

The social system of an endemic lava lizard, *Microlophus
atacamensis*: the interplay between social structure and social
organization

By
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Abstract

Animal social systems can be described through 4 main components: social structure, social organization, mating system, and care system. Social structure describes the relationships between individuals in a population, while social organization describes the group composition, size and spatiotemporal variation of a population. I use these two frameworks to study the social system of *Microlophus atacamensis*, an endemic lizard found along the Chilean coast that inhabits the rocky intertidal zone between the Pacific Ocean and the Atacama Desert. Lizards in the genus *Microlophus* generally exhibit territorial behaviors, but their exact social system is largely undescribed. The area *M. atacamensis* inhabits poses specific challenges stemming from their use of two distinct habitat types: they forage in the cooler intertidal zone and use large rocks in more inland areas for basking. I characterized the social system of *M. atacamensis* using social structure and social organization as a framework, hypothesizing that social structure would be independent of habitat type, while social organization based on space use would differ with habitat type. My assessment focused on 2 separate populations: one to characterize social structure by means of focal observations and social network analysis, and a second to assess social organization by examining space use through home range and core area analyses. Social network analysis revealed that in the social structure of *M. atacamensis* larger individuals were more central to the social network and body size influenced the outcomes of aggressive interactions. Interactions were more common in the intertidal zone where lizards foraged, where males had more associates and more repeated interactions with those associates than females. Spatial analyses revealed that the social organization of *M. atacamensis* is characterized by high home range overlap, specifically in the intertidal zone where foraging occurs, but also by relatively exclusive core areas dispersed across both habitat types. I suggest that *M. atacamensis*

has a shifting social system in which small exclusive territories are maintained on large rocks in inland areas, while a system of dominance relationships promotes access food in the intertidal zone.

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Chapter 1: Introduction

Animal social systems influence many aspects of a species' ecology. Understanding social systems has been a major topic of interest, with various studies examining the evolution of social systems in relation to environmental factors like microhabitat and resource availability as well as the ways in which social systems vary across different phylogenetic groups (Doody et al., 2013; Kappeler et al., 2013; Thierry et al., 2000). Because access to limited resources often modifies behavior and leads to complex interactions, variations in social systems can be expected to emerge, making studies on animal sociality and its plasticity based on the species' ecology a topic of significant interest.

Only recently has a comprehensive framework describing and comparing social systems across animal taxa been proposed, one that contains 4 core components: social structure, social organization, mating system, and care system (Kappeler, 2019). One component, social structure, describes how individuals in a social unit interact and the relationships that form from repeated interactions (e.g., dominance relationships). A second component, social organization, describes the group size, composition, and kinship patterns of a social unit (i.e., solitary, pair-living, or group-living) including spatial and temporal variation in group size and composition. *Social structure* and *social organization* have frequently been used interchangeably, which has led to confusion in the literature. Their subtle distinction lies with social organization describing characteristics of the social unit like spatial and temporal variation, while social structure describes the nature of relationships among individuals forming the social unit. The other two components are more intuitive and less often confused, with mating system describing which individuals actually mate and reproduce, allowing for categorical classifications that describe the mating pattern (i.e., monogamous, polygynous, polyandrous, polygynandrous, promiscuous) and

care system, describing who cares for dependent young, which can include the absence of parental care as well as parental and allo-parental care (Kappeler, 2019).

Social Structure

Social structure can be analyzed via social network analysis, which delineates the relationships between individuals. Network analysis is versatile and can be applied to social structure in relation to the acquisition of food resources (Eifler et al., 2016), the spread of disease or parasites (Godfrey et al., 2006, 2009), and shifts in relationships inherent to fusion-fission societies (Chaverri, 2010; Mbizah et al., 2020). Furthermore, many studies describe social structure with respect to environmental characteristics like habitat complexity (Edenbrow et al., 2011; Leu et al., 2016) and seasonality (Mbizah et al., 2020). Within populations, network analyses can be used to explore which individuals are important to the social structure, which in turn can reveal phenotypic characteristics that influence sociality (Croft et al., 2008).

Social networks have been studied in various vertebrate taxa including mammals (de Silva & Wittemyer, 2012; Mbizah et al., 2020; Vance et al., 2009), birds ((Moyers et al., 2018; Snijders et al., 2014) and fish (Atton et al., 2012; Edenbrow et al., 2011), but relatively little has been done on reptiles. Historically, reptiles are not thought to have societies complex enough to merit network analysis, but increasingly the complexity of their social systems is being recognized (Doody et al., 2021). Recent studies indicate complexity in lizard social systems (Gardner et al., 2016; While et al., 2019), with the genus *Egernia* documented as exhibiting group-living (Bull et al., 2017; Chapple & Scott Keogh, 2006; Leu et al., 2015) and *Pholidoscelis* demonstrating cooperative and coordinated behavior (Eifler et al., 2016, Eifler et al. in review).

Social Organization

Group size and composition, as well as the nature of the social unit in an animal's social system, often depends on numerous factors including population density, habitat structural complexity, and resource availability (Maher & Lott, 2000). When essential resources are scarce but concentrated in specific locations, animal distributions are often linked to the location of the resources. For example, large ungulates and carnivores in the African savanna often are limited to areas near watering holes, especially in the dry season (Valeix, 2011). Ectotherms are especially influenced by habitat features that control thermoregulation. Among saxicolous lizards, rock characteristics like width and height regulate the spatial and temporal distribution of lizards across their habitat (Eifler et al., 2017; Hedman et al., 2021; Schlesinger & Shine, 1994). In addition, crevice temperatures can be important to space use (Diaz et al., 1996; Hedman et al., 2021), even influencing physiological functions during the next active period (Croak et al., 2008). The distribution of suitable locations for thermoregulation can thus influence group size and composition. Finally, age class interacts with microhabitat use, as shifts in body size change thermal requirements as well as the ability to exclude other individuals from higher quality locations (Eifler et al., 2007; Eifler et al., 2017; Vasconcelos et al., 2012). Examining microhabitat use can provide vital information on how spatial segregation between individuals, as a function of sex and life history traits, can modulate social organization.

Space use is inexorably related to social organization as sharing space or excluding individuals from a location affects group composition. In lizards, spatial analyses that examine space use and occupancy overlap commonly have been used as measurements of social organization (Godfrey et al., 2012; Hagen & Bull, 2011; Osterwalder et al., 2004). Many studies examine space use via home range analysis, which defines the area traversed during an individual's daily activities (Burt, 1943) and core area analysis, which defines the area of

concentrated activity for an individual (Vander Wal & Rodgers, 2012). The extent to which home ranges or core areas overlap provides an assessment of the social organization of a population. For example, although the lizard *Aspidoscelis uniparens* exhibits extensive home range overlap, core areas are largely isolated, with small, exclusive areas maintained behaviorally through aggressive displacements (Eifler & Eifler, 1998). Moreover, resource distribution often plays a role in determining suitable habitat and, as a consequence, the resulting distribution of individuals or segregation of the sexes across that habitat. A manipulation of food availability can lead to *A. uniparens* altering its social organization to one with extensive core area overlap (Eifler, 1996). Among some lizard species, female home ranges are often distributed according to food or perch resources, whereas males in the breeding season can have home ranges distributed based on access to females (Brown et al., 1995; Ferner, 1974; Haenel et al., 2003; Osterwalder et al., 2004; Rose, 1982; Smith, 1985).

Social System

The social system of a species results from both their evolutionary history and the environmental characteristics of their habitat. Because of this, the overall social system of a species can differ considerably among populations from territoriality, in which the social system is centered around exclusive areas defended by an individual, to dominance hierarchies, where the social system depends on relationships between individuals independent of location. Social structure and social organization represent different characteristics of social systems, such that a species can be territorial and still exhibit dominance relationships (Effenberger & Mouton, 2007). Spatial analyses and habitat use reveal whether the social organization includes territoriality, while social network analyses can be used to identify and quantify social structure and evaluate whether dominance hierarchies exist. Linkages between spatial and network

analyses can reveal nuanced aspects of social systems that would not be evident if only one analysis were used. For example, *Pholidoscelis corax*, a lizard species endemic to a single small island off the coast of Anguilla with limited food resources. Spatial analysis revealed an uneven distribution of fruits, eggs, and chum that form the basis of their diet, while social network analysis delineated relationships among animals as a function of their size and sex (Eifler et al., 2016). The spatial distribution of resources serves to link the social organization and social structure because only larger lizards can easily gain access to the richest food sources. Social network analysis revealed that larger males were most central in the social network and that larger lizards of both sexes were more connected (i.e., larger body size = more social links; Eifler et al., 2016). I explore the social system of *Microlophus atacamensis* for a similar connection between the spatial distribution of resources and their social network.

The highly endemic South American genus *Microlophus* is comprised of > 20 species, some of which were previously placed in the genus *Tropidurus*. Their sociality has been explored somewhat, with dominance displays and territorial behaviors observed in both males and females of several species (Carpenter, 1966). *Microlophus atacamensis* is particularly interesting because of the unique habitat it occupies, being restricted to the intertidal zone along the Chilean coast between the Pacific Ocean and the Atacama Desert (Vidal et al., 2002). The Atacama Desert is a challenging ecosystem with resource limitations that likely affect lizard social behavior and space use. Although thermodynamically unfavorable, the intertidal zone is necessary for feeding whereas rocky inland areas (i.e., the adjacent Atacama Desert) are thermodynamically favorable, but limited in food resources.

Microlophus atacamensis is sexually dimorphic, with males attaining larger body sizes, and omnivorous, eating a variety of plant and insect matter depending on resource abundance in

different parts of their range (Farina et al., 2008). They use the rocky inland areas adjacent to the open desert for refuges, thermoregulation, and for some feeding (Vidal et al., 2002). Adults remain on large rocks in the inland area until attaining a minimum active body temperature (Heisig, 1993). However, they primarily forage in the intertidal zone, which at any given time is composed of both dry and wet areas. The splash zone is the wet area typically covered by water throughout most of the day, while a majority of the intertidal zone remains dry most of the time, with the inland edge only reached by the high tide. The ocean currents circulate cold waters off the coast of Chile during all seasons, creating a thermodynamically unfavorable region in intertidal areas. At the same time, the tides also bring significant marine subsidies like algae and organic matter that attracts marine detritivores, flies and other insects that *M. atacamensis* can use as food sources (Richardson et al., 2019; Spiller et al., 2010; Wright et al., 2013).

