, may be coordinated by way of conspecific attraction or familiarity, resulting in social (communication) networks which ultimately leads to the partitioning of individuals into subgroups and to the observed network modularity [17, 21, 75].

Remarkably, over the 15-year period of study, the focal group of adults showed near absolute fidelity to communal den sites. Several females, however, alternated year-to-year from communal dens to overwintering singly in shelters such as rodent middens and small mammal burrows [28, 29]. Adult males in our population, on the other hand, never occupied these kinds

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were obtained from the Arizona Game and Fish Department [Clark et al. 2014; Levine et al. 2021].

Data accessibility. The data used in the present analysis are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.3xsj3txjr

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Appendix

Definitions of important terms in social network ecology that were used in the present study.

Association index – Any measure of the strength of association between two species [23, 30].
Centrality – The extent to which a given node (e.g., individual) occupies a position that is important in the structure of the network [23, 30].

Closeness centrality – A measure of centrality that quantifies the proximity of a node (e.g., individual) to all other nodes in the network and thus indicates nodes that are more connected and highly influential in the social network [65, 66],
Edge – A line between two nodes (e.g., individuals) representing a social interaction [23, 30]

Fission-Fusion Dynamics – The extent of variation in spatial cohesion and individual membership in a group over time [47].

Modularity – A measure of subsets (groups, clusters, or communities) of entities (e.g., individuals) that interact with each other more frequently than with other individuals in a population; groups or modules of highly connected individuals. High modularity networks have dense connections between nodes within modules but few connections (between nodes) in different modules [30, 60].

Nestedness – Interactions of less connected elements (e.g., individuals) that form proper subsets of the interactions of more connected elements, e.g., individuals [30, 61, 62, 73].

Node – An object in a network, such as an individual [23, 30].

Social Preference – Selection of one element (e.g., individual) more frequently over another element (e.g., individual) in the context of a social environment. Nonrandom, repeated interactions with certain individuals that are the foundation of social relationships. Also termed preferred association [20, 21 23, 30].

Network Analysis Details

In an interaction matrix, each node (column *i* or row *j*) represents an individual and each social interaction observed between two individuals (a*ij*) is an edge. Modularity occurs when subsets of individuals interact more among themselves than with other individuals in the population, forming modules of highly connectriNetw-15h(984)-1500 (ine)1 (lements, e.g., i)1 99 TD.69ilements, e.g., iE1he where *n*

Sex	0.026	0.014	-0.001	0.054
MCP	-0.010	0.007	-0.022	0.003
SVL	0.001	0.007	-0.014	0.014

Table A3. Model selection results (encompassing 95% of the total model weight) for predicting

MCP	0.004	0.004	-0.005	0.011
Sex	-0.004			

CA094f	female	0.04419564	CA094f	female	0.00000000	CA006m	male	0.00000000
CA095f	female	0.00000000	CA095f	female	0.00000000	CA076m	male	0.00000000
CA100f	female	0.00000000	CA100f	female	0.00000000	CA079m	male	0.00000000
CA101f	female	0.00000000	CA101f	female	0.00000000	CA092m	male	0.00000000
CA102f	female	0.04419564	CA102f	female	0.07784758	CA096m	male	0.00000000
CA112f	female	0.00000000	CA112f	female	0.00000000	CA097m	male	0.04761905
CA113f	female	0.00000000	CA113f	female	0.05462988	CA098m	male	0.00000000
CA114f	female	0.00000000	CA114f	female	0.00000000	CA099m	male	0.00000000
CA115f	female	0.00000000	CA115f	female	0.00000000	CA117m	male	0.00000000
CA116f	female	0.00000000	CA116f	female	0.00000000	CA122m	male	0.00000000
CA120f	female	0.00000000	CA120f	female	0.00000000			
CA121f	female	0.00000000	CA121f	female	0.00000000			
CA124f	female	0.00000000	CA124f	female				

