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Evolution of social position and structure – a multilevel selection perspective

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Evolution of social position and structure – a multilevel selection perspective

A dissertation submitted in partial satisfaction
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Doctor of Philosophy in Biology

by

Conner Steven Philson

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ABSTRACT OF THE DISERTATION

Evolution of social position and structure – a multilevel selection perspective

by

Conner Steven Philson

Doctor of Philosophy in Biology

University of California, Los Angeles, 2023

Professor Daniel T. Blumstein, Chair

The extent the evolution of sociality was shaped by multilevel selection – a theoretical framework for natural selection occurring at levels of biological organization other than the gene – is a classic debate in biology. Though common examples are focused on social behavior, we do not know if multilevel selection significantly acts on social behavioral phenotypes in the wild. For multilevel selection to contribute to evolution, social phenotypes must be variable, replicable, and have unique fitness consequences from two or more discrete levels (e.g., the individual and the group). While the individual fitness consequences of the individual social phenotype (e.g., how connected or social an individual is) have been demonstrated, the individual fitness consequences of the group's social phenotype (e.g., the structure and pattern of all social interactions in the group) for each individual who lives in the group is largely unknown. Here I quantify individual fitness consequences of the group social phenotype, providing evidence that the individual and group social phenotypes are discrete and quantifiable levels of biological organization. Chapters 2 and 3 show how residing in more connected social groups is associated with decreased individual reproductive success but increased individual winter survival in a wild, free-living population yellow-bellied marmots (*Marmota flaviventer*), a harem polygynous, facultatively social, hibernating rodent with variable and genetically heritable social behaviors. Not only does the type of group an individual resides in have fitness consequences for those individuals, but the fitness consequences of the group social phenotype are *different* than those of the individual social phenotype (e.g., less social individuals in more connected groups experience higher winter survival). Thus, chapter 3 quantifies the independent contributions of the individual and group social phenotypes to individual fitness by exploring the two phenotypes together in a unified, multilevel selection framework. We show that multilevel selection is indeed occurring, with selection for the group social phenotype stronger than selection for the individual social phenotype. Thus, given the social phenotype is variable, heritable, and under selection in this system, this work has shown that evolution (directly or indirectly genetic) for both social position and social structure as discrete phenotypes is possible.

The dissertation of Conner Steven Philson is approved.

Noa Pinter-Wollman

Peter Nicholas Nonacs

Zachary Steinert-Threlkeld

Daniel T. Blumstein, Committee Chair

University of California, Los Angeles

2023

DEDICATION

There is something to be said, in a dissertation on the consequences of social relationships and groups, about the consequences these two levels of sociality have had on me over the last four years. While an isolating journey, no doctorate is done in a silo. Countless social relationships – direct and indirect, strong and weak, directed and reciprocal – and countless social groups – sparce and dense, random and assortative, decentralized and centralized – have underlined my personal development and the research herein. While the social network minded brain of mine wants to quantify each connection and group in a mathematical and systematic fashion, too many of these tangible connections and groups have had intangible impacts to quantify. Thus, a list, while incomplete, will have to suffice.

Thank you to the following individuals for your time, energy, motivation, love, friendship, and so much more: Steven Philson, Shannon Philson, Mr. Mike Weinstein, Dr. Jason Davis, Dr. Sarah Foltz, Dr. Joel Hagen, Dr. Sara O'Brien, Dr. Matt Close, Dr. Judy Guinan, Dr. Christine Small, Dr. Cassady Urista, Joey Curti, Eva Sofia Horna Lowell, Albert Chung, Tanner Dulay, Sean O'Fallon, Cayden Williamson, Dr. Kenta Uchida, Dr. Dana Williams, Dr. Watcharapong Hongjamrassilp, Dr. Rachel Blakey, Dr. Gabriela Pinho, Dr. Chase Alexander, Gina Johnson, Kyle Voss, Dewey Overholser, Dr. Mick Demi, Dr. Scott Thomas, Dr. Susan Washko, Dr. Jared Balik, Jackie Fitzgerald, Dr. Tori Reynolds, Izzy Rodelius, Benn Schmatz, Jade McLaughlin, Mairead Brogan, the billy barr, Katie Harper, Brady Harper, Brett Biebuyck, Rick Reavis, Dr. Ian Billick, Dr. Jennie Reithel, Erik Hulm, Katie Lawn, Lisa Lucas, Steve Jennison, Rick Horn, Louis Bliard, Stavi Tennenbaum, Megan Edic, Dr. Rachel Chock, Dr. Dave Daversa, Emily

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A special thank you to my dissertation committee for dealing with an astounding lack of brevity and for your guidance every step of the way: Dr. Noa Pinter-Wollman, Dr. Peter Nonacs, and Dr. Zachary Steinert-Threlkeld.

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TABLE OF CONTENTS

LIST OF FIGURES

Chapter 4

Figure 4.1. Selection gradients (plotted as marginal effects) for the individual and group social phenotypes. Adult female reproductive success (A-B) was under positive individual selection for more social partners and closer social distances. Yearling male (C) and adult female (E) hibernation survival was under positive selection for social groups less fragmentable into two or more groups. Adult male hibernation survival (D) was under positive group selection for the number of social links between the two most distant members of the social group. Adult female hibernation survival (F) was under negative group selection for the proportion of connected triads.

LIST OF TABLES

Chapter 2

Chapter 3

Chapter 4

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I confirm the contents of this dissertation are my own work and all sources quoted, paraphrased, or otherwise are properly acknowledged in the references. I confirm that this dissertation has not been previously submitted for the awarding of a degree to this, or any other university. Any portions of this dissertation that resulted from the contributions of others are detailed below.

Chapters 2 to 4 were written as independent manuscripts for publication. While these chapters were all conducted with co-authors (acknowledged below), I developed the questions, conducted analysis, and drafted the original manuscripts myself with advice and supervision by my advisor, Dr. Daniel T. Blumstein. Manuscripts were prepared following the formatting of the respective journals or target journal. Therefore, there are minor formatting or structural differences between all chapters.

Chapter 2 was published in *Behavioral Ecology* in 2023 (DOI 10.1093/beheco/arac102) under the title “Group social structure has limited impact on reproductive success in a wild mammal”. Thus, this chapter follows the *Behavioral Ecology* formatting and is reproduced here with permission from Oxford University Press Academic. The publication was co-authored with Daniel T. Blumstein.

Chapter 3 was published in *Biology Letters* in 2023 (DOI 10.1098/rsbl.2022.0511) under the title “Emergent social structure is typically not associated with survival in a facultatively social mammal”. Thus, this chapter follows the *Biology Letters* formatting and is reproduced here with permission from The Royal Society. The publication was co-authored with Daniel T. Blumstein.

Chapter 4 was prepared and originally submitted to, and sent out for peer review in, *Science*. Thus, this chapter follows the *Science* formatting. The publication was co-authored with Daniel T. Blumstein and Julien G.A. Martin.

Data for chapters 2 to 4 were collected under the research protocol ARC 2001-191-01 (approved by the UCLA Animal Care Committee on 13 May 2002 and renewed annually), protocols approved by the Rocky Mountain Biological Laboratory, permits issued annually by the Colorado Division of Wildlife (TR-917). Thank you to the countless “marmoteers” who collected the 19 years of data used in this dissertation – you made this research possible. Thank you to Julien G.A. Martin for managing the RMBL Marmot Project database. Thank you to the staff of the Rocky Mountain Biological Laboratory for making long-term field research like this possible. Funding for this research was provided by the Rocky Mountain Biological Laboratory, Animal Behavior Society, American Society of Mammalogists, UCLA Canadian Studies Program, UCLA Graduate Division Dissertation Year Fellowship, and UCLA Department of Ecology and Evolutionary Biology.

VITA

Education

B.S. – Biology – Radford University (2019)

Selected Publications

†denotes undergraduate mentee; [Δ]denotes co-first or co-senior author

Pfau M †, Degregori S, Johnson G, Tennenbaum SR, Barber PH, Blumsten DT[Δ], **Philson CS**[Δ] (2023) The social microbiome: gut microbiome diversity and abundance are negatively associated with sociality in a wild mammal. *Royal Society Open Science* 10: 231305.

Philson CS, Blumstein DT (2023) Emergent social structure is typically not associated with survival in a facultatively social mammal. *Biology Letters* 19: 20220511.

Philson CS, Blumstein DT (2023) Group social structure has limited impact on reproductive success in a wild mammal. *Behavioral Ecology* 34(1): 89-98.

Barbee BE †, Lin MKR †, Min IA †, Takenami AM †, **Philson CS**, Blumstein DT (2022) Nutrient Enrichment Alters Risk Assessment in Giant Clams. *Journal of Zoology* 319(2): 112-118.

Philson CS[Δ], Todorov S[Δ]†, Blumstein DT (2022) Marmot mass gain rates relate to their group's social structure. *Behavioral Ecology* 33(1): 115-125. [Cover Article]

Philson CS, Grey L, Pedroncelli L, Ota W (2021) Mitigating climate change's impact on tick-borne zoonotic disease emergence. *Journal of Science Policy and Governance* 19(1).

Robin AN, Denton KK, Horna Lowell ES, Dulay T, Ebrahimi S, Johnson GC, Mai D, O'Fallon S, **Philson CS**, Speck HP, XP Zhang, Nonacs P (2021) Major evolutionary transitions and the roles of facilitation and information in ecosystem transformations. *Frontiers in Ecology and Evolution* 9:711556.

Philson CS, Nawathe R, Wagner L (2021) Mitigating California wildfire impact through zoning and housing policy. *Journal of Science Policy and Governance* 18(1).

Selected Presentations

Philson CS (2023) Evolution of social position and structure, a multilevel selection perspective. *UCLA*. Department of Ecology and Evolutionary Biology, Seminar. Los Angeles, CA.

Philson CS (2023) Evolution of social position and structure, a multilevel selection perspective. *Princeton University*. Integrated Behavioral Research Group, Seminar. Online.

Philson CS (2023) Evolution of social position and structure, a multilevel selection perspective. *California Polytechnic State University, Pomona*. Department of Biological Sciences, Seminar. Pomona, CA.

Philson CS, Bruebach C, Bastian T, barr b, Blumstein DT (2023) Environmental correlates of social network position in a wild mammal. *Animal Behavior Society Annual Meeting*. Portland, OR.

Philson CS, Blumstein DT (2023) Multilevel selection of individual and group social behaviors varies with age and sex in a social mammal. *UCLA EEB Research Symposium*. Los Angeles, CA (Poster). **Awarded First Place*

Philson CS, Blumstein DT (2023) Survival consequences of group social structure in a wild hibernating mammal. *Society for Integrative and Comparative Biology Annual Meeting*. Austin, TX.

Philson CS, Blumstein DT (2022) Group social structure relates to reproductive success in yellow-bellied marmots. *Animal Behavior Society Annual Meeting*. Virtual.

Philson CS, Todorov S, Blumstein DT (2021) Consequences of social structure for mass gain in an alpine hibernator. *Animal Behavior Society Annual Meeting*. Virtual.

Selected Research Grants

2023	Dissertation Year Fellowship – UCLA	$38,000
	Research Award – UCLA Canadian Studies Program	$1,000
2022	Graduate Fellowship – Rocky Mountain Biological Laboratory (RMBL)	$1,400
	Grants-in-Aid of Research – American Society of Mammalogists	$1,500
2021	Holmes O. Miller Fellowship – UCLA	$25,000
	Student Research Grant – Animal Behavior Society	$2,000
	Grants-in-Aid of Research – American Society of Mammalogists	$1,500
	Bartholomew Research Grant – UCLA	$1,500
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2020	Departmental Research Award – UCLA EEB	$1,675

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2022	**Teaching Associate** – Field Biology Quarter - Mo'orea (Dr. Dan Blumstein)
	Teaching Associate – Conservation Biology (Dr. Alison Lipman)
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Students Mentored *(*denotes published/submitted their undergraduate research)*

Sophia Todorov* (UCLA, 2020-‘21), Vanessa Ho* (UCLA, 2020), McKenna Sanchez* (RMBL, 2022), Carla Bruebach* (UCLA 2022-‘23), Madison Pfau* (UCLA 2022-’23), Sara Schneidman* (RMBL, 2023), Tali Szulanski* (RMBL, 2023)

Selected Service

2022-2023	**Member** – RMBL Board of Trustees’ Strategic Planning Committee
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2023	**Assistant Editor-in-Chief** – *Journal of Science Policy and Governance*
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CHAPTER 1: THE LEVELS OF SELECTION AND THE REQUIREMENTS FOR EVOLUTION

Charles Darwin's theory of evolution is universally celebrated for its explanatory power. The theory is a conceptual framework that can be applied to any question about any organism and seamlessly integrates functional, historical, mechanistic, and developmental perspectives. In the *Origin of Species* (1859), Darwin proposed three requirements for the evolution of a trait to occur: variation, replication, and selection (Darwin 1859; Jablonka & Lamb 2014; Wilson et al. 2023). Only when this triad is met is evolution possible.

Darwin thought his theory of evolution could explain all aspects of design – everything that works must have a functional basis. However, upon further thought, Darwin came upon a dilemma when thinking about social groups: why do some traits that are disadvantageous on the individual level result in benefits within the context of group living? While relatively more "recent" developments like kin selection in the context of inclusive fitness is a widely accepted answer in some contexts (Hamilton 1964a, 1964b; Eberhard 1975), Darwin had a different idea. Darwin acknowledged he couldn't explain everything by the product of natural selection unless he added something – to think of natural selection at a slightly larger scale. Writing in *The Decent of Man* (1871), Darwin suggested that the evolution of group living could affect individual survival. The extension of this today is known as group selection (Wynne-Edwards 1962; Maynard-Smith 1964; Dawkins 1986; Wilson & Sober 1994; Okasha 2006; Nowak et al. 2010; West et al. 2011).

The classic example of group selection puts forth that while individual A may dominate individual B, groups of B individuals dominate groups of A individuals. As David Sloan Wilson says, "Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary" (Wilson and Wilson 2007, p. 345). Thus, the most common way this idea has been thought about and debated is differential individual survival versus differential group survival – that groups as themselves are an entity trying to survive (Okasha 2006). While this is a case relevant to the natural world in some cases (Crow & Aoki 1982; Nowak et al. 2010), and kin selection and inclusive fitness plays an explanatory role, it is not the only case where the group selection idea is relevant. This is not to say the individuals are behaving for the good of the group, but rather, individuals can *benefit* from the *type of group* they *reside in*. In other words, it's not just who you are that impacts your individual fitness, it's the structure of the group you live in that also impacts your individual fitness. Thus, certain group structures can proliferate through time not for their ability to outcompete other groups, but because of the fitness benefits individuals gain from residing in these groups. From this logic comes a broader way of thinking about individual versus group selection.

Multilevel selection is a theoretical framework positing that natural selection occurs at multiple levels of biological organization at once, and at levels other than only on the gene (Damuth & Heisler 1988; Wilson & Sober 1994; Okasha 2005; Wilson and Wilson 2008; West et al. 2011; Goodnight 2013; Wilson et al. 2023). It is a framework for understanding the multiple selective forces acting on phenotypes and does not pit individual-level selection against group-level selection, but instead proposes selection can *simultaneously occur* and *be measured* at both levels. For example, this may be selection acting simultaneously at the level of the gene, cell, organism, or group. Multilevel selection has already been documented as a driving force in the emergence of the first multicellular organisms (Yu et al. 2020) to the structure of entire ecosystems (Johnson & Gibson 2021) and cultures (Wilson et al. 2023). Multilevel selection also acts on morphological phenotypes in plants and animals (Stevens et al., 1995; Weinig et al., 2007; Formica et al. 2021).

However, despite social behavior being the most common example in the case for multilevel selection (Wilson 1997; Wilson & Kniffin; Wilson & Wilson 2007, 2008; O'Gorman et al. 2008; Kramer & Meunier 2016), no work to date has explored if multilevel selection for social behavior occurs in wild populations. While some work has explored multilevel sexual conflict (Eldakar et al. 2010) and multilevel selection for social behaviors in laboratory settings (Costello et al. 2023), the debate for multilevel selection as an evolutionary force on social behaviors in natural settings is largely a theoretical, not analytical, debate. Given social behavior is found in numerous taxa and underpins human societal institutions, this question has the potential to reshape our understanding of the evolutionary origins of friendship across species, and governments across nations.

Social behavior is further a particularly interesting phenotype to ask about multilevel selection because the costs, benefits, and evolution of social group living is relatively well established (Tinbergen 1963; Alexander 1974; Hinde 1976). Individuals reside in social groups to avoid predators, acquire resources, or attract mates (Alexander 1974). From social group living comes two discernable and discrete levels of biological organization: (1) how social an individual is within their social group and (2) the overall structure and pattern of all social interactions within their social group (Hinde 1976; Wasserman & Faust 1994; Moore et al., 1997; Croft et al. 2016; Kappeler 2019). This individual social position and group social structure vary within many species (Hinde 1976; Kurvers et al. 2014; Croft et al. 2016; Ilany & Akcay 2016; Kappeler 2019; Shizuka & Johnson 2020). Individual social behavior and position is also genetically heritable in many species (Lea et al. 2010; Brent et al. 2013; Ilany & Akcay 2016). By contrast group social structure is modulated via the genetics of individuals that comprise the group, indirect genetic effects, cultural inheritance, and social learning (Gardner 2015; Moore et al., 1997; Ilany & Akcay 2016; Cantor et al. 2021). Thus, individual social position and group social structure satisfy the variation and replication components of the Darwinian triad, leaving only selection (Darwin 1859; Jablonka & Lamb 2014; Wilson et al. 2023). It's also important to note that "natural selection acts on phenotypes, regardless of their genetic basis" and "can be measured without recourse to principles of heredity or evolution. In contrast, evolutionary response to selection, the genetic change that occurs from one generation to the next, does depend on genetic variation" (Lande and Arnold 1983, p. 1210). In other words, selection can occur and be measured regardless of any genetic evolution.

