HARSH AND VARIABLE ECOLOGICAL CONDITIONS MODULATE THE RELATIONSHIP BETWEEN SOCIAL STRUCTURE AND DIRECT FITNESS IN A PLURALLY BREEDING SMALL MAMMAL

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ABSTRACT

Evidence suggests that harsh and variable environmental conditions modulate the fitness benefits associated with increased group size in some species. Social network analysis is a more powerful approach to examine this relationship, as the quality of interactions is more important than quantity. Using 9 years of data, I determined how mean and coefficient of variation (CV) of nine ecological variables modulated the relationship between social network metrics on direct fitness in the plurally breeding rodent, *Octodon degus*. As predicted, increased social structure was most beneficial when food abundance was more variable, mean monthly rainfall was highest, predator abundance was more variable, soil hardness was more variable, and ectoparasitic flea intensity was low and more variable. In contrast, the observed effect of the CV of burrow density and mean food abundance on the relationship between strength and direct fitness contradicted our predictions. Overall, our results illustrate that the harshness and unpredictability of ecological conditions are not mutually exclusive explanations for social structure-direct fitness covariation.

DEDICATION

For JM, may the completion of this work be the gateway to many wanderings and adventures.

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LIST OF ABBREVIATIONS

AIC, Akaike Information Criterion

ANCOVA, analysis of covariance

ENSO, El Niño/Southern Oscillation

EFI, ectoparasitic flea intensity

ID, individual’s ear tag number, individual may have more than one number associated with them

PCOS, per capita offspring surviving to reproductive age

PCOW, per capita number of offspring weaned

SNA, social network analysis

LIST OF TERMS

Allee effect — positive relationship between population growth rate and density at low animal densities

Breeding system — the extent to which direct reproduction is monopolized by and parental care is shared among group members

Burrow System — burrow openings directly surrounding a central location, burrow systems were determined through telemetry of collared individuals

Cooperative breeding — see singular breeding

Direct fitness — the contribution of an individual to the gene pool of a subsequent generation based only on the reproductive success of that individual

Eigenvector centrality — a measure of how well an individual is associated with other individuals and how well its close associates are themselves associated

Fitness — the contribution of an individual to the gene pool of subsequent generations

Inclusive fitness – the sum of an individual's direct and indirect fitness

Mating system — the number of mates an individual has

Plural breeding — a breeding system in which multiple individuals within a group breed; this can be with communal care (nursing or provisioning of offspring that one did not produce) or without communal care

Singular breeding — a breeding system in which one or few breeding individuals dominate reproduction, other individuals act as non-breeding helpers (synonymous: cooperative breeding)

Social behavior — species-typical pattern of relationships among all members of a group (including spatial distribution patterns, inter-individual relationships involving dominance hierarchies or territoriality, mating systems, parenting and dispersal)

Social network analysis — a method for mathematically measuring relationships between individuals that overlap spatially and temporally

Social organization — group composition and size

Social structure — types and patterns of interactions between adult individuals

Social systems — conspecifics that interact regularly and do so more with each other than with other individuals in the ‘background’ population. There are three fundamental components of social systems: social organization (group composition), social structure (individual interactions), and mating system.

Strength — the sum of an individual’s associations including both the number of associates and the intensity of associations (synonym: gregariousness).

CHAPTER 1

INTRODUCTION

Social Behavior and Social Systems

Social systems characterize the extent to which individuals overlap and interact with conspecifics in the population (Kappeler and van Schaik 2002) and represent emergent properties of individual social behavior and strategies (Hinde 1976). Being a member of a social group may increase individual fitness through benefits such as reduced predation risk (through collective vigilance or dilution) or improved food or territory acquisition (Caro 1994; Mosser and Packer 2009). To date, a major aim of social system research has been to examine the associated reproductive fitness consequences of variation in social systems. In some groups of organisms, physical and ecological constraints allow for fairly easy classification and description of social systems (Whitehead 1997). However, classification of social systems can be challenging and often varies between and within species (Whitehead 1997). Social systems can range from long-term associations, often kin-groups such as in elephant herds (Emlen 1995; Wittemyer et al. 2005), to temporal aggregations or colonies, such as in socially roosting bats (Kappeler and van Schaik 2002; Kerth et al. 2002; Krause and Ruxton 2002). Although often defined differently (Whitehead 1997; Müeller and Thalmann 2000) there are three widely accepted and interrelated components of social systems: mating systems, social organization, and social structure (Kappeler and van Schaik 2002).

One component of social systems, mating systems, is defined as social interactions between mates, called the social mating system, and the reproductive consequences of those interactions, referred to as the genetic mating system (Kappeler and van Schaik 2002). Thus, when determining the fitness consequences of mating systems, both social and genetic components must be examined (Kappeler and van Schaik 2002). Across species, there is a wide array of mating systems ranging from long-term monogamy to promiscuity (Clutton-Brock 1989). In mammals, variation in mating systems between different genders is dependent on a large number of ecological and physiological factors including territory quality, defensibility of mates, and offspring care (Clutton-Brock 1989).

Social organization, or the composition and size of a social unit (typically group size), is the most widely used of the three components when studying the fitness consequences of social systems. However, across and within vertebrate taxa, there are inconsistent patterns in the direct fitness consequences of social organization (Balshine et al. 2001; Clayton and Emery 2007; Ebensperger et al. 2012a; Schradin et al. 2012). Studies of social organization show that the reproductive success of breeders can be unaffected, decrease, or increase with increasing number of adults per group (Vehrencamp and Quinn 2004; Silk 2007; Ebensperger et al. 2012a). Similarly, there is considerable variation in the effects of adult group composition (Silk et al. 1981) and the number of non-breeding “helpers” in groups (Moehlman 1979; Russell et al. 2003) on direct fitness. These inconsistent patterns are likely due to the fact that social organization, alone, cannot capture the complexity and variation across social systems (Kappeler and Van Schaik 2002; Wey et al. 2008).

Social structure, the third component of social systems, is defined as the patterns of interactions between individuals and the resulting relationships those interactions produce (Kappeler and Van Schaik 2002). These relationships often persist because they represent fitness maximizing behavioral strategies (Van Schaik 1989). Social structure can be characterized by examining the difference in the frequency, types, or intensity of interactions between two conspecifics. Determining the fitness consequences associated with social structure involves comparing these interactions across groups or populations.

Ecological Constraints on Social Systems

The concept that environmental or ecological variables modulates or constrains social systems emerged in the 1970s (Crook 1970; Emlen and Oring 1977; Terborgh and Janson 1986). Since then, many socio-ecological models have been proposed that examine the relationships between components of social systems and ecological variables (Emlen 1982; Terborgh and Winter 1983; Van Schaik and Van Hooff 1983; Terborgh and Janson 1986; Emlen 1995). In particular, socio-ecological research has focused on the causes of delayed dispersal and group formation (Emlen 1982; Komdeur 1992; Emlen 1995; Schoech 1996; Arnold and Owens 1999; Lucia et al. 2008) and the costs and benefits of cooperation (Hamilton 1964; Trivers 1971; Cockburn 1998). More recently, studies have focused on determining how species distributions (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011) and reproductive consequences of social systems (Rubenstein 2011; Ebensperger et al. 2012a, 2014) are influenced by spatio-temporal variation in ecology. However, the modulating role of spatio-temporal variation in ecology on the fitness consequences of social systems is still a topic of debate in behavioral ecology (Cockburn and Russell 2011; Gonzalez et al. 2013). In most social vertebrates, determining this effect requires multi-generational, long-term studies of individually marked animals (Clutton-Brock and Sheldon 2010). Two recent long-term studies, one on mammals (Ebensperger et al. 2014) and one on birds (Rubenstein 2016), shed light on how ecological conditions may modulate the relationship between social organization and fitness. Ebensperger et al. (2014) determined that the relationship between the number of adult female group members (an indicator of communal care) and direct fitness in a plurally breeding mammal was modulated by inter-annual variation in mean food availability, animal density, and precipitation. Their study, an analysis of an 8-year database, revealed an important modulating effect of ecological “harshness” on the relationship between social organization and direct fitness in a plurally breeding species. Specifically, their study indicated that increased group size was more beneficial under harsh conditions, represented by low rainfall, low food abundance and low animal density (Ebensperger et al. 2014). Using a 10-year dataset, Rubenstein (2016) found that variation in annual precipitation influenced all aspects of superb starling (*Lamprotornis superbus*) life history (i.e., breeding role, helping behavior), supporting the hypothesis that plural breeding and "helpers at the nest" may reduce environmentally induced variation in fecundity.

Social Network Analysis

Finding measures that accurately reflect the complexities of social relationships among individuals is one of the biggest challenges when studying social species. Social network analysis (SNA) allows researchers to study and measure complex social relationships directly (Wey et al. 2008). Social network models are made up of nodes, which represent individuals or groups, and ties, which represent some form of connection between two nodes at a given time. For example, a tie can represent any type of social interaction such as grooming, learning, or pathogen transfer (Wasserman and Faust 1994). Social network analysis (SNA) provides the tools necessary to examine variation in social structure across all levels of organization in social species using formal descriptors (Wey et al. 2008). Thus, SNA provide the quantitative measures necessary to test statistical models that examine the relationships in the network (Wasserman and Faust 1994; Wey et al. 2008; Farine and Whitehead 2015). Network analyses are broadly applicable across a wide range of topics including disease transmission (Wey et al. 2013), hierarchical position (Formica et al. 2012), kin structure and fitness (Hirsch et al. 2013; Davis et al. 2015), and fission-fusion dynamics (where group size and composition are fluid; Carter et al. 2013). A particularly important aspect of SNA is that relationships among individuals can be measured directly through trapping overlap or behavioral observations, and unlike group size, more accurately represent the frequency or intensity of interactions between members of a group or population (Wey et al. 2008). Additionally, SNA can be linked to fitness, which allows an examination of social systems in an evolutionary context (Farine and

Whitehead 2015). A current challenge in developing a comprehensive model for sociality using network studies is that, despite the broad range of topics that network analyses can be used to examine, network analyses have been focused on a limited number of contexts (Kurvers et al. 2014). Recent evidence suggests that social structure affects a broader range of ecological and evolutionary processes that have not been fully explored (Kurvers et al. 2014).

Thesis Objectives

The extent to which spatio-temporal ecological variation modulates the relationship between social structure and reproductive success is unknown. Thus, the goal of this research is to describe the modulating effect of spatio-temporal variation in ecological conditions on the relationship between social network structure and per capita direct fitness, shown in Figure 1.1 below. This figure illustrates the conceptual framework for the present study, showing how ecological variables influence different components of a social system and two resulting per capita fitness correlates. Each of the four components of social systems are likely effected by changes in ecological conditions and the reference (Ebensperger et al. 2014) listed below social organization denotes a study in which the fitness consequences of this component were previously examined. Between the two fitness correlates is dispersal, where offspring can leave their natal burrow system, or philopatry, where an individual can remain at their natal burrow (Quirici et al. 2011). The decision by an individual to remain at or leave their natal burrow typically occurs between weaning and reproductive age (Quirici et al. 2011). The aim of this study was to determine if certain ecological variables had a modulating effect on the relationship between social structure (in bold below) and the two fitness correlates aforementioned.

Here, we use a 9-year dataset to examine this relationship in the Common degu (*Octodon degus*, herein referred to simply as degu), a caviomorph rodent endemic to central Chile. Specific predictions and models were used test two hypotheses: the "benefits under harsh conditions" using the mean values of ecological variables and "benefits under variable conditions" using the coefficient of variation values of ecological variables.