CA040m	male	0.000000000	CA040m	male

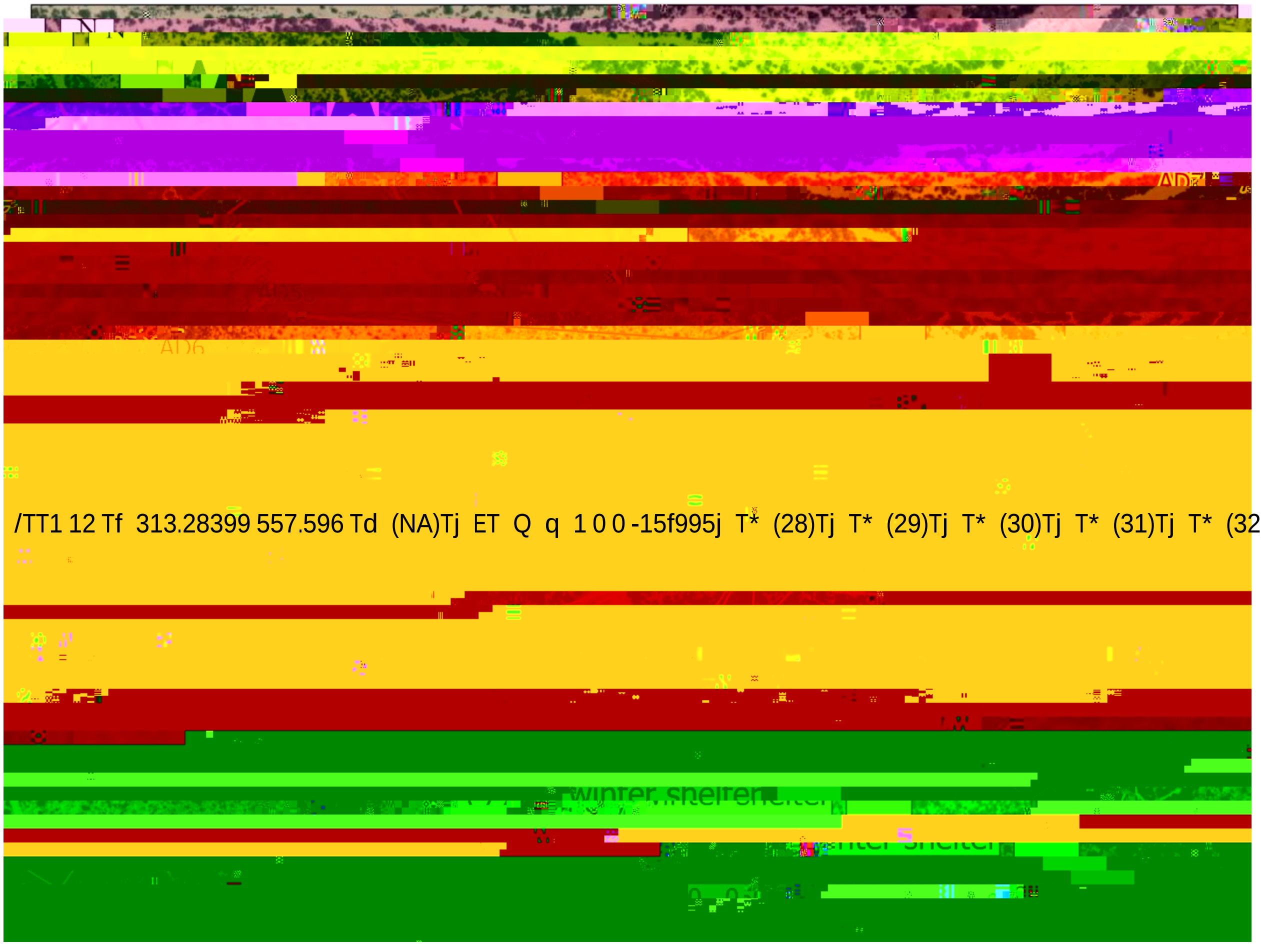
CA119m	male	0.000000000	CA119m	male	0.00000000
CA122m	male	0.000000000	CA122m	male	0.00000000
CA123m	male	0.000000000	CA123m	male	0.00000000
CA126m	male	0.000000000			