The cooler intertidal zone temperatures influence both daily and seasonal activity for *M. atacamensis* (Sepúlveda et al., 2014). During cool seasons, there are decreased activity periods, while the warm summer and spring seasons lead to increased foraging periods (Sepúlveda et al., 2014). The shifting location of food within the intertidal zone further complicates the social system of *M. atacamensis*. The tides can randomly bring marine subsidies to shore, but the frequency and density of subsidies are unpredictable. In addition, rising and receding tides can both cover and uncover feeding areas so the location of food in the intertidal zone is variable. The separation of food and thermoregulatory resources presents a challenge to an individual, both creating a trade-off between thermoregulation and feeding and making the possibility of monopolizing resources by maintaining an exclusive territory very costly. Thus, despite the fact that territorial behaviors have been observed in the genus *Microlophus*, I postulate that *M. atacamensis* is not strictly territorial. As lizards move between the intertidal zone and warmer

rocks, they are likely making compromises between obtaining food, finding optimal temperatures, and establishing social dominance. I used social network and home range analyses in combination to explore the interplay between social organization and social structure in *M. atacamensis* society. Understanding these two main components of their social system in combination allows me to describe their social system in a more nuanced way. I test two main hypotheses, that in *M. atacamensis* (1) social structure is independent of habitat type and (2) social organization, as reflected in patterns of space use, will vary with habitat type.

Chapter 2: Materials and Methods

I studied the social system of *M. atacamensis* in two field sites separated by 1.5 km along the rocky intertidal zone near Peña Blanca, ca. 40 km south of Huasco, Huasco Province, Atacama Region, Chile (Site 1: 28.6979°S, 71.3182°W; Site 2: 28.6901°S, 71.3076°W; datum = World Geodetic System 84 (WGS84)). The distance between the two sites ensured that the lizards at each site represented separate populations. Both sites were characterized by two distinct habitat types: (1) *large rocks* that consisted of isolated boulders (3 – 6 m in height) and rock walls (> 3 m in height) forming the boundaries of central arenas running from the Pacific Ocean inland to the edge of the Atacama Desert and (2) *cobble fields*, which were the central arenas bounded by the large rocks, that contained cobble-sized stones (Figure 1). Site 1 consisted of a single cobble field bounded by large rocks and site 2 was composed of multiple cobble fields, each bounded by large rock edges that collectively formed a contiguous block. At site 2, some interior large rocks bounded two cobble fields (Figure 2, Figure 3). Two separate sites were chosen based on the different functions of each site. Site 1 provided a small enough area from which to observe interactions and social structure but was not logistically practical for collection of spatial data. Many large rocks on site 1 were very tall and could only be viewed from one side, such that collecting spatial data would have caused behavioral changes in the lizards and compromised the data we could collect. Site 2 was more suited to spatial analysis as the habitat was more open and although the rock walls and boulders were also tall, they were more easily traversed.

Based on my preliminary observations, I thought that large rocks would be important basking and displaying locations where lizards could choose whom to associate with, while the cobble fields, which are important for feeding, provided lizards with less choice in their



Figure 1:

The central cobble field on site 1 surrounded by rock walls on both sides and some of the large interspersed boulders. The transition from sandy desert to the cobble field is visible in the foreground and the transition into the ocean in the background. Photo by M. Eifler.



Figure 2:

An example of a smaller cobble field bordered by two rock walls (site 2, cobble field 2). Photo by M. Eifler



Figure 3:

The largest cobble field on site 2 where many of the interactions occurred. This is the cobble field outlined in red in figures 11 and 12. Photo by M. Eifler.

associates. On site 1, I explored social structure assessing whether relationships differed between the large rock and cobble field habitats. I predicted that social networks and dominance relationships present in the cobble fields would be preserved on the large rocks (hypothesis 1). On site 2, I determined social organization, predicting that there would be sex-based differences in space use, as well as largely exclusive use of space (hypothesis 2).

Data Collection

Prior to collecting data, I marked most of the animals in the study populations. Lizards on both sites were captured using a lasso attached to an extendable pole, measured (mass (g) and snout-vent length (SVL, mm)), sexed via cloacal probing, and uniquely marked using non-toxic paint pens. Lizards were released at their initial sighting location within 5 h. Any additional unmarked lizards were captured after sampling periods were completed on site 1 or when encountered during surveys on site 2. I did not collect data for lizards that were not successfully captured, measured, and marked. All data collection started once lizards had become active for the day, which varied with the weather.

Site 1

Site 1 (area = 0.134 ha) was characterized by a central cobble field bordered by 12 large rocks (3 – 6m) (Fig. 1). From 22 Dec 2019 – 4 Jan 2020 between 1300 – 1830 h, four people simultaneously monitored the lizards in the central cobble field to record all occurrences of interactions. The sampling periods lasted 30 – 120 mins, depending on lizard activity levels. For behavioral sampling, one person was positioned in each corner of the cobble field to ensure that the entire central arena could be monitored. Simultaneously, a fifth person surveyed the bordering large rocks every 30 mins, scanning each to record occupancy and interactions between marked lizards. To ensure that surveys did not interfere with behavioral sampling, the

observer walked around the edges of the large rocks as far from the central cobble field as possible and used binoculars for sighting and identifying lizards. Interactions between two or more lizards were categorized as spatial proximity (Figure 4), chases, fights, displacements, and retreats (Table 1).

Site 2

Site 2 (area = 1.02 ha), consisted of 6 large rocks interspersed with 5 cobble fields. Site 2 occupied a longer strip of coast than site 1, but was contiguous so that a single lizard could travel across multiple large rocks and cobble fields within the site (Figure 2, Figure 3). I studied home ranges and space use of *M. atacamensis* by obtaining location information through surveys conducted every 90 mins from 10 – 17 Jan 2020, between 1000 – 1900 h. Four surveyors walked evenly spaced transects parallel to the shore, using binoculars to scan for and identify individuals. Each time a marked animal was observed, I recorded the animal's identity, time, and location (i.e., which large rock or cobble field and GPS coordinates (myTracks GPS-logger for iPhone)). To ensure independence, I only used locations for any single animal that were at least 1 h apart. Each day, I alternated whether surveys began at the north or south end of the study site. I moved in the same direction throughout each day, to ensure that animals had ca. 90 mins to recover from any disturbance that my presence on the plot might have caused. In addition, I opportunistically collected behavioral data on Site 2 when I observed lizards interacting during surveys, classifying interactions as on site 1 (Table 1).

Analysis

Social Structure

Social networks were constructed and analyzed using Ucinet (ver. 6.671; Borgatti et al., 2002) and the igraph package in R (ver. 4.0.0; R Core Team, 2020). To assess social structure,



Figure 4:

Spatial proximity of a marked male and female M. atacamensis. Photo by M. Eifler.

Table 1:

Interaction types and their definitions. Spatial proximity is non-directional, but all other interactions involve a winner and loser (specified).

Interaction	Description
Spatial Proximity	≥ 2 animals within 30 cm of each other or connected by a chain (Croft et al. 2008)
Chase	one animal pursues (winner) a second animal that flees (loser) without physical contact occurring
Fight	≥ 2 animals engage in aggressive physical contact, with one animal breaking contact and fleeing to a further location (loser) while the other remains (winner)
Displacement	one animal approaches another and occupies the other's current location (winner) while the approached animal departs to another location (loser)
Retreat	one animal departs to another location (loser) when approached by another (winner) without physical contact occurring

all lizards were treated as nodes and individuals observed interacting were connected via edges.

Edges are social links between individuals and were directional for all interaction types except spatial proximity, which is a non-directional social link (Figure 4). Directional social links represented relationships with a dominant (i.e., winning) and subordinate (i.e., losing) lizard. To measure linear dominance in my population, I calculated Landau's index (h) using directional social links (Whitehead, 2008):

$$h = \frac{12}{n^3 - n} * \sum_{l=1}^n \left(v_l - \frac{(n-1)}{2} \right)^2$$

where n is the number of individuals in the population and v_l is the number of individuals dominated by individual l . Landau's index ranges from 0 to 1 where 1 represents a completely linear dominance hierarchy and 0 indicates that there is no consistent pattern of dominance relationships. To assess a lizard's centrality, a measure of the relative importance of the position of the node (i.e., individual) to the structure of the social network (Croft et al., 2008), I calculated degree, strength, betweenness, and assortativity (defined in Table 2) (Croft et al., 2008). For network analysis, I focused on the core animals using the study site, determined by filtering the data to include only individuals with degree ≥ 1 (Bejder et al., 1998; Croft et al., 2004, 2008; Lusseau et al., 2003; Wolf et al., 2007). Unconnected individuals (i.e., degree = 0) could have been transients or individuals only occasionally using the study site and were not part of the social network I assessed. I also determined network density, calculated as the proportion of social links present relative to the total possible social links, and identified network components, which are sets of nodes (i.e., individuals) connected to each other, but not connected to the rest of the network. On site 1, I analyzed the social network in three ways: (1) population-level network analysis using all interactions collected for an individual (= overall network), (2) interactions observed on large rocks only (= rock network), and (3) interactions observed in the

Table 2:

Definitions for each network measure used to assess an individual lizard's centrality to the network.

Centrality	
Measures	Definition
Assortativity	A comparison of an animal's characteristic of interest (i.e., sex, SVL, etc.) with the average of the same characteristic for that animal's associates. Values range from -1 to 1. Negative values indicate that animals tend to associate with individuals possessing dissimilar characteristics, whereas positive values indicate a tendency to associate with similar individuals. Values near zero indicate random mixing or no tendency to associate with individuals based on similarity in specific characteristics.
Betweenness	The number of shortest social paths between all possible pairs of animals that pass through a focal animal.
Degree	A unitless measure of the number of animals that interacted with a specific individual.
Strength	The total number of interactions for each individual.

cobble field only (= cobble field network). On site 2, I only had sufficient data to analyze the overall network.