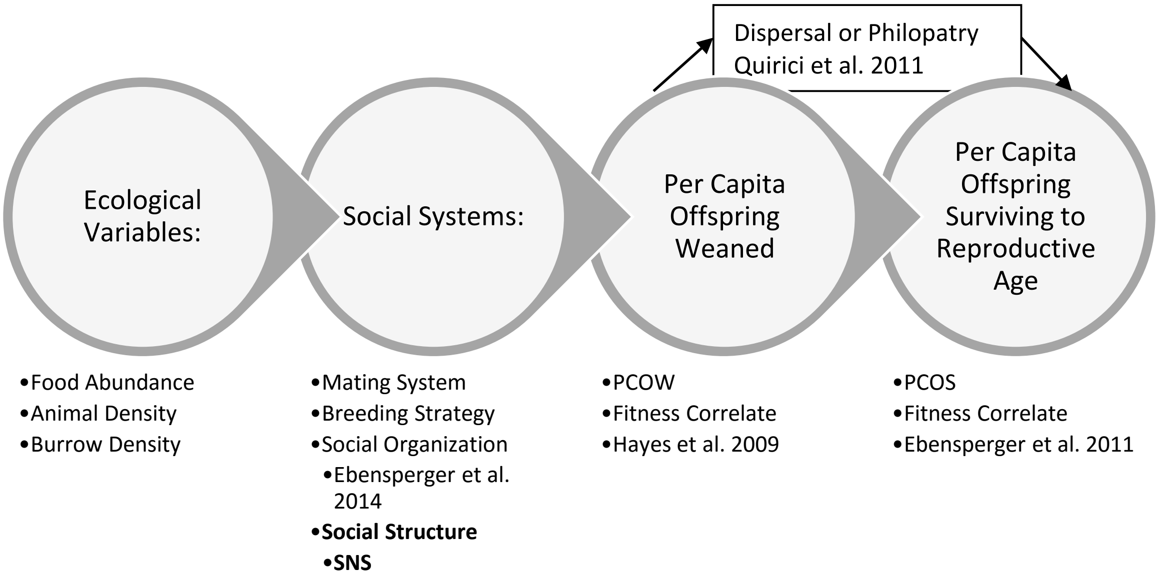

Figure 1.1 Conceptual framework of the present study. This framework was designed based on previous research conducted by Hayes et al. 2009, Quirici et al. 2011, and Ebensperger et al. 2014. This figure illustrates that ecological variables influence all components of social systems which not only influence individual fitness but also the decision of offspring to disperse or remain philopatric to their natal territory.

Significance

Research on the fitness consequences of social systems often uses group size (a component of social organization) as a proxy for social systems. The use of group size in social system studies has not been successful in revealing patterns of fitness consequences of different social systems and has generated conflicting results. The contradictory results generated by group size studies only further the confusion about the importance of social systems on direct fitness. Alternatively, social network analysis, an indicator of social structure, provides the tools necessary to study social complexity (Stanton and Mann 2012) in species where social interactions are challenging to observe or document (Wey et al. 2008). The use of social structure, as opposed to social organization, may reveal novel and exciting insights into the direct fitness consequences of social systems. Additionally, with the use of a long-term dataset, the modulating effect of spatio-temporal variation in ecological conditions on social structure and direct fitness covariation may be elucidated. These long-term studies can potentially provide important insight into how future changes in ecological conditions (due to human impacts i.e., climate change or habitat modification) will affect the social structure and direct fitness of plurally breeding species.

CHAPTER 2

HARSH AND VARIABLE ECOLOGICAL CONDITIONS MODULATE THE RELATIONSHIP BETWEEN SOCIAL STRUCTURE AND DIRECT FITNESS IN A PLURALLY BREEDING SMALL MAMMAL

Introduction

Social systems characterize the extent to which individuals overlap and interact with conspecifics in the population (Kappeler and Van Schaik 2002). A major aim of research on social systems is to identify sources of inter- and intraspecific variation and to analyze the associated reproductive fitness consequences. This is challenging because social systems can be complex (Wittemyer et al. 2005) and group stability varies extensively (Port and Johnstone 2013), with some species exhibiting frequent changes in group membership (Aureli et al. 2008). Moreover, there is a diverse spectrum of social systems ranging from temporal aggregations or colonies which are typically formed to exploit a resource or group size benefit (Kappeler and Van Schaik 2002; Kerth et al. 2002; Krause and Ruxton 2002) to relatively stable, long-term associations which are typically kin groups (Emlen 1995).

Understanding the evolutionary significance of long-term associations among conspecifics requires an understanding of four inter-related components of a social system: i) mating system, ii) breeding strategy, iii) social organization, and iv) social structure. The mating system describes the number of mates that individuals have (i.e., monogamy, polygyny) and is thought to be influenced by ecology, the potential to monopolize mates, and sex-specific strategies of investment in reproduction (Bateman 1948; Emlen and Oring 1977; Kokko and Johnstone 2002; Kokko and Jennions 2008). Breeding strategy describes the extent to which direct reproduction is monopolized by and parental care is shared among group members (Silk 2007). Breeding strategies includes singular breeding where one dominant breeder and non-breeders care for offspring; also cooperative breeders (Lukas and Clutton-Brock 2012) and plural breeding where multiple group members breed, with and without communal offspring care (Brown 1978; Silk 2007). Social organization refers to the composition and size of social groups, while social structure includes the types and patterns of interactions among adult group members (Kappeler and Van Schaik 2002). Our understanding of the evolutionary significance of vertebrate social systems is based largely on studies of social organization, mainly the number and composition of adult group members (Silk et al. 1981; Forrester 1991; Ebensperger et al. 2012a). This is problematic because of the interdependent nature of the different components of a social system (Kappeler and Van Schaik 2002). For example, there is strong evidence that individual direct fitness is affected by both breeding strategy (Ebensperger et al. 2012a) and social structure, including the extent of cooperation among adult group members (Clutton-Brock et al. 1976) and the type of care provided by “helpers” (König 1997; Cockburn 1998; Taborsky et al. 2007). Thus, how two or more components of social systems interact to influence fitness should enhance our understanding of the evolutionary significance of social systems significantly.

This understanding also requires a theoretical framework linking individual fitness-enhancing behavior (the level at which selection occurs) to group traits (the level at which social system research is conducted; Kappeler and Van Schaik 2002). The socio-ecological model provides this link and indicates that ecological factors shape interactions between conspecifics (Kappeler and Van Schaik 2002). Although there is evidence that ecology plays a role in shaping the direct fitness consequences of social organization (Rubenstein 2011; Ebensperger et al. 2012b), the extent to which spatio-temporal variation in ecology modulates the fitness consequences of different components of a social system is a topic of debate in behavioral ecology (Cockburn and Russell 2011; Gonzalez et al. 2013). In particular, spatio-temporal variation in ecology can alter or reinforce social interactions (i.e., cooperative vs. competitive) among group members, which in turn could affect the fitness consequences of variation in social organization (Ebensperger et al., in review).

Two non-mutually exclusive hypotheses for the modulating effect of spatio-temporal variation in ecology on the relationship between social organization and direct fitness are the "benefits under harsh conditions" and "benefits under variable conditions" (Rubenstein 2011; Ebensperger et al. 2014). The "benefits under harsh conditions" hypothesis posits that increasing group size improves direct fitness under extreme or harsh environmental conditions. Support for this hypothesis comes from research on cooperatively breeding birds (Magrath 2001; Covas et al. 2008; Shen et al. 2012) and a plurally breeding mammal (Ebensperger et al. 2014). The "benefits under variable conditions" hypothesis posits that increasing group size enhances direct fitness or allows some reproductive success when environmental conditions are variable, including both inter- and intra-annual variation (Rubenstein and Lovette 2007; Rubenstein 2016). This hypothesis is supported by comparative studies showing cooperative breeding in birds is positively associated with unpredictable inter-annual rainfall and most commonly occurs in semiarid habitats (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011). Further support comes from a long-term field study in which variation in annual precipitation influenced all aspects of superb starling (*Lamprotornis superbus*) life history (including breeding roles, helping behaviors, etc.), supporting the hypothesis that plural breeding reduces environmentally induced variation in fecundity (Rubenstein 2011; 2016).

The aim of our study was to determine if the "benefits under harsh conditions" and "benefits under variable conditions" hypotheses explain social structure-direct fitness relationships in a plurally breeding mammal where the relationship between social organization and direct fitness has already been examined (Ebensperger et al. 2014). To quantify social structure, we used social network analyses, a powerful method of determining variation in social structure across groups and populations (Wasserman and Faust 1994; Farine and Whitehead 2015). When social interactions are difficult to observe, social network analysis can be used to estimate interactions in species with complex social structure (Wey et al. 2008) and under a wide range of ecological conditions (Wey et al. 2013; Farine and Whitehead 2015; Firth and Sheldon 2015). Furthermore, social network analyses reveal important information about the quality and nature of social interactions, which is more important than the number of associations (group size) alone (Stanton and Mann 2012). Variation in social structure can be described using social network metrics that indicate (i) how connected an individual is to other individuals (strength) and (ii) how well connected an individual is and to whom (eigenvector centrality) (Whitehead 2009). Here, we use a 9-year dataset to examine how mean and variation in ecological conditions modulate the relationship between social network structure and direct fitness in the common degu (*Octodon degus*, herein degu), a caviomorph rodent endemic to central Chile. Our study builds on previous field work that revealed an important modulating role of spatio-temporal variation in ecology on the direct fitness consequences of group size in degus (Ebensperger et al. 2014) and patterns in direct fitness of plural breeding in mammals (Ebensperger et al. 2012a). In light of this previous work, our study of social structure will generate important insights into the evolutionary significance of social systems.

Model Species and Hypotheses

Degus forage aboveground during the daytime and share underground nests with conspecifics at night (Ebensperger et al. 2014). Degu social groups vary in size and composition (Hayes et al. 2009; Ebensperger et al. 2011, 2014). The average relatedness of individuals within groups is not different from the average relatedness of randomly selected individuals in the population (Quirici et al. 2011;

Davis et al. 2015), suggesting that direct reproduction is the primary avenue to inclusive fitness. Within social groups, all adult females reproduce (>95%; Hayes et al. 2009; Ebensperger et al. 2011) and nurse offspring communally (Ebensperger et al. 2006; Jesseau et al. 2009), implying that degus are plural breeders. Previous studies of 2-3 years in duration suggests that increasing group size has direct fitness costs to females (Hayes et al. 2009; Ebensperger et al. 2011). A recent analysis of an 8-year dataset suggests that increasing group size is most beneficial in years or in patches with the lowest mean food abundance (Ebensperger et al. 2014). Degu social network structure is highly variable at the group (Davis et al. 2015) and population (Wey et al. 2013) level. The extent to which spatio-temporal ecological variation modulates the relationship between network structure and direct fitness is unknown. To test the “benefits under harsh conditions” and “benefits under variable conditions” hypotheses, we quantified the extent to which mean and variance in ecological factors modulate social network structure–direct fitness covariation, respectively. Based on relevant ecological conditions and social theory we considered harsh environmental conditions to be represented by i) low mean food abundance ii) high mean degu density (due to high competition for resources; based on the between-group contest competition hypothesis; Harris 2006) iii) low mean precipitation iv) high mean predation risk, including high predator abundance and low availability of burrows (refuges), v) high mean soil hardness vi) extreme (high or low) monthly ambient temperature, and vii) high mean ectoparasitic flea intensity (EFI; Burger et al. 2012; Ebensperger et al. 2014). We consider variable environmental conditions to be represented by i) variable food abundance ii) variable degu density iii) variable precipitation iv) variable predation risk, including variable predator abundance and variable availability of burrows (refuges), v) variable soil hardness vi) variable monthly ambient temperature and vii) variable ectoparasitic flea intensity (Ebensperger et al. 2014). Specific predictions and models (i.e., food abundance and degu density) used to test predictions for the two are outlined in Table 2.1.