Table A8. Predictor variable measured for each *C. atrox*

CA063f	female	910	386	NA	NA	0
CA064f	female	940	513	407.71	0.93725	3
CA065f	female	790	347	NA	NA	0
CA066f	female	845	393	501.89	1.40	2
CA070f	female	910	485	NA	NA	0
CA071f	female	940	454	NA	NA	0
CA077f	female	850	379	963.32	4.41	1
CA081f	female	845	419.5	2085.79	7.23	3
CA085f	female	775	243	NA	NA	0
CA086f	female	350	18.5	NA	NA	0
CA087f	female	705	257.3	NA	NA	0
CA089f	female	310	21	NA	NA	0
CA008f	female	845	347	NA	NA	0
CA090f	female	298	19	NA	NA	0
CA093f	female	825	399	944.4	3.35	3
CA094f	female	775	370	633.28	1.87	2
CA095f	female	905	476	648.33	1.82	1
CA103m	male	910	505	NA	NA	0
CA104m	male	900	429	NA	NA	0
CA105m	male	1003	625	NA	NA	0
CA106m	male	700	265	NA	NA	0
CA107m	male	1040	905	NA	NA	0
CA108m	male	810	405	NA	NA	0
CA109m	male	1004	816	NA	NA	0
CA110m	male	780	386	NA	NA	0
CA111m	male	875	451	NA	NA	0
CA117m	male	965	535	1326.72	6.02	2
CA118m	male	875	453	NA	NA	0
CA119m	male	1020	604	NA	NA	0
CA122m	male	864	433	1351.75	9.18	1
CA123m	male	786	384	NA	NA	0
CA126m	male	900	632	NA	NA	0
CA127m	male	935	600	NA	NA	0
CA128m	male	1070	842	NA	NA	0
CA129m	male	1060	775	NA	NA	0
CA130m	male	1045	859	NA	NA	0
CA132m	male	1015	740	NA	NA	0
CA134m	male	738	243	NA	NA	0
CA013m	male	1060	673	1723.93	17.85	3
CA018m	male	950	470	NA	NA	0
CA001m	male	NA	NA	NA	NA	0
CA020m	male	850	452	NA	NA	0
CA021m	male	960	563	NA	NA	0

CA022m male

CA082m	male	875	597.5	NA	NA	0
CA083m	male	850	413.5	NA	NA	0
CA084m	male	980	633	NA	NA	0
CA088m	male	1005	622	NA	NA	0
CA091m	male	320	24	NA	NA	0
CA092m	male	980	686	1491.76	13.33	1
CA096m	male	920	570	2366.75	21.94	2
CA097m	male	965	653	2024.56	16.69	2
CA098m	male	1040	859	2334.71	17.95	2
CA099m	male	1065	735	NA	NA	0
CA009m	male	990	517	NA	NA	0



3Tj T* (2600 g /TT1 12 Tf 313.28399 557.596 Td (NA)Tj ET Q q 1 0 0 -15f995j T* (28)Tj T* (29)Tj T* (30)Tj T* (31)Tj T* (32)Tj T* (geM7.5j

Figure A1. Minimum convex polygons (MCP) showing home ranges for females CA-02 and CA-77 that alternated between communal dens (den ID: AD-1 and AD-5) and private winter shelters in different years. Note the consistency in CA-02's annual home range size and shape. See main text for additional details.

Supplementary Material from “Fission-Fusion Dynamics in the Social Networks of a North American Pitviper”

Rattlesnakes in social network analysis

Numerous moderate- to large-sized species of rattlesnakes (e.g., *Crotalus atrox*, *C. cerberus*, *C. oreganus*, *C. stephensi*, and *C. viridis*) possess several attributes that allow their study in nature to be manageable and thus good candidate models for longitudinal studies using network analysis. The changing academic milieu and publication stance on social behavior in animals, in general, and rattlesnakes and other reptiles, in particular, is summarized by Schuett and colleagues [1, 2] and inspired by Doody and colleagues [3, 4] and Van Dyke and colleagues [5].