Social metrics (betweenness, degree, and strength) were not normally distributed so I used non-parametric tests for comparisons. I used paired Wilcoxon tests to compare social metrics between habitat type on site 1 (i.e., large rock network vs cobble field network), using only lizards present in both networks. I compared the frequency of interactions, as well as social links within and between the sexes, using chi-square goodness of fit tests. For some analyses, the different types of directional interactions were pooled to compare with non-directional interactions (i.e., spatial proximity). The expected values were calculated based on the sex ratio present in the overall network. To assess the significance of the assortativity values, I used permutation tests (2000 permutations). I randomly reassigned social links in our network, recalculated assortativity for each network, and compared our observed values to the randomized distribution for identifying the level of statistical significance. Additionally, to examine if assortativity differed between the cobble field and large rock habitats, I calculated assortativity using the interactions seen in each habitat type and used permutation tests to check significance. General linear models were developed to compare social metrics (degree, betweenness, and strength) to demographic measures. A step-wise model selection process was employed, using sex, SVL, and their interaction for the model examining relationships to degree, and additionally adding in degree for strength and betweenness models. I used a square root transformation for normality. On site 2, I assessed the social network by examining network density and network components in addition to calculating degree and betweenness, but did not do further analyses as the data were insufficient and the sampling scheme more opportunistic (Table 2).

Social Organization

Home range estimates for site 2 animals were calculated using Ranges (ver. 7; Kenward et al., 2014) and statistical analyses were done in R (ver. 4.0.0; R Core Team, 2020). Home range size was estimated using minimum convex polygons (MCP; Rose, 1982) and neighbors were defined as individuals whose home range polygons overlapped. I calculated percent home range overlap for each individual relative to all other individuals in the population and summed pairwise overlap, resulting in many individuals with percent overlap values >100%. Core areas were estimated using 50% MCPs, which is the smallest polygon containing 50% of an individual's locations. I chose to use 50% of the points to delineate core area because, when plotting the sequence of home range estimates using 50% – 100% of the points (by 10% increments), there was no sharp increase in size from 50% – 90% indicating that 50% of the locations sufficiently define core areas for this population (Figure 5). Core area overlap was calculated for each lizard relative to all other lizards in the population, using each individual's 50% MCP. As with the social network measures, I developed general linear models to examine home range measures with sex, body size, and location as factors in a step-wise model selection process, which resulted in 6 models, one each for home range size, core area size, home range overlap, core area overlap, number of home range neighbors, and number of core area neighbors. In addition, we tested for nested influence, where aspects of home range predicted aspects of core area, and whether overlap predicted number of neighbors. Per capita home range overlap and per capita core area overlap was the average home range or core area overlap for each individual with its neighbors. I used paired Wilcoxon tests to examine the variation in the per capita male and female home range or core area overlap. Spearman's correlations were used to examine how space use variables were related with the sex of neighbors.

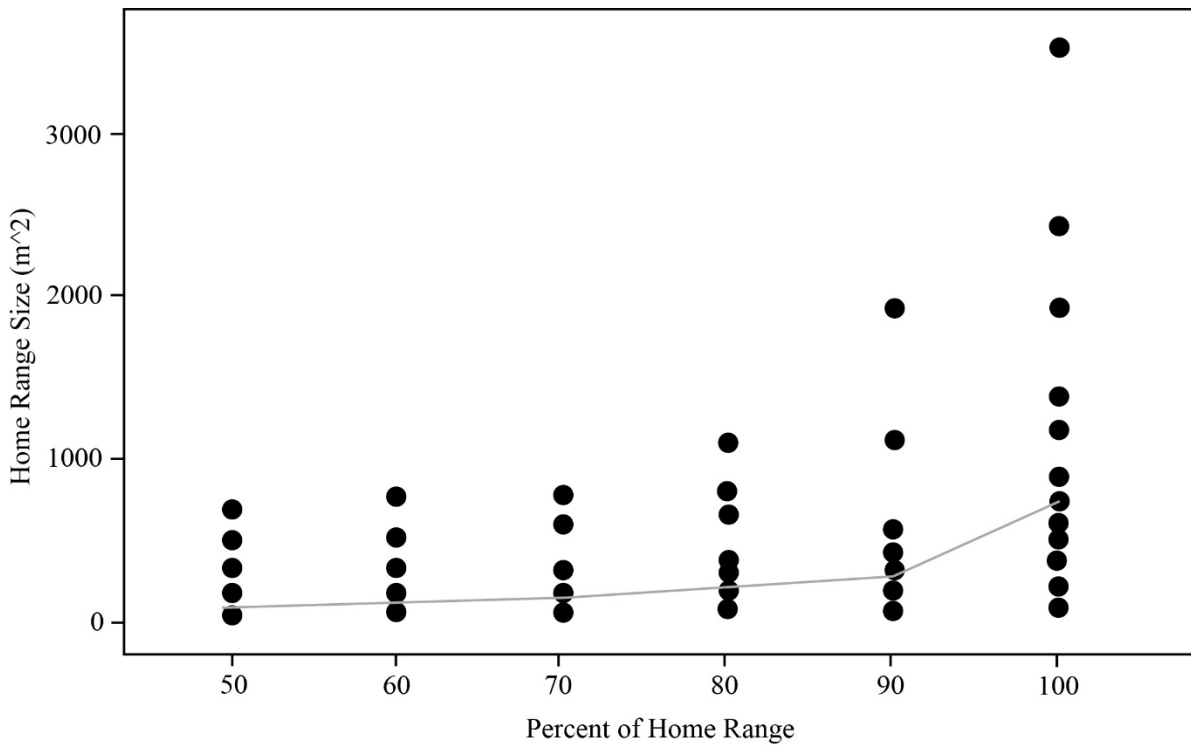


Figure 5:

*Plot of home range size as a function of the percentage of points (50% MCP to 100% used to calculate the home range estimate in 10% increments. The gray line shows the average value for the population. The increase in home range size is minimal until the jump from 50 – 90% MCP, indicating 50% is sufficient to describe the core area for *M. atacamensis*.*

I examined home range overlap and core area overlap in relation to the habitat type in ArcGIS Pro (version 2.7.26828). For each lizard, 100% MCPs were constructed by plotting the GPS location of each sighting. I then overlaid all the individual polygons into a new layer to compute the number of individuals overlapping in each cell (1x1m) throughout the study site. Additional polygons representing the two habitat structures (cobble fields vs large rocks) were added to the overlain polygons based on GPS coordinates taken in the field along the edges of the large rocks and the cobble fields. To create a similar map of overlap for core areas the same method was used with the 50% MCP locations.

Using the opportunistically collected interaction data on site 2, I computed a basic network analysis including calculations of degree and betweenness. Social and morphological metrics were not normally distributed and I used non-parametric tests for comparisons. I used Spearman's correlations to examine the relationship between degree and space use metrics.

Chapter 3: Results

The population size on both sites was similar (site 1, $n = 44$; site 2, $n = 43$), as was the number of males and females (19 males on each site; 25 females on site 1, 24 females on site 2), but site 1 was $\approx 1/10^{\text{th}}$ the size of site 2 (0.134 ha vs 1.02 ha, respectively) resulting in a density that was almost 10-fold higher than site 2 (328.4 vs 42.2 lizards/ha, respectively). Based on our captures, the sex ratio of adults does not differ significantly from 1:1 (1-sample proportion test: Site 1, $P = 0.45$; Site 2, $P = 0.54$) and is the same on both sites (Fisher's exact test: $P = 1$). On both sites, males were larger than females (SVL and mass; Table 3).

Social Structure

Site 1 Social Network Analyses

Of the 44 individuals on site 1, 30 (68%) lizards had social links and were part of the network, while 14 lizards were unconnected to the network. On site 1, our network had 1 main component and 2 smaller components consisting of pairs of individuals (dyads) (Figure 6). In the main component, both sexes were equally represented and the individuals with the highest degree included both males and females (Table 3). There was no sex difference in the proportion of individuals with a degree of 0 (i.e., unconnected to the network; females (10/25; 40%) vs. males (4/19; 21%): Fisher's exact test: $P = 0.21$). I observed 172 interactions on site 1, 37 of which (22%) occurred on the large rocks and 135 (78%) in the cobble field. The interactions composed 68 social links yielding a network density of 15.6%.

Network Structure. Most lizards in the network were somewhat peripheral, having relatively low degree, betweenness and strength values, while a small subset of the network seemed very interconnected (Figure 6, 7, 8, 9). Male and female degree, betweenness, and

Table 3:

Summary demographic and social network measures (mean \pm SE). Sample sizes are given for adult males (M) and females (F), as well as the t-test results between the sexes for demographic measures.