Given that individual social position and group social structure, like most biological traits, are not completely independent, we must simultaneously understand their selection *relative to each other*. Thus, if we are to modify Darwin's triad: we're looking for variation, replication, and multilevel selection.

For multilevel selection to occur for two seemingly similar phenotypes, there must be unique fitness consequences for each of the two phenotypes. That is, the fitness consequences of group social structure cannot be identical to the fitness consequences of individual social position as this could, and perhaps should, be interpreted as non-independence and thus individual level selection manifesting at different levels (though this doesn't apply in case of identical or nearly identical genetic makeups across levels, such as some eusocial insects). In other words, to be confident that it is truly multilevel selection, we must be able to quantify that individual social position and group social structure have mostly unique individual fitness consequences (given the difficulties of quantifying two levels of selection if identical in direction and magnitude). That is, more socially connected individuals residing in more socially connected groups cannot always have the same fitness consequences for example. While the fitness consequences of individual social position are well studied across taxa (Formica et al. 2012; Royle et al. 2012; Kurvers et al. 2014; Croft et al. 2016; Fisher & McAdam 2017; Snyder-Mackler et al. 2020), not much is known about the individual fitness consequences of social group structure in the wild (Solomon-Lane et al. 2015; Croft et al. 2016; Philson et al. 2022; Costello et al. 2023; Philson & Blumstein 2023a, 2023b).

The following chapters leverage a long-studied population of yellow-bellied marmots (*Marmota flaviventer*) at the Rocky Mountain Biological Laboratory, a subalpine field station in Colorado to explore these questions. Yellow-bellied marmots live in matrilineal social groups where the coefficient of relatedness is relatively high across groups and thus kin selection between groups is not as strong of a factor, as all groups have a relatively high coefficient of relatedness (Schwartz & Armitage 1983). Yellow-bellied marmots are further a well-suited system for the exploration of the evolution of social position and structure via multilevel selection given they are socially variable (Armitage 2014) and have genetically heritable social positions (Lea at al.

2010). Thus, yellow-bellied marmot's social phenotypes satisfy two of the three components of the Darwinian Triad. Further, the fitness consequences of more social and connected individual social positions are well documented in this system (increased summer survival: Montero et al. 2020; decreased winter hibernation survival: Yang et al. 2016, decreased reproductive success: Wey & Blumstein 2012; decreased longevity: Blumstein et al. 2018). Lastly, we have nearly 20 years of long-term, detailed behavioral, demographic, life history, and fitness data on individually marked individuals – a unique and powerful dataset in the fields of ecology and evolutionary biology (Clutton-Brock & Sheldon 2010; Blumstein 2013; Armitage 2014).

To leverage this system to ask about the evolution of social position and structure with a multilevel selection perspective, we must first ensure that the individual fitness consequences of individual social position and group social structure are not the same. Thus, Chapters 2 and 3 assess the individual fitness consequences of group social structure. While we can't easily quantify fitness directly in this system (i.e., gene contributions to the population), we can quantify representative fitness correlates such as reproductive success (Chapter 2) and survival (both summer and winter survival given this system is an obligate hibernator with different selection pressures for survival in each season; Chapter 3).

While more social individual marmots experience increased summer survival (Montero et al. 2020), I show in Chapter 3 that there is no relationship between the structure of the social group an individual resides in and their probability of surviving summer (Philson and Blumstein 2023b). While more social individual marmots experience decreased winter survival, I also show in Chapter 3 that individuals residing in more connected and less breakable (into two or more) social groups have increased winter survival (Philson and Blumstein 2023b). In Chapter 2 I show that individuals residing in more breakable social groups (Philson and Blumstein 2023a), in addition to more socially connected individuals (Wey & Blumstein 2012), have decreased reproductive success.

Thus, not only are the individual fitness consequences of individual social position largely different than the individual fitness consequences of group social structure, but traits at one level are not necessarily consequential at the other. Thus, in some biologically relevant cases, there are unique fitness consequences between the two of biological organization of interest. This allows for the possibility of multilevel selection.

Given that there is documented variation and replication of individual social position and group social structure, and that individual social position and group social structure have non-aligned individual fitness consequences, Chapter 4 explores if multilevel selection simultaneously occurs for social position and social structure in this system. If multilevel selection is present, then, and only then, would the evolution of social position and structure be possible. Using contextual analysis to partition selection among the two levels of social organization (Lande and Arnold 1983; Damuth & Heisler 1987; Goodnight et al. 1992; Goodnight and Stevens 1997), we fit four analogous pairs of social network traits that tell a similar story across the two levels and have had documented fitness consequences in previous studies. These analogous network trait pairs quantify four core components in human and non-human animal social networks (including yellow-bellied marmots) at the two levels of social network organization: connectivity, closeness, breakability, and clustering (Wasserman & Faust 1994; Krause et al. 2009). We additionally included other biologically relevant variables (e.g., body mass, predator index, location, social group size) to ensure that we were not measuring selection for the two levels of social traits in isolation, but in relevance other selective forces or traits that may buffer selection in this system.

I show, in Chapter 4, that multilevel selection is occurring for both individual social position and group social structure (Philson et al. *in review*). There is both negative and positive selection for more social individual social phenotypes for female reproductive success and negative selection for more connected group social phenotypes for winter survival across age-sex groups. Because the two levels of the social phenotype were scaled prior to analysis, we can compare the strength of selection with the model estimates. The mean absolute strength of selection for individual traits is 0.76 whereas the mean strength of selection for group traits 1.03. This suggests selection is, on average, stronger for the group social phenotype. I found no case for selection within the analogous pairs of social network traits or the same fitness-age-sex setting, suggesting that traits at one level are not also under selection at another level but that some traits are under selection at the individual level and *different* traits are under selection at the group level within specific age-sex classes. Lastly, summer survival wasn't under selection at either level, and given the selection for group living in this system is largely contributable to predator avoidance, this suggests the selection for group living is different than the selection for social position and social structure, which are a subsequent byproduct of group living.

In summary, I have shown that there is variation, replication, and selection for both social position and social structure. Therefore, the evolution of social position and structure is indeed possible, and can be interpreted, using a multilevel selection perspective.

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CHAPTER 2: GROUP SOCIAL STRUCTURE AND REPRODUCTIVE SUCCESS

Abstract

The frequency and type of dyadic social interactions individuals partake in has important fitness consequences. Social network analysis is an effective tool to quantify the complexity and consequences of these behaviors on the individual level. Less work has used social networks to quantify the social structure – specific attributes of the pattern of all social interactions in a network – of animal social groups, and its fitness consequences for those individuals who comprise the group. We studied the association between social structure, quantified via five network measures, and annual reproductive success in wild, free-living female yellow-bellied marmots (*Marmota flaviventer*). We quantified reproductive success in two ways: (1) if an individual successfully weaned a litter and (2) how many pups were weaned. Networks were constructed from 38,968 interactions between 726 unique individuals in 137 social groups across 19 years. Using generalized linear mixed models, we found largely no relationship between either measure of reproductive success and social structure. We found a modest relationship that females residing in more fragmentable social groups (i.e., groups breakable into two or more separate groups of two or more individuals) weaned larger litters. Prior work showed that yellow-bellied marmots residing in more fragmentable groups gained body mass faster – another important fitness correlate. Interestingly, we found no strong relationships between other attributes of social group structure, suggesting that in this facultatively social mammal, the position of individuals within their group, the individual social phenotype, may be more important for fitness than the emergent group social phenotype.

Introduction

Dynamic social structures and relationships arise as a result of behavioral interactions between individuals (Hinde 1976), and social behavior and aggregation have demographic and evolutionary consequences (Alexander 1974; Wilson 1975; West-Eberhard 1979; Wey et al. 2008; Farine and Sheldon 2015). To advance our knowledge of the adaptive value of sociality, we must expand our understanding of precisely how animals are affected by their social interactions (Hinde 1976; Krause et al. 2007; Silk 2007; Croft et al. 2008; Kurvers et al. 2014).

Over the past decade social networks have been used to quantify a variety of measures of sociality and have shed novel insights on the adaptive value of sociality (Wey et al. 2008; Whitehead 2008; Pinter-Wollman et al. 2014; Croft et al. 2016). Prior work exploring the fitness consequences of sociality using animal social networks can be broadly summarized into three main areas: [1] how an individual's social interactions affect them (e.g., copulation success in male forked fungus beetles (*Bolitotherus cornutus*); Formica et al. 2012), [2] how an individual's social mate's interactions affect them (e.g., survival in bottlenose dolphins (*Tursiops sp.*); Stanton and Mann 2012), and [3] how individual social interactions influence group and population processes (territory selection in great tits (*Parus major*); Farine and Sheldon 2015). In summary, the pattern and makeup of interactions individuals participate in has direct consequences for their fitness, the structure of their group, and population processes (Lusseau 2003; Oh and Badyaev 2010; Formica et al. 2012; Kurvers et al. 2014; Croft et al. 2016; Leu et al. 2016).

However, these prior network studies have largely overlooked the role of the social group as a whole in influencing an individual's success (i.e., group-level selection; Wilson 1983; Okasha 2006). That is, current animal behavior network research has under addressed how the resulting feedback from all the interactions between individuals in a group subsequently influences each individual who comprises the group. This is separate from asking how individuals contribute to the social structure – specific attributes of the pattern of all social interactions in a group – but instead explores the consequences of social structure, which is an emergent property (Moore et al. 1997; Kappeler 2019). Social structure, or the group's social phenotype, is more complex than averages of individual-level network values (the individual social phenotype). Therefore, to better map the consequences of sociality for individuals, the influence of social structure must be explored directly.

Prior research has already suggested a relationship between the social group and individual fitness correlates. For example, individuals residing in groups with regular intragroup conflict experience reduced reproductive opportunity and success and increased chronic stress in a variety of primates (de Waal 2000; Flack et al. 2006), as well as water striders (*Aquarius remigis*; Sih and Watters 2005) and meerkats (*Suricata suricatta*; Young et al. 2006). While suggesting the social group may influence an individual's success, these studies did not identify specific attributes of the social group. Work on humans has quantified social structure via social network analysis and explored team success in English Premier League soccer (Grund 2012) and professional e-sports (Mora-Cantallops and Sicilia 2019), the vitality of Western Chinese housing markets (Zhang et al. 2012), the inefficiency of the U.S. Congress (Neal 2020), and work in non-human primates has explored the social structure factors impacting primate group size (Balasubramaniam et al. 2017) and movement patterns (Dufour et al. 2011). How animal's group social structures respond to altered ecological conditions (Leu et al. 2016; Costello et al. 2022) and how social structure emerges based on the group's composition of individual personalities (Cook et al. 2022) has also been quantified with social network analysis. Though, the connection between specific attributes of social structure and its fitness consequences is greatly understudied, in both humans and non-humans.

Reproductive success is a key fitness component (Clutton-Brock 1988). Different aspects of reproductive success are influenced by biotic and abiotic factors such as weather (Thompson 1997; Krüger 2002), prey and predator abundance (Lack 1947; Martin 1987; Durant 2000), and population density (Kunin 1997; Luijten et al. 2000). Reproductive success is also influenced by the performance and outcome of social behaviors (Alexander 1974; Silk 2007). Prior work has used social networks to explore this relationship on the individual level in a range of taxa including, but not limited to, some insects (Formica et al. 2012), lizards (Godfrey et al. 2012), birds (McDonald 2007; Ryder et al. 2008; Oh and Badyaev 2010), fishes (Solomon-Lane et al. 2015), and mammals (Silk et al. 2009; Wey et al. 2013; Wyman et al. 2021). These prior studies focused almost entirely on individual level sociality, and not that of group social structure.

Few studies have explored the social structure-fitness relationship. One such study explored displacement networks in captive bluebanded gobies (*Lythrypnus dalli*), an obligatorily social species, and identified a negative relationship between individual reproductive success and aggressive reciprocity (rate at which aggressive behaviors were both initiated and received between social ties across the group; Solomon-Lane et al. 2015). This study demonstrated how social network analysis can be applied to both describe the attributes of a group's social structure and quantify its consequences at the individual level. However, how this important relationship transpires in wild populations, or in facultatively social species, is not known. Here we explore the social structure-reproductive success intersection in a long-studied population of free-living wild yellow-bellied marmots (*Marmota flaviventer*), a facultatively social rodent.

Yellow-bellied marmots are an ideal system in which to study the consequences of social group structure for several reasons. First, they are socially plastic which creates variation in social structure (Blumstein 2013). Second, social connections at the individual level have been related to reproductive success. Males (who fight with other males to control matrilines and gain or maintain reproductive access) who participate in more agonistic behaviors experience reproductive benefits (Wey and Blumstein 2012). Adult female marmots (the central figures in social groups) who are more social in affiliative (e.g., greeting, allogrooming, play) networks experienced reproductive determents (Wey and Blumstein 2012), potentially due to the time and energy costs of social interactions. This finding corroborated previous work in this system that found social factors differentially influenced reproductive success across sexes (Armitage 1991). Third, prior work in this system showed that group social structure is associated with a key fitness trait – the rate at which marmots gain mass in the summer, which is highly correlated with over-winter survival because fat reserves are the primary metabolic energy source during hibernation (Philson et al. 2022). Specifically, marmots residing in less connected, more socially homogeneous, and more stable social groups tended to gain less body mass during the summer growing season than those residing in social, heterogeneous, and unstable groups. Together, these past studies strongly suggest sociality has significant implications for marmot reproductive success and that social structure has the potential to influence reproductive success. These results also provide the background knowledge to develop specific hypotheses. Lastly, the long-term dataset on this population, with a large number of replicate social group measurements, and associated fitness measures over two decades, enabled us to explore the social structure-fitness relationship beyond a few social groups in laboratory settings.

We developed *a priori* hypotheses for the relationship between five attributes of social structure (density, transitivity, reciprocity, positive degree assortativity, and cut points; Table 1) and two measures of reproductive success in adult female marmots: (1) if offspring were successfully weaned and (2) the number of offspring weaned, if offspring were weaned. These five network measures have homologous measures on the individual level, which facilitated the development of *a priori* hypotheses as well as our understanding of the consequences of social behavior across social scales.

Our specific *a priori* hypothesis was that individuals in more connected and sociable groups would experience lower reproductive success. This hypothesis was informed by previous network studies in this system showing strong individual social relationships are often costly for reproductive success (Wey and Blumstein 2012) and that residing in connected groups reduced mass gain during the summer – a key fitness-related trait for marmots (Philson et al. 2022).

Also based on our previous social structure study (Philson et al. 2022), we hypothesized individuals residing in socially homogeneous groups would experience higher reproductive success. Social homophily within a group may lead to a reduction in social stressors because interactions are more predictable and reliable (Massen and Koski 2014). Additionally, less stressed female marmots have higher reproductive success (Monclús et al. 2011; Blumstein et al. 2016; Pinho et al. 2019). Being surrounded by similarly social individuals may facilitate avoidance of stressful and aggressive interactions and instead allow for more time and energy to be allocated towards tending to offspring. Thus, we hypothesized social homophily would enhance reproductive success.

Finally, we hypothesized that attributes of social structure would be more strongly related to the number of offspring that weaned from the burrow than it would be related to whether an individual successfully weaned offspring. Individuals that are involved in many interactions may become socially stressed, energetically depleted, and may have less time and energy for parental care, and consequently may wean fewer offspring. Thus, variance in the number of offspring weaned may be explained more by attributes of social structure than if an individual weaned any offspring at all.

Overall, this work will help us contextualize the potential role that social structure, an emergent property, plays in influencing reproductive success. By doing so, it adds to our understanding of the adaptive value of sociality across social scales. We use a well-studied population of a wild social mammal with a large number of replicate social groups across 20 years to address this question.

Methods

Data collection

The yellow-bellied marmot population around the Rocky Mountain Biological Laboratory (RMBL) in the Upper East River Valley, Gothic, Colorado (38°57’N, 106°59’W; ca. 2900 m elevation) has been continuously studied since 1962. Yellow-bellied marmots are a facultatively social, harem-polygynous species of ground-dwelling squirrel that live in matrilineal colonies with one or two territorial males (Frase and Hoffmann 1980; Armitage 1991). Active for five months annually (early May to mid-September), marmots mate soon after emerging from hibernation, with new pup emergence and yearling dispersal occurring around late-June/early-July. Annually, nearly half of females and most males disperse with most dispersal resulting in movement out of the study area (Armitage 1991).

From 2002 to 2020, marmots were observed and repeatedly live trapped during their active season. Using Tomahawk-live traps placed near burrow entrances, individuals were trapped and immediately transferred to cloth handling bags to record body mass, sex, and other morphological and physiological measures. Only adults are reproductively mature (pups <1 year, yearlings =1 year, and adults ≥2 years. All marmots are given two uniquely numbered permanent metal ear tags (Monel self-piercing fish tags #3, National Band and Tag, Newport, KY) and marked on their dorsal pelage with nontoxic Nyanzol fur dye (Greenville Colorants, Jersey City, NJ) to aid identification from a distance. Virtually all marmots in our study population are trapped and marked annually, permitting us to accurately identify interacting individuals. Since most other marmots at each colony site were marked, we can often identify the individuals that may have not been recaptured after molting their pelage (and thus marks). Colony sites can be grouped into a higher classification of higher elevation and lower elevation sites (five are at higher elevation sites, seven are at lower elevation sites). Higher elevation sites are ~166 m higher than lower elevation sites and experience harsher weather conditions (Van Vuren and Armitage 1991; Blumstein et al. 2006; Maldonado-Chaparro et al. 2015b).