1) In the five rattlesnake taxa mentioned above, individuals often assemble to form highly localized groups (two to several hundred) in communal winter shelters (communal dens) from fall to spring, or even longer [1, 2, 6–9]. Rarely observed in other species of snakes, this attribute permits one not only to observe most adult snakes (and sometimes neonates and juveniles) of a population [1, 2, 8, 10–14], but also to capture them for processing such as inserting permanent PIT tags (identification), performing radio-telemetry surgery (radio-tracking), and procuring tissues (e.g., blood, scale clips) for subsequent DNA analysis [2, 9]. See Schuett and colleagues [1, 2, 11] for a discussion of other attributes of communal shelters in rattlesnakes for studies of social behavior.

2) With the advent of affordable commercial radio-telemetry for terrestrial snakes since the late 1980s, it is now possible to implant radio-transmitters into the body cavity of moderate- to large-sized individuals for long periods (e.g., months to years) before removal or replacement [15]. Radio-telemetry provides a unique radio-signal for each individual. Coupled with the use of PIT tags and other forms of identification methods (e.g., unique painting of rattles, photographs), radio-tracking and locating individuals can be done with high precision.

3) As a group, rattlesnakes tend to be slow-moving, ambush (sit-and-wait) predators [16, 17]. Consequently, their movements are limited and distances traveled per movement session (e.g., evening) tend to be short (e.g. 0.1–1km). Thus, unlike many other organisms such as birds, felids, and ungulates, radio-tracking can be done by foot and managed on a daily basis if needed. Furthermore, when compared to other snake species, rattlesnakes as sit-and-wait predators are often exposed on the ground-surface and visible for observation purposes [17; R. Repp and G. Schuett, pers. observ., 2001–2015].

4) Nearly all large species of rattlesnakes are long-lived, with some attaining lifespans exceeding four decades [18–19]. Longevity is especially desirable in that overlapping generations can be studied simultaneously and by a single researcher. Maturation in females is from 3 to 12 years dependent on the species and location [18–19].

Communal denning and relatedness analysis

CAMD2_S6 M

CASD-083	M	CA-83	u	u	u	u	u	u	u	u	u	HS	u	x

CAMD2_S1 6	M	CA-13

Table S4. Genotype results of adult Western Diamond-backed Rattlesnakes (*Crotalus atrox*) from Den AD-6 at the Suizo Mountains, AZ, USA. Site was sampled from 2001 to 2010. HS = half-sibs. See Clark et al. (2014) and Schuett et al. (2014).

Relatedness matrix			CASD-044	CASD-046	CAMD007	CASD-068	CASD-082	CASD-084	CASD-111
			F	F	M	M	M	M	M
			CA-44	CA-46	CA-7	CA-68	CA-82	CA-84	CA-111
CASD-044	F	CA-44	x						
CASD-046	F	CA-46	0.04	x					
CAMD007	M	CA-7	0	0.03	x				
CASD-068	M	CA-68	0.03	0.05	0	x			
CASD-082	M	CA-82	0.06	0	0	0.03	x		
CASD-084	M	CA-84	0.04	0.05	0	0.03	0.05	x	
CASD-111	M	CA-111	0.04	0	0	0.04	0.03	0	x