	Site 1		
	F (n = 15)	M (n = 15)	t, P
SVL (mm)	98.0 \pm 2.8	116.5 \pm 4.8	t ₂₂ = 3.3, P = 0.003
Mass (g)	35.4 \pm 2.6	63.5 \pm 6.5	t ₁₈ = 3.9, P = 0.001
Degree	4.5 \pm 0.9	4.6 \pm 0.9	
Betweenness	13.7 \pm 5.1	16.1 \pm 6.0	
Strength	9.5 \pm 2.6	13.4 \pm 3.6	

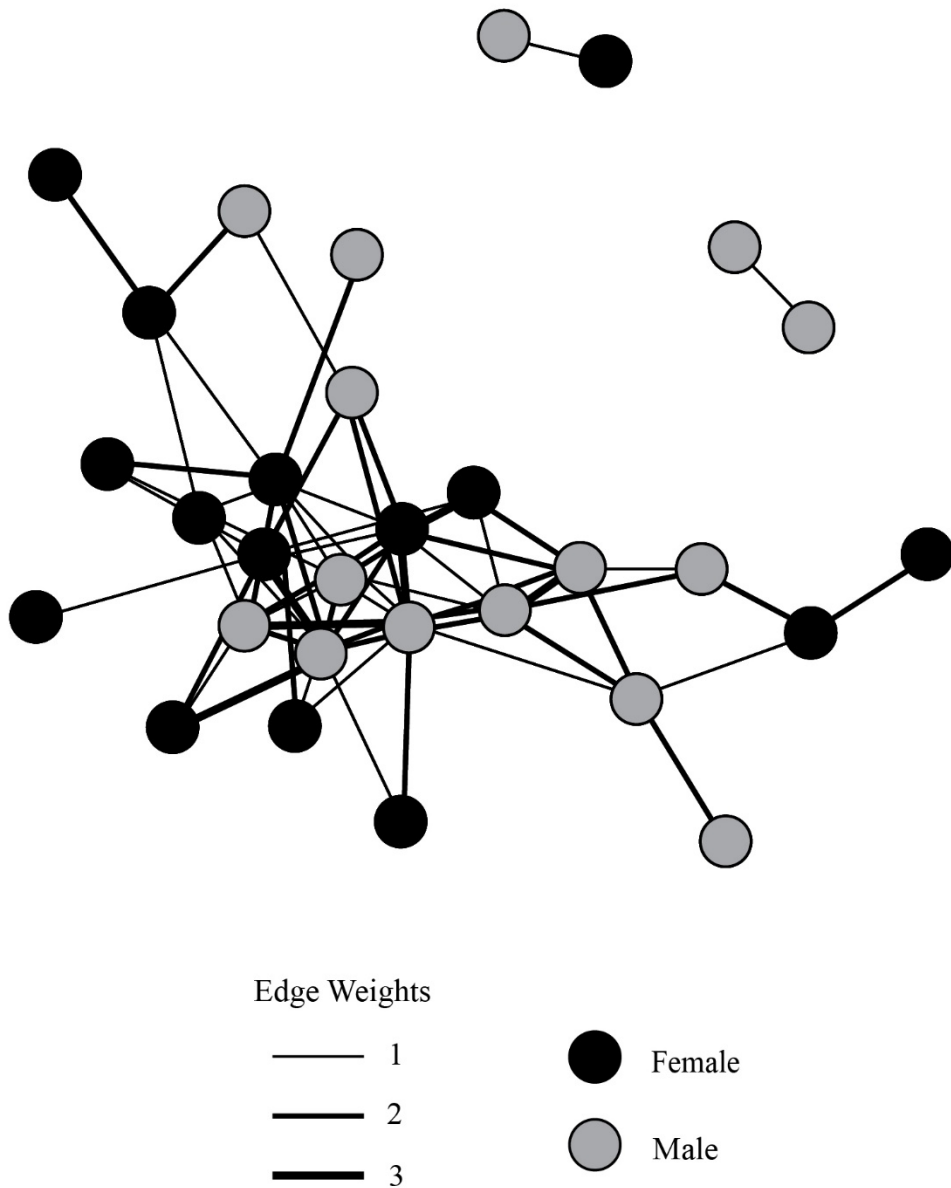


Figure 6:

Site 1 social network (n = 43 individuals): Each circle is a node and represents a unique individual with males in gray and females in black. Lines between nodes are edges and represent social links between lizards. Edges are weighted by the number of interactions that were observed among a pair of individuals. Social links that only occurred once have a weight = 1, links that occurred 2 – 5 times have a weight = 2, and links that occurred 6 – 14 times have a weight = 3.

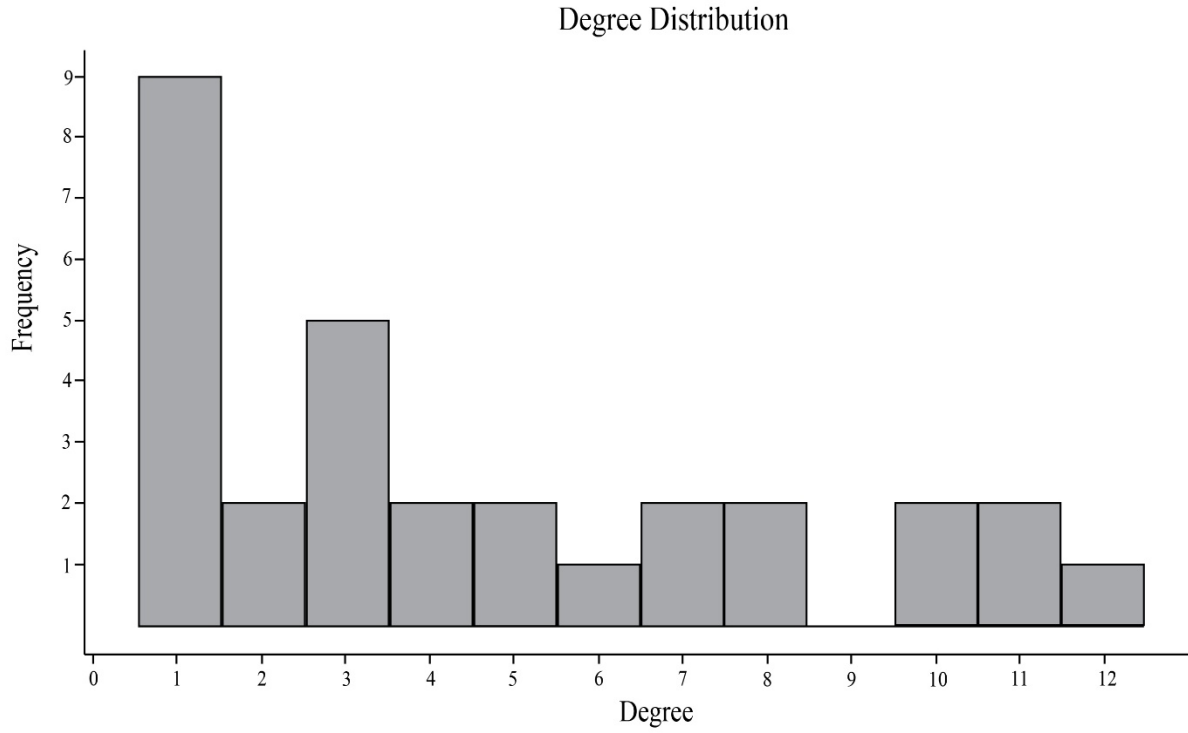


Figure 7:

Degree distribution for Site 1 ($n = 30$). Degree is the number of other lizards a specific individual interacted with.

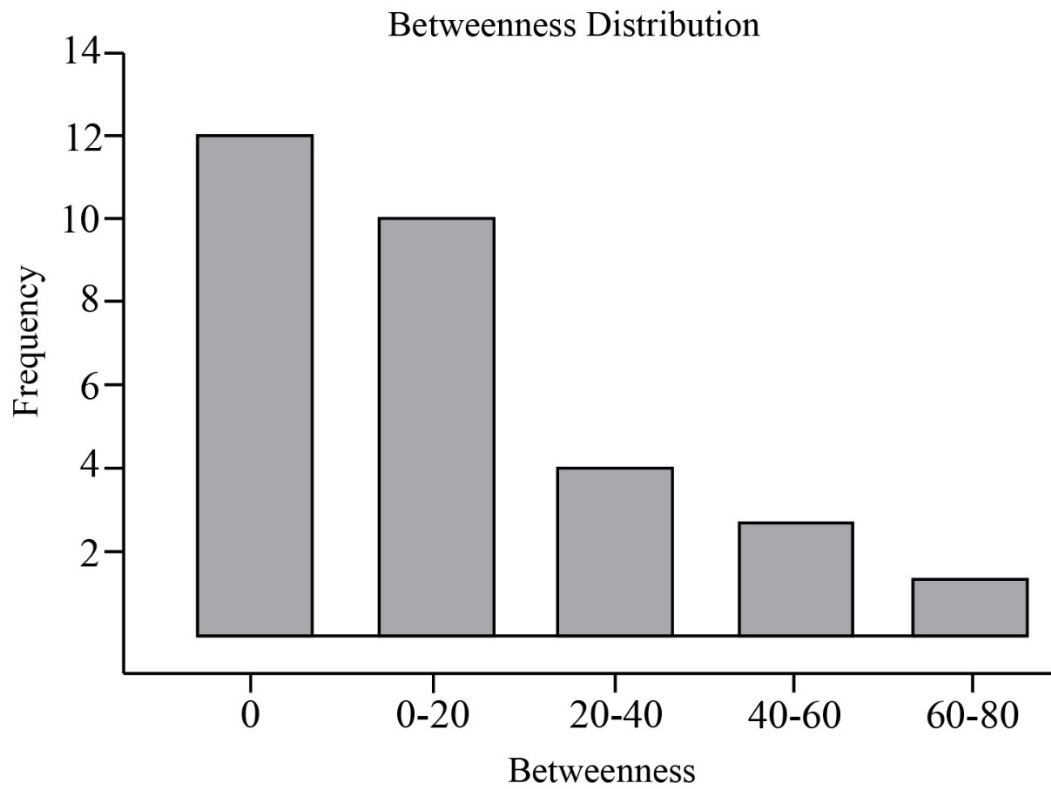


Figure 8:

Betweenness distribution for Site 1 ($n = 30$). Betweenness is the number of shortest social paths between all possible pairs of animals that pass through a focal animal and indicates centrality to the overall social network.