Table 2.1 Models, predictions and trends of modulating ecological variables. Models, predictions and trends examining how ecological variables modulate the relationship between social network metrics and direct fitness for two hypotheses. Direct fitness metrics included both per capita offspring weaned (PCOW) or per capita offspring surviving to reproductive age (PCOS). Best fit models are based on decreasing Akaike Information Criterion (AIC) and included null model as possible best fit. Only relationships between strength and direct fitness are included, as eigenvector centrality models never had AIC values lower than the null models (Table G1). CV=coefficient of variation

Model	Prediction(s)	Best fit model	Observed trend*
(1) Benefits under harsh (mean) conditions			
Food and degu density (*within groups)*	Relationship between PCOW (or PCOS) and strength of all adult group members females (or female group members) becomes more positive with decreasing mean food abundance and increasing mean degu density	Food, only PCOW-All	Less negative relationship with increasing mean food abundance.
Burrow density and predation (*within groups)*	Relationship between PCOS and strength of all adult group members females (or female group members) becomes more positive with increasing mean predation and increasing mean burrow density (many places to hide)	Null model	No predictor interactions detected.
Soil hardness and precipitation (*within groups)*	Relationship between PCOW (or PCOS) and strength of all adult group members females (or female group members) becomes more positive with increasing mean soil hardness and decreasing mean monthly precipitation	Precipitation, only PCOS-All	Less negative relationship with decreasing mean monthly precipitation.
Ectoparasitic flea intensity (*within groups)*	Relationship between PCOW (or PCOS) and strength of all adult group members females (or female group members) becomes more positive with increasing mean ectoparasitic flea intensity (EFI)	EFI PCOS-All	Less negative relationship with decreasing mean EFI.
		EFI PCOW-Females	Less negative relationship with decreasing mean EFI.
Ectoparasitic flea intensity (*population level)*	Relationship between PCOW (or PCOS) and strength (or eigenvector centrality) of all adult group members females (or female group members) becomes more positive with decreasing mean EFI	EFI PCOS-All	Less negative relationship with decreasing mean EFI.

Table 2.1 Continued

(2) Benefits under variable (CV) conditions

Food and degu density (*within groups*)	Relationship between PCOW (or PCOS) and strength of all adult group members females (or female group members) becomes more positive with more variable food abundance and more variable mean degu density	Food abundance, only PCOW-All	Less negative relationship with decreasing CV of food abundance.
		Food abundance, only PCOW-Females	Less negative relationship with increasing CV of food abundance.
Burrow density and predation (*within groups*)	Relationship between PCOS and strength of all adult group members females (or female group members) becomes more positive with more variable predation and more variable burrow density (many places to hide)	Burrows, only PCOW-All	Less negative relationship with decreasing CV of burrow density.
		Predation, only PCOS-All	Less negative relationship with increasing CV of predator abundance.
Soil hardness and precipitation (*within groups*)	Relationship between PCOW (or PCOS) and strength of all adult group members females (or female group members) becomes more positive with more variable soil hardness and more variable monthly precipitation	Soil hardness, only PCOW-All	Less negative relationship with decreasing CV of soil hardness.
		Soil hardness, only PCOW-Females	Less negative relationship with increasing CV of soil hardness.
Ectoparasitic flea intensity (*within groups*)	Relationship between PCOW (or PCOS) and strength of all adult group members females (or female group members) becomes more positive with more variable ectoparasitic flea intensity (EFI)	EFI PCOS-All	Less negative relationship with increasing CV of EFI.
Ectoparasitic flea intensity (*population level*)	Relationship between PCOW (or PCOS) and strength (or eigenvector centrality) of all adult group members females (or female group members) becomes more positive with less variable EFI	EFI PCOS-All	Less negative relationship with increasing CV of EFI.
		EFI PCOS-Females	Less negative relationship with increasing CV of EFI.

*Abbreviated trends

PCOW-All: relationship between PCOW and strength (or eigenvector centrality) of all adult group members

PCOW-Females: relationship between PCOW and strength (or eigenvector centrality) of adult female group members

PCOS-All: relationship between PCOS and strength (or eigenvector centrality) of all adult group members
PCOS-Females: relationship between PCOS and strength (or eigenvector centrality) of adult female group members

Methods

Study Site

Field work was conducted at the Universidad de Chile Estación Experimental Rinconada de Maipú (33°23’S, 70°31’ W, altitude 495 m) in 2005-2013. The study site is characterized by a Mediterranean climate with strong inter-annual and seasonal variation in rainfall and plant abundance (Ebensperger et al. 2014). The landscape consists of uniformly distributed grasses and shrubs (*Proustia pungens, Acacia caven, and Baccharis* spp.) that on average cover 14.5% of the ground (Ebensperger and Hurtado 2005). The abundance of adult degus in this population at this site ranged between 25 and 109 over the period of study.

Social Group Identification and Membership

Social group composition was determined between late August and early November, a time encompassing the period of parturition to weaning (Hayes et al. 2007; Ebensperger et al. 2014). The main criterion used to assign degus to social groups was the sharing of burrow systems during the night-time (Ebensperger et al. 2004; Hayes et al. 2009). A burrow system was defined as a group of burrow openings surrounding a central location where individuals were repeatedly found during telemetry (Fulk 1976). Burrow sharing was determined by means of burrow trapping and night telemetry conducted between August–October, the period of pregnancy and lactation of degus. Each year, Tomahawk

(Tomahawk model 201, Tomahawk Live Trap Company, Tomahawk, WI) and locally produced traps (similar to Sherman live traps [H. B. Sherman Traps, Inc., Tallahassee, FL] in design) were placed at burrow systems covering an area of 1-2 hectares. The area was dependent on the abundance and spacing of degu groups each year. Traps were set prior to the emergence of adults during morning hours (06:00 h) and remained opened for 1.5 hours (Ebensperger et al. 2014). Eight to fourteen traps were opened during the early morning and closed 1–2 hours after sunrise. Some burrow systems were added to trapping effort after animals were tracked to these systems during telemetry observations made during August-September (see below). Burrow systems were trapped for 13–36 days per month during September and October. Trapping ended when less than 5% of captured offspring were new individuals, always by late October or early November.

We determined the identity, location, sex, and body mass (to 0.1 g) of all degus, and reproductive condition of all females (perforated, pregnant, or lactating). Each degu was marked with unique tags (Monel 1005-1, National Band and Tag Co., Newport, KY) on each ear at the time of first capture. Adult individuals weighing greater than 170 g were fitted with a 6–7 g radio collar (BR radio-collars, AVM Instrument Co., Colfax, CA) with unique pulse frequencies. Approximately one hour after sunset, radio-collared adults were radiotracked to their burrows through “homing” (Kenward 2001). Nighttime telemetry was conducted using a LA 12-Q receiver (for radio-collars tuned to 150.000–151.999 MHz frequency) or FM-100 receiver (for radio-collars tuned to 164.000–164.999 MHz; Advanced Telemetry Systems, Isanti, MN, USA) and a hand-held three-element Yagi antenna (AVM Instrument Co. or Advanced Telemetry Systems).

Social group membership was determined following methods described in Hayes et al. 2009 and Ebensperger et al. 2014. To determine overlap of individuals, we calculated similarity matrices based on pairwise associations using SOCPROG 2.5 software (Whitehead 2009). For each pair of individuals, we calculated a “simple ratio” index which is defined as the number of times two individuals are caught at the same burrow, divided by the total number of times those individuals are caught on the same day (Ginsberg and Young 1992). The association indices for pairs of individuals indicate the proportion of burrow use overlap within the population (Wey et al. 2013). These values ranged from 0 “never caught together” to 1 “always caught together” (Wey et al. 2013). Only associations with a value greater than 0.1 (i.e., 10% overlap of trapping/telemetry locations) were used to assign individuals to groups (Hayes et al. 2009; Ebensperger et al. 2011; Ebensperger et al. 2014). We confirmed the fit of data with the cophenetic correlation coefficient, a correlation between the actual association indices and the levels of clustering in the diagram. In this procedure, values above 0.8 indicate that hierarchical cluster analysis has provided an effective representation of the data (Whitehead 2008). We chose maximum modularity criteria (Newman 2004) to cut off the dendrogram and define social groups. All adults with radio collars that survived the period of parturition and lactation (September–October) were included in this analysis. Additionally, adults without radio collars had to be captured with another individual in the same burrow system at least four times to be included in this analysis (Hayes et al. 2009; Ebensperger et al. 2011).

Social Network Analysis

Only degus that were trapped on at least five days were included in social network analyses to exclude individuals that were poorly sampled (Wey et al. 2013). Using the program SOCPROG 2.5 (Whitehead 2009), we calculated the social network metrics strength and eigenvector centrality from pairwise association matrices:

(i) *Strength (s)* is defined as the sum of an individual’s associations (where a_{IJ} is the association index of interaction rate between individuals I and J) including both the number of associates and the intensity of associations, representing gregariousness (Whitehead 2008).

$$s_I = \sum_J a_{IJ}$$

High strength indicates a high total amount of spatial and temporal overlap between individuals, resulting from strong associations, many associations, or a combination of both. There were two metrics of strength. *Within group* strength refers to strength calculated from pairwise association matrices for group members only (separately for all adults, adult females). Within group strength is important because direct fitness is measured at the level of the social group (parental care is shared by group members) and DNA based maternity analyses were not conducted. *Population level* strength indicates the extent of interaction among group members and other individuals in the population (i.e., non-group members). Calculating *population level* strength required two steps (Davis et al. 2015). First, we calculated pairwise association matrices for all adults with five or more captures, regardless of social group membership. We then calculated average strength of individuals assigned to the same group (separately for all adults, adult females). This analysis was only conducted for EFI and was important in examining how ectoparasitic fleas, which can move between individuals, influenced interactions of individuals across the population.

(ii) *Eigenvector centrality (e)* is a measure of how well an individual is associated to other individuals and how well its close associates are themselves associated (where *a* is the association index and *I* represents an individual).

$$e_I = (\text{the first eigenvector of } a)_I$$

This index ranks importance, based on accessibility to a single individual within the network taking into account the degree of connectivity of its neighbors: high eigenvector centrality indicates that an individual is globally important for being connected to other individuals that have also strong associations. Eigenvector centrality was only examined at the population level (Whitehead 2008).

Ecological Sampling

Ecological conditions thought to be relevant to degus included food availability, soil hardness, predation risk (burrow density and predator abundance), ambient temperature, precipitation levels, degu density, and ectoparasitic flea intensity (EFI; sum of two flea species: *Xenopsylla cheopis* and *Leptopsylla segnis*; Burger et al. 2012). For each variable, we calculated means (benefits under harsh conditions hypothesis) and coefficients of variation (CV; benefits under variable conditions hypothesis).

Food availability was quantified by collecting all the above ground vegetation within a 250 x 250 mm area at 3 m and at 9 m from the center of each burrow system in one of the cardinal directions and was randomly selected for each distance at each burrow system. The biomass of food was determined by drying above-ground green herbs at 60°C degrees for 72 hours to determine abundance of primary food (Ebensperger et al. 2014). Data from 3 and 9 m was averaged per burrow system, values were standardized to grams per square meter for analysis. Mean and CV of values were calculated for groups based on data collected at burrow systems used by each group.

Soil hardness was recorded because it is related to the energetic cost of burrow digging (Ebensperger and Bozinovic 2000a, 2000b). Soil hardness was determined using soil penetrability measurements taken at 3 and 9 m from the center of each burrow system using a handheld soil compaction meter (Lang Penetrometer Inc., Gulf Shores, AL) in a randomized cardinal direction (Ebensperger et al. 2014). We calculated the mean value of samples collected at 3 and 9 m for each burrow system and transformed units to kPa.

Burrow density, an indicator of predation risk (i.e., available refuges to evade predators), was determined by counting the number of burrow openings within a 9 m radius from the center of each burrow system and standardized to burrows per square meter. Scan sampling for predators was conducted at two fixed vantage points approximately 50-100 m from areas of active degus. Predators known to prey on degus (i.e., culpeo fox, *Lycalopex culpaeus*; and birds of prey) were recorded every 30 minutes during a 20 minute circular sweep of the entire area. A total of 40 scan samples were conducted per year from 2006 to 2013 during morning (7:30-12:00h) and afternoon hours (17:00-19:30h), times when degus were observed aboveground.

Mean monthly temperature (°C) and precipitation (mm) were recorded 5-10 km north of the study site (at the Pudahuel weather station, 33°23'S, 70°47'W, 475 m of altitude) from June through October. Ambient temperature and precipitation were examined as monthly values at the level of the study population (Ebensperger et al. 2014).