Relationship matrix			CASD-044	CASD-046	CAMD00

Relatedness matrix			CASD-047	CASD-058	CASD-040	CASD-076	CASD-078	CASD-079	CASD-092	CASD-043	CASD-073	CASD-074	CASD-X057
			F	F	M	M	M	M	M	M	M	M	M
			CA-47	CA-58	CA-40	CA-76	CA-78	CA-79	CA-92	CA-43	CA-73	CA-74	CA-x57
CASD-047	F	CA-47	x										
CASD-058	F	CA-58	0	x									
CASD-040	M	CA-40	0	0	x								
CASD-076	M	CA-76	0	0.02	0.06	x							
CASD-078	M	CA-78	0	0	0.09	0	x						
CASD-079	M	CA-79	0	0.06	0.06	0.03	0	x					
CASD-092	M	CA-92	0.02	0	0	0	0	0	x				
CASD-043	M	CA-43	0	0	0.02	0	0	0.03	0	x			
CASD-073	M	CA-73	0.002	0.01	0	0.06	0	0	0	0	x		
CASD-074	M	CA-74	0	0.007	0.06	0.07	0	0	0	0	0	x	
CASD-X057	M	CA-x57	0	0.02	0	0	0.08	0	0	0.003	0	0.05	x

Relationship matrix			CASD-047	CASD-058	CASD-040	CASD-076	CASD-078	CASD-079	CASD-092	CASD-043	CASD-073	CASD-074	CASD-X057
			F	F	M	M	M	M	M	M	M	M	M
			CA-47	CA-58	CA-40	CA-76	CA-78	CA-79	CA-92	CA-43	CA-73	CA-74	CA-x57
CASD-047	F	CA-47	x										
CASD-058	F	CA-58	u	x									
CASD-040	M	CA-40	u	u	x								
CASD-076	M	CA-76	u	u	u	x							
CASD-078	M	CA-78	u	u	u	u	x						

CASD-079	M	CA-79	u	u	u	u	u	x					
CASD-092	M	CA-92	u	u	u	u	u	u	x				
CASD-043	M	CA-43	u	u	u	u	u	u	u	x			
CASD-073	M	CA-73	u	u	u	u	u	u	u	u	x		
CASD-074	M	CA-74	u	u	u	u	u	u	u	u	u	x	
CASD-X057	M	CA-x57	u	u	u	u	u	u	u	u	u	u	x

Table S6. Genotype results of adult Western Diamond-backed Rattlesnakes (*Crotalus atrox*) from Den AD-8 at the Suizo Mountains, AZ, USA. Site was sampled from 2001 to 2010. HS = half-sibs. See Clark et al. (2014) and Schuett et al. (2014).

Relatedness matrix			CASD-064	CASD-101	CASD-102	CASD-097
			F	F	F	M
			CA-64	CA-101	CA-102	CA-97
CASD-064	F	CA-64	x			
CASD-101	F	CA-101	0	x		
CASD-102	F	CA-102	0.07	0.04	x	
CASD-097	M	CA-97	0	0.01	0	x

Relationship matrix			CASD-064	CASD-101	CASD-102	CASD-097
			F	F	F	M
			CA-64	CA-101	CA-102	CA-97
CASD-064	F	CA-64	x			
CASD-101	F	CA-101	u	x		
CASD-102	F	CA-102	u			

R matrix			CASD-040	CASD-052	CASD-053
			M	M	M
			CA-40	CA-52	CA-53
CASD-040	M	CA-40	x		
CASD-052	M	CA-52	0	x	
CASD-053	M	CA-53	0.24	0.02	x
Relationship matrix			CASD-040	CASD-052	CASD-053
			M	M	M
			CA-40	CA-52	CA-53
CASD-040	M	CA-40	x		
CASD-052	M	CA-52	U	x	
CASD-053	M	CA-53	HS	U	x

Table S8. Genotype results of adult Western Diamond-backed Rattlesnakes (*Crotalus atrox*) from Den 1 at the Suizo Mountains, AZ, USA. Site was sampled from 2001 to 2010. HS = half-sibs. See Clark et al. (2014) and Schuett et al. (2014). There was no relatedness between these two male snakes.Refs bnc(en these t x)Tj/TT14.5