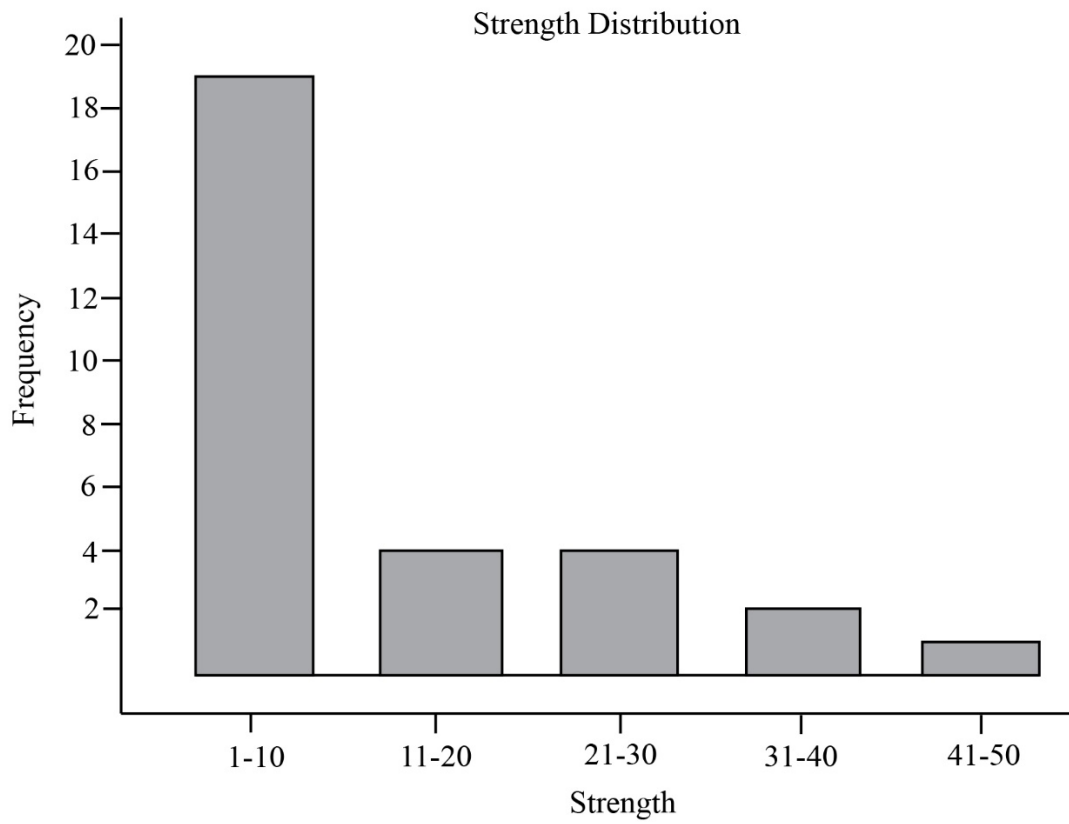


Figure 9:

Strength distribution for Site 1 ($n = 30$). Strength is the total number of interactions for each individual.

strength distributions did not differ (Chi-square test: degree, $X^2 = 0.6$, $df = 2$, $P = 0.76$; betweenness, $X^2 = 1.4$, $df = 2$, $P = 0.49$; strength, $X^2 = 3.9$, $df = 2$, $P = 0.14$). In the step-wise model selection process, no model was identified for a relationship between degree and demographic measures demonstrating that degree was not related to SVL, sex, or their interaction. The best fit model for betweenness included SVL ($F_{1,27} = 2.4$, $P = 0.13$) and showed that betweenness was strongly related to degree ($F_{1,27} = 45.6$, $P < 0.001$; overall $R^2 = 66.4\%$). In the strength model, strength was positively related to both SVL ($F_{1,27} = 5.3$; $P = 0.03$) and degree ($F_{1,27} = 131.5$; $P < 0.001$; overall $R^2 = 84.4\%$). Examining associative tendencies for sex, SVL, and degree yielded values ≈ 0 (Table 4:), indicating no strong inclination to associate with the same sex, similar-sized lizards, or with lizards of similar connectedness, respectively. I did not detect a linear dominance hierarchy in *M. atacamensis* (Landau's index: $h = 0.02$), but the dominance matrix used for the calculation was largely unpopulated (i.e., low network density), which might have prevented the determination of dominance patterns.

Interactions. About half of the total interactions were spatial proximity (51%), with the remaining interactions being directional and containing a clear winner (49%). Similar proportions of spatial proximity (78% vs 79%) and directed interactions (22% vs 21%) occurred in cobble fields and on large rocks, respectively. Male-male directional and male-female spatial proximity interactions were more common than random expectations, while female-female interactions were similar to random predictions (Chi-square test: $X^2 = 8.97$, $df = 2$, $P = 0.011$; Table 5). Among the directional interactions, larger individuals won interactions more often (79%) than smaller individuals (21%). For same-sex interactions, larger lizards won most often (n (% larger victors): males 34 (97%), females 13 (77%)). In male-female interactions ($n = 37$), larger lizards won 62% of the time and among interactions where larger individuals won, the

Table 4:

*Assortativity values calculated using all interactions based on the habitat where each interaction occurred. Statistical significance (P) calculated from permutation tests reported in parentheses. Significant probabilities are in **bold**.*

	Sex	SVL	Degree
Overall Network	0.029 (0.16)	0.068 (0.09)	0.072 (0.08)
Cobble Field	-0.062 (0.56)	0.024 (0.19)	-0.04 (0.64)
Large Rocks	0.041 (0.3)	-0.039 (0.56)	0.237 (0.04)

Table 5:

Frequency and percent of each type of interaction on site 1 (n (%)) for same sex (MM = male-male, FF = female-female) or opposite sex (MF) pairs of M. atacamensis. Percentages sum across each row.

	MM	MF	FF	Total
Chase	16 (41%)	16 (41%)	7 (18%)	39
Displacement	11 (41%)	12 (44%)	4 (15%)	27
Fight	0 (0%)	3 (100%)	0 (0%)	3
Retreat	7 (47%)	6 (40%)	2 (13%)	15
Spatial Proximity	19 (22%)	58 (66%)	11 (12%)	88
Total	53 (31%)	95 (55%)	24 (14%)	172

winners were male in all but 1 interaction (96%). In male-female interactions where the smaller individual won, all winners were female (Table 6). Of the male-female interactions, 16 were chases with females winning 25% of the time and 12 were displacements with females winning 67% of the time.

Between Habitats. Of the 68 social links I observed, most occurred on the cobble field (59%), where there were almost twice as many as on the large rocks (32%); only 6 pairs of lizards were seen interacting in both habitats (9%; Table 7). When examined by sex, nearly half of the social links occurred between males and females (49%). Among same-sex social links, equal numbers occurred among males and among females (26% and 25%, respectively; Table 7). In the cobble field and on large rocks, same sex and intersex social links were similar to random expectations (Chi-square goodness of fit test: cobble field, $X^2 = 1.62$, $df = 2$, $P = 0.44$; large rocks, $X^2 = 2.16$, $df = 2$, $P = 0.34$). Male ($n = 8$) degree and strength was significantly larger in the cobble fields than on the large rocks (paired Wilcoxon test: degree, $V = 0$; $P = 0.022$; strength, $V = 1$; $P = 0.016$) but did not differ for females ($n = 7$; degree, $V = 3.5$; $P = 0.341$; strength, $V = 2$; $P = 0.093$). Betweenness did not differ significantly between habitats for either sex (males, $V = 8$, $P = 0.35$; females, $V = 7$, $P = 0.529$). When split by habitat, assortativity values for sex, SVL, and degree were ≈ 0 , indicating that there was no trend in a lizard's assortative mixing except for degree on large rocks where lizards with similar degree values tended to interact ($P = 0.042$; Table 4).

Site 2 Social Network Analysis

On site 2, our population consisted of 43 lizards that took part in 43 interactions ($n = 21$ in cobble fields, $n = 22$ on large rocks). The interactions accounted for 28 unique social links

Table 6:

Site 1 directional interactions of same sex or opposite sex pairs by the number of times larger or smaller individuals won each interaction.

	Total Interactions	Frequency of Larger Winner	Frequency of Smaller Winner
MM	34	33 (97%)	1 (3%)
FF	13	10 (77%)	3 (23%)
MF	37	23 (62%)	14 (38%)
Total	84	66 (79%)	18 (21%)

Table 7:

Number of edges (social links) in each habitat type for each site by same sex (MM or FF) or opposite sex (MF) pairings.

Habitat	Site 1				Site 2			
	MM	MF	FF	Total	MM	MF	FF	Total
Large Rocks	4 (18%)	9 (41%)	9 (41%)	22	3 (23%)	8 (62%)	2 (15%)	13
Cobble Field	13 (33%)	20 (50%)	7 (17%)	40	5 (42%)	7 (58%)	0 (0%)	12
Both	1 (17%)	4 (66%)	1 (17%)	6	1 (33%)	2 (67%)	0 (0%)	3
Total	18 (26%)	33 (49%)	17 (25%)	68	9 (32%)	17 (61%)	2 (7%)	28

(Table 7), yielding a network density of 7.4%. The proportion of males and females with degree = 0 did not differ (females (42%) vs. males (26%), Fisher's Exact Test: $P = 0.35$).

Social Organization

Space Use

I conducted 21 surveys on site 2, using 557 locations obtained from lizards with > 3 sightings for the home range analyses ($n = 39$ lizards, $\bar{X} = 14$ points per lizard, range = 6 – 22 points). Mean home range size was 715 m², while mean core area was 89 m² (Table 8). Home range size was strongly related to the number of locations used to calculate the MCPs ($F_{1,27} = 11.63$, $P = 0.002$; overall $R^2 = 23.9\%$). Core area size was strongly related to both the number of locations used ($F_{1,27} = 19.83$, $P < 0.001$) and home range size ($F_{1,27} = 11.38$, $P = 0.002$ overall $R^2 = 55.8\%$). No variable was strongly related to home range overlap, but home range size was kept in the model $F_{1,27} = 2.22$, $P = 0.145$; overall $R^2 = 5.7\%$). Core area overlap was positively related to home range overlap ($F_{1,27} = 19.59$, $P < 0.001$; overall $R^2 = 35.2\%$). The number of home range neighbors was significantly related to home range size ($F_{1,27} = 19.92$, $P < 0.001$; overall $R^2 = 35\%$), while the number of core area neighbors was related to home range overlap ($F_{1,27} = 6.4$, $P = 0.016$), core area overlap ($F_{1,27} = 17.14$, $P < 0.001$), and core area size ($F_{1,27} = 5.96$, $P = 0.02$; overall $R^2 = 63.2\%$). Sex and body size were not related to any of the metrics. Finally, degree did not correlate with home range size, core area size, or number of home range or core area neighbors (Table 9).