Degu density was estimated on two permanent trapping grids approximately 150 m apart with similar distribution of plants (Hayes et al. 2007). The grids were approximately 0.18 ha (30 x 60 m; grid 1) and 0.25 ha (50 x 50 m; grid 2) in size respectively. Grid trapping was conducted over 5 days in June using locally produced metal live traps (similar to Sherman live traps [H. B. Sherman Traps, Inc., Tallahassee, FL] in design). Traps baited with rolled oats were set at fixed stations ever 5 m resulting in 91 traps and 121 traps in grids 1 and 2 respectively. Traps were opened during the morning prior to degu emergence from burrows and closed in the afternoon (8:00-3:00h). Data from the two grids were used to calculate mean and coefficient of variation (CV) of degu density yearly from 2005-2013.

EFI (*X. cheopis* and *L. segnis*) was sampled during burrow trapping conducted in September-October 2007 to 2013. Using a flea comb, we removed ectoparasitic fleas following methods in Burger et al. (2012). Ectoparasites were stored in 95% ethanol and identified using a dissecting microscope at 4x magnification (Burger et al. 2012). Identification of ectoparasites was conducted in the Laboratorio de

Química Clínica Especializada (LQCE), Santiago, Chile. Data from sampled individuals were used to calculate mean and CV of EFI (synonymous parasite load; Bush et al. 1997) each year.

Measures of Reproductive Success

We determined the total number of offspring emerging from burrow systems (weaned) by each social group during the months of September and October. Per capita offspring weaned (PCOW, a measure of direct fitness) was calculated by dividing the number of offspring caught at a group's burrow systems by the number of adult female degus in those groups (Ebensperger et al. 2014). Per capita estimates of direct fitness are reliable indicators of individual direct fitness in degus (Hayes et al. 2009; Ebensperger et al. 2011) and correlate well with estimates based on DNA based maternity analyses (Ebensperger, L.A. and Hayes, L.D., unpublished). In the wild the mortality of degu offspring by 2 months of life is high at >65% (Meserve and Rodriguez 1984). Thus, per capita number of offspring surviving to reproductive age (PCOS) was also examined. PCOS values were based on the number of offspring recaptured in the austral autumn (May to June) divided by the number of females from the social group in which offspring were born (Ebensperger et al. 2014). The values for PCOS were likely not underestimated because both sexes are equally likely to disperse and adult degus typically settle within 30 to 40 m of their natal burrow systems (Quirici et al. 2011).

Statistical Analysis

We used a Pearson correlation to verify that group size is an inherent component of within group strength (all adult group members: slope= 0.24; r=0.43; r^2=0.20; P=0.00006; adult female group members: slope= 0.37; r=0.46; r^2=0.21; P=0.0008) (Whitehead 2008). To determine the modulating effect of ecological conditions on the relationship between social network measures (i.e., strength) and direct fitness, we used hierarchical regression and random effects techniques (i.e., linear mixed effects models) similar to those used by Ebensperger et al. (2014). These models are appropriate to examine data sets with a nested or hierarchal structure. All models predicted the effect of mean and CV of ecological conditions on direct fitness (PCOW or PCOS). For all groups, we determined how the relationship between strength and direct fitness was affected by: i) mean and coefficient of variance (CV) of food abundance and degu density, ii) mean and CV of soil hardness and rainfall, iii) mean and CV of predation risk, iv) mean and CV of temperature, and v) mean and CV of EFI. Additionally, we examined mean and CV of EFI both within groups and for the population (parasite transmission). Separate models were used for strength estimates for female group members and all adult group members. For analyses of adult female group members, 2010 and 2011 were excluded because there were fewer than three social groups in those years. A total of 76 different models are reported for a total of 24 independent statistical tests of hypothesis (Supplementary Document; S1).

For each analysis, a hierarchical model was defined where social variables were declared at level 1 layer and ecological factors were declared at level 2 in the model hierarchy. Study years were used as grouping factors to control for correlations among contrasting ecological conditions. Slope and intercept of predictors at level 1 were allowed to vary between years, and effects of level 2 ecological variables on the social network-direct fitness slopes were tested by means of interactive terms involving the level 1 predictors (i.e., strength and eigenvector centrality), all customary routines in mixed modeling analysis (Zuur et al. 2009). Model fit was tested against a null random intercept model with study year as a grouping variable only. The Akaike information criterion (AIC) accompanied by likelihood ratio test were used to assess goodness of fit of each full model against their respective null models. We further verified model fit with the use of heterogeneous variance structure followed by examination of residuals and outliers. All analyses were conducted in R Statistical Software (version 3.2.2, R Development Core Team 2015) using library lme4.

Results

Modulating Effect of Ecological Variables

The 76 models examined are listed in Supplementary Table G2 and the outputs of the 11 significant models are outlined in Table G1. The modulating effects of mean and CV of ambient temperature are not reported in detail below because all models for ambient temperature were not statistically significant (models 49-56).

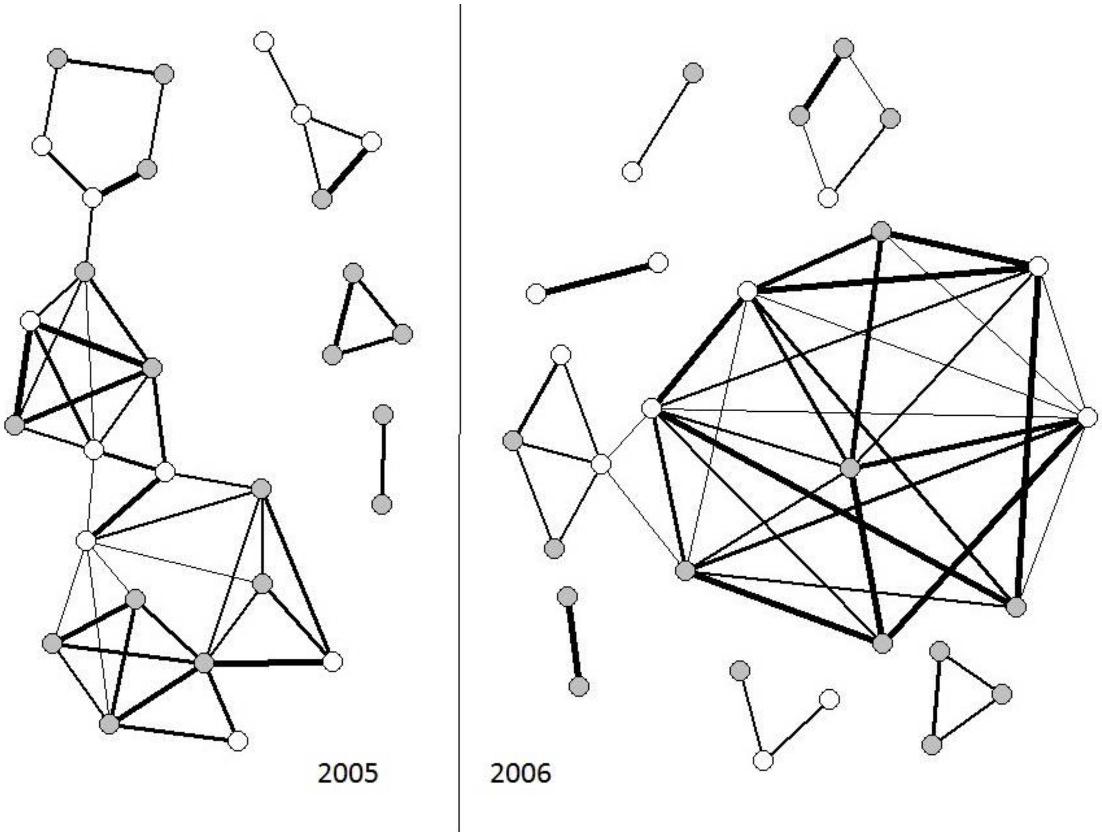

Figure 2.1 Representative social network maps. These maps are from 2005 and 2006 and show all individuals assigned to a social group. Males are represented by white circles, females by grey circles, and the thickness of the lines indicates the amount of trapping overlap between any two individuals. There were 8 social groups in both 2005 and 2006. However, there were three solitary adult males (no trapping overlap with any other individuals) in 2006 that are not shown in the network map. This figure illustrates that the individuals studied interact both within their social group as well as with individuals in other groups. Network maps were visually examined to determine how social structure varied year to year relative to ecological conditions. In 2005, CV of food abundance, CV of burrow density, and mean monthly temperature (°C) were the lowest of all years examined (2005-2013). Additionally, mean monthly precipitation was highest in 2005. In 2006, CV of food abundance, CV of burrow density, mean predator abundance, and CV of soil hardness were highest of all years examined and CV of predator abundance was the lowest. Social network maps for all other years are available in Appendix I.

Modulating Effect of Food Abundance and Degu Density

The models for food abundance and degu density included food abundance, degu density, and a food abundance x degu density factor interaction. The model with the lowest AIC was food abundance only (Figure 2.2a, b, c; models 1-16). Yearly mean and CV of food abundance influenced the relationship between strength and per capita offspring weaned (PCOW), but not per capita offspring surviving to adulthood (PCOS). The relationship between strength among adult group members (but not strength among adult female group members) and PCOW became less negative in social groups using burrows with increasing mean food abundance (Figure 2.2a; model 2). The relationship between strength and PCOW among all adults in groups became less negative in social groups using burrows with decreasing CV of food abundance (Figure 2.2b; model 2). The relationship between strength and PCOW of adult female group members became less negative in groups with increasing CV of food abundance (Figure 2c; model 6).

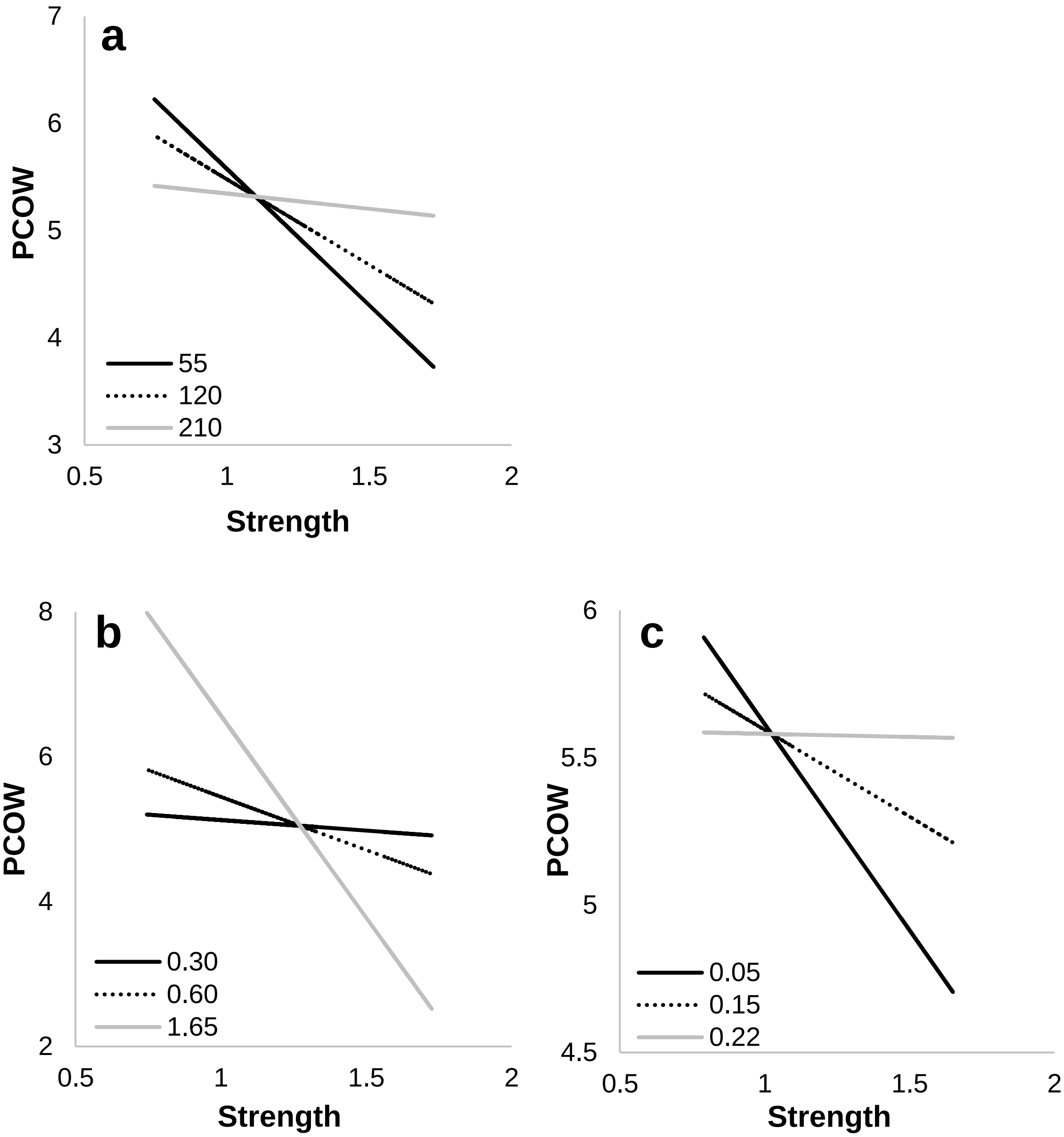

Figure 2.2 Modulating effect of food abundance. Relationship between strength of all adult group members (panels a, b) or strength of adult female group members (c) and the per capita number of offspring weaned (PCOW). Panel a illustrates how this relationship becomes more negative with decreasing mean food abundance. Panel b illustrates how this relationship becomes more negative with increasing CV of food abundance. Panel c illustrates how this relationship becomes more negative with decreasing CV of food abundance. Levels of food abundance represent the conditions below, near and above mean and CV of recorded values based on samples collected at active degu burrow systems. These results correspond to model numbers 2 and 6.