Detailed social interactions in this population have been recorded since 2002. Behavioral observations are made during hours of peak activity (07:00–10:00 h and 16:00–19:00 h; Armitage 1962) using binoculars and spotting scopes from distances that did not disrupt normal social behavior (20–150 m; Blumstein et al. 2009). We classified each interaction as either affiliative (e.g., greeting, allogrooming, play) or agonistic (e.g., fighting, chasing, biting; detailed ethogram in Blumstein et al. 2009). We also recorded the initiator and recipient, time, and location of each interaction. Most interactions (79%) occurred between identified individuals. The direction of the remaining 21% interactions could not be identified because the marmot's dorsal fur mark was not visible, due to the marmot's posture or visual obstructions, and thus we excluded these interactions from our data. Excluding these interactions between unidentified individuals should not significantly influence social structure (Silk et al. 2015). Our data also only consisted of yearlings and adults because these cohorts were present early in the season, when social interactions were the most common. We excluded pups from our data because of their mid-season emergence and as they primary only interact with each other and their mother (Nowicki and Armitage 1979). Additionally, we filtered out individuals observed or trapped fewer than five times in a year to eliminate those dispersing through the study area (Wey and Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018).

Social network measures

Using this refined social observation data collected from 2002 to 2020 and the R package "igraph" (Csardi and Nepusz 2006; version 1.2.11; R Development Core Team 2021; version 4.1.2), weighted (accounting for the number of interactions in a social connection) and directed (accounting for who initiates and receives each interaction) social interaction matrices were constructed from affiliative interactions between individuals for each year. We focused on affiliative interactions because they relate to female marmot reproductive success on the individual level (Wey and Blumstein 2012) and because they comprised 88% of interactions in our refined data. These affiliative matrices consisted of 38,968 social interactions between 726 individuals (626 of whom were observed across multiple years). 18,438 of these interactions and 313 unique individuals were at our lower elevation sites and 20,530 interactions and 417 unique individuals were at the higher elevation sites. From these matrices we defined a social group as each network isolate (set of connected individuals with no other external connections) that appeared naturally within a valley location (higher elevation or lower elevation; Philson et al. 2022) in a given year. This produced 137 social groups in total. The number of social groups that emerged from a valley location ranged from 1 to 6, while the total number of social groups in our study area annually ranged from 4 to 11. Group sizes ranged from 3-58 individuals with a mean of 20.51 (SE = 0.52) across the dataset.

For each social group we calculated five social network measures to quantify social structure (described in Table 1). Density, transitivity, and cut points represent specific attributes of connectivity; reciprocity and degree assortativity represent specific attributes of homophily. We selected these five social network measures due to their importance in past papers in our system (transitivity: Wey et al. 2019; density, transitivity, cut points, reciprocity, and degree assortativity: Philson et al. 2022), other systems (density: Weinig et al. 2007; reciprocity; Soloman-Lane et al. 2015) and/or because these network measures have analogous measures on the individual level, aiding our understanding of consequences of social behavior across social scales (Wasserman and Faust 1994). Our observations of marmot social groups across their entire active season (mean n observations per individual across years = 28.81, range of each year = 6.79– 75.14) and low rate of unknown individuals involved in social interactions facilitated the reliability of the five social network measures (Silk et al. 2015; Davis et al. 2018; Sánchez-Tójar et al. 2018). Because some network measures cannot be calculated for certain group sizes or group configurations (e.g., transitivity for a group of two or a linear group) we systematically removed all N/A's for network measures from the data. If an individual had an N/A in any of its measures, it was removed from the data entirely. This can be attributed to some individuals only being observed a few times a year or their membership in a small group (e.g., a group of two; Wasserman and Faust 1994).

Because group size is associated with many social network measures (Wasserman and Faust 1994; e.g., density, cut points), as seen in previous analyses in our system (Maldonado-Chaparro et al. 2015a), we ensured each measure was standardized for group size by dividing the social network measures by group size. Some measures already are 'standardized' because of how they are calculated (density, reciprocity, and transitivity; Wasserman and Faust 1994). Thus, we manually divided degree assortativity and cut points by group size so all five of our network measures were standardized for group size.

Reproductive success

While both males and females are in the social networks, we focus only on female reproductive success because male reproductive success mostly depends on dominance and tenure length (Armitage 1998; Huang et al. 2011). Yellow-bellied marmots are harem-polygynous; males fight for control of harems with more aggressive males with better body conditions experiencing greater reproductive success (Huang et al. 2011). Additionally, the smaller number of males in the population diminishes analysis power, requiring models with different covariates from the female models and thus inhibiting comparisons between sexes. We focused on two attributes of female reproductive success: (1) a binary measure if a female successfully weaned a litter from the burrow and (2) if a female successfully weaned a litter, a continuous measure of the number of pup/s that weaned. Offspring were assigned to each female based on behavioral observations and a comprehensive pedigree (see Blumstein et al. 2010 and Olson and Blumstein 2010 for pedigree details). Because we use weaned pups for both measures, this methodology does not account for pups that may have been born in the burrow but died before emergence (i.e., weaned; all pups are born in the burrow and emerge ~30 days after birth; Armitage 2014).

Data analysis

To test the relationships between social structure and female reproductive success, we fitted two (one for each measure of reproductive success) generalized linear mixed models in R using the “lme4” package (Bates et al. 2015b; version 1.1-27.1). Whether a female successfully weaned offspring from the burrow was the first dependent variable. We fitted a binomial distribution using the "logit" link function and a bobyqa optimizer with 1,000 function evaluations (Bates et al. 2014; Bates et al. 2015a). This model had 654 observations of female reproductive success and group measures consisting of 306 unique individuals in 92 social groups across 19 years. For the females that had pup/s wean from the burrow, our second dependent variable was the number of pup/s that weaned. We fitted a Poisson distribution using the "log" link function. This model had 234 total observations of female reproductive success and group measures consisting of 109 unique individuals in 78 social groups across 19 years.

Both models included the five network measures, group size (number of individuals in the social group), age, June mass, and valley location as fixed effects. We included the individual attributes June mass, age, and location because the correlates of reproductive success are multicausal and we want to account for these important attributes. Group size was included as a fixed effect due to its relationship with fitness correlates in this system (Wey and Blumstein 2012; Maldonado-Chaparro et al. 2015a). Age was included because older females are more likely to wean smaller litters than younger mothers under stressful conditions (Monclús et al. 2011) and because marmots become less social as they age (Wey and Blumstein 2010). Age was squared in our models to account for senescent declines as female reproductive success increases linearly with age until age seven, at which point female reproductive success declined (St. Lawrence et al. 2022). June mass was included because adult relative mass is positively associated with annual reproductive success (Huang et al. 2011; Blumstein et al. 2016).

We included year and individual ID as random effects (random effects were crossed as an individual may be seen in multiple years). We included year as a random effect to acknowledge annual environmental and demographic differences (Maldonado-Chaparro et al. 2015b; Kroeger et al. 2018; Heissenberger et al. 2020). Individual identity was included as a random effect to account for individuals that were observed over multiple years. While using social group ID would have accounted for multiple members of the same group that shared a network measure within a given year (as done in Philson et al. 2022), we did not include this as a random effect due to model convergence and overfitting issues. When we do fit our two models with social group ID, despite model fitting issues, results of our models did not change and <0.93% of additional conditional variance was explained in both models. Because of this, and because we control for individuals within and across years, we are confident that by not including social group ID we are not misrepresenting our results or attributing all among-group differences to the network traits. Additionally, groups often have one or few reproductive females, thus there is little to no variation of within group reproductive success that requires explanation, further bolstering our confidence that the exclusion of group ID is not creating misleading results.

Valley location was our only categorical fixed effect and we mean-centered it following Schielzeth (2010); lower elevation sites were coded as “+1” whereas higher elevation sites were coded as “-1". Group size and age were $\log_{10}$ transformed and all variables then were standardized (mean-centered and divided by one SD using the “scale” function in base R; Becker et al. 1988). We checked for collinearity by calculating correlation coefficients between continuous predictors. We originally attempted to fit models with two additional network measures (average path length and centralization), though due to their high correlation coefficient of >0.8 with other network measures (group size and degree assortativity, respectively), we did not include average path length and centralization in our models (Franke 2010; Shrestha 2020). After fitting each model, we checked model assumptions with the “check_model” function in the “performance” package in R (Lüdecke et al. 2021). We calculated the marginal and conditional R^2 values for the whole model and calculated the semi-partial marginal and conditional R^2 to estimate the variance explained by each of our fixed effects using the "partR2" package in R (Nakagawa and Schielzeth 2013; Stoffel et al. 2021; version 0.9.1). The marginal R^2 gives an estimate of the variance explained by all fixed effects for the model. The conditional R^2 gives an estimate of the variance explained by all fixed effects plus all random effects for the model. The marginal semi-partial R^2 gives an estimate of the variance explained by each individual fixed effect whereas the conditional semi-partial R^2 gives an estimate of the variance explained by each individual fixed effect plus the variance explained by all the random effects. We use marginal semi-partial R^2 values in the remainder of the primary text, and report conditional semi-partial R^2 values in Table 2. We estimated 95% confidence intervals for our R^2 and semi-partial R^2 values using 100 parametric bootstrap iterations. The figures were generated using "ggplot2" package in R (Wickham 2016; version 3.3.5).

Results

Social structure is not associated with the number of offspring weaned

We found no significant main effects of social structure in our model for whether a female successfully weaned offspring (Table 2), suggesting social structure does not play a primary role in successfully weaning a litter. Our model explained 54.48% of the marginal variance and 61.71% of the conditional variance. These results thus reject our *a priori* hypotheses which stated that female marmots in more connected and less homogeneous groups would have reduced reproductive success.

Breakable social structures are modestly associated with the number of offspring weaned

Overall, four of the five measures of social structure did not have a significant statistical relationship with the number of offspring weaned. However, one did; there was a statistically significant positive main effect of cut points on the number of offspring weaned (B = 0.091; P = 0.037; Std. Error = 0.044; Figure 2; Table 2). This suggests as social groups become more fragmentable (i.e., breakable into two or more separate groups of two or more individuals), females may have higher reproductive success. This result is consistent with our *a priori* hypothesis. This model had a marginal R^2 value of 13.78% and a conditional R^2 value of 23.50%. Cut points as a fixed effect alone explained 1.51% of the marginal semi-partial R^2 variance suggesting that the effect is relatively modest.

Discussion

In exploring the relationship between group social structure and reproductive success in a facultatively social rodent, only one measure of social structure was related with female reproductive success suggesting that, overall, group structure has a limited impact on this key fitness attribute in yellow-bellied marmots. Social structure is an emergent property of the group and thus exists on a different phenotypic scale than an individual’s direct social interactions (Moore et al. 1997; Croft et al. 2016; Kappeler 2019). In this system, how many social partners an individual has, how often they interact with their social partners, and their position within their group are much stronger predictors of reproductive success (Wey and Blumstein 2012), and fitness overall (alarm call propensity: Fuong et al. 2015; survival: Yang et al. 2017; longevity: Blumstein et al. 2018), than social structure. Individual social phenotypes (e.g., individual position) playing a more consequential role than group social phenotypes (e.g., social structure) is not unexpected (Wilson 1983; Okasha 2006). While residing in a certain type of group may have some effect, in species with low intergroup interactions, such as our system, an individual's direct social interactions are more impactful on an individual's fitness than an emergent property like social structure. Our results imply that, while potentially important, group-level selection is less evolutionarily consequential than individual-level selection in the context of reproductive success, at least in this facultatively social mammal. This is not to say that this group-level selection plays no role because growing evidence shows that both individual and group traits both influence individual fitness (Lusseau 2003; Oh and Badyaev 2010; Formica et al. 2012; Kurvers et al. 2014; Solomon-Lane et al. 2015; Croft et al. 2016; Leu et al. 2016; Philson et al. 2022), often differentially (Goodnight et al. 1992; Weinig et al. 2007; Laiolo and Obeso 2012). Thus, more research in this system and others should incorporate measures of both individual position and group social structure to better understand the directional selection on these two scales of social phenotypes.

Our modest statistically significant positive relationship between female reproductive success and group social structure (Figure 2; Table 2) suggests that females in groups with more cut points wean larger litters. Thus, as social groups become more fragmentable (breakable into two or more separate groups), females may experience higher reproductive success. This result supports our specific *a priori* hypothesis for cut points, though with the other network measures having no significant statistical relationship with reproductive success, we mostly reject our broader *a priori* hypothesis that social structure is generally related to female reproductive success. Our two measures of reproductive success happen after social behavior seasonally attenuates in this system. It is possible that reproductive events more closely tied to peak social activity (e.g., the likelihood of mating) could result in stronger associations.

The cut points result is interesting for a few reasons. Females in more fragmentable groups experiencing a fitness benefit aligns with our previous study of the social structure-fitness relationship in this system which showed that marmots have higher rates of proportional mass gain in more fragmentable and less social groups (Philson et al. 2022). These two sets of results are plausible because yellow-bellied marmots are facultatively social and experience many fitness costs from being more connected on the individual level (decreased female reproductive success: Wey and Blumstein 2012; decreased winter survival: Yang et al. 2017; shorter lifespan: Blumstein et al. 2018). Since marmots may mostly gain anti-predator benefits from social living, and because alarm calls can be heard across separate social groups (Armitage 2014), residing in fragmentable groups may limit the costs of increased sociality. This study and our previous study show marmots may experience fitness costs from residing in more connected groups as well, adding to our understanding of the adaptive value of sociality across social scales (Blumstein 2013). The tools and implications of our work extend to more social species, especially in species for which work has focused on implications of social interactions on the individual level. Thus, to comprehensively understand the consequences of sociality, group social structure must be explored in both facultatively and obligatory species in the wild.

Reproductive suppression may also play a role in our results. Reproductive suppression is widely reported in social animals, including rodents (Solomon and French, 1997; Hacklander et al., 2003). When closely living females compete reproductively, not all females may breed or litter sizes are reduced (Hacklander et al., 2003). Despite affiliative interactions being more likely between related females due to the matrilineal nature of yellow-bellied marmot social groups (Armitage 1998), older females have been shown to suppress their daughters' reproduction (Armitage 1991). The statistical significance of age in our model exploring if a female reproduced may be partly related to this age-based suppression. Additionally, the positive statistical significance of body mass in both models suggests larger females experience higher reproductive success, and when thinking about reproductive suppression, may be better able to suppress smaller females. The main effect of cut points – females residing in more fragmentable groups wean larger litters – also fits in with the reproductive suppression seen in this system. Residing in more fragmentable groups may limit the social opportunities for older females to suppress younger females' litter sizes. The social environment is primary predictor of female-female reproductive suppression in some primates (Beehner and Lu 2013), carnivores (Montgomery et al. 2018), and rodents (Sherman 1981; Wolff 1993; Wolf 1997; Freeman 2021). More fragmentable groups may be spread across a larger area, potentially leading to younger females raising litters in burrows separate from their mothers, facilitating reproductive suppression avoidance. As female marmots age, they become less social (Wey and Blumstein 2010), and this may further provide less social opportunity for older females to reproductively suppress younger females, which may be compounded in fragmentable groups. For younger females, fewer interaction opportunities with older females may also allow for unrestricted mating with the dominate male (often their father, whom they will mate with), or, in groups that contain multiple males, with sub-dominate males.

In summary, we found that group social structure is only modestly associated with higher reproductive success. Nevertheless, this work is a valuable addition to analysis of the fitness consequences of the individual social phenotype and has larger evolutionary implications, namely it has increased our understanding of the consequences of social behavior across social scales. This work is also consistent with the observation that while potentially important, group-level selection is often less evolutionarily consequential that individual-level selection (Okasha 2006). However, this does not mean emergent properties like social structure should not be explored (Kappeler 2019). Because both individual and group traits influence individual fitness, often differentially, more basic research across animal systems is required to better understand social structure's relationship with fitness. Ultimately, this understanding will enhance our understanding about selection on individual and group social phenotypes across animal systems.