Overlap

Core areas overlapped significantly less than home ranges (paired Wilcoxon test: $V = 741$, $P < 0.05$; Figure 10). The average lizard had a home range on site 2 with an average of 14.5 other neighbors, but had a core area with an average of only 2.5 neighbors. When examining

Table 8:*Summary of space use metrics on site 2 for each sex (n = 39).*

	mean \pm SE (range)
Home range size (m ²)	715 \pm 123 (43 – 3532)
Core (50%) area (m ²)	89 \pm 22 (0 – 698)
Home range overlap (%)	458 \pm 35 (24 – 854)
Number of home range neighbors (n)	14.5 \pm 1.2 (2 – 30)
Core area overlap (%)	62 \pm 9 (0 – 189)
Number of core area neighbors (n)	2.5 \pm 0.3 (0 – 10)

Table 9:

Spearman's correlations (Rho) and their significance (P-value) comparing degree and space use metrics on site 2.

Comparison	Rho	P-value
Degree & Home Range Size	0.069	0.68
Degree & Core Area Size	0.079	0.63
Degree & # of Home Range Neighbors	0.149	0.37
Degree & # of Core Area Neighbors	0.209	0.21

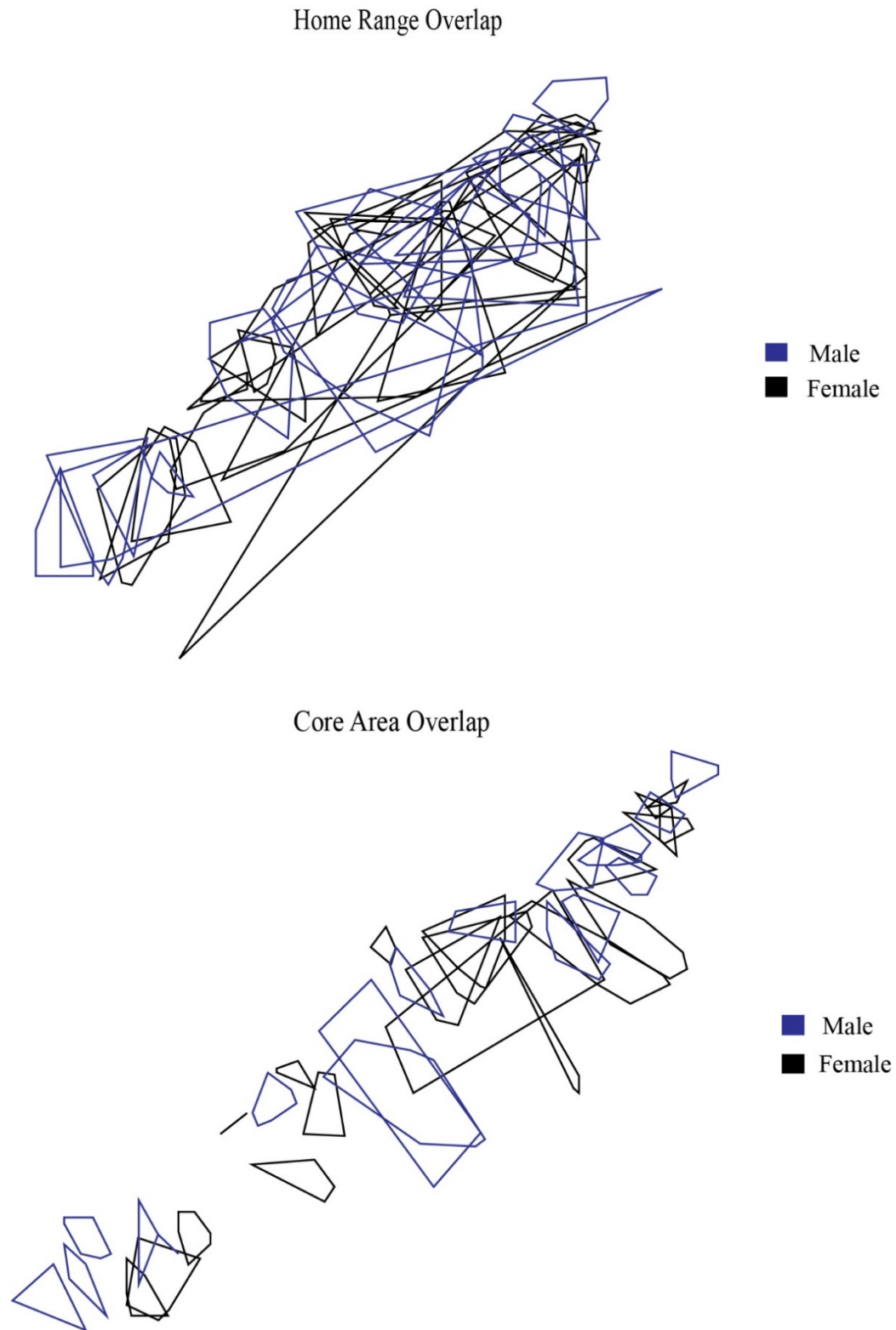


Figure 10:

Core area and home range overlap comparison.

overlap in home range compared to overlap in core area, a similar trend is evident: on average a single lizard has a mean home range overlap of 458%, while mean core area overlap was 62% (Table 8). When examining overlap by location on the study site, most home range overlap occurred in the largest cobble field (Figure 11). For mapped locations, up to 14 lizards shared space (i.e., home ranges) in that single cobble field with areas of high overlap extending onto the edges of the large rocks along the cobble field borders. Most areas outside of the largest cobble field were used by 3 – 5 individuals (Figure 11). When core areas were mapped by location, most core areas were exclusive and a maximum of 3 individuals overlapped (Figure 12).

Sex Differences

Per capita overlap in home range and core area did not differ significantly between the sexes (Mann-Whitney test: home range, $W = 181$, $P = 0.83$; core area: $W = 211$, $P = 0.35$). Per capita home range overlap with females was larger than per capita home range overlap with males (paired Wilcoxon test: $V = 224$, $P = 0.03$). However, per capita core area overlap did not differ between the sexes (paired Wilcoxon test: $V = 150$, $P = 0.23$).

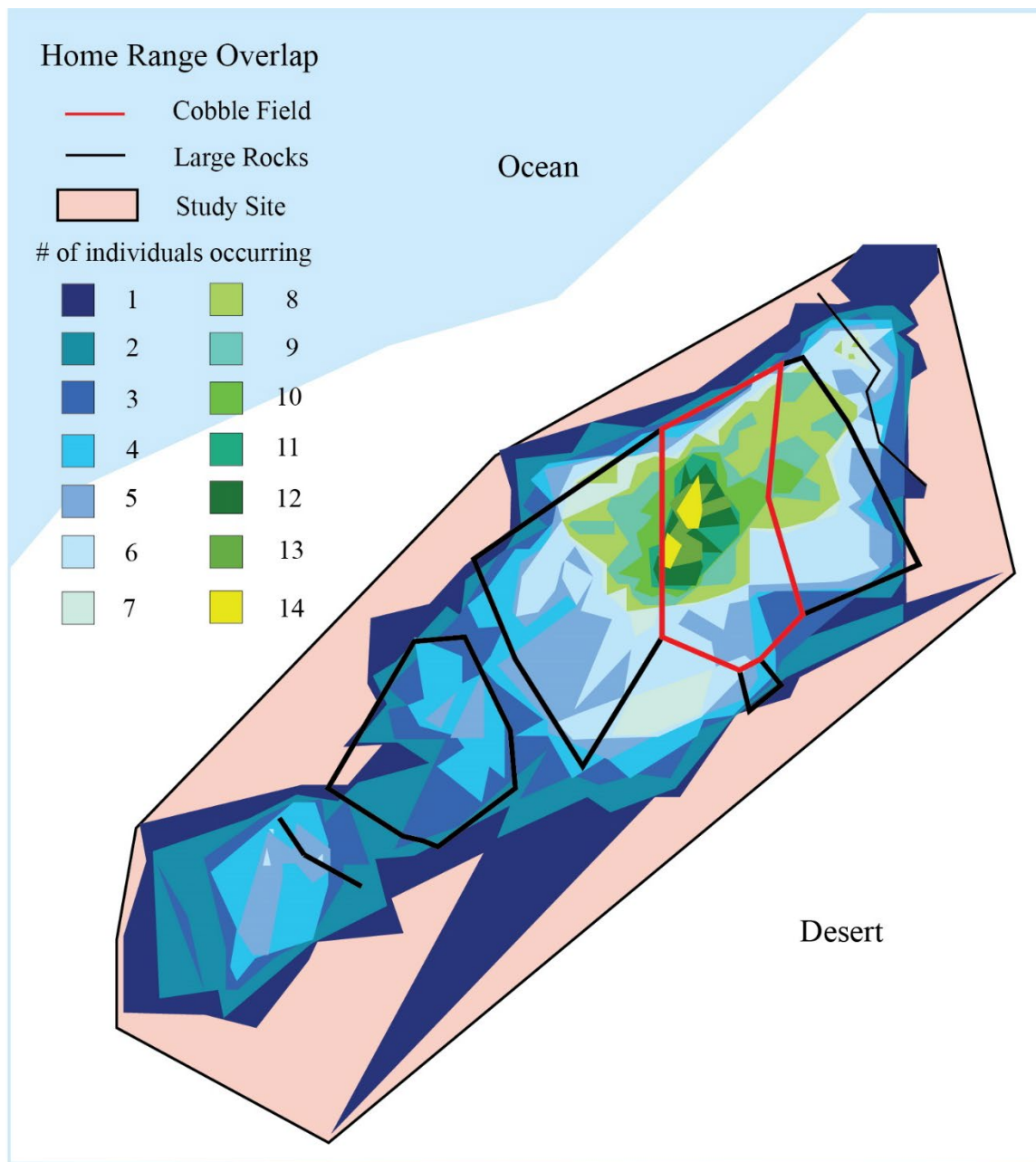


Figure 11:

Map of the site 2 100% MCPs. Home range overlap is concentrated in the largest cobble field outlined in red.