Modulating Effect of Predation Risk

The models for predation risk included burrow density, predator abundance, and a burrow density x predator abundance factor interaction. The models with the lowest AIC values were burrow density for PCOW (Figure 2.3a), and predator abundance for PCOS (Figure 2.3b; models 17-32). The relationship between strength among all adult group members (but not adult female group members) and PCOW became less negative in social groups using burrow systems with decreasing CV of burrow density (Figure 2.3a; model 18). The relationship between strength among all adult group members (but not all adult female group members) and PCOS changed from negative to positive during years with increasing CV of predator abundance (Figure 2.3b; model 27).

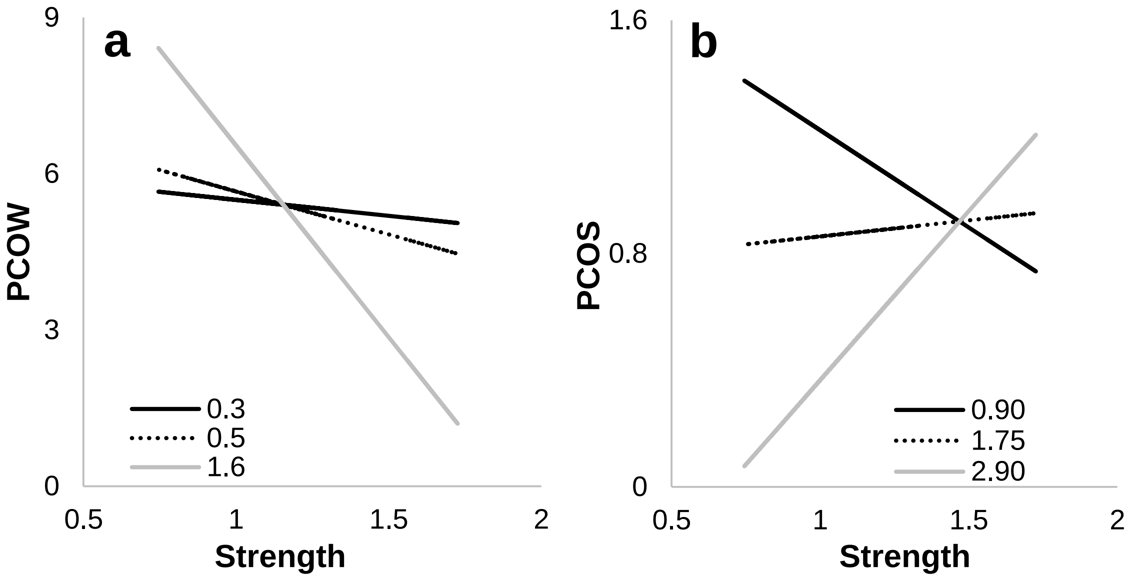

Figure 2.3 Modulating effect of predation risk. Relationship between strength of all adult group members and the per capita number of offspring weaned (PCOW; panel a) or per capita offspring surviving to reproductive age (PCOS; panel b). Panel a illustrates how this relationship becomes more negative with increasing CV of burrow density. Panel b illustrates how this relationship becomes more positive with decreasing CV of predator abundance. Levels of

burrow density and predator abundance represent the conditions below, near and above CV of recorded values. These results correspond to model numbers 18 and 27.

Modulating Effect of Soil Hardness and Precipitation

The models examined included soil hardness, precipitation, and a soil hardness x precipitation factor interaction. The models with the lowest AIC values were precipitation (with all group members and PCOS; Figure 2.4a), CV soil hardness (with all adult group members and PCOW; Figure 2.4b), and CV soil hardness (with adult female group members and PCOW; Figure 2.4c) (models 33-48). The relationship between strength and PCOS (all adult group members) became more positive in years with decreasing mean monthly precipitation for all adult group members (Figure 2.4a; model 43). The relationship between soil hardness and PCOW (all adult group members) became less negative with decreasing CV of soil hardness across burrow systems used (Figure 2.4b; model 34). The same relationship (soil hardness and PCOW) switched from negative to positive for adult female group members with increasing CV of soil hardness (Figure 2.4c; model 38).

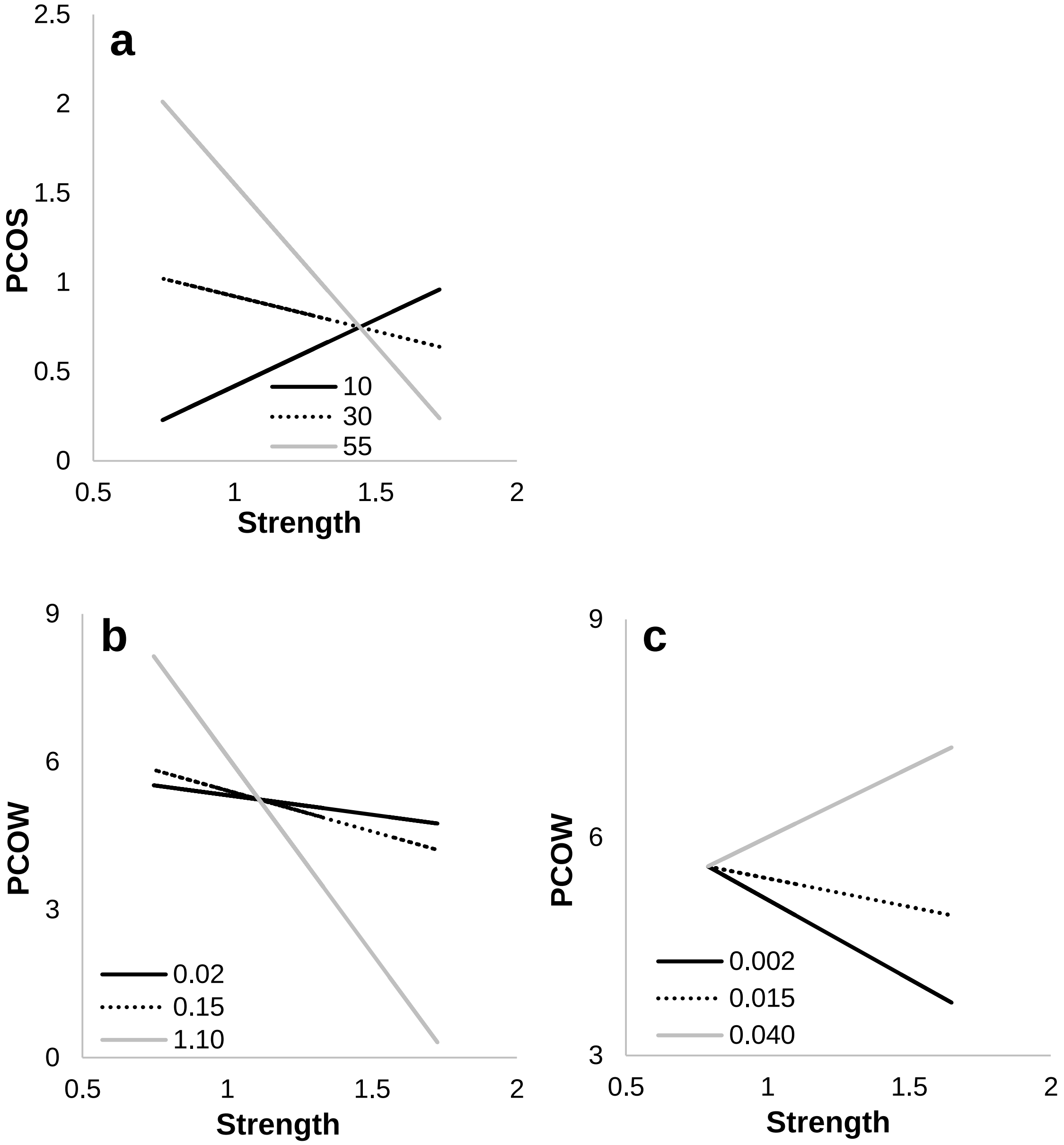

Figure 2.4 Modulating effect of precipitation and soil hardness. Relationship between strength of all adult group members (panel a, b) or strength of female adult group members (panel b) and per capita offspring surviving to reproductive age (panel a) or per capita offspring weaned (panel b, c). Panel a illustrates how this relationship becomes less negative with decreasing mean monthly precipitation. Panel b illustrates how this relationship becomes more negative with increasing CV of soil hardness. Panel c illustrates how this relationship becomes more positive with increasing CV of soil hardness. Levels of monthly precipitation and soil hardness represent the conditions below, near and above mean or CV of recorded values. These results correspond to model numbers 34, 38 and 43.

Modulating Effect of Ectoparasitic Fleas

The effect of EFI (total number of *X. cheopis* and *L. segnis* fleas) on strength-direct fitness relationships was calculated for both within group (Figure 2.5a, b, e) and population level strength (Figure 2.5c, d, f). Thus, there were 12 models included in this analysis (models 57-68). The models with the lowest AIC values were within group strength of adult female group members and PCOW, within group strength of all adult group members and PCOS, and population level strength of both adult female group members and all adults and PCOS. Within groups, the relationship between PCOS and strength of all adult group members changed from negative to positive as mean EFI decreased (Figure 2.5a; model 64). The relationship between PCOS and within group strength of all adult group members became positive with increasing CV of EFI (Figure 2.5b; model 64). The relationship between PCOW and within group strength of adult female group members became less negative with decreasing mean EFI (Figure 2.5e; model 61). At the population level, the relationship between strength of all adult group members and PCOS switched from negative to positive as mean EFI decreased (Figure 2.5c; model 65). Additionally, at the population level the relationship between strength of both adult female group members and all adult group members and PCOS switched from negative to positive with as CV of EFI increased (Figure 2.5d, f; models 68 and 65 respectively). For all best-fit population level models, there was not a statistically significant relationship between eigenvector centrality and PCOW or PCOS (; models 69-76).