Figures

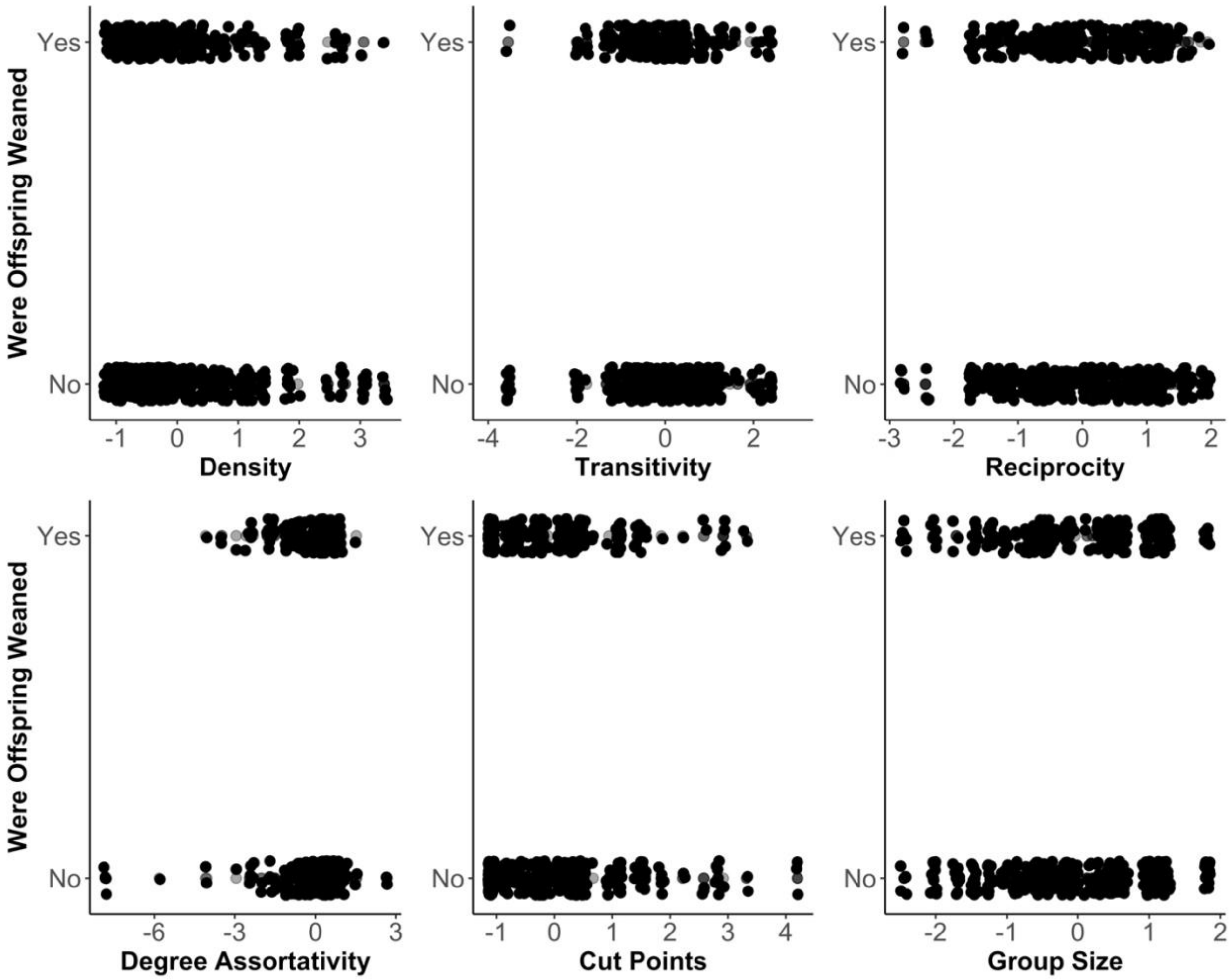


Figure 2.1. Relationship between whether offspring were weaned and social structure. The predictor variable is scaled (mean-centered and divided by one SD); the response variable is binary (1 = weaned a litter, 0 = did not wean a litter). Darker points indicate more overlaid data whereas lighter points indicate less overlaid data.

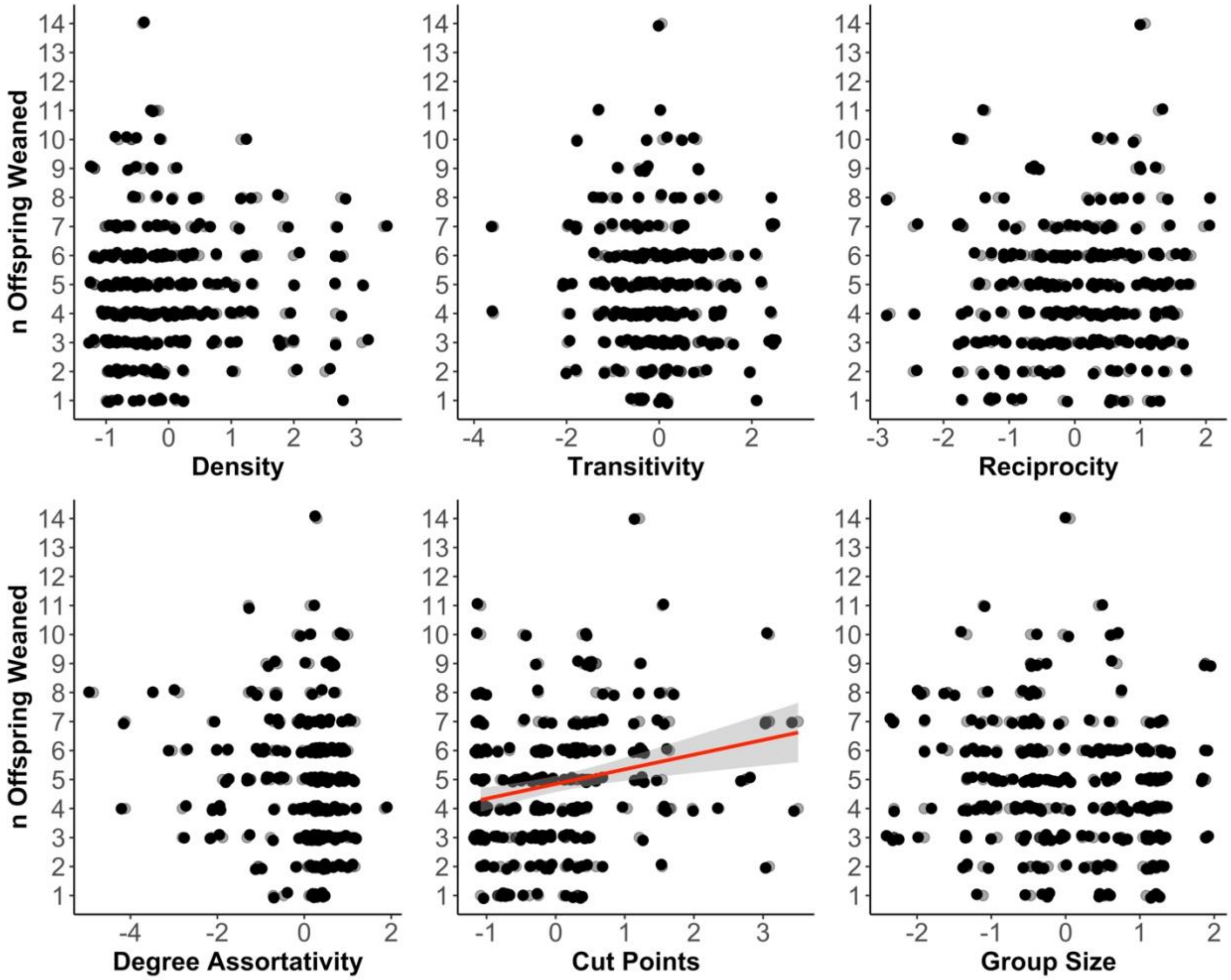
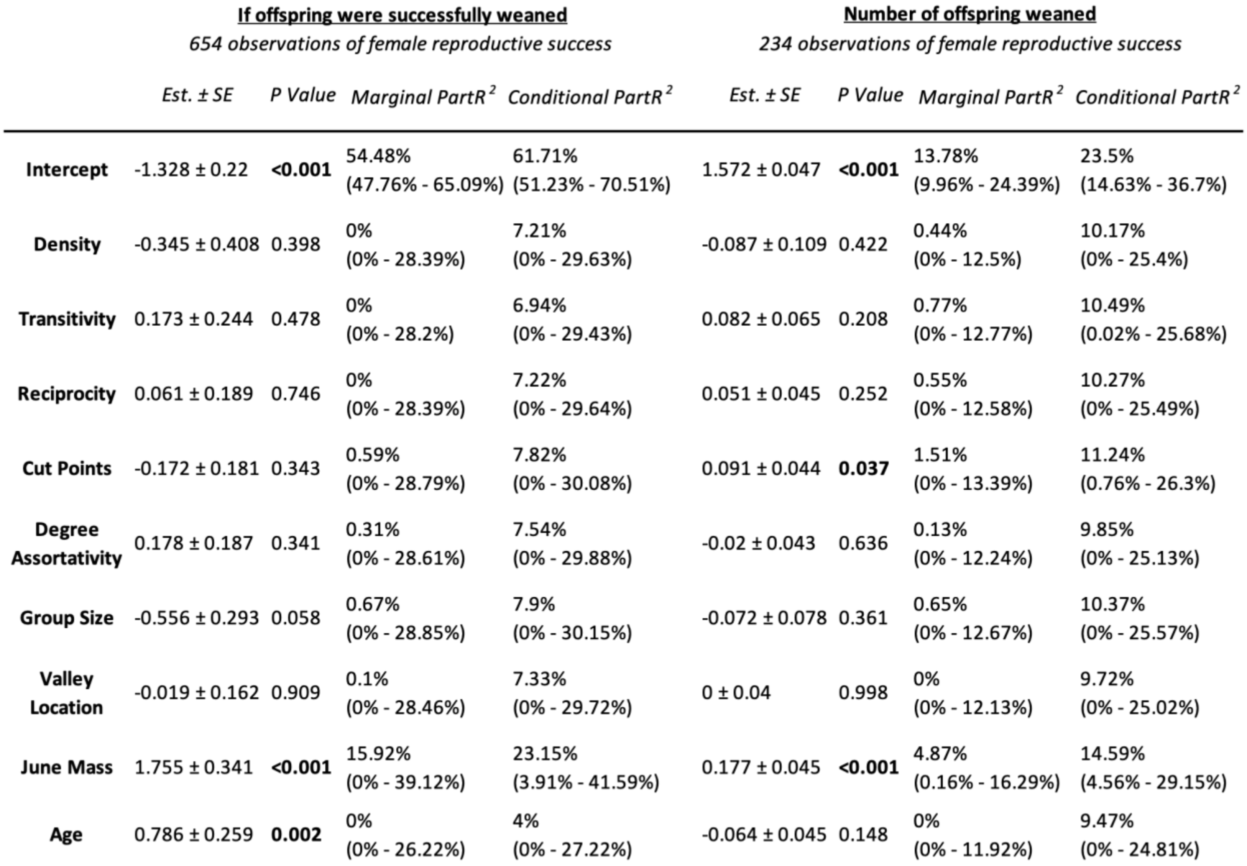


Figure 2.2. Relationship between the number of offspring weaned and social structure. The predictor variable is scaled (mean-centered and divided by one SD); the response variable is a count. A predicted regression (with 95% CIs) is plotted for the significant relationship and was created using R package "sjPlot" (Lüdecke 2022) to account for both fixed and random effect. Darker points indicate more overlaid data whereas lighter points indicate less overlaid data.

Tables

Measure	Description	References	Interpretation	Hypothesized Direction
Density	Number of interactions observed represented as a fraction of all possible interactions	Burt 1992; Wasserman and Faust 1994; Grund 2012	How connected a group is	-
Transitivity	Proportion of completely connected triads out of the total possible triads	Wasserman and Faust 1994; Milo et al. 2002; Faust 2010	How cyclically connected a group is. There are more transitive components in affiliative networks in this system (Wey et al. 2019)	-
Reciprocity	The number of mutual interactions divided by the number of possible mutual interactions	Wasserman and Faust 1994; Kankanhalli et al. 2005; Squartini et al. 2013	Used to quantify how mutual or one-sided interactions are in a group	+
Degree Assortativity	Tendency for social ties to share similar individual degree measures	McPherson et al. 2001; Currarini et al. 2016	How socially homogeneous a group is, in terms of individual's number of social partners	+
Cut points	Number of social ties that if cut will result in two or more separate networks.	Wasserman and Faust 1994; Borgatti 2006	How stable or fragmentable (breakable) a group is	+

Table 2.1. Network-level measures used to quantify social structure along with the *a priori* hypothesized direction of the relationship between the social measure and reproductive success.



	If offspring were successfully weaned *654 observations of female reproductive success*				**Number of offspring weaned** *234 observations of female reproductive success*			
	Est. ± SE	*P Value*	*Marginal PartR²*	*Conditional PartR²*	*Est. ± SE*	*P Value*	*Marginal PartR²*	*Conditional PartR²*
Intercept	-1.328 ± 0.22	**<0.001**	54.48% (47.76% - 65.09%)	61.71% (51.23% - 70.51%)	1.572 ± 0.047	**<0.001**	13.78% (9.96% - 24.39%)	23.5% (14.63% - 36.7%)
Density	-0.345 ± 0.408	0.398	0% (0% - 28.39%)	7.21% (0% - 29.63%)	-0.087 ± 0.109	0.422	0.44% (0% - 12.5%)	10.17% (0% - 25.4%)
Transitivity	0.173 ± 0.244	0.478	0% (0% - 28.2%)	6.94% (0% - 29.43%)	0.082 ± 0.065	0.208	0.77% (0% - 12.77%)	10.49% (0.02% - 25.68%)
Reciprocity	0.061 ± 0.189	0.746	0% (0% - 28.39%)	7.22% (0% - 29.64%)	0.051 ± 0.045	0.252	0.55% (0% - 12.58%)	10.27% (0% - 25.49%)
Cut Points	-0.172 ± 0.181	0.343	0.59% (0% - 28.79%)	7.82% (0% - 30.08%)	0.091 ± 0.044	**0.037**	1.51% (0% - 13.39%)	11.24% (0.76% - 26.3%)
Degree Assortativity	0.178 ± 0.187	0.341	0.31% (0% - 28.61%)	7.54% (0% - 29.88%)	-0.02 ± 0.043	0.636	0.13% (0% - 12.24%)	9.85% (0% - 25.13%)
Group Size	-0.556 ± 0.293	0.058	0.67% (0% - 28.85%)	7.9% (0% - 30.15%)	-0.072 ± 0.078	0.361	0.65% (0% - 12.67%)	10.37% (0% - 25.57%)
Valley Location	-0.019 ± 0.162	0.909	0.1% (0% - 28.46%)	7.33% (0% - 29.72%)	0 ± 0.04	0.998	0% (0% - 12.13%)	9.72% (0% - 25.02%)
June Mass	1.755 ± 0.341	**<0.001**	15.92% (0% - 39.12%)	23.15% (3.91% - 41.59%)	0.177 ± 0.045	**<0.001**	4.87% (0.16% - 16.29%)	14.59% (4.56% - 29.15%)
Age	0.786 ± 0.259	**0.002**	0% (0% - 26.22%)	4% (0% - 27.22%)	-0.064 ± 0.045	0.148	0% (0% - 11.92%)	9.47% (0% - 24.81%)

Table 2.2. Model estimates, standard error, *P* value, marginal and conditional part R^2, and marginal and conditional semi-partial part R^2 values for both models. Values in bold represent statistical significance ($P < 0.05$). In addition to estimated part R^2 and semi-partial part R^2 values, estimated 95% confidence intervals based on 100 parametric bootstrap iterations are reported in paratheses. The model exploring if offspring were successfully weaned had 654 observations of female reproductive success and group measures consisting of 306 unique individuals in 92 social groups across 19 years. The model exploring the number of offspring weaned had 234 total observations of female reproductive success and group measures consisting of 109 unique individuals in 78 social groups across 19 years.

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CHAPTER 3: GROUP SOCIAL STRUCTURE AND SURVIVAL

Abstract

For social animals, group social structure has important consequences for disease and information spread. While prior studies showed individual connectedness within a group has fitness consequences, less is known about the fitness consequences of group social structure for the individuals who comprise the group. Using a long-term dataset on a wild population of facultatively social yellow-bellied marmots (*Marmota flaviventer*), we showed social structure had largely no relationship with survival, suggesting consequences of individual social phenotypes may not scale to the group social phenotype. An observed relationship for winter survival suggests a potentially contrasting direction of selection between the group and previous research on the individual level; less social individuals, but individuals in more social groups experience greater winter survival. This work provides valuable insights into evolutionary implications across social phenotypic scales.

Introduction

An individual's social phenotype has important implications for its fitness in group-living species (Alexander 1974). Survival, an important fitness correlate, is influenced by the degree, rate, and context of social interactions in some species, as measured by social network analysis. For example, stronger social relationships have been associated with greater survival in male bottlenose dolphins (*Tursiops sp.*; Stanton and Mann 2012), chacma baboons (*Papio hamadryas ursinus*; Cheney et al. 2016), Barbary macaques (*Macaca sylvanus*; McFarland and Majolo 2013;

Lehmann et al. 2016), and feral horses (*Equus caballus*; Cameron et al. 2009; Nuñez et al. 2015). Several mechanisms contribute to this positive sociality-survival relationship, such as predator defense and detection (Hamilton 1971; Janson and Goldsmith 1995; Clutton-Brock et al. 1999) and resource exploitation (Blundell et al. 2002; Lancaster et al. 2006). Yet, higher rates of sociality can also be costly in terms of survival, as seen in female bottlenose dolphins (Stanton and Mann 2012) and is often associated with predator attraction and disease acquisition (Freeland 1976; Côté and Poulinb 1995; Lucatelli et al. 2021).

This previous work exclusively explored the fitness consequences of an individual's social phenotype, leaving the consequences of the group social phenotype unstudied (Croft et al. 2016; Fisher and McAdam 2017; Costello et al. 2023). Group social structure – emergent network traits generated by the interactions of all group members – quantifies the group social phenotype in a way more complex than averages of individual-level network values (Hinde 1976; Wasserman and Faust 1994; Ilany et al. 2015; Kappeler 2019). Social structure influences key ecological and evolutionary processes (Kurvers et al. 2014) such as group formation and regulation (Balasubramaniam et al. 2017) and movement patterns (Dufour et al. 2011). Social structure is in turn influenced by ecological conditions (Leu et al. 2016; Costello et al. 2022) and group composition of individual social and non-social phenotypes (Farine et al. 2015; Cook et al. 2022). In most species, social structures are non-random, repeatable across years, group compositions, and environmental gradients and conditions (Godfrey et al. 2013; Shizuka et al. 2014; Wilson et al. 2014; Aplin et al. 2015; Wilson et al. 2015; Maldonado-Chaparro et al. 2015; Blaszczyk 2018; Cook et al. 2022; Costello et al. 2023).

Social structure may also have fitness consequences. Captive bluebanded gobies (*Lythrypnus dalli*), an obligately social species, have reduced reproductive success when living in groups with more reciprocated aggressive interactions (Solomon-Lane et al. 2015). In wild yellow-bellied marmots, adult female reproductive success modestly increases when living in more fragmentable social groups (Philson and Blumstein 2023). Adults also gain body mass more slowly when living in more connected groups, though yearlings gain mass more quickly in socially homogeneous groups (Philson et al. 2022). These studies highlight how social structure may have different fitness consequences across species, demographic roles, and social systems (Croft et al. 2016; Fisher and McAdam 2017). However, how social structure specifically relates to patterns of survival in animal populations is not understood.