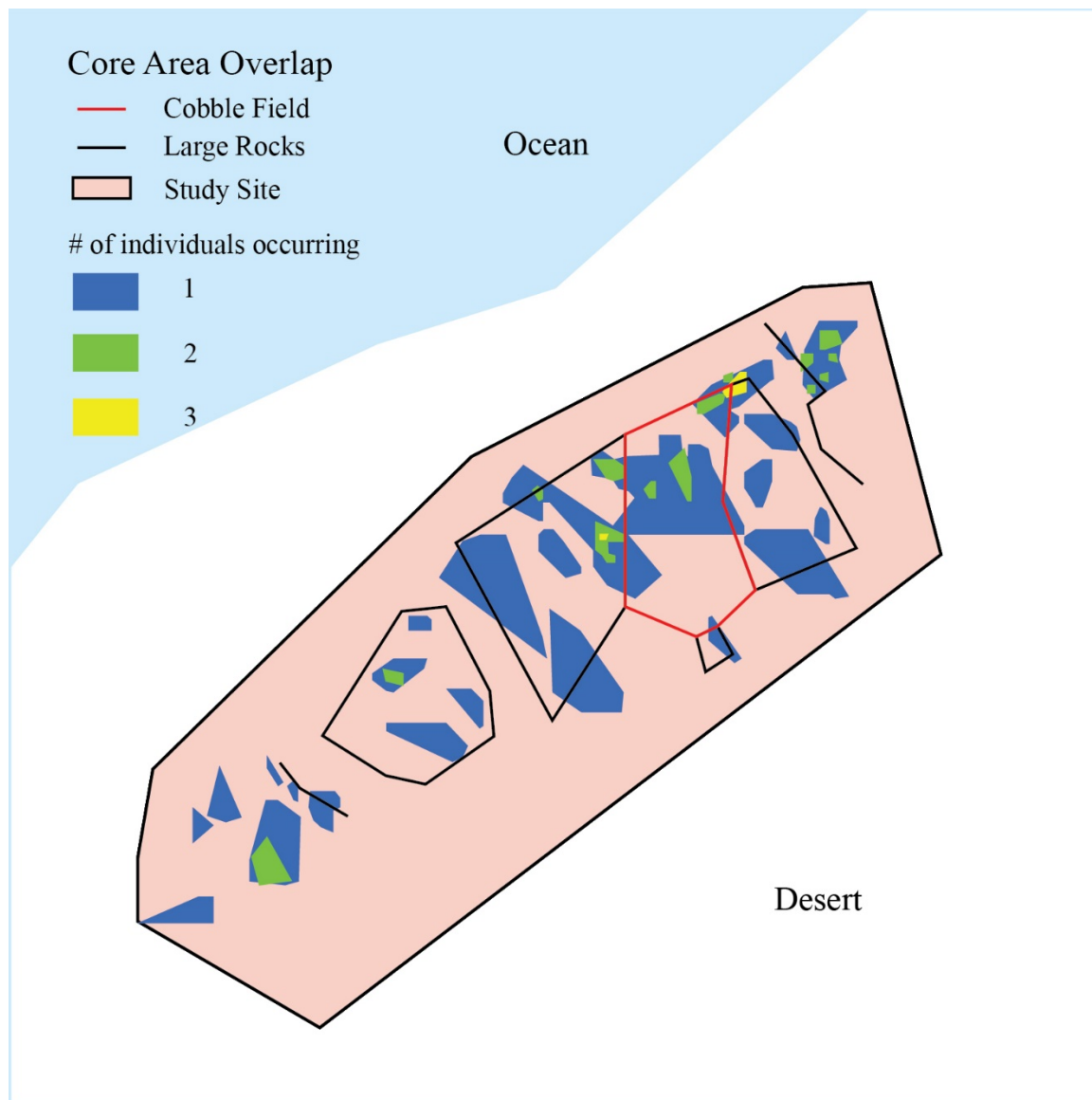


Figure 12:

Map of the site 2 50% MCPs. Core area overlap is considerably less than home range overlap.

Chapter 4: Discussion

Animal social systems often are complex, even when described from the singular point of view of the social structure, social organization, mating system, or care system. The complexity of the social system of *M. atacamensis* can be best understood by examining data through more than one conceptual framework. Their use of space (i.e., social organization) is intimately linked to their ability to interact (i.e., social structure). Only through an understanding of both frameworks can their social system be fully understood.

Microlophus atacamensis uses 2 main habitat types, each filling fundamental ecological needs necessitating that both are utilized. The cobble fields, which are in the intertidal zone, have more abundant food resources, but are submerged daily with the shifting of the tides, whereas the large rocks can provide resources that include basking locations, refugia, home crevices, and places to monitor threats. The separation of essential resources means that *M. atacamensis* is compelled to use both habitats, and although both male and female lizards have been reported to show aggressive behaviors (Carpenter, 1966; Heisig, 1993), they do not readily fit into a traditional “territorial” or “non-territorial” classification. Territorial behavior can be expected when essential resources are sufficiently abundant and concentrated to yield benefits from resource defense, so that at low or high food abundance territoriality is less cost effective (Maher & Lott, 2000). However, territorial behaviors like location defense does not mean that a species is always territorial, but rather could indicate that the species or population is living under territorial conditions (Lott, 1984). The distinction between territoriality and territorial behavior is not made often enough when describing animal social systems. Territoriality is location-specific and occurs when the benefits of defending an area outweigh costs, whereas territorial behavior can occur as part of a dominance relationship when the benefits of resource defense are not high

enough. I suggest that *M. atacamensis* is not a strictly territorial species and that their social system is a hybrid of location-dependent (i.e., territoriality) and location-independent dominance relationships resulting from an interplay between their social structure (i.e., the pattern of their social relationships) and their social organization (i.e., the spatial variation of individuals across the habitat).

Social Structure

The social network of *M. atacamensis* contained many interconnected individuals, but most had only a few associates (i.e., low degree) and relatively few of the possible social links were realized (i.e., low betweenness and low network density (15.6%)). The low connectedness by all three measures could result from indirect rather than direct interactions holding the social network together. Indirect interactions hold the network together when the social structure relies on a few highly central individuals. Theoretically, if central individuals were removed the network would fragment into smaller components, each of which is comprised of fewer individuals with direct social links. The major component of the social network on site 1 contained a few individuals that were highly central to the network (Figure 6), with males and females both among the individuals with the highest degree and strength (i.e., degree was not sex or size-dependent). However, social links were not formed on the basis of degree. Social links for both sexes tended toward expectations consistent with random mixing (assortativity ≈ 0). Low connectedness in combination with random mixing argues for the importance of indirect links in the social system of *M. atacamensis*. The prevalence of indirect links in this population of *M. atacamensis* might result from the separation of resources that establishes high levels of movement between habitats and increases the likelihood of contacting a variety of individuals.

Although body size in *M. atacamensis* was unrelated to the number of associates (i.e., degree), body size played an important role in determining the abundance (i.e., strength) and outcome of interactions. In directed interactions, larger individuals were more likely to be dominant (i.e., win), with the exception of the few females that won aggressive interactions. Body size is often important in determining which individuals can acquire, defend, or access resources like mates, food, refugia, and basking sites (Eifler et al., 2016; Noble et al., 2013; Torr & Shine, 1996). The influence of body size on winning aggressive interactions in *M. atacamensis* indicates that body size could affect the outcome of competition for resources, hinting at the possibility of a size-based dominance hierarchy. I did not find evidence of a linear dominance hierarchy using Landau's index, which is typically used to test the pattern of dominance relationships among well-known and highly social animals over long periods of study (i.e., months to years). The timeframe of my study and the fact that I only observed a small fraction of the possible social links might have influenced my inability to detect a dominance hierarchy. My observation was that larger lizards win a majority of the agonistic interactions and that a few of the larger males held socially dominant positions, often displaying from the highest locations in the cobble field and seeming to control which individuals could access the splash zone (personal obs). In addition, strength (the number of interactions for an individual) was positively related to both degree and body size, meaning that more connected, larger lizards were more likely to have repeated interactions with the same individuals. Larger *M. atacamensis* might have higher resource holding potential and be better able to defend small, high-quality areas within the cobble fields whose locations rotate based on the resources that tides both uncover and wash away. However, a truly territorial system in the cobble field is unlikely when the unpredictability of resources lowers the net benefit of territoriality (Maher & Lott, 2000), as

in Sanderlings (*Calidris alba*), where the distribution of individual birds and their foraging locations along beaches shifts based on changing prey availability caused by tides (Connors et al., 1981). Monitoring interactions in *M. atacamensis* over longer periods of time might result in more of the possible social links being realized so that Landau's index could provide a more robust assessment of dominance. Future research examining the possibility that *M. atacamensis* shift their foraging locations and the location of their aggressive interactions in response to changes in food abundance in the cobble field is merited.

In *M. atacamensis*, male-male aggressive and male-female non-aggressive interactions were most common and important in shaping social structure. Male-male aggression is common in lizards (Langkilde & Shine, 2007; Lewis & Saliva, 1987; Martín & López, 2009). It is commonly observed when the sex ratio is skewed. When the ratio is female skewed a harem defense mating system can emerge (Carothers, 1981), but when the sex-ratio is male skewed, it can result in male-male aggression and female mate guarding (Marco & Perez-Mellado, 1998). Male-male aggression is also common when there is competition for resources (Knell, 2009). In my population, the sex ratio was not skewed at either site so resource competition might be prompting male-male aggression. Some individuals attempted to control access to certain parts of the cobble field, but future research would be necessary to quantify location-specific interactions on a finer scale. Although male *M. atacamensis* are reported to exhibit territorial behavior in the form of mate guarding during the breeding season, how interactions were recorded and quantified is unclear (Heisig, 1993). The interactions reported as signifying territoriality simply might have occurred to establish dominance relationships. The higher rate of male-male aggression in the cobble fields than on the large rocks could result from a shift from location-specific defense of rocks to dominance interactions in the cobble fields as individuals

search for areas in which to forage. While male-female associations could be common as a way of strengthening reproductive pairs or alliances via spatial proximity interactions. In the Australian sleepy lizard, *Tiliqua rugosa*, long-term male-female associations increases reproductive success (Leu et al., 2015) and in primate societies male-female bonds are also known to have reproductive benefits like decreased infanticide (Baniel et al., 2016; Van Schaik, 1996; Van Schaik & Kappeler, 1997). The high frequency of male-female associations suggests that these bonds play an important role in the social system. Future research should explore the nature and context of male-female associations. Among directional male-female interactions, females tended to displace males, but only occasionally did females chase a male. Surprisingly, we did not observe any intrasexual fights. The only fights observed occurred between males and females ($n = 3$) in the cobble field, with females winning $\frac{1}{3}$ of the fights, which could have been an instance of a female rejecting a male as an associate or mating partner. Future research should investigate the frequency of fights and the potential mechanisms causing agonistic interactions.