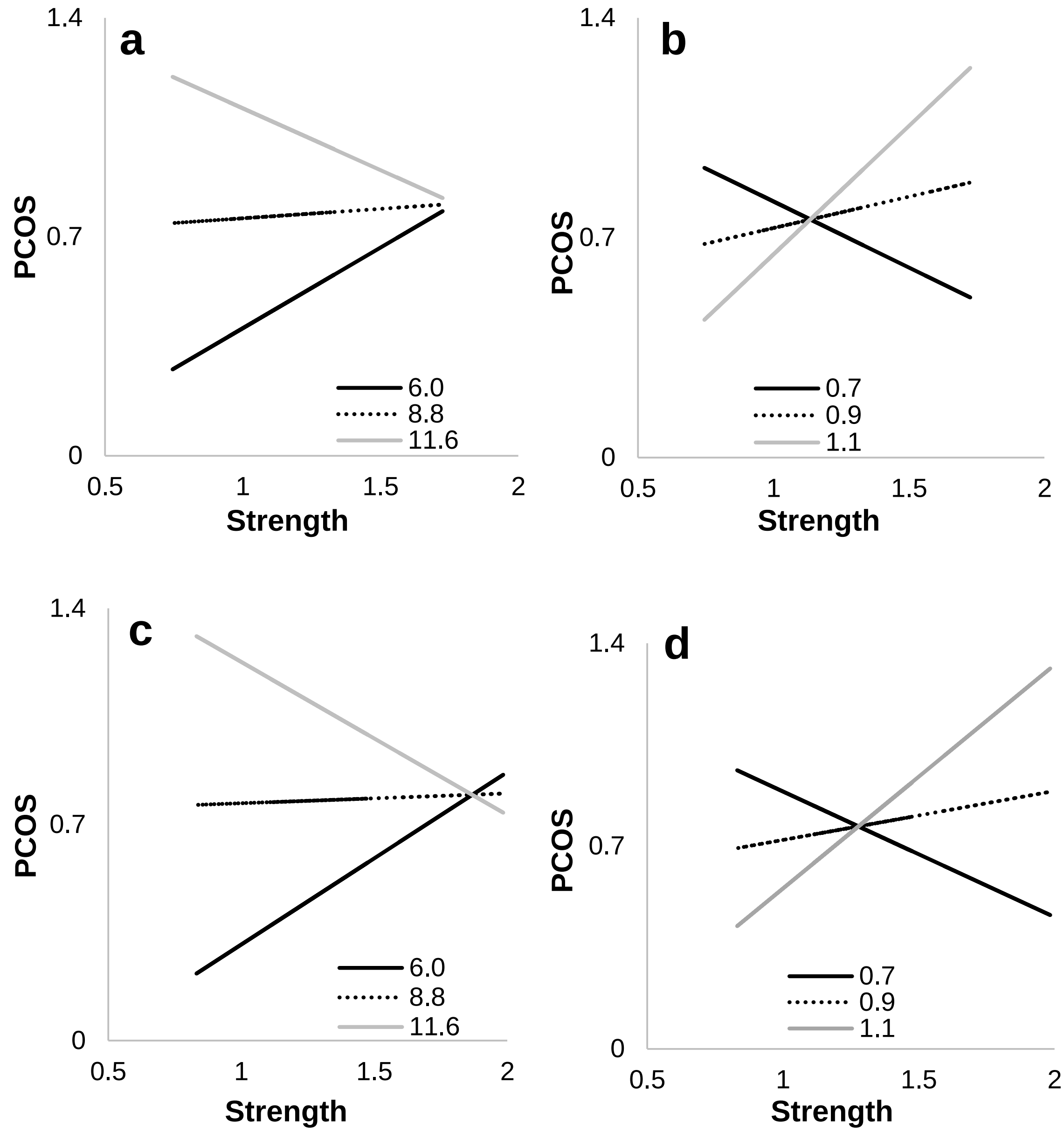

Figure 2.5 continued on next page.

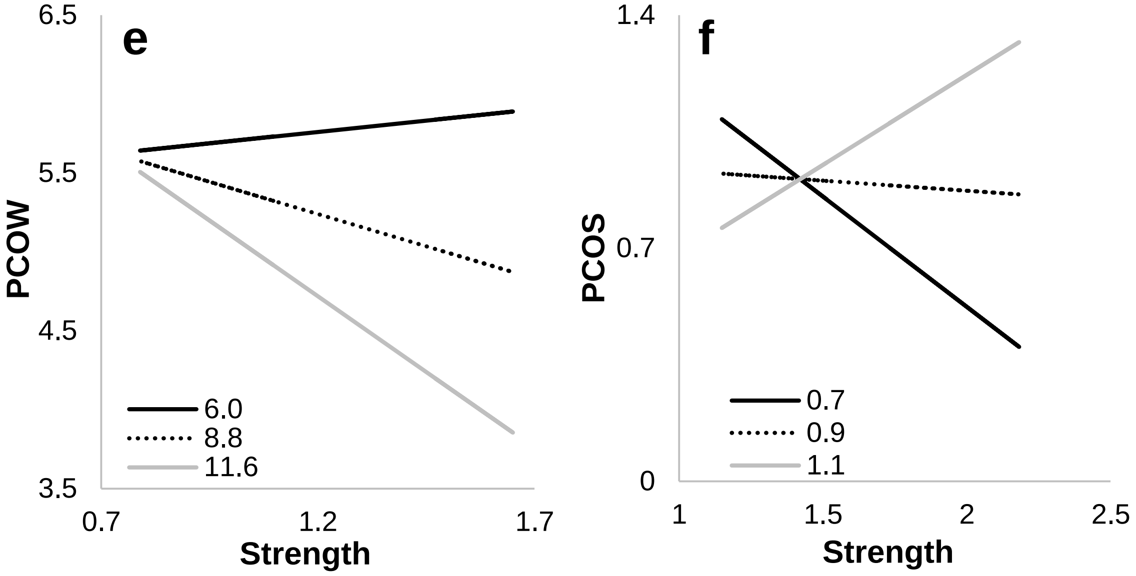

Figure 2.5 Modulating effect of ectoparasitic flea intensity. Relationship between within group strength of all adult group members (panels a, b) or adult female group members (e) and PCOS or PCOW. Relationship between population level strength of all adult group members (c, d) or adult female group members (f) and PCOS. Panels a, c, and e illustrate how this relationship becomes less negative with decreasing mean ectoparasitic flea intensity (EFI). Panels b, d, and f illustrate how this relationship becomes more positive with increasing CV of EFI. Levels of EFI represent the conditions below, near and above mean and CV of recorded values based on samples collected from individual degus. These results correspond to model numbers 61, 64, 65, and 68.

Discussion

Summary of Main Results

Best-fit models that supported the “benefits under harsh conditions” hypothesis included mean precipitation and population level EFI models (models 34 and 65). All other models either were not the best-fit model (based on AIC) or generated contradictory predictions (models 2, 61, and 64). Best-fit models supporting the “benefits under variable conditions” hypothesis included CV of food abundance and soil hardness (adult female group members), CV of predator abundance (all adult group members), and CV of EFI within groups (models 6, 27, 38, and 64). All other models for CV of ecological conditions either were not the best-fit model (based on AIC) or generated contradictory predictions (models 2, 3, 18, 34, 65, and 68). To summarize, we observed that increased strength of interactions among adult females group members has the most positive (or least negative) relationship with per capita direct fitness (PCOW or PCOS) when i) food abundance is less predictable (high CV), ii) soil hardness is less predictable (high CV), and iii) EFI is low but less predictable (low mean, high CV). Alternatively, increased strength of all adult group members has the most positive (or least negative) relationship with per capita direct fitness (PCOW or PCOS) when i) food abundance is high and more predictable (high mean, low CV), ii) soil hardness is more predictable (low CV), iii) predator abundance is less predictable (high CV), iv) burrow density is more predictable (low CV), v) mean monthly precipitation is low (low mean), and vi) EFI is low but less predictable (low mean, high CV). Moreover, when comparing adult female group members and all adult group members, differences in the relationship between social structure and direct fitness (for food abundance and soil hardness) emerge, suggesting that the interactions among females and males have different impacts on direct fitness, adding further complexity to this story.

Modulating Effects of Ecology on Social Structure-Direct Fitness Relationships

The effect of spatio-temporal variation in ecology on animal social systems has re-emerged as a prominent and exciting topic in behavioral ecology. For decades, emphasis was on the causes of delayed dispersal and group formation (Emlen 1982; Komdeur 1992; Emlen 1995; Schoech 1996; Arnold and Owens 1999; Lucia et al. 2008) and the costs and benefits of cooperation (Hamilton 1964; Trivers 1971; Cockburn 1998). Recently, attention has turned to determining how species distributions (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011) and reproductive consequences of social systems

(Rubenstein 2011; Ebensperger et al. 2012a, 2014) are influenced by spatio-temporal variation in ecology. In passerine birds, the prevalence of cooperative breeding is associated with variation in precipitation (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011) and reproductive success declines with increasing group size, territory quality, and environmental quality (Rubenstein 2011). Conversely, in two non-passerine birds, "helpers at the nest" have the most beneficial effect on fitness in environments characterized by less variable or less harsh conditions (Koenig et al. 2011; Gonzalez et al. 2013; Koenig and Walters 2015).

Taken together, our results and those of recent studies on social vertebrates (Jetz and Rubenstein 2011; Gonzalez et al. 2013; Ebensperger et al. 2014; Rubenstein et al. 2016) suggest that the effects of spatio-temporal variation in ecology on social system-direct fitness relationships are complex and depend, not only on what component of social system is under examination, but also on whether interactions are between females (primary care-givers in degus; Hayes et al. 2009) or all adults. For example, our observation that the relationship between strength and PCOW became less negative in years with high mean (all adult group members) and less variable food abundance (all female group members) aligns with observations in non-passerine birds (Koenig et al. 2011; Gonzalez et al. 2013) and singularly breeding mammals (Harrington et al. 1983; Solomon and Crist 2008). Increased overlap during early morning trapping could suggest greater social cohesion and cooperation (Poirier et al. 1978; Drea et al. 1996) or could suggest that adults forage more closely together due to the benefits of reduced predation risk (Ebensperger and Wallem 2002). Our observation that the relationship between strength of adult female group members and PCOW switched from negative to positive when food abundance was variable supported our prediction that increased interactions between potential care-givers is important to increasing offspring survival when food resources are not reliably abundant (Rubenstein and Lovette 2007). Future intraspecific comparisons should examine how variation in food abundance during different life history stages selects for different social interactions among male and female group members, adults and juveniles, and group members of different social status. Interspecific comparisons should also focus on how food abundance influences social interactions and direct fitness in social species with different modes of parental care.

Similar to food abundance, the modulating effect of soil hardness on social structure and reproductive success is complex in degus. The modulating role of soil hardness on strength-direct fitness covariation was opposite for all adult group members and adult female group members. One explanation for these results is that the costs of burrowing (Ebensperger and Bozinovic 2000b) are driven by intrinsic factors (i.e., body condition: Zelová et al. 2010) that differ between sexes (Scantlebury et al. 2006). Alternatively, variation in social structure within the timeframe of our study may have limited benefits in terms of the construction of new burrows. Unlike some fossorial species, such as the African bathyerids (mole-rats; Luna and Antinuchi 2006), degus do not excavate burrows to search for food or mates (Vleck 1979, 1981; Bennett and Faulkes 2000; Ebensperger and Bozinovic 2000a). Degu social groups often use the same burrow systems repeatedly or move into existing burrow systems, minimizing the current utility of coordinated digging among group members.

Predation risk plays an important role in shaping social organization (Ebensperger et al. 2012b) and social structure (Eggleston and Lipcius 1992) and can affect population dynamics (Hik 1995). In small mammals, predation risk includes two interrelated components, predator abundance (or the number of potential predators) and availability of shelter (burrow density for degus; Hayes et al. 2007). While foraging above-ground during the daytime, degu offspring are vulnerable to predators such as a foxes (*Lycalopex culpaeus*), raptors (*Geranoaetus melanoleucus, Parabuteo unicinctus, Buteo polyosoma*), and owls (*Tyto alba, Bubo virginianus, Speotyto cunicularia, Glaucidium nanum*). Thus, we expected the relationship between within group network strength and per capita offspring surviving to adulthood

(PCOS) to increase with increasing mean and CV of predation abundance and mean and CV of burrow density. Our observation that relationship between strength and PCOS increased with increasing CV of predator abundance, but not burrow density, partially supports this hypothesis and suggests that predation pressure has a greater impact on degu social structure and fitness than burrow density. Interestingly, we observed that the relationship between strength and PCOW became more positive with increasing CV of burrow density. Predation of degu offspring by snakes is relatively low (Green and Jaksic 1992), suggesting that predation risk prior to emergence from burrows is not a driving force for social structure-direct relationships. Since degus also use burrows to rear offspring (Hayes et al. 2009; Ebensperger et al. 2012b), variation in PCOW may be more sensitive to the number of care-givers (Ebensperger et al. 2014) and the types of care they provide (König 1997; Cockburn 1998; Taborsky et al. 2007). Other factors including the distance to cover during foraging (Molvar and Bowyer 1994; Whitfield 2003; Hayes et al. 2007) and foraging group size which is related to vigilance or dilution effect (Roberts 1996; Ebensperger and Wallem 2002; Ebensperger et al. 2006) affect risk in degus and other species, but were not measured in the present study.