CASD-096	M	CA-96
CASD-x023	M	CA-x23

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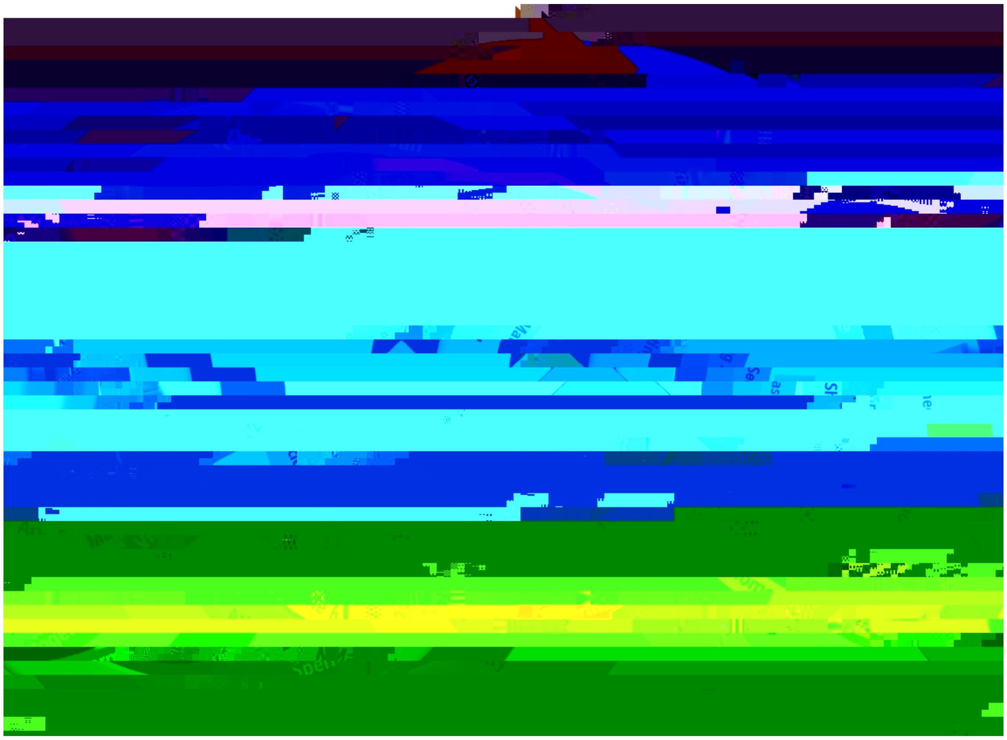

Figure 1. Annual cycle and phenology of behavioral, physiological, reproductive, and life history events for adult Crotalus atrox at Suizo Mountains (Pinal County, Arizona), and nearby areas, based on 15 consecutive years (2001–2015) of research [28, 29, 36–40]. Note: Shed Cycle refers to skin shedding (ecdysis).

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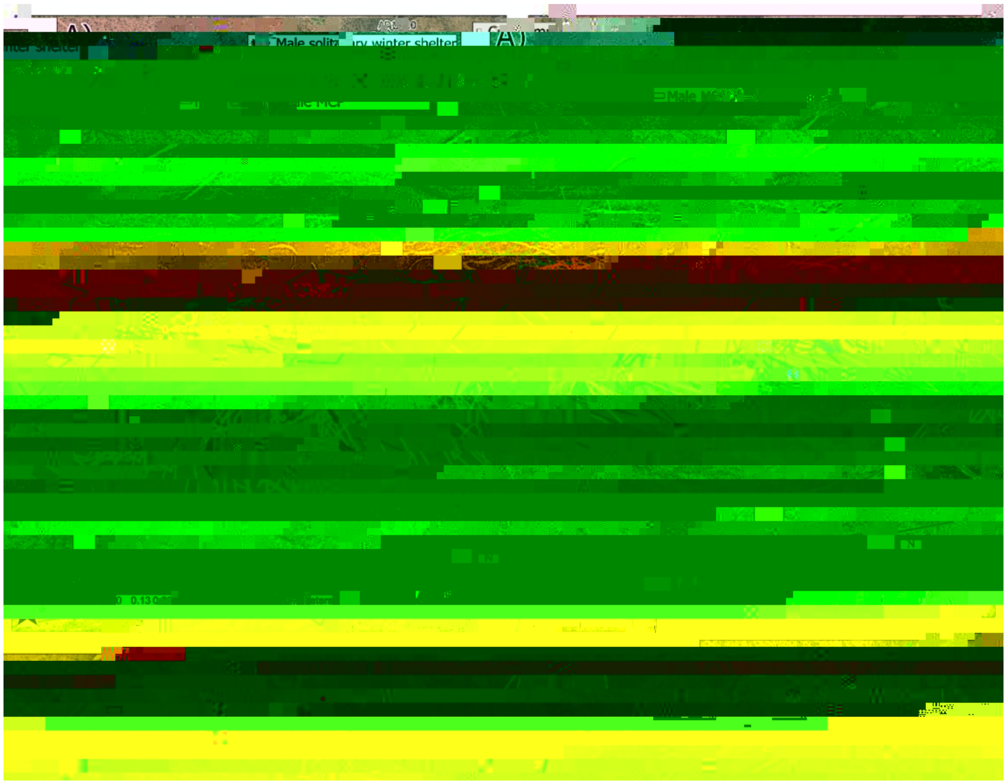