Habitat Specific Social Structure

Most lizards did not interact with the same associates on both large rocks and in the cobble field (Table 7), suggesting that some pairs of lizards interacted only on specific habitat structures (i.e., cobble field or large rocks). To access the intertidal zone to feed, all *M. atacamensis* must enter the cobble fields, while large rocks are necessary for thermoregulation and as refuges. When comparing habitat-specific social networks, most social links occurred in the cobble field, as animals traveled through the cobble field to forage.

In the cobble field, males had more associates (i.e., higher degree) and interacted more often with their associates (i.e., higher strength) than on large rocks, while females associated with similar numbers of individuals at similar frequencies in both habitats. Additionally, same

sex and intersex social links were similar to random expectations in the cobble field (Table 7), indicating that there are no differences in sex-based social links occurring in the cobble field. As the larger sex, males should have a size advantage in aggressive interactions and be better at controlling access to resources. Some of the larger males did seem to be trying to control access to the intertidal zone, but there also seemed to be a few dominant females (i.e., high degree and high strength) that could win aggressive interactions with males. Individuals could be organized based on dominance such that a few dominant males and females are positioned at the top. Both males and females use the cobble fields to forage, but also to establish and solidify dominance, which could be supported by more intensive data delineating dominance relationships.

Tradeoffs evaluated on the basis of estimated costs and benefits of aggressive interactions in the context of foraging can vary enormously (Dubois & Giraldeau, 2003). The outcome of aggressive encounters often depends on characteristics of the individuals involved, as well as on the benefits accrued, number of competitors, and frequency of encounters. The intertidal zone represents a difficult to defend food resource where aggression across large areas would be highly costly. However, defending smaller areas or controlling access based on dominance among individuals is possible. Among shorebirds, Sanderlings (*Calidris alba*) exhibit territorial defense of feeding sites, but as food density decreases and the number of competitors increases the shifting cost-benefit ratio results in a decrease in territorial and aggressive behaviors (Myers et al., 1979). The entire cobble field cannot be defended by a single individual, but a lizard's "personal space" (i.e., radius around themselves) can be monitored and relationships sorted out therein. Lizards in the cobble fields could be defending small areas around themselves whose locations shift as the tides rise and recede, with the size of the areas defended varying with the resources contained and a lizard's resource holding potential. Whether dominant lizards control

access to better or larger stores of resources in this system (Torr & Shine, 1996) merits future investigation.

On the other hand, large rocks serve as locations for displaying, basking, and seeking shelter. Because *M. atacamensis* primarily relies on behavioral mechanisms to thermoregulate (Sepúlveda et al., 2008) and because large rocks are more spatially and temporally stable, large rocks could represent locations that can be defended in a more strictly territorial sense. Although I did not quantify the position of lizards while basking and displaying on large rocks, my general impression was that smaller lizards tended to be found lower on the large rocks, while larger lizards were seen higher on the rocks. Higher points are generally associated with higher dominance (Eifler et al., 2007; Greenberg & Crews, 1990; Tokarz, 1985). Given how body size influences dominance, future research should quantify microhabitat characteristics and the distribution of refugia as well as their use relative to body size and social standing. Microhabitat features often influence a lizard's fitness by affecting their body temperature and physiological functions in the active period that follows (Croak et al., 2008). Thus, features like crevice abundance (Eifler et al., 2017; Hedman et al., 2021), crevice size or orientation (Shah et al., 2004), rock dimensions (Eifler et al., 2017; Howard & Hailey, 1999; Schlesinger & Shine, 1994), substrate temperature (Diaz et al., 1996; Langkilde & Shine, 2004; Vasconcelos et al., 2012), and basking locations are all potential features affecting *M. atacamensis* fitness and social interactions. The Mexican spiny-tailed iguana, *Ctenosaura pectinata*, inhabits a similar ecological situation around the outskirts of villages in Mexico, where they can be found on rock walls surrounding bean fields and males exhibit territory defense. A single dominant male is able to “trespass” or move around the territories of subordinate males on the wall, but territorial behavior stops when lizards enter the bean fields to forage or move away from their territory to

access water sources (Evans, 1951). For *M. atacamensis*, the location of the large rocks provides the potential for territory defense.

Social Organization

My hypothesis that social organization, as reflected by patterns of space use and overlap, would vary with habitat was supported. Home range overlap among individuals was significantly higher than core area overlap. While the amount of overlap is interesting, information on where within an animal's home range the overlap is occurring is more relevant to their social organization. When mapped, much more of the home range overlap was shown to occur in the cobble field than on large rocks (Figure 11), illustrating the different use of the two habitat features. Core areas overlapped much less, tended to be more exclusive, and were more spread out across the study site compared to home range (Figure 12). For *M. atacamensis*, food resources are more plentiful in the cobble fields, both on the cooler rocks reached by high tides and in the actual splash zone, making the cobble fields the areas more likely to have overlapping use, whereas large rocks can be used more exclusively. The high home range overlap demonstrates the large number of lizards utilizing the cobble field for activities like foraging, while choosing more isolated areas to spend a majority of their time (i.e., low core area overlap). Additionally, degree did not correlate to any space use metrics (i.e., home range or core area size and number of home range or core area neighbors), indicating that social structure and social organization do not always follow the same pattern. Thus, the benefit of using both frameworks is a fuller understanding of the overall social system. For example, various lizard species spatially segregate, but the method of separation can vary. The desert grassland whiptail, *Aspidoscelis uniparens*, maintains exclusive core areas using aggressive interactions like chases (Eifler & Eifler, 1998), while others like the Mexican pygmy whiptail, *Aspidoscelis parvisocius*,

have a system of mutual avoidance in which individuals utilize larger areas with minimal overlap (Maslin & Walker, 1973). Not all systems are spatially organized by aggression, but the many aggressive interactions I observed supports the idea of dominance relationships organizing the social system for *M. atacamensis* in the cobble fields.

The resource use of *M. atacamensis* might be best understood by comparing them to animals in seemingly different ecological situations. Many African ungulate species are spatially constrained to areas near watering holes, especially during the dry season (Redfern et al., 2003; Valeix, 2011). The coast of Chile contains a mixture of habitat features, including intertidal zones (i.e., cobble fields) and their associated large rocks, but also sheer cliffs meeting deeper water and sparse sandy beaches meeting shallows. The cobble fields could serve a purpose similar to watering holes in deserts or savannas, as they are isolated and contain a limited resource, thereby limiting the distance lizards can reside away from these areas.

Sex Differences in Social Organization

Home range and core area size estimates did not differ significantly between the sexes, indicating similar overall space use for males and females. For both sexes, core areas were only a small proportion of their home range. During my surveys, many lizards could be found repeatedly near the same location on a large rock. The large home range estimates point out the broad areas used by lizards to access both the cobble fields and the large rocks, while the small core areas characterize the specific basking sites or refuges where the majority of their time is spent. Home ranges could be large as a result of the space required to access the cobble fields, but also spread out far enough to maintain exclusive core areas. Generally, the more time an individual spends at a location the more ably that individual can defend the space (Lott, 1984), which lends more support to a territorial organization on the large rocks where core areas are

located. Although I did not measure the amount of time lizards spent in each habitat type, 50% of their locations were in a small area, indicating concentrated use. Coupled with their low overlap in core areas, I suggest that *M. atacamensis* uses territorial defense in terms of their space use on the large rocks.

While home range overlap did not differ between the sexes, for all individuals per capita home range overlapped significantly more with females than with males. Males of many species are known to have home ranges that overlap with multiple females (Alberts, 1993; Bonatto et al., 2015; Madikiza & San, 2020; Mendez et al., 2017; Rose, 1982) likely for the purpose of increasing reproductive success and access to potential mates (Schoener & Schoener, 1980; Stamps, 1977). On the other hand, higher home range overlap of females with other females could indicate that female-female competition is comparably less, even while males tend to maintain higher levels of exclusivity in relation to other males. Although home ranges are configured relative to the home ranges of females, core areas are isolated among all individuals regardless of sex.

Conclusions

By examining social organization and social structure, I was able to more aptly reveal patterns in the social system of *M. atacamensis*. Body size played a role in determining the winner and abundance of aggressive interactions, indicating the potential for size-based dominance hierarchies. Activity in the cobble fields was greater than on large rocks as indicated by both social structure (i.e., higher frequency of interactions), and social organization (i.e., greater home range overlap), illustrating the importance of the cobble fields to the social system. In terms of same-sex and opposite sex social links, male-male aggressive and male-female non-aggressive links were most common indicating the importance of male-male competition and

male-female associations. Males interacted more and with more individuals in the cobble field compared to females. On the other hand, the large rocks were used similarly by both sexes, but tended to be more exclusively used with less overlap among individuals. Home range overlap occurred much more in the cobble field and with females, while core areas were much more exclusively maintained regardless of sex. *Microlophus atacamensis* has a shifting pattern of organization to its social system, with territoriality more likely determining relationships on large rocks, while dominance relationships play a larger role in the cobble fields. Future research should investigate the specific dynamics involved in defense of basking sites on large rocks and dominance interactions relative to food abundance in the cobble fields.

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