In vertebrates, there are energetic (Khokhlova et al. 2002) and reproductive (Møller 1993) costs of ectoparasitism. Living in groups may reduce these costs if individuals reduce ectoparasites by allogrooming. This hypothesis is supported by observations of negative relationships between ectoparasite infection and group size (Bordes et al. 2007; Viljoen et al. 2011) and our observation that PCOS increased with strength (among all adult group members) in years with increasing CV of EFI. However, our observation that the relationship between strength (among adult female and all adult group members) and PCOS became more negative in years with low mean EFI and that increasing group size does not result in reduced ectoparasitic flea loads in degus (Burger et al. 2012) and other species (i.e., Stanko et al. 2002; Altizer et al. 2003; Hillegass et al. 2008) suggest otherwise. The effectiveness of allogrooming in reducing ectoparasites may decrease with increasing ectoparasite intensity (Johnson et al. 2004). We could not quantity allogrooming directly because most degu social interactions occur below ground and allogrooming above ground is rare (Ebensperger and Hurtado 2005). Allogrooming aligns well with other social interactions in several mammals (Wilkinson 1986; Hart and Hart 1992; Kutsukake and Clutton-Brock 2006). Thus, we expect allogrooming to increase with increasing strength in degus. A comparison of allogrooming and strength under laboratory conditions or with the use of underground cameras will be necessary to test this hypothesis.

During the daytime, degus forage in temporary groups consisting of social group members and conspecifics from other social groups (Ebensperger and Wallem 2002). Under these conditions, ectoparasitism of group members could be influenced by contact with non-group members during the daytime. Our observations suggest partial support for the prediction that EFI is influenced by social interactions of group members with members outside the group. However, modulating effects of mean and CV of EFI on the relationship between strength and direct fitness were nearly identical within groups (Figure 2.5a, b, e) and at the population level (Figure 2.5c, d, f). The slopes of lines reflecting the modulating effect of mean EFI on strength-PCOS relationships and maximum PCOS values (compare y-axes of Figure 2.5a, c) were similar when comparing within group strength (Figure 2.5a) and population level strength (Figure 2.5c). This was also true for the modulating effect of CV of EFI on strength-PCOS (Figure 2.5b, d, f) when comparing within groups to the population level. These comparisons suggest that population level trends (Figure 2.5c, d, f), which include estimates of strength based on group members and all other adults in the population, are largely driven by strength between individuals within the same group and not interactions between non-group members.

Concluding Remarks

Our understanding of the evolutionary significance of social systems largely comes from short-term studies that focus on social organization. Recent long-term field studies (Rubenstein 2011; Ebensperger et al. 2014) and meta-analyses (Ebensperger et al. 2012a) have shed light on the evolutionary significance of plural breeding. Studies focusing on the direct fitness consequences of social structure focus primarily on singular breeders. By using social networks to assess social structure, our study revealed that the impact of spatio-temporal variation in ecology on the relationship between social systems and direct fitness is complex. Furthermore, the relationships we observed for social structure are not the same as those from a previous study evaluating social organization in degus (Ebensperger et al. 2014), suggesting that selection pressures affect components of social systems differently. Ecological harshness and variability interact with elements of social organization (i.e., adult sex composition; the present study) and life history attributes to influence social structure-fitness relationships (Gonzalez et al. 2013). Disentangling the complexity of these relationships will require the further examination of how various components of social systems impact direct fitness in different environments. Most attempts to understand the modulating role of ecology on social systems and fitness are based on short-term datasets (1-4 years; i.e., White and Cameron 2009; Hayes et al. 2009). Complex results generated by long–term studies such as ours reinforce the growing sentiment that understanding the evolutionary significance of social living requires the examination of long-term data sets (Clutton-Brock and Sheldon 2010). Moreover, long-term studies on the modulating effect of ecological conditions may become particularly important as ecological conditions change due to human impacts (i.e., climate change, habitat loss) or in response to periodic evens such as El Niño/Southern Oscillation (ENSO).

CHAPTER 3

CONSERVATION IMPLICATIONS

The objective of the present study was to examine the modulating role of ecological conditions on social structure-direct fitness covariation. To date, this effect has been poorly examined in social vertebrates, in part because social systems are complex and vary across and within species. Evidence from comparative studies on birds suggests that cooperative breeding is positively associated with unpredictable inter-annual environmental conditions (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011). My study, along with a previous study on the degu (Ebensperger et al. 2014), suggest that harsh or variable ecological conditions modulate the relationship between social systems and direct fitness. Thus, when making conservation management decisions for social species, understanding the effect of ecological or environmental conditions (i.e., animal population density, temperature, rainfall) on social structure-direct fitness covariation could have broad ranging conservation implications.

Understanding the effect of population density, which is often influenced by food abundance, on the relationship between sociality and fitness is vital in the conservation management of many social species. For example, a socially obligate species, the African wild dog (*Lycaon pictus*), is reliant on non-breeding “helpers” for breeding and resource defense (Courchamp and Macdonald 2001). If the number of members in the pack drops too low, a positive feedback loop arises wherein poor reproduction and survival further decreased pack size. This feedback loop eventually leads to a loss of the entire pack (Courchamp and Macdonald 2001). This phenomenon, known as the Allee effect (Figure 3.1), increases the likelihood of a population going extinct because of the cost of retaining sufficient group size and structure (Allee 1931; Courchamp et al. 1999; but see Creel et al. 2015).

The Allee effect has potential impacts on conservation strategies and harvest rates of social species. Social constraints, such as the Allee effect, influence a variety of taxa including fish (Stephens and Sutherland 1999; Kuparinen et al. 2014), birds (Marvelde et al. 2009; Votier et al. 2009), and mammals (Courchamp and Macdonald 2001; Morris 2002). The collapse of many east coast commercial fisheries operating under maximum sustainable yield principles is thought to be a byproduct of Allee-type dynamics (Stephens and Sutherland 1999). While the present study does not focus on the Allee effect specifically, understanding the impact of ecological variability on social structure could prove vital to conserving populations under the Allee effect. Typically, conservation efforts for species under the Allee effect have focused on maintaining sufficient group or population size, but the present study illustrates that social structure is also an important component of social systems that affects the reproductive success of social species. In the future, conservation biologists working with threatened or endangered species should not only focus on group size but should also examine social structure.

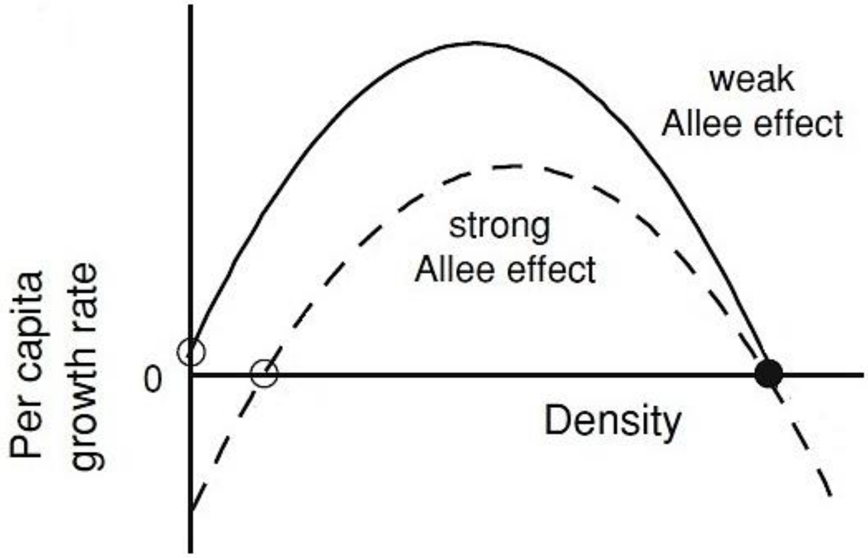

Figure 3.1 Allee effect. Representation of the Allee effect showing the positive relationship between population growth rate and density at low animal densities.

One cause of spatio-temporal variation in ecological conditions is climate change. Climate change induced variability in available food is correlated with social group size in bottlenose dolphins (*Tursiops truncatus*) and orca whales (*Orcinus orca;* Lusseau et al. 2004). This suggests that ecological variability influences social organization in some marine mammals (Lusseau et al. 2004). Furthermore, studies on African striped mice (*Rhabdomys spp*.) indicate that behavioral or social flexibility, despite being costly, may be vital to the persistence of species under shifting environmental conditions (Rymer et al. 2013). However, there is limited research on how climate variability, either anthropogenic or natural in origin, affects social structure in mammals (Holmgren 2006; Previtali et al. 2010).

The present study builds on years of existing research, potentially informing theory on how highly variable long-term ecological processes, such as El Niño/Southern Oscillation (ENSO), influence social structure. ENSO helps explain irregular variation in climate (i.e., rainfall, ocean surface temperature) globally (Philander 1990). Historically, ENSO events have led to population crashes in commercial fisheries, such as the Peruvian anchovy population collapse during the 1997-98 El Niño (Broad et al 2002). Long-term studies that examine the effects of environmental variability, like ENSO, may prove essential to the conservation of both economically important species and species at risk of extinction in the future. As human impacts continue to alter habitats globally and ecological conditions become less predictable, conservation biologists will likely rely on studies that examine how social species are impacted by ecological variation. The present study illustrates how social network analysis can be used to examine changes in social systems under variable environmental conditions. In the future, the conceptual framework of the present study could be applied directly to conditions associated with ENSO events or anthropogenic climate change.

Understanding social structure, using social network analysis (SNA), has already proven useful in the conservation of threatened or endangered species, particularly in marine mammals. SNA was used to improve the conservation efforts for the threatened Indo-Pacific humpback dolphin (*Sousa chinensis)* in

China (Wang et al. 2015). SNA yielded important insights into how dolphin communities interact and suggested that geographic segregation and habitat shifts of two dolphin communities were likely adaptations to intensive anthropogenic activities (Wang et al. 2015). Another study, on an endangered population of orcas (*Orcinus orca*), also utilized SNA to aid in the conservation of species under variable ecological conditions (Foster et al. 2011). In this study, orca social network structure correlated with food availability and was invaluable in the design of conservation management plans (Foster et al. 2011). Overall, social network analyses have already been applied and proven useful in helping conservation biologists make informed management decisions, particularly in marine mammal research. The present study, though not conservation based, provides novel insight into how spatiotemporal variability modulates the social network structure and fitness relationship in a plurally breeding mammal and may help conservation biologists make informed management decisions in two ways. First, the present study further illustrates the utility of social network analysis, in particular for species living in harsh or variable habitats. Second, the present study indicates the interdependent nature of different components of social systems and illustrates the necessity of understanding not only group size, but other components as well. Insights from the present study can be used to maximize management strategies for protecting endangered or threatened species living in harsh, unpredictable, or highly variable environments.