We explored the relationship between group social structure and survival over both the active summer season and winter hibernation in a long-studied population of yellow-bellied marmots. In this system, an individual's social phenotype predicts survival (Yang et al. 2017; Montero et al. 2020) and other fitness correlates (alarm call propensity: Fuong et al. 2015; reproductive success: Wey and Blumstein 2012; longevity: Blumstein et al. 2018). Informed by previous work on the individual and group levels in this system, we developed *a priori* hypotheses (Table 1) for six network measures, capturing the connectedness, mutuality, and homophily of a group, and both summer and winter survival. Females living in larger social groups and yearling females engaging in more social interactions experience enhanced summer survival (Montero et al. 2020). Predation is the primary driver of summer mortality in this system (Van Vuren 2001), thus more social individuals, or those residing in more connected groups, may better detect and avoid predators (Hamilton 1971; Janson and Goldsmith 1995; Clutton-Brock et al. 1999). We predict that residing in more connected, reciprocal, and socially homogeneous groups will be associated with increased summer survival. However, more social marmots are less likely to survive hibernation (Yang et al. 2017). Since body condition is the primary driver of winter mortality, this may be a function of social interaction time costs (Pollard and Blumstein 2008) and/or individuals in groups having more costly periodic arousals during social hibernation (Arnold 1990; Armitage et al. 2003). Thus, we predict that residing in more connected, less reciprocal, and socially heterogeneous groups will be associated with decreased winter survival, as was seen for mass gain and reproductive success (Philson et al. 2022; Philson and Blumstein 2023).

Methods

Study system

Yellow-bellied marmots are harem-polygynous, facultatively social ground-dwelling squirrels living in matrilineal colonies with one to two territorial males (Frase and Hoffmann 1980; Armitage 1991). The population at the Rocky Mountain Biological Laboratory in Colorado (38°57’N, 106°59’W; ca. 2900 m elevation) has been continuously studied since 1962. These marmots are active for five months annually (mid-April to mid-September). Following their winter hibernation, they mate soon after emergence with yearlings dispersing and new pups emerging in late-June to early-July. Annually, most males and about half of females disperse as yearlings, typically resulting in movement out of the study area (Armitage 1991). We only explore adult summer and winter survival because yearling dispersal creates uncertainty about yearling survival.

Data collection

We repeatedly trapped and observed marmots during their active season from 2002 to 2020. All individuals studied in our population have unique nontoxic dye marks on their dorsal pelage, allowing accurate identification of interacting individuals and precise estimates of survival. A detailed ethogram and behavioural observational methodology are outlined in Blumstein et al. (2009). The initiator, recipient, location, time, and type of each interaction is recorded, with most interactions (79%) occurring between identified individuals. The remaining 21% interactions could not be identified because of interacting individuals' posture or visual obstructions. We excluded these interactions from our data, which should not significantly influence our estimates of social structure (Silk et al. 2015).

Only adults and yearlings are included in our social interaction data because only these cohorts were present in spring, when social interactions were most common. Pups were excluded because of their mid-season emergence and primary interaction with their mother and each other (Nowicki and Armitage 1979). We eliminated transients by excluding individuals observed or trapped fewer than five times in a given year (Wey and Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018). Colony sites are grouped into higher and lower elevation sites (five are at higher and seven are at lower elevation sites). Higher elevation sites are ~166 m higher and experience harsher weather conditions (Van Vuren and Armitage 1991; Blumstein et al. 2006; Maldonado-Chaparro et al. 2015b).

Social network measures

Directed and weighted interaction matrices were constructed from affiliative interactions for each year (2002 to 2020) the package "igraph" (version. 1.3.5; Csardi and Nepusz 2006) for R 4.2.0 (R Development Core Team 2021). We focused on affiliative interactions (e.g. allogrooming, greeting, play) because they relate to summer and winter survival on the individual level (Yang et al. 2017; Montero et al. 2020) and affiliative interactions comprised 88% of interactions. These affiliative matrices consisted of 38,968 social interactions between 726 individuals (626 of whom were observed across multiple years). A social group is defined as a network component (set of connected individuals with no other external connections) appearing naturally within a valley location (higher elevation or lower elevation) in a given year. This operationalisation produced 137 social groups with group sizes ranging from 3-58 individuals with a mean of 20.51 (SE = 0.52). Details on identical behavioural observation and network methods can be found in Philson and Blumstein (2023).

Six social network measures were calculated for each group to quantify social structure (Table 1). Density, transitivity, average path length, and cut points quantify connectivity; reciprocity and degree assortativity quantify homophily. We selected these measures due to their importance in our system (Wey et al. 2019; Philson et al. 2022; Philson and Blumstein 2023), other systems (Weinig et al. 2007; Soloman-Lane et al. 2015; Costello et al. 2022; Costello et al. 2023), and because these network measures have analogous measures on the individual level (e.g. density and degree; transitivity and clustering coefficient; Costello et al. 2023), aiding our understanding of consequences of social behaviour across social phenotypic scales (Wasserman and Faust 1994). The reliability of the social network measures is facilitated by our observations of marmot social groups across their entire active season (mean n observations per individual across years = 28.81, range of each year = 6.79– 75.14) and low rate of unknown individuals involved in social interactions (Silk et al. 2015; Davis et al. 2018; Sánchez-Tójar et al. 2018). Because group size is associated with many marmot social network measures (e.g. density, cut points; Maldonado-Chaparro et al. 2015a; Philson et al. 2022; Philson and Blumstein 2023), we standardised each measure not already 'standardised' (i.e. degree assortativity and cut points) by dividing the network measures by group size (Wasserman and Faust 1994; Philson et al. 2022; Philson and Blumstein 2023).

Data analysis

Summer survival was defined as individuals seen or trapped after 1 August or in the following years. Winter survival was defined as individuals seen the following year/s. Survival data was paired with network measures from the current active season (for summer survival) or the active season before hibernation (for winter survival). We fitted two generalised linear mixed models (summer and winter) with a binomial distribution and a bobyqa optimiser with 20,000 iterations using "lme4" (Bates et al. 2014; Bates et al. 2015a; Bates et al. 2015b). Model assumptions and zero inflation were checked after fitting. The summer survival model included the six network measures, social group size, age, sex, June mass, valley location, and a predation index as fixed effects. The winter survival model included the six network measures, group size, age, sex, August mass, valley location, and the date bare ground was first visible because of melting snowpack in the center of our colony areas. Models had 559 observations consisting of 252 unique individuals in 91 social groups across 19 years.

We included the individual attributes age, sex, mass, and location because survival is multicausal and we wished to account for important attributes with known fitness implications (Wey and Blumstein 2010; Huang et al. 2011; Blumstein et al. 2016). Group size was included due to its relationship with fitness correlates in this system (Wey and Blumstein 2012; Maldonado-Chaparro et al. 2015a). Predation index is a binary variable calculated by whether the number of predators observations at that colony was below or above the median number of predator observations across all colony areas in that year (Nash et al. 2020), providing a value relative to all other years (Montero et al. 2020). Individual ID and year were included as random effects to account for annual environmental and demographic differences (Maldonado-Chaparro et al. 2015b; Kroeger et al. 2018; Heissenberger et al. 2020) and individuals observed over multiple years.

All continuous variables were standardised (mean-centered and divided by one SD using the "scale" function in base R; Becker et al. 1988). Group size was log10 transformed before scaling, but we employed no other transformations. We checked for multicollinearity between fixed effects and found each had a correlation coefficient of <0.8 (Franke 2010; Shrestha 2020), though, both density and group size had a VIF of >5 in both the summer and winter models (supplementary material, table S1). Because group size has known relationships with fitness in this system (Wey and Blumstein 2012; Maldonado-Chaparro et al. 2015a; Philson et al. 2022; Philson and Blumstein 2023), we removed density from both models and the interpretation of the results for the measures of social structure did not change (supplementary material table S2). Since this suggests our models were relatively robust, we report models that included both density and group size here.

Marginal and conditional R^2 values for each model and the semi-partial marginal and conditional R^2 that estimate variance explained by each fixed effect were calculated using “partR2” (Nakagawa and Schielzeth 2013; Stoffel et al. 2021). We estimated 95% confidence intervals for our R^2 values using 100 parametric bootstrap iterations. Figures were generated with “ggplot2” (Wickham 2016).

Results

Contrary to our *a priori* hypothesis, we found a statistically significant negative main effect of cut points on winter survival (B = -0.359; P = 0.031; Std. Error = 0.167; Figure 1; Table 2), suggesting individuals residing in more fragmentable – breakable into two or more separate groups of two or more individuals – social groups experienced reduced winter survival. Overall, five of the six measures of social structure did not have a significant statistical relationship with winter survival, suggesting the relationship is modest. This model had a marginal R^2 value of 6.28% and a conditional R^2 value of 7.93%. Cut points explained 1.11% of the marginal semi-partial R^2 variance further suggesting the relationship is modest.

Rejecting our *a priori* hypotheses, we found no significant main effects of social structure in our summer survival model (Figure 3; Table 2), suggesting social structure does not play a primary role in summer survival. This model explained 7.39% of the marginal variance and 19.17% of the conditional variance.

Discussion

We found no strong and consistent evidence that social structure is related to summer survival in this system. However, because one measure of social structure (cut points) was related to winter survival, group structure may have a limited impact in specific contexts. Because group social structure exists on a larger, emergent phenotypic scale than an individual's direct social interactions (Moore et al. 1997; Croft et al. 2016; Kappeler 2019), its logical that the relationship between social structure and fitness may be quite modest because of its indirect nature, as seen in previous work (Solomon-Lane at al. 2015; Philson and Blumstein 2023; Costello et al. 2023).

Social structure not relating to summer survival is surprising given that more connected groups might excel at predator detection and/or avoidance (Hamilton 1971; Turner and Pitcher 1986; Wrona and Dixon 1991; Janson and Goldsmith 1995; Clutton-Brock et al. 1999). However, the lack of a statistically significant relationship may result from the emergent, and hence indirect nature of social structure (Hinde 1976; Wasserman and Faust 1994; Ilany et al. 2015; Kappeler 2019; Costello et al. 2023). Since these facultatively-social marmots experience mostly fitness costs from more social individual and group phenotypes (Wey and Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018; Philson et al. 2022; Philson and Blumstein 2023), the consequences of more social individual phenotypes may not scale linearly to the group social phenotype, as seen in male forked fungus beetles (Costello et al. 2023). That is, residing in a more connected group may not incur the same benefits as increased individual sociality. A marmot may have modest benefits at an individual level of being more socially connected with others, but still regulate their social interactions by residing in less connected groups. Because of the few associations with winter survival, the strength of group-level selection is likely less than the strength of individual-level selection for survival in this system. However, targeted exploration of multilevel selection is required to specifically test this hypothesis.

Interestingly, the one statistically significant relationship we identified (between winter survival and cut points) may have interesting evolutionary implications and further suggests that the individual social phenotype may not scale to the group phenotype (Costello et al. 2023). In this system, more socially connected individuals have decreased winter survival (Yang et al. 2017), suggesting selection acts against more social individual phenotypes. As we have shown here, individuals residing in less fragmentable (or more closely socially connected) groups have increased winter survival, suggesting selection acts towards more social group phenotypes. The mechanisms for this are entangled. Winter survival is closely associated with body mass (Kroeger et al. 2018). Thus, more social individuals in more social groups may have less time to forage to develop energy reserves and may be more likely to socially hibernate, increasing the risk of costly torpor interruptions (Arnold 1990; Armitage et al. 2003). However, residing in a less fragmentable group, where individuals may be more likely to share space and hear conspecific alarm calls (Godfrey et al, 2013; Leu et al. 2016; He et al. 2019; Costello et al. 2022) may facilitate predator avoidance and allow for more time to gain mass. This potential explanation is muddled, but not dismissed, by the lack of an observed relationship for summer survival.

Importantly, residing in a less fragmentable group does not necessarily imply that individuals within that group are significantly more social (Hinde 1976; Wasserman and Faust 1994; Ilany et al. 2015; Kappeler 2019). This also does not imply more connected social structures are beneficial in this species (Philson et al. 2022; Philson and Blumstein 2023), but rather that in specific contexts some benefits to increased sociality may emerge at different social scales. As mentioned, the strength and potential contrasting direction of selection between individual and group traits in this system requires further exploration. Opposing selection has been observed across species for non-social traits (Stevens et al. 1995; Tsuji 1995; Weinig et al. 2007; Eldakar et al. 2010; Laiolo and Obeso 2012; Van Vliet and Doebeli 2019; Cordes et al. 2020), though less research investigates selection acting on social behaviour across social scales (Eldakar et al. 2010; Laiolo and Obseo 2012; Royle et al. 2012). Bluebanded gobies (Solomon-Lane et al. 2015), chacma baboons (*Papio hamadryas ursinus*; Cheney et al. 2016), and social bumble bees (*Bombus sp*.; Otterstatter and Thomson 2007; Figueroa et al. 2020) experience fitness benefits across social scales. However, not all species may experience, or experience via the same mechanisms, aligned fitness consequences across social scales (Costello et al. 2023).

Understanding the evolution of social behaviour requires directly measuring the fitness consequences of natural behavioural variation (Solomon-Lane et al. 2015). While the ranging fitness consequences of individual social network position is well documented (Wey et al. 2008; Whitehead 2008; Stanton and Mann 2012; Formica et al. 2012; Pinter-Wollman et al. 2014; Farine and Sheldon 2015; Croft et al. 2016), growing research supports group level social network traits also have a range of fitness consequences across species (Solomon-Lane et al. 2015; Philson et al. 2022; Philson and Blumstein 2023; Costello et al. 2023). This work highlights evolutionary implications across social scales and our main finding is that group social phenotype has a complex relationship with fitness that does not necessarily scale. Our observed relationship may further suggest complexity via contrasting selection between the individual and group social phenotypes on winter survival. However, because the relationship is modest and little research investigates selection acting on behaviour across social scales, future work using a multilevel selection approach is essential to better understand the adaptive value of sociality.

Figures

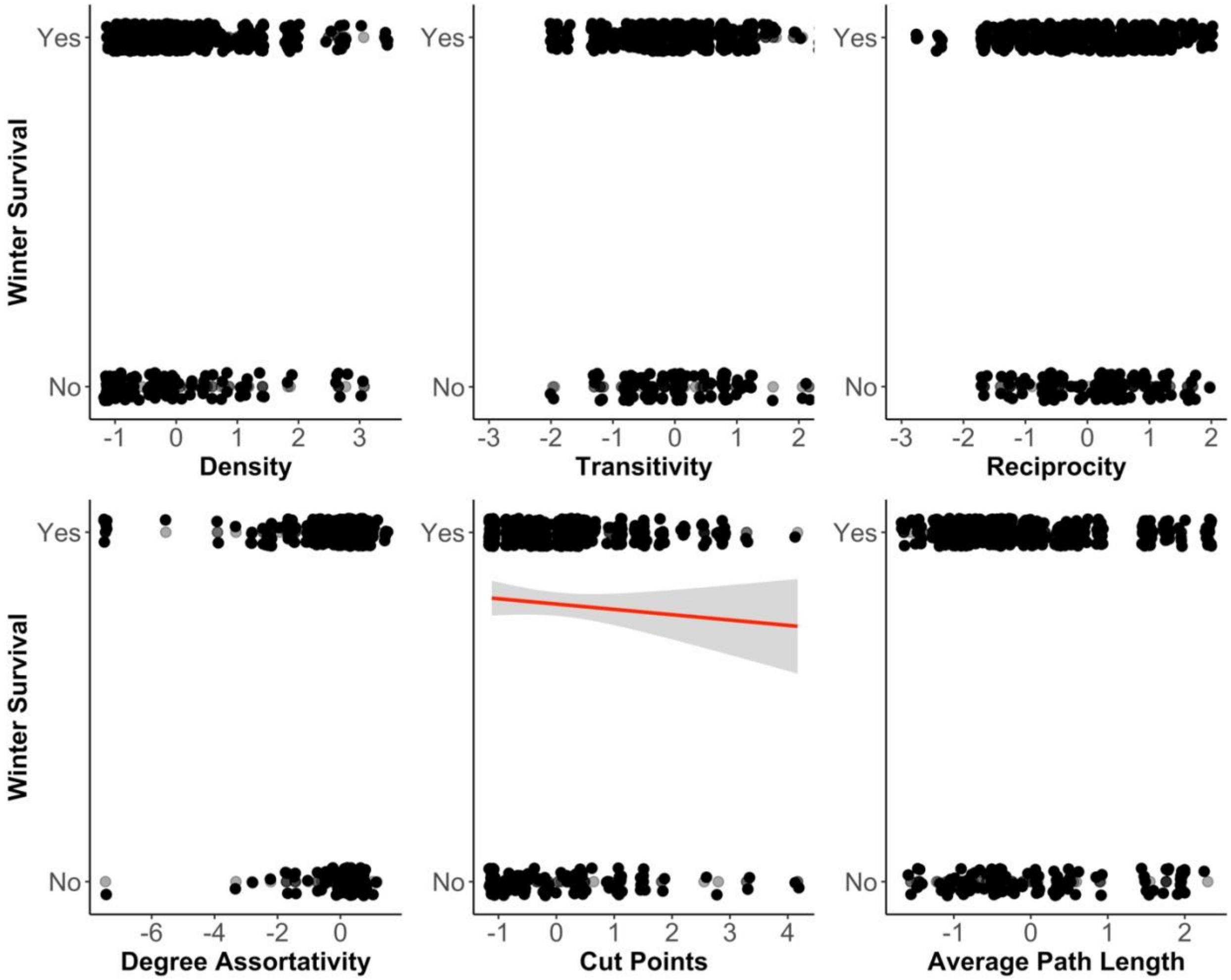


Figure 3.1. Relationship between winter survival and social structure. The predictor variable is scaled. Darker points indicate overlaid data.