Figure 3. Spatial data on our focal group (22 males, 28 females) of adult Crotalus atrox. A) Annual home ranges (minimum convex polygons; MCP) of males (blue) and females (orange) that were observed overwintering in communal dens (AD = den ID). B) Sites where males overwintered in isolation (pink diamonds) or communal dens in relation to their annual home range; C) Home ranges of males and females that were observed engaging in reproductive behaviors. D) Sites where females gave birth (blue triangles) and overwintered privately (pink circles) or in communal dens (white squares) in relation to their home range.

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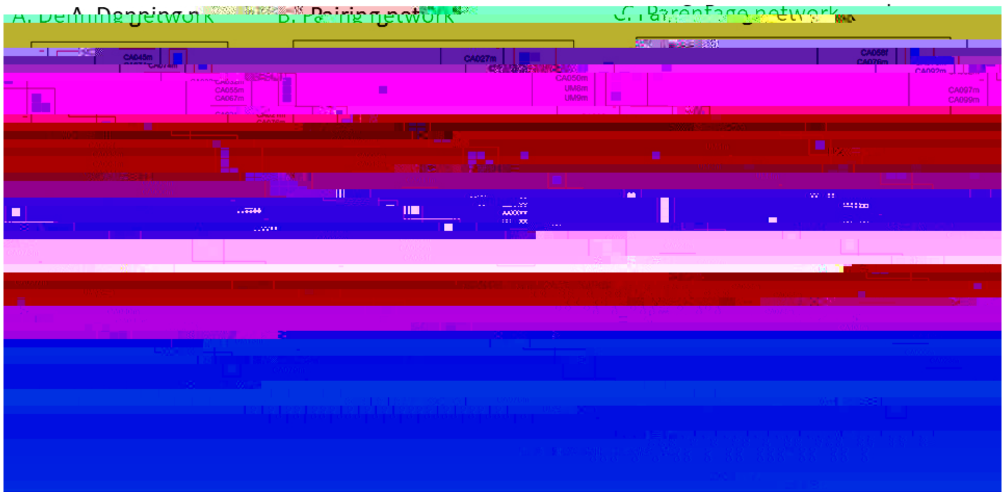

Figure 4. Modularity of individuals' A) denning network, B) pairing network, and C) parentage network of Crotalus atrox subjects in this study. Inner boxes indicate subsets of individuals interacting preferentially with each other (i.e., modules). In A), individuals of both sexes can be at the x and y axis since multiple males and females may share a communal den. In C) color intensity indicates the number of offspring sired. In C), UM indicates "unidentified male" (sampled but not radio-tracked; see text). Nine unidentified males were genotyped in the analysis: UM 1–4, 7–9, and 10, 13. See [46].

254x127mm (96 x 96 DPI)