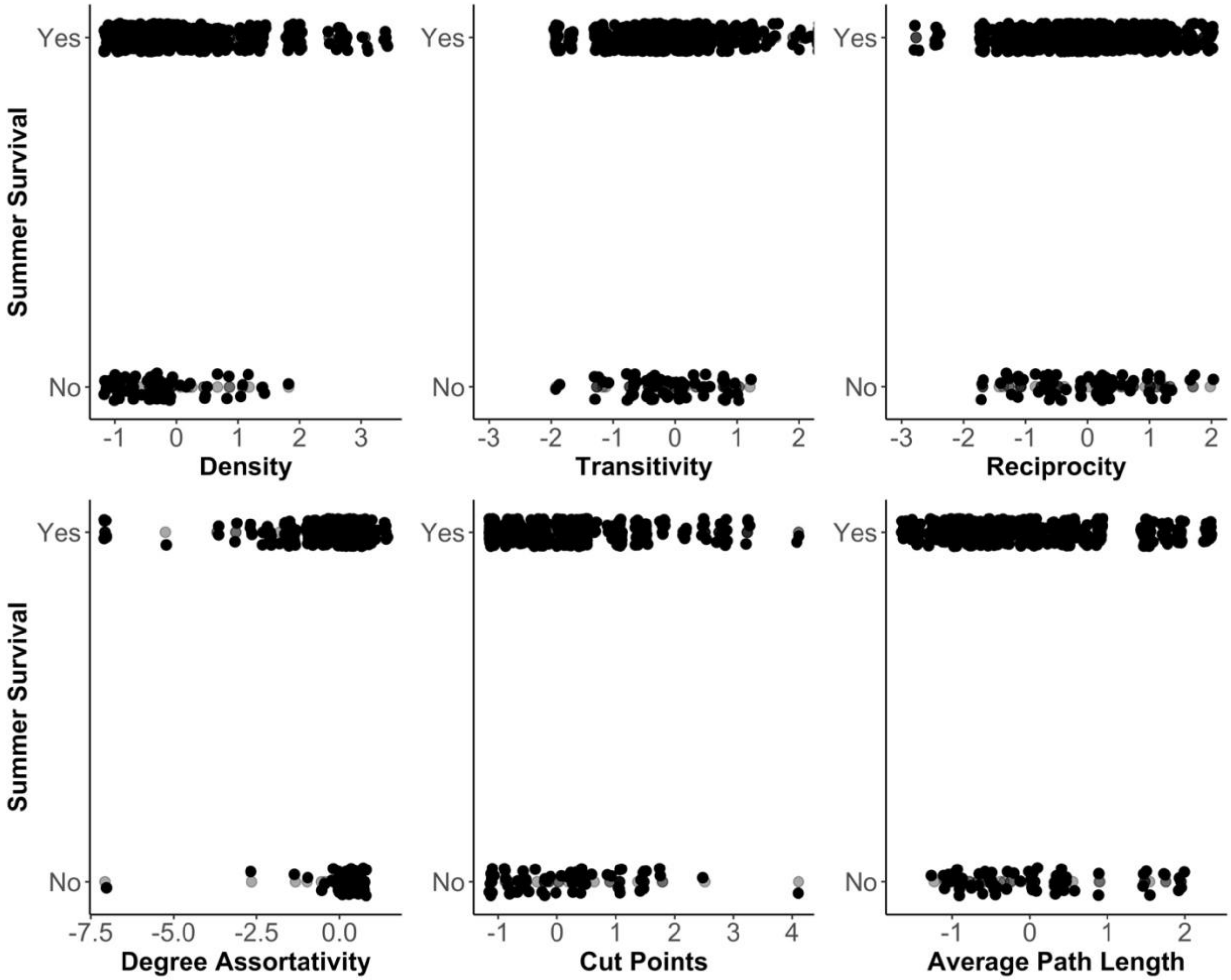


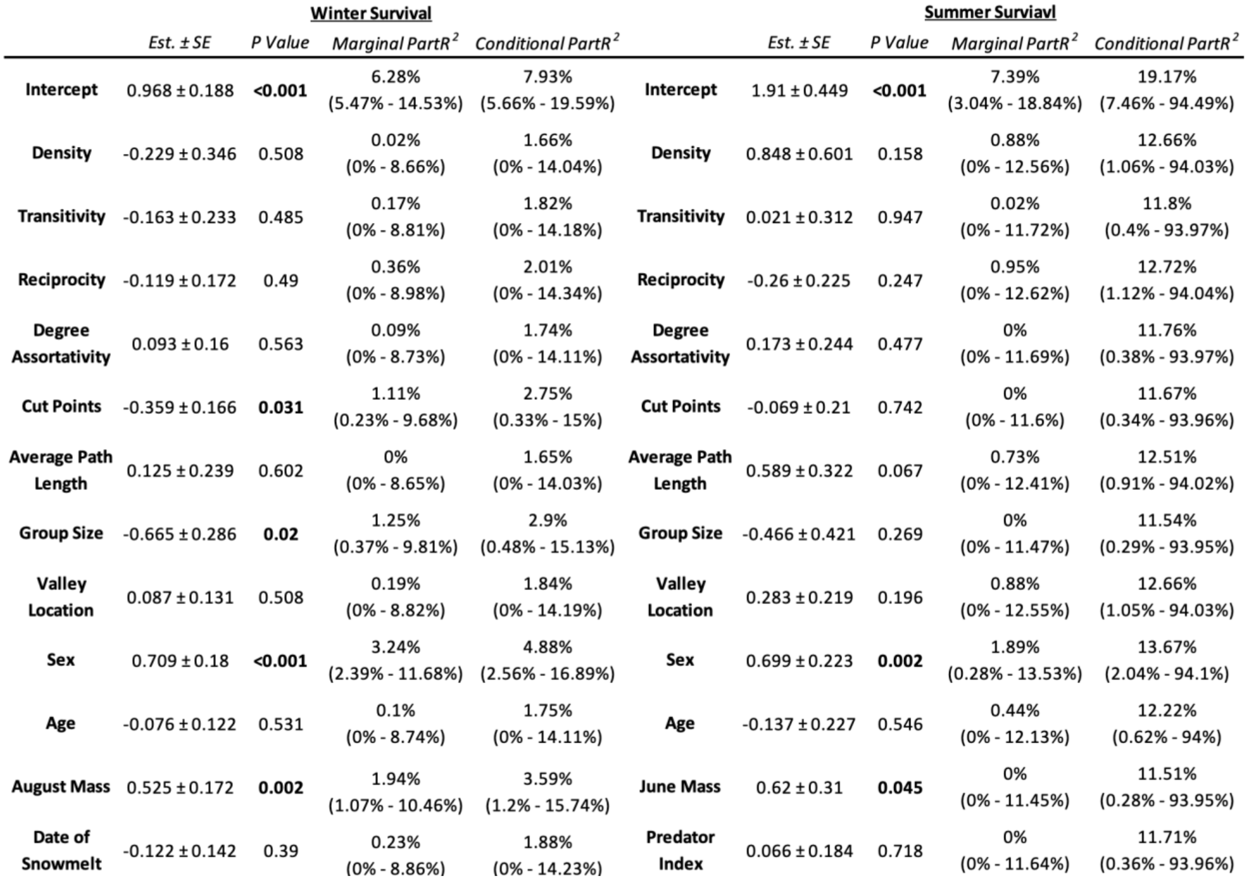
Figure 3.2. Relationship between summer survival and social structure. The predictor variable is scaled. Darker points indicate overlaid data.

Tables

Measure	Description	References	Interpretation	Summer Hypothesis	Winter Hypothesis
Density	Number of interactions observed represented as a fraction of all possible interactions	Burt 1992; Wasserman and Faust 1994; Grund 2012	How connected a group is	+	-
Transitivity	Proportion of completely connected triads out of the total possible triads	Wasserman and Faust 1994; Milo et al. 2002; Faust 2010	How cyclically connected a group is. There are more transitive components in affiliative networks in this system (Wey et al. 2019)	+	-
Reciprocity	The number of mutual interactions divided by the number of possible mutual interactions	Wasserman and Faust 1994; Kankanhalli et al. 2005;	Used to quantify how mutual or one-sided interactions are in a group	+	+

		Squartini et al. 2013			
Degree Assortativity	Tendency for social ties to share similar individual degree measures	McPherson et al. 2001; Currarini et al. 2016	How socially homogeneous a group is, in terms of individual's number of social partners	+	+
Average Path Length	Average of the shortest paths between all pairs of nodes	Watts and Strogatz 1998; Broder et al. 2000	Identifies the size of a network, in addition to raw group size	-	+
Cut points	Number of social ties that if cut will result in two or more separate networks.	Wasserman and Faust 1994; Borgatti 2006	How stable or fragmentable (breakable) a group is	-	+

Table 3.1. Measures of social structure with the *a priori* hypothesised direction of the relationship.



	Winter Survival					Summer Surviavl			
	Est. ± SE	*P Value*	*Marginal PartR^2*	*Conditional PartR^2*		*Est. ± SE*	*P Value*	*Marginal PartR^2*	*Conditional PartR^2*
Intercept	0.968 ± 0.188	**<0.001**	6.28% (5.47% - 14.53%)	7.93% (5.66% - 19.59%)	**Intercept**	1.91 ± 0.449	**<0.001**	7.39% (3.04% - 18.84%)	19.17% (7.46% - 94.49%)
Density	-0.229 ± 0.346	0.508	0.02% (0% - 8.66%)	1.66% (0% - 14.04%)	**Density**	0.848 ± 0.601	0.158	0.88% (0% - 12.56%)	12.66% (1.06% - 94.03%)
Transitivity	-0.163 ± 0.233	0.485	0.17% (0% - 8.81%)	1.82% (0% - 14.18%)	**Transitivity**	0.021 ± 0.312	0.947	0.02% (0% - 11.72%)	11.8% (0.4% - 93.97%)
Reciprocity	-0.119 ± 0.172	0.49	0.36% (0% - 8.98%)	2.01% (0% - 14.34%)	**Reciprocity**	-0.26 ± 0.225	0.247	0.95% (0% - 12.62%)	12.72% (1.12% - 94.04%)
Degree Assortativity	0.093 ± 0.16	0.563	0.09% (0% - 8.73%)	1.74% (0% - 14.11%)	**Degree Assortativity**	0.173 ± 0.244	0.477	0% (0% - 11.69%)	11.76% (0.38% - 93.97%)
Cut Points	-0.359 ± 0.166	**0.031**	1.11% (0.23% - 9.68%)	2.75% (0.33% - 15%)	**Cut Points**	-0.069 ± 0.21	0.742	0% (0% - 11.6%)	11.67% (0.34% - 93.96%)
Average Path Length	0.125 ± 0.239	0.602	0% (0% - 8.65%)	1.65% (0% - 14.03%)	**Average Path Length**	0.589 ± 0.322	0.067	0.73% (0% - 12.41%)	12.51% (0.91% - 94.02%)
Group Size	-0.665 ± 0.286	**0.02**	1.25% (0.37% - 9.81%)	2.9% (0.48% - 15.13%)	**Group Size**	-0.466 ± 0.421	0.269	0% (0% - 11.47%)	11.54% (0.29% - 93.95%)
Valley Location	0.087 ± 0.131	0.508	0.19% (0% - 8.82%)	1.84% (0% - 14.19%)	**Valley Location**	0.283 ± 0.219	0.196	0.88% (0% - 12.55%)	12.66% (1.05% - 94.03%)
Sex	0.709 ± 0.18	**<0.001**	3.24% (2.39% - 11.68%)	4.88% (2.56% - 16.89%)	**Sex**	0.699 ± 0.223	**0.002**	1.89% (0.28% - 13.53%)	13.67% (2.04% - 94.1%)
Age	-0.076 ± 0.122	0.531	0.1% (0% - 8.74%)	1.75% (0% - 14.11%)	**Age**	-0.137 ± 0.227	0.546	0.44% (0% - 12.13%)	12.22% (0.62% - 94%)
August Mass	0.525 ± 0.172	**0.002**	1.94% (1.07% - 10.46%)	3.59% (1.2% - 15.74%)	**June Mass**	0.62 ± 0.31	**0.045**	0% (0% - 11.45%)	11.51% (0.28% - 93.95%)
Date of Snowmelt	-0.122 ± 0.142	0.39	0.23% (0% - 8.86%)	1.88% (0% - 14.23%)	**Predator Index**	0.066 ± 0.184	0.718	0% (0% - 11.64%)	11.71% (0.36% - 93.96%)

Table 3.2. Model estimates, standard error, P value, marginal and conditional and semi-partial part R2.

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CHAPTER 4: MULTILEVEL SELECTION ON INDIVIDUAL AND GROUP SOCIAL BEHAVIOUR IN THE WILD

Abstract

The degree to which phenotypes are shaped by multilevel selection – the theoretical framework proposing natural selection occurs at levels of biological organization more than only the gene – is a classic debate in biology with roots in group selection. Though social behavior is a common example for multilevel selection, we do not know if multilevel selection acts on these social phenotypes in the wild. Here we studied the relative strength of selection for both individual and emergent group social network traits using 19 years of data from a wild, free-living mammal with genetically heritable social traits. Contextual analysis (partitioning selection among social phenotypic levels) revealed multilevel selection for both individual and group social phenotypes in specific fitness and life history contexts, with group selection exerting a stronger force than individual selection. Given sociality has ranging consequences across levels of organization from individual health to community disease transmission and national economies, our work provides, for the first time, empirical evidence for the importance of multilevel selection on social relationships and structures in the wild and provides direct evidence for a classic, unanswered question in biology.

Main

The evolution of sociality is a central question in biology (Tinbergen 1963; Alexander 1974; Hinde 1976). For species living in social groups, both individual position within the group and the overall structure of the group arise from interactions between all group members (Wasserman

& Faust 1994). Social network analysis is a powerful and common tool to analytically quantify social relationships and structures (Wasserman & Faust 1994; Croft et al. 2016; Kappeler 2019). These social interactions, and the resulting group social structures, have both fitness and population dynamic consequences in wild populations (Formica et al. 2012; Royle et al. 2012; Kurvers et al. 2014; Solomon-Lane et al. 2015; Croft et al. 2016; Fisher & McAdam 2017; Snyder-Mackler et al. 2020; Philson et al. 2022; Philson & Blumstein 2023a; Philson & Blumstein 2023b) and in economics can affect business profitability and trading markets (Coleman 1988). Social behaviors are often considered an individual phenotype but inherently involve interactions among individuals within a group leading to emergent group phenotypes (Moore et al., 1997; Kappeler 2019). Group social structure is an emergent phenotype more complex than the sum of a groups' individual behaviors (Hinde 1976; Kappeler 2019). Thus, social behaviors exist and can be quantified on multiple discrete levels of biological organization, potentially allowing for selection to act on both the individual and group levels independently.

While natural selection acts on phenotypes regardless of genetic heritability, evolution is the genetic response to this selection (Lande & Arnold 1983). Traditionally, the theory of evolution by natural selection dictates only differences among individuals can be selected on, implying only individual social phenotypes can undergo direct selection. The individual social phenotype is genetically heritable (Lea et al. 2010; Brent et al. 2013). Emergent group phenotypes, though not directly genetically heritable, are more complex than the sum of multiple individual genotypes (Gardner 2015) and inheritance may be instead derived from indirect genetic effects (Moore et al. 1997). How group phenotypes experience genetic evolution in the wild is unknown

(Maynard-Smith 1964), but the group phenotypic response to natural selection is an evolutionary prerequisite (Lande & Arnold 1983; Moore et al., 1997; Gardner 2015; Kappeler 2019). To understand the evolution of individual social position and emergent group structures, we must first understand how natural selection acts on these two social phenotypes.

The idea of group selection has undergone many transformations over the years through healthy debate (Wynne-Edwards 1962; Maynard-Smith 1964; Dawkins 1986; Wilson & Sober 1994; Okasha 2006; Nowak et al. 2010; West et al. 2011). The modern argument proposes group phenotypes driving individual fitness variation may be under natural selection (as seen in some birds, fishes, and mammals: Royle et al. 2012; Solomon-Lane et al. 2015; Philson et al. 2022; Philson & Blumstein 2023a; Philson & Blumstein 2023b). Multilevel selection combines individual and group selection into one conceptional framework (Damuth & Heisler 1988; Wilson & Sober 1994; Okasha 2005; Wilson and Wilson 2008; West et al. 2011).

The proposition that natural selection can act simultaneously, and potentially in opposing directions, on differences across levels of biological organization (such as individual and group social phenotypes), means that multilevel selection may be an important evolutionary mechanism. For instance, multilevel selection was a driving force in the emergence of multicellular organisms (Yu et al. 2020) and the structure of entire ecosystems (Johnson & Gibson 2021) and also acts on morphological phenotypes in plants (Stevens et al., 1995; Weinig et al., 2007) and animals (Eldakar et al., 2010; Fisher et al., 2017; Formica et al. 2021).

Despite social behavior being a common example in making the case for multilevel selection, no work has explored the presence and strength of multilevel selection for social behaviors in wild, free-living populations. Thus, the decades old debate of individual versus group selection for social behaviors (Leigh 2010), and more recently multilevel selection (Nowak et al. 2010; Goodnight 2013), remains largely a theoretical, not analytical, debate (Okasha 2006). This open question in evolutionary biology has the potential to reshape our understanding of the evolutionary origins of friendship and social organization that underpin social lives across species and governments across nations.

To address this question, we used 19 years of continuous social, fitness, and life history data on a well-studied, wild, free-living population of yellow-bellied marmots (Marmota flaviventer). Yellow-bellied marmots, a hibernating harem polygynous rodent, have genetically heritable social positions (Lea et al. 2010) and experience individual fitness consequences from both their individual and group social phenotypes (Wey & Blumstein 2012; Yang et al. 2017; Montero et al. 2020; Philson et al. 2022; Philson & Blumstein 2023a; Philson & Blumstein 2023b), providing a strong foundation to explore multilevel selection in the same model with a unified statistical approach for the first time. We calculated four pairs of analogous individual and group social network measures to quantify the independent contributions of the individual and group phenotypes (Table 1; Costello et al. 2023) from social networks for consisted of 172 unique social groups comprised of 723 unique individuals. These analogous network trait pairs quantify four core components in human and non-human animal social networks at the two levels of social network organization: connectivity, closeness, breakability, and clustering (Wasserman & Faust 1994). We used contextual analysis, an extension of the Lande-Arnold selection analysis using partial regression to partition selection among levels (Lande and Arnold 1983; Goodnight et al. 1992), to evaluate the distinct contributions of group and individual social phenotypes to four annual fitness correlates (summer survival, hibernation survival, if a female weaned offspring, and how many offspring a mother had). Contextual analyzes are sensitive to the scale of standardization and should be based on the biological and ecological processes that generate selection in the context of the study system (De Lisle and Svensson 2017; Costello et al. 2023). Thus, we mean-variance standardized individual-level social network measures at the scale of each social group and group-level social network measures across all social groups across all 19 years. Because of fundamental differences in life history strategies between age classes (adult and yearling) and sexes in this system, we fitted separate models for the four sex and age classes separately. This analysis allowed the quantification of independent contributions to individual fitness of qualitatively similar traits at different levels of social organization and between age-sex cohorts while accounting for natural variation in group size across a nearly two-decade dataset.

If only individual traits were under selection, we could dismiss the presence of group selection as a selective force of social behavior in this system. If both individual and group traits, or just group traits, were under selection, the role of multilevel selection for sociality would be demonstrated for the first time across generations in the wild. Based on previous work exploring individual fitness consequences of the individual and group social phenotypes in this system (Wey & Blumstein 2012; Yang et al. 2017; Montero et al. 2020; Philson et al. 2022; Philson & Blumstein 2023a; Philson & Blumstein 2023b), we predicted negative multilevel selection would be present and the strength of individual-level selection would be stronger.

Our results revealed quantitative differences in the presence, strength, and direction of multilevel selection for individual and group social traits (Figure 1). Individual traits quantifying connectivity and closeness were under negative selection for reproductive success in adult females, suggesting sociality is selected against in this fitness context (Figure 1A-B; Supplementary Table 1). Group traits that quantified closeness and clustering were under negative selection and group traits for breakability were under positive selection for hibernation survival in three of the four age-sex cohorts (only female yearlings did not experience selection for winter survival; Figure 1C-F; Supplementary Table 2 and 3). These results suggest group selection acts on adult females and yearling males residing in less breakable social groups and opposes adult males who reside in more closely connected social groups. Interestingly, adult females experienced negative group selection when residing in more transitive groups, suggesting emergent group structure can experience both negative and positive group selection for the same fitness correlate dependent on life history. Sociality was not under selection for summer survival (Supplementary Table 4). These results largely align with previous work in this system identifying costly reproductive and hibernation survival consequences of these social behaviors (Yang et al. 2017; Philson & Blumstein 2023a; Philson & Blumstein 2023b). Results here now suggest these behaviors are under multilevel selection in specific contexts, a prerequisite the evolution of social relationships and group social structure.

When considering the evolution of group traits, whether social network structures in the wild or the structure of businesses, if group-level selection acts on group averages of individual traits or on emergent group traits is an ongoing debate (Gardner, 2015; Goodnight, 2013). When exploring averages of individual traits (e.g. Royle et al. 2012), the argument for group/multilevel selection claims the evolutionary response to individual-level selection will be stronger and more consequential than group-level selection because evolutionary response is still at the level of the individual genotype. In other words, the distinction between individual- and group-level selection is irrelevant as the genetic response is only at the individual level (Okasha 2006; Eldakar and Wilson 2011). For multilevel selection to occur, the response must be at multiple levels of biological organization (Goodnight and Stevens 1997; Okasha 2005; West et al. 2011).

We have provided empirical evidence of group-level selection acting on emergent group traits without selection for an analogous individual-level trait in the wild. Thus, in some systems, group selection (and thus multilevel selection) cannot be ignored as a potentially important selective force. However, since the genetic response to selection on the group social phenotype has not been fully established, how this multilevel selection shapes evolution requires further investigation of evolutionary theory, quantitative genetics, and indirect genetic effects in novel ways. Furthermore, as individual and group social network traits may correlate across levels, selection at one level may either accelerate or constrain evolution at another level (Maynard-Smith, 1964; Goodnight, 2013), further complicating the discrete role of different levels of selection.

When exploring multilevel selection for social behaviors across taxa, the social system is relevant. Yellow-bellied marmots are a facultatively social mammal and do not rely on social relationships to the same extent as more gregarious and obligately social species (Snyder-Mackler et al. 2020). We suggest that obligately social animals may experience stronger multilevel selection than the yellow-bellied marmots studied here. While not a wild population, in a captive population of forked fungus beetles (Bolitotherus cornutus) with a fixed group size, more socially connected males experienced positive individual selection where females residing in more connected social groups experienced negative group-selection for reproductive success (Costello et al 2023). This study quantified individual and emergent group social phenotypes with a similar analogous social network trait and contextual analysis approach here we do here, but without quantifying the independent contributions of selection for multiple analogous pairs in the same model. Combined with our results showing multilevel selection acts on social phenotypes in wild populations for the first time, multilevel selection is likely present across taxa. Further research in the wild is required to test this hypothesis.

Interestingly we found no selection on either social phenotype in the context of summer survival. Predation accounts for 98% of summer mortality in this system (Van Vuren 2001) and the evolutionary origins of yellow-bellied marmot group living are contributed to predator avoidance (Armitage 2014). This suggests selection driving group living can be, and is in some cases, different than the selection driving individual position and social structures within groups. Again, work in more gregarious species where the evolutionary origins of group living may be attributable to grooming, heat retention, resource acquisition, or other non-predator avoidance drivers may find that the selection for group living and individual position and group structure are more aligned.

A common argument against group selection (and thus multilevel selection) that has been used since the 1960s focused on differences in individual lifespan versus group duration (Maynard-Smith 1964; Wade, 1977). Where individual lifespans are shorter than group duration, selection proceeds faster at the level of the individual. However, in yellow-bellied marmots, dispersal, mortality, and births ensure that groups restructure annually. Individuals surviving to adulthood have a mean lifespan of 4.07 and are thus part of multiple social groups in their lifetime (Armitage, 2014). Because individual lifespan is longer than group turnover in our population, this argument does not apply. Indeed, this same logic would predict stronger selection at the level of the group, which is what we found.

By leveraging a 19-year dataset from a wild, free-living mammal and using social network analysis to quantify individual and group social phenotypes in an analogous and comparative way, we provided evidence for multilevel selection as an important and complex force in the evolution of social behaviors in the wild. Indeed, because we show that selection acts on multiple levels of social behavior in the wild, multilevel selection as a conceptional framework more accurately represents how natural selection acts on social position and structure than either individual or group selection independently.

Methods

Study System

We used a 19-year dataset (2003-2021) on wild, free-living yellow-bellied marmots (*Marmota flaviventer*) studied at and around the Rocky Mountain Biological Laboratory in Colorado (38□570N, 106□590W; ca 2,895m above sea level). Yellow-bellied marmots are hibernating harem polygynous facultatively social ground-dwelling squirrels with matrilineal colony structures. This population is active for five months annually (mid-April to mid-September). Mating soon after emergence from hibernation, yearlings disperse and new pups emerge in late-

June to early-July. Annually, most males and about half of females disperse as yearlings, typically resulting in movement out of our study area. Marmots were studied annually at seven colony sites spread across 5 km at the bottom of the valley. Colonies are grouped into higher and lower elevation sites (four are at higher and three are at lower elevation sites). Higher elevation sites are approximately 166 m higher and experience harsher weather conditions (Van Vuren & Armitage 1991; Blumstein et al. 2006; Maldonado-Chaparro et al. 2015).

Throughout the active season, marmots were repeatedly live trapped and observed from 2003 to 2021. Recapture rate is above 86% in all colonies for all sex and age classes considered (Ozgul et al 2006). In addition to unique ear tags, all individuals were marked with unique non-toxic dye marks on their dorsal pelage to allow for accurate identification. Marmots were weighted when trapped and these data were used to predict 1 June and 15 August body mass (to estimate early and late season body condition) via a best linear unbiased predictions (BLUPs) model (Ozgul et al. 2010; Kroeger et al. 2018). June mass reflects the energy trade-off between left over energy from hibernation and available energy for spring reproduction whereas August mass reflects gain in fat mass during the active season and predicts overwinter survival (Ozgul et al. 2010; Armitage 2014; Kroeger et al. 2018). Data used in our BLUPs consisted of 25,979 observations across 4,330 individuals and 58 years with a mean of 5.99 observations per individual (range: 1.0–107.0; Median = 4.0), facilitating the accuracy and reliability of the BLUPs (Martin & Pelletier 2011; Dingemanse et al. 2019; Philson et al. 2022).

Marmots were studied under the research protocol ARC 2001-191-01 (approved by the UCLA Animal Care Committee on 13 May 2002 and renewed annually), protocols approved by the

Rocky Mountain Biological Laboratory, and trapped under permits issued annually by the Colorado Division of Wildlife (TR-917).

Social Networks

Detailed behavioural observational methodology and ethogram are outlined in Blumstein et al. (2009). For social interactions, the initiator, recipient, location, time, and type of each interaction is recorded, with most interactions (79%) occurring between identified individuals. The remaining 21% interactions could not be identified because of the interacting individuals' posture or visual obstructions. We excluded these interactions from our data, which should not significantly influence our estimates of social structure (Silk et al. 2015; Sánchez-Tójar et al. 2018). We only included adults and yearlings because only these cohorts were present in spring, when social interactions were most common. Pups were excluded because of their mid-season emergence and primary interaction with their mother and each other (Nowicki & Armitage 1979). We eliminated transients by excluding individuals observed or trapped fewer than five times in a given year (Wey & Blumstein 2012; Fuong et al. 2015; Yang et al. 2017; Blumstein et al. 2018). Only interactions in April, May, and June (~2.5-month time frame is when marmots emerge from hibernation/mate to when pups emerge from natal burrows) because this is when most social interactions occur and when we have the highest resolution of observation data (the growth of vegetation begins to impair observations as the summer progresses). Lastly, we focused on affiliative interactions (e.g. allogrooming, greeting and play) because they relate to fitness on both the individual and group levels (Wey & Blumstein 2012; Yang et al. 2017; Blumstein et al. 2018; Montero et al. 2020; Philson et al. 2022; Philson & Blumstein 2023a; Philson & Blumstein 2023b) and affiliative interactions comprised 88% of interactions.

Marmots share space with a subset of all possible individuals within their colony area, we therefore defined social groups based on space-use overlap per year (two individuals observed using the same burrow or seen/trapped at the same location and time within one-day intervals). Simple-ratio pairwise association indices based on colony space-use overlap were (Cairns & Schwager 1987) calculated with SOCPROG (version 2.9; Whitehead 2009) and run through the random walk algorithm Map Equation (Csardi & Nepusz, 2006; Rosvall & Bergstrom, 2008; Rosvall et al., 2009) to assemble association indices and identify social groups (network isolates within an association index). While Map Equation assigns each individual to only one social group (per year in our case), this can exclude key social connections, such as those with adult males. Because adult males often mate with females from multiple matrilines and have important interactions with members of multiple groups, we added adult males to each social group for which they had at least one social interaction with a member of that group to enable more accurate social network measures. However, each year, a male's network measures were only calculated from their originally assigned group.

From these spatially defined groups, directed and weighted social interaction matrices were constructed from affiliative social interactions for each group each year with the R (version 4.2.0; R Development Core Team 2023) package "igraph" (version 1.4.2; Csardi & Nepusz 2006). These affiliative social interaction matrices consisted of 42,369 social interactions between 1,294 individuals (338 of whom were observed across multiple years). This operationalisation produced 180 social groups with group sizes ranging from 2 to 35 individuals with a mean of 7.65 ± 5.92 (mean ± standard deviation). Individuals had an average of 66.23 ±

90.72 social interactions per year, ranging from 1 to 694. Within social groups, social interactions averaged 447.35 ± 653.18, ranging from 2 to 4,118.

We calculated (using "igraph") four pairs of analogous individual and group social network measures to quantify the independent contributions of the individual and group phenotypes (Table 1). These analogous network trait pairs quantify four core components in human and non-human animal social networks (including yellow-bellied marmots) at the two levels of social network organisation: connectivity, closeness, breakability, and clustering (Wasserman & Faust 1994; Krause et al. 2009). Degree (how may social partners an individual has; Wasserman & Faust 1994) and density (proportion of possible social connections that are observed in a group; Opsahl 2009) are paired to quantify social connectivity. Closeness (social distance between all other individuals in the group; Wasserman & Faust 1994) and average path length (mean social distance between all individuals in the group; Opsahl 2009) quantify social closeness. Embeddedness (individual connectedness based on their direct and indirect relationships with their cluster and group; Moody and White 2003) and cut points (number of social links that if broken result in two or more social groups of at least two individuals; Borgatti 2006) quantify social breakability. Local clustering coefficient (proportion of an individual's direct social partners who are also social partners, forming a triad/s; Croft et al. 2008) and transitivity (proportion of possible social triads that are observed in a group; i.e. global clustering coefficient; Wey et al. 2019) quantify social clustering.

The reliability of the social network measures is facilitated by our regular observations of marmot social groups (mean n observations per individual across years= 28.81, range of each year = 6.79– 75.14) and low rate of unknown individuals involved in social interactions (Silk et al. 2015; Sánchez-Tójar et al. 2018; Davis et al. 2018). Group size is associated with many group-level social network measures (Wasserman and Faust 1994; e.g. density, cut points) which may buffer the strength of selection. Because density, average path length, and transitivity are already "standardised" based on their equations, we standardised cut points by group size so all four group-level measures account for group size. We then fitted group size (measured as social network size) as a fixed effect in all models to further account for group size.

Fitness Measures

Summer survival was defined when individuals were seen or trapped after 1 August or in subsequent years, and over-winter/hibernation survival was defined as those individuals having survived the summer being seen the following spring or in subsequent years (Philson and Blumstein 2023b). For summer survival, only adults (>2 years old) were included in the analysis because of uncertainty quantifying survival for yearlings because a majority disperse (Armitage 1991). Predation accounts for 98% of summer mortality (Van Vuren 2001) and poor body condition and winter snowpack are primary predictors of hibernation mortality (Van Vuren and Armitage 1991; Armitage et al. 2003). Summer survival was paired with network measures from the current active season and hibernation survival with the active season before winter.

Only female reproductive success is quantified because male reproductive success mostly depends on dominance, body condition, and tenure length (Armitage 1998; Huang et al. 2011), is difficult to quantify, and the smaller number of males in the population diminishes analysis power. We quantified two attributes of female reproductive success: if a female successfully weaned offspring from the burrow and the number of offspring a mother weaned (if at least one pup was weaned) (Philson and Blumstein 2023a). Behavioural observations and a comprehensive genetic pedigree (Blumstein et al. 2010; Olson and Blumstein 2010) were used to assign offspring to mothers. This method does not account for pups that may have been born in the burrow but died before emergence (all pups are born in the burrow and emerge ~30 days after birth; Armitage 2014).

Contextual Analysis

We used contextual analysis, an extension of the Lande-Arnold selection analysis using partial regression to partition selection among levels (in this case, the individual and group social phenotypes; Lande and Arnold 1983; Goodnight et al. 1992). Our contextual analysis differed from classic contextual analysis (Heisler and Damuth 1987; Goodnight et al. 1992; Goodnight and Stevens 1997) since we used emergent group traits instead of using the mean of all individuals within a group.

Contextual analyses are sensitive to the scale of standardisation and should be based on the biological and ecological processes that generate selection in the context of the study system (De Lisle and Svensson 2017; Costello et al. 2023). Thus, we mean-variance standardised individual-level social network measures at the scale of each social group. Because group-level selection inherently operates across groups, we standardised group-level social network measures across all social groups across all 19 years. We further mean-variance standardised group size on the global scale across all social groups across all years. Overall, the model can be expressed as:

$$w_{jkl} = \beta_0 + \beta_{w,\Delta P_i} \Delta P_{i_{jkl}} + \beta_{w,\Delta P_g} \Delta P_{g_{jkl}} + e_{jkl}$$

Where w_{jkl} is the relative fitness of individual *j* in group *k* in year *l*, P_i are the social traits of an individual (individual social phenotype) and P_g are the emergent social traits at the group level (group social phenotype). $\Delta P_{i_{jkl}}$is the deviation of social trait for individual *j* from the mean of its group *k* in year *l.* $\Delta P_{g_{jkl}}$is the deviation of the emergent group social trait for group *k* of individual *j* in year *I* from the overall mean of group social trait across all groups and all years. $\beta_{w,\Delta P_g}$ and $\beta_{w,\Delta P_i}$ are the among-group and among-individual within a group selection gradients. $\beta_0$and e_{jkl} are the intercept and residual terms respectively (Lande and Arnold 1983; Fisher et al. 2017).

Due to fundamental differences in life history strategies between age classes (adult and yearling) and sexes in this system (Armitage 2014), we fitted separate models for each cohort. Each model included the fitness measure as the response variable, the four pairs of analogous social network traits, group size, and valley location (higher or lower elevation) as fixed effects. Individual ID and year were fitted as random effects. Eight models were fitted in total and the final models, after correcting fit for multicollinearity, met their respective assumptions. Models were fitted with “lme4” (version 1.1-33; Bates et al. 2015) and assumptions were checked with the car (version 3.1-2; Fox & Monette 1992; Fox & Weisberg 2019) and DHARMa (version 0.4.6; Hartig 2012) packages in R (version 4.2.0; R Development Core Team 2023).

The set of models (adult females only) for both measures of reproductive success additionally fit June body mass as a fixed effect given body condition’s importance for reproductive success in this system (Armitage 2014) and neither model had multicollinearity issues. The model for whether or not a female weaned a litter was fitted with a binomial distribution with a bobyqa optimiser of 10,000 function evaluations and had 363 observations across 157 unique individuals. The model for the number of offspring (if a litter was weaned) was fitted with a Poisson distribution and had 191 observations across 98 unique individuals (Extended Data Table 1).

The four sets of models (one for each age-sex cohort) for hibernation survival additionally included August body mass as a fixed effect (Armitage 2014). These models were fitted with a binomial distribution and a bobyqa optimiser of 10,000 function evaluations. Multicollinearity was again an issue between the network traits and thus the degree-density analogous pair was removed from all four models. With 19 years of data, the yearling male and female models had 119 and 209 observations, respectively (Extended Data Table 2). The adult male model had 109 observations across 58 unique individuals and the adult female model had 324 observations across 134 unique individuals across 19 years (Extended Data Table 3).

The two models for summer survival (male and female adults) additionally included June body mass and a predator index as fixed effects (Armitage 2014). The predation index was calculated by dividing the number of predators seen in a colony by the time spent observing that colony for that year (Blumstein et al. 2023). These models were fitted with a binomial distribution and a bobyqa optimiser of 10,000 function evaluations. Both of these models had VIF > 5 for density, thus we removed the degree-density analogous pair and ran the models again. The summer model included 19 years of data with 138 observations across 80 unique individuals for males and for females had 363 observations across 157 unique individuals (Extended Data Table 4).

Because of the standardization approach we used as part of this contextual analysis, model estimates can be interpreted as the effect size. To account for potential non-linear selection, we fitted models with a quadratic transformation for both the individual and group social network measures as fixed effects in each model. However, as these non-linear variables were not statically significant in any model, we chose to report the models without these non-linear variables for model fit, statistical simplicity, and interpretability. We also controlled for multiple comparisons by calculating False Discover Rate (FDR) adjusted *P*-values (Shaffer 1995; Verhoeven et al., 2005; Pike, 2011) based on eight comparisons for the eight models, which still showed multilevel selection occurred (despite losing statistical significance for some group measures after the FDR adjustment; Extended Data Table 5).

In all, these analyses allowed the quantification of independent contributions to individual fitness of qualitatively similar traits at different levels of social organisation and between age-sex cohorts while accounting for natural variation in group size across a nearly two-decade dataset.

Figures

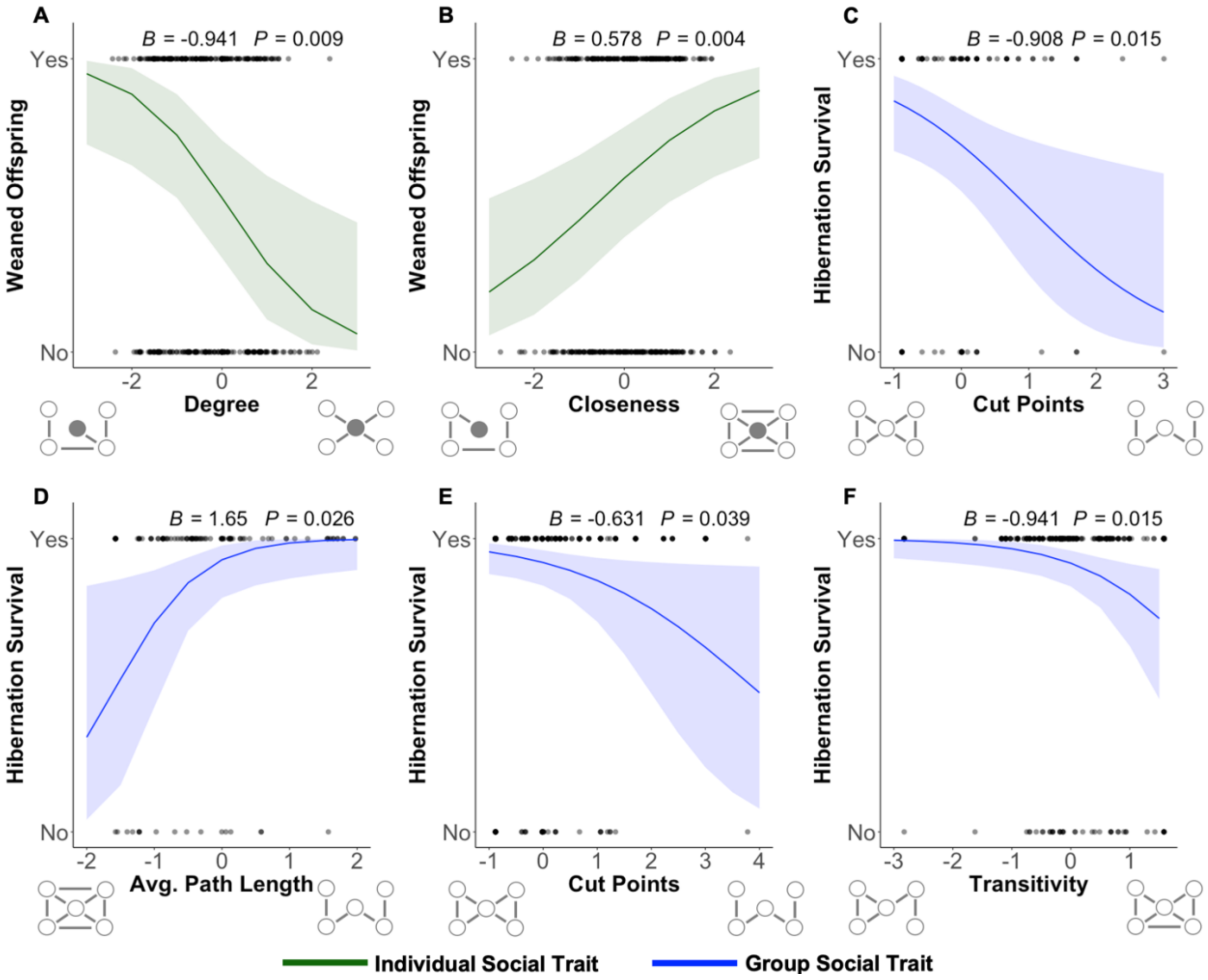
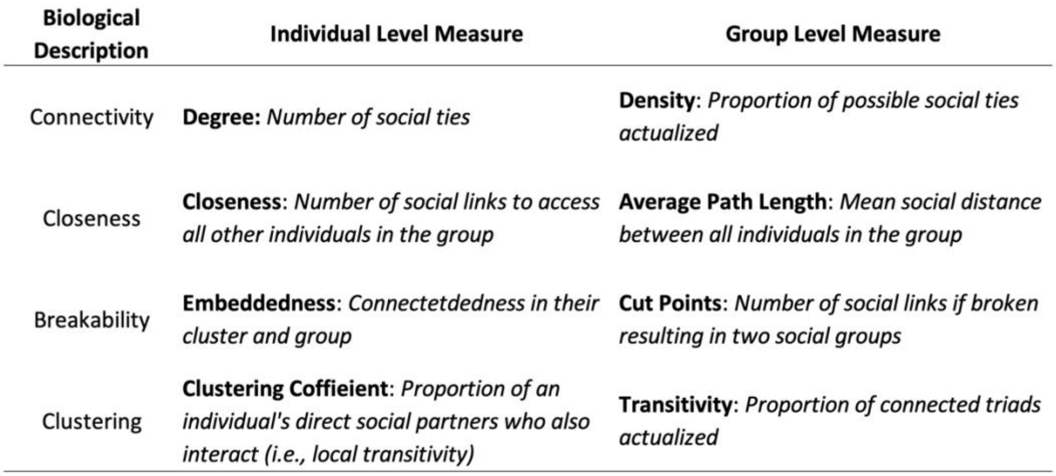


Figure 1. Selection gradients (plotted as marginal effects) for the individual and group social phenotypes. Adult female reproductive success (A-B) was under positive individual selection for more social partners and closer social distances. Yearling male (C) and adult female (E) hibernation survival was under positive selection for social groups less fragmentable into two or more groups. Adult male hibernation survival (D) was under positive group selection for the number of social links between the two most distant members of the social group. Adult female

hibernation survival (F) was under negative group selection for the proportion of connected triads.

Tables



Biological Description	Individual Level Measure	Group Level Measure
Connectivity	**Degree:** *Number of social ties*	**Density**: *Proportion of possible social ties actualized*
Closeness	**Closeness**: *Number of social links to access all other individuals in the group*	**Average Path Length**: *Mean social distance between all individuals in the group*
Breakability	**Embeddedness**: *Connectetdedness in their cluster and group*	**Cut Points**: *Number of social links if broken resulting in two social groups*
Clustering	**Clustering Coffieient**: *Proportion of an individual's direct social partners who also interact (i.e., local transitivity)*	**Transitivity**: *Proportion of connected triads actualized*

Table 1. The four pairs of analogous individual and group social network measures to quantify the independent contributions of the individual and group phenotypes.

Additional Information

Description	**Social Level**	**Variable**	**Estimate**	**Standard Error**	**Z value**	**P value**
		(Intercept)	-0.985	0.529	-1.864	0.062
Connectivity	Individual	**Degree**	-0.941	0.359	-2.624	**0.009**
	Group	**Density**	-0.138	0.383	-0.359	0.720
Closeness	Individual	**Closeness**	0.578	0.203	2.847	**0.004**
	Group	**Avg Path Length**	-0.057	0.350	-0.164	0.870
Fragmentable	Individual	**Embeddedness**	0.415	0.296	1.402	0.161
	Group	**Cut Points**	-0.313	0.249	-1.260	0.208

Clustering	Individual	**Clustering Coefficient**	-0.133	0.202	-0.659	0.510
	Group	**Transitivity**	0.147	0.263	0.559	0.576
		Age	0.212	0.089	2.395	**0.017**
		Valley Location	-0.291	0.369	-0.789	0.430
		Social Group Size	-0.323	0.307	-1.052	0.293
		1-June Mass	0.557	0.419	1.329	0.184
		(Intercept)	1.434	0.111	12.930	< **0.001**
Connectivity	Individual	**Degree**	-0.009	0.090	-0.101	0.920
	Group	**Density**	-0.059	0.087	-0.683	0.494
Closeness	Individual	**Closeness**	-0.043	0.046	-0.945	0.345
	Group	**Avg Path Length**	-0.118	0.078	-1.513	0.130
Fragmentable	Individual	**Embeddedness**	0.037	0.076	0.492	0.623
	Group	**Cut Points**	-0.010	0.058	-0.173	0.862
Clustering	Individual	**Clustering Coefficient**	-0.007	0.049	-0.142	0.887
	Group	**Transitivity**	-0.038	0.061	-0.619	0.536
		Age	-0.023	0.018	-1.313	0.189
		Valley Location	0.013	0.080	0.166	0.868
		Social Group Size	-0.032	0.071	-0.455	0.649
		1-June Mass	0.344	0.095	3.621	< **0.001**

Extended Data Table 1. Estimates, standard error, Z value, and P value from the two contextual analyses for adult female reproductive success: if at least one offspring was successfully weaned from the burrow (top) and the number of offspring a mother weaned (if at least one pup was weaned; bottom).

Description	Social Level	Variable	Estimate	Standard Error	Z value	P value
		(Intercept)	1.228	0.403	3.048	**0.002**
Closeness	Individual	**Closeness**	0.637	0.333	1.910	0.056
	Group	**Avg Path Length**	0.536	0.498	1.076	0.282
Fragmentable	Individual	**Embeddedness**	-0.246	0.377	-0.654	0.513
	Group	**Cut Points**	-0.908	0.373	-2.437	**0.015**
Clustering	Individual	**Clustering Coefficient**	-0.122	0.363	-0.336	0.737
	Group	**Transitivity**	-0.408	0.393	-1.037	0.300
		Valley Location	1.086	0.602	1.802	0.072
		Social Group Size	-1.005	0.410	-2.453	**0.014**
		15-August Mass	0.031	0.358	0.087	0.931
		(Intercept)	1.558	0.437	3.568	**< 0.001**
Closeness	Individual	**Closeness**	0.119	0.266	0.446	0.656
	Group	**Avg Path Length**	0.140	0.374	0.374	0.709
Fragmentable	Individual	**Embeddedness**	-0.400	0.387	-1.032	0.302
	Group	**Cut Points**	-0.122	0.359	-0.339	0.734
Clustering	Individual	**Clustering Coefficient**	0.279	0.309	0.901	0.367
	Group	**Transitivity**	-0.162	0.375	-0.431	0.666

		Valley Location	0.689	0.465	1.481	0.139
		Social Group Size	-0.381	0.335	-1.138	0.255
		15-August Mass	-0.152	0.424	-0.359	0.720

Extended Data Table 2. Estimates, standard error, Z value, and P value from the two contextual analyses for yearling male (top) and yearling female (bottom) hibernation survival.

Description	Social Level	Variable	Estimate	Standard Error	Z value	P value
		(Intercept)	1.027	0.865	1.188	0.235
Closeness	Individual	**Closeness**	-0.327	0.389	-0.840	0.401
	Group	**Avg Path Length**	1.648	0.739	2.228	**0.026**
Fragmentable	Individual	**Embeddedness**	0.716	0.480	1.491	0.136
	Group	**Cut Points**	0.074	0.485	0.152	0.879
Clustering	Individual	**Clustering Coefficient**	0.209	0.356	0.588	0.556
	Group	**Transitivity**	0.060	0.493	0.121	0.904
		Valley Location	0.003	0.690	0.005	0.996
		Social Group Size	-1.378	0.682	-2.022	**0.043**
		15-August Mass	0.747	0.390	1.918	0.055
		(Intercept)	2.498	0.418	5.971	**< 0.001**
Closeness	Individual	**Closeness**	-0.388	0.244	-1.591	0.112
	Group	**Avg Path Length**	0.001	0.372	0.001	0.999

Fragmentable	Individual	**Embeddedness**	0.316	0.230	1.371	0.170
	Group	**Cut Points**	-0.631	0.306	-2.063	**0.039**
Clustering	Individual	**Clustering Coefficient**	-0.079	0.219	-0.361	0.718
	Group	**Transitivity**	-0.941	0.385	-2.444	**0.015**
		Valley Location	-0.168	0.420	-0.400	0.689
		Social Group Size	-0.647	0.358	-1.806	0.071
		15-August Mass	0.144	0.303	0.477	0.634

Extended Data Table 3. Estimates, standard error, Z value, and P value from the two contextual analyses for adult male (top) and adult female (bottom) hibernation survival.

Description	**Social Level**	**Variable**	**Estimate**	**Standard Error**	**Z value**	**P value**
		(Intercept)	0.840	0.685	1.226	0.220
Closeness	Individual	**Closeness**	0.333	0.299	1.114	0.266
	Group	**Avg Path Length**	-0.618	0.434	-1.424	0.154
Fragmentable	Individual	**Embeddedness**	0.272	0.318	0.854	0.393
	Group	**Cut Points**	-0.022	0.318	-0.070	0.944
Clustering	Individual	**Clustering Coefficient**	-0.072	0.277	-0.261	0.794
	Group	**Transitivity**	-0.026	0.371	-0.070	0.944
		Valley Location	0.175	0.531	0.329	0.742
		Social Group Size	-0.135	0.434	-0.310	0.756

		1 June Mass	0.551	0.318	1.733	0.083
		Predator Index	-0.339	0.528	-0.642	0.521

		(Intercept)	2.108	0.484	4.357	**< 0.001**
Closeness	Individual	**Closeness**	-0.112	0.230	-0.488	0.625
	Group	**Avg. Path Length**	0.323	0.357	0.905	0.366
Fragmentable	Individual	**Embeddedness**	0.412	0.215	1.920	0.055
	Group	**Cut Points**	-0.156	0.264	-0.588	0.556
Clustering	Individual	**Clustering Coefficient**	-0.187	0.208	-0.900	0.368
	Group	**Transitivity**	0.305	0.262	1.162	0.245
		Valley Location	-0.567	0.447	-1.268	0.205
		Social Group Size	-0.344	0.365	-0.943	0.346
		1 June Mass	1.156	0.382	3.027	**0.002**
		Predator Index	0.095	0.401	0.238	0.812

Extended Data Table 4. Estimates, standard error, Z value, and P value from the two contextual analyses for adult male (top) and adult female (bottom) summer survival.

Fitness Measure	Network Measure	Estimate	Standard Error	Z value	P value	FDR Adjusted P value
If Offspring Was Weaned	**Closeness**	0.57768	0.20291	2.847	0.004	0.035
If Offspring Was Weaned	**Degree**	-0.94128	0.35876	-2.624	0.009	0.035
Hibernation Survival (Adult Female)	**Transitivity**	-0.9405215	0.3848622	-2.444	0.015	0.039
Hibernation Survival (Yearling Male)	**Cut Points**	-0.90812	0.37269	-2.437	0.015	0.030
Hibernation Survival (Adult Male)	**Avg Path Length**	1.647839	0.739472	2.228	0.026	0.041
Hibernation Survival (Adult Female)	**Cut Points**	-0.631057	0.3058272	-2.063	0.039	0.052

Extended Data Table 5. False Discover Rate (FDR) adjusted P-values (for eight comparisons due to running eight models) for the six statistically significant network measures.

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