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APPENDIX A

SOCIAL GROUPS

2005

ID	ID	ID	ID	ID	ID	ID	ID
0010 (F)	1003 (M)	0033 (M)	2004 (M)	0200 (F)	0023 (F)	0005 (F)	0012 (M)
2200 (F)	4020 (M)	3050 (F)	3002 (F)	3001 (F)	1001 (M)	0011 (M)	0015 (M)
3100 (F)			4100 (F)		4200 (F)	0120 (F)	0024 (M)
			4301 (M)			3003 (F)	0300 (F)
			0140b (F)			4005 (F)	1300 (M)
							3010 (F)
							4400 (F)

2006

ID	ID	ID	ID	ID	ID	ID	ID	ID	ID	ID
0040 (F)	0320 (M)	1015 (M)	0053 (M)	0045 (M)	3403 (M)	0441 (M)	3402 (M)	0141 (F)	0115 (F)	0111 (F)
0455 (F)	0451 (F)			0233 (M)	3410 (M)	1201 (M)		0155 (F)	0143 (F)	0124 (F)
	1043 (F)			4010 (F)		3330 (F)		0232 (M)	0352 (F)	0141 (F)
	3032 (F)							0444 (M)		0151 (F)
										0153 (F)

2007

ID	ID	ID	ID	ID	ID	ID
1103 (F)	0141 (F)	1253 (F)	0143 (F)	1312 (F)	1111 (F)	0134 (F)
1115 (M)	0154 (F)	1354 (F)	2434 (F)	1314 (F)	2453 (F)	1445 (M)
3102 (F)	0155 (F)	4010 (F)	3323 (M)	2223 (F)	4002 (M)	2053 (F)
3210 (F)	1012 (M)	4012 (F)		4441 (F)		2202 (F)
	2352 (F)	4052 (M)				2341 (F)
	2454 (F)	1041 (F)				3011 (F)
	4443 (F)					

2008

ID	ID	ID	ID	ID	ID	ID
0100 (M)	0410 (F)	1041 (F)	1311 (F)	0054 (M)	0124 (F)	0252 (F)
0240 (F)	1021 (M)	3252 (M)	4144 (F)	0243 (F)	3355 (F)	0412 (F)
0251 (F)	3400 (F)	4243 (F)	4322 (F)	1015 (F)		
0315 (F)	4325 (F)					
1023 (F)						

2008 cont.

ID	ID	ID	ID	ID	ID
0221 (F)	0001 (F)	4422 (F)	0411 (F)	0214 (F)	1150 (F)
13(15)1 (F)	0203 (F)	4423 (F)	1445 (M)	0255 (F)	
		4455 (F)		3005 (F)	
				3221 (F)	

2009

ID	ID	ID	ID	ID	ID	ID
1027 (F)	883 (F)	986 (F)	879 (M)	989 (F)	1011 (F)	874 (M)
1033 (F)	1102 (M)	1037 (F)	994 (F)	1029 (M)	1194 (F)	939 (M)
1034 (M)	1144 (F)	1124 (M)	1089 (M)	1062 (F)	1015 (F)	1066 (F)
1074 (M)	0130 (F)		1259 (F)		4324 (F)	1261 (F)
						0252 (F)

ID	ID	ID
1101 (F)	866 (M)	974 (F)
1104 (M)	1106 (M)	1021 (F)
1108 (F)	1262 (M)	1073 (F)
	3024 (F)	3025 (F)
	4325 (F)	4144 (F)

2010

ID	ID	ID	ID	ID	ID
1135 (F)	1181 (M)	1177 (M)	1218 (F)	1163 (F)	1270 (M)
1381 (M)	1247 (F)	1209 (F)	1367 (M)		
	1376 (M)	1368 (M)	1372 (M)		
		1374 (M)	1375 (M)		

2011

ID	ID	ID	ID	ID	ID	ID
1163 (F)	1467 (F)	2010 (M)	1506 (F)	1218 (F)	1473 (M)	1488 (F)
1504 (M)	1483 (M)	2015 (M)	2136 (F)	1418 (M)	1491 (F)	1503 (M)
		2132 (F)		1471 (M)		
		2133 (F)				

ID	ID	ID	ID
1478 (M)	1516 (M)	1372 (M)	1515 (F)
1520 (F)	2123 (M)	1405 (M)	1517 (F)
	2127 (M)	2121 (F)	

2012

ID	ID	ID	ID	ID	ID	ID	ID	ID
1723 (F)	1722 (F)	1696 (F)	1418 (M)	1714 (F)	1654 (F)	1721 (F)	1561 (F)	1726 (F)
		1702 (F)	1603 (F)	1717 (F)	1655 (F)	2012 (F)		
		1703 (F)		1719 (M)	1657 (F)	2024 (F)		
		1710 (F)			1727 (M)			

2013

ID	ID	ID	ID	ID	ID	ID	ID
1655 (F)	1668 (F)	1561 (F)	1925 (F)	1789 (F)	1758 (F)	1847 (F)	1833 (F)
1746 (F)	1809 (F)	1772 (M)					1859 (F)
1757 (F)	1813 (F)	1876 (M)					
1836 (F)		1909 (M)					

ID	ID	ID	ID	ID	ID
1853 (M)	1872 (F)	1794 (F)	1867 (F)	1812 (F)	1717 (F)
1901 (F)	1883 (F)	1796 (M)	5545 (M)	1903 (F)	1733 (M)
	1904 (F)	1838 (F)		1905 (M)	1748 (F)
	1926 (M)	1915 (F)		1910 (F)	

APPENDIX B

ECOLOGICAL DATA

Yearly Averages for All Variables

Degu Density and Food Abundance

Year	Mean Degu Density (degus/ha)	CV of Degu Density (degus/ha)	Mean Food Abundance (g/m2)	CV of Food Abundance (g/m2)
2005	132.56	0.30	137.05	0.31
2006	198.78	0.76	86.52	1.64
2007	223.78	0.83	106.72	0.34
2008	62.33	1.23	117.09	0.53
2009	77.78	1.41	76.06	0.53
2010	36.11	1.41	124.77	0.55
2011	22.22	1.41	58.27	0.55
2012	20.33	0.26	174.17	0.46
2013	17.11	0.42	207.57	0.78

Soil Hardness and Monthly Precipitation

Year	Mean Soil Hardness (kPa)	CV of Soil Hardness (kPa)	Mean monthly Precipitation (mm)	CV of Monthly Precipitation (mm)
2005	2875.91	0.06	26.94	1.48
2006	3037.60	1.04	22.99	1.54
2007	3031.21	0.04	11.20	1.52
2008	3109.16	0.02	18.54	1.38
2009	3042.77	0.03	17.29	1.90
2010	2978.64	0.04	13.42	1.27
2011	3020.80	0.05	9.30	1.63
2012	2865.70	0.06	13.85	1.35
2013	2925.51	0.04	10.32	2.11

Burrow Density and Predator Abundance (together Predation Risk)

Year	Mean Burrow Density (#/m2)	CV of Burrow Density (#/m2)	Mean Predator Abundance (sightings/hour)	CV of Predator Abundance (sightings/hour)
2005	0.13	0.37		
2006	0.13	1.54	13.04	0.93
2007	0.14	0.38	6.45	0.93
2008	0.11	0.37	2.18	1.32

2009	0.12	0.38	1.95	1.37
2010	0.12	0.37	0.45	2.84
2011	0.17	0.36	0.83	2.01
2012	0.11	0.40	0.60	2.58
2013	0.13	0.43	1.05	2.00

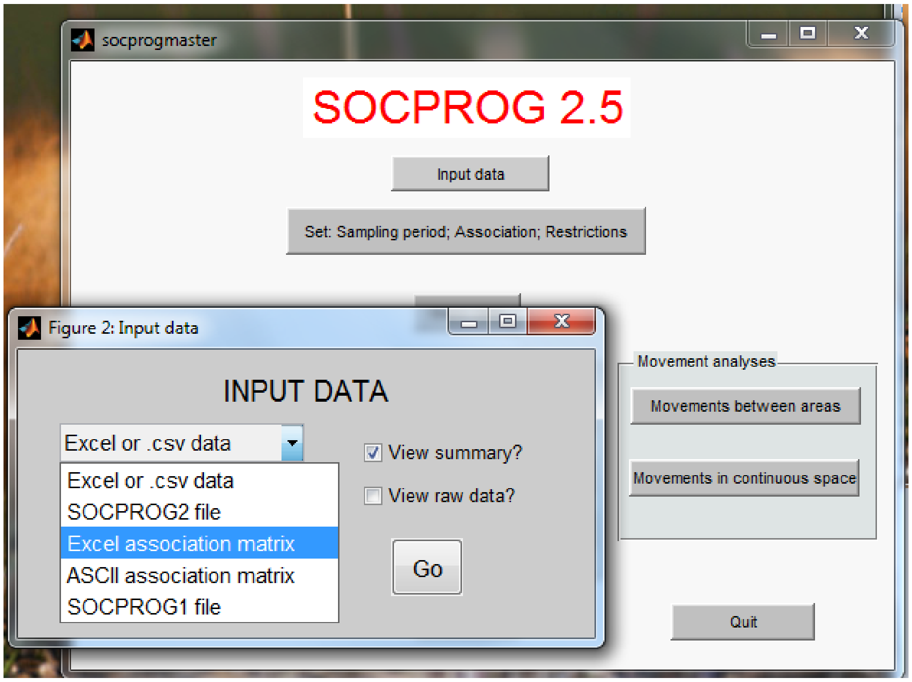
Monthly Temperature and Ectoparasitic Flea Intensity (EFI)

Year	Monthly Mean Temperature (°C)	Monthly CV of Mean Temperature (°C)	Mean EFI (ectoparasites/host)	CV of EFI (ectoparasites/host)
2005	10.6	0.17		
2006	11.2	0.19		
2007	8.8	0.39	9.39	1.06
2008	11.2	0.24	11.12	0.73
2009	10.4	0.27	6.10	0.81
2010	9.6	0.33	7.33	0.79
2011	10.0	0.36	8.37	0.82
2012	10.4	0.23	11.52	1.00
2013	10.4	0.28	7.14	0.83

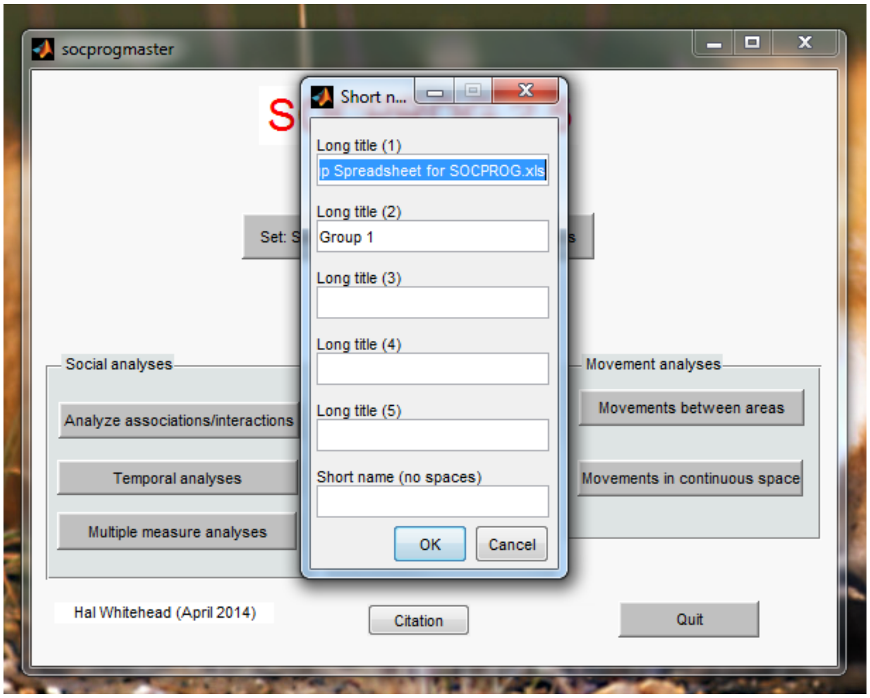
APPENDIX C

SOCPROG PROCEDURE

Select “Input data”



Under data input select “Excel association matrix”



Long title (1): p Spreadsheet for SOCPROG.xls
Long title (2): Group 1
Long title (3):
Long title (4):
Long title (5):
Short name (no spaces):

After selecting the tab that contains the matrix hit ‘OK’ and leave the long title the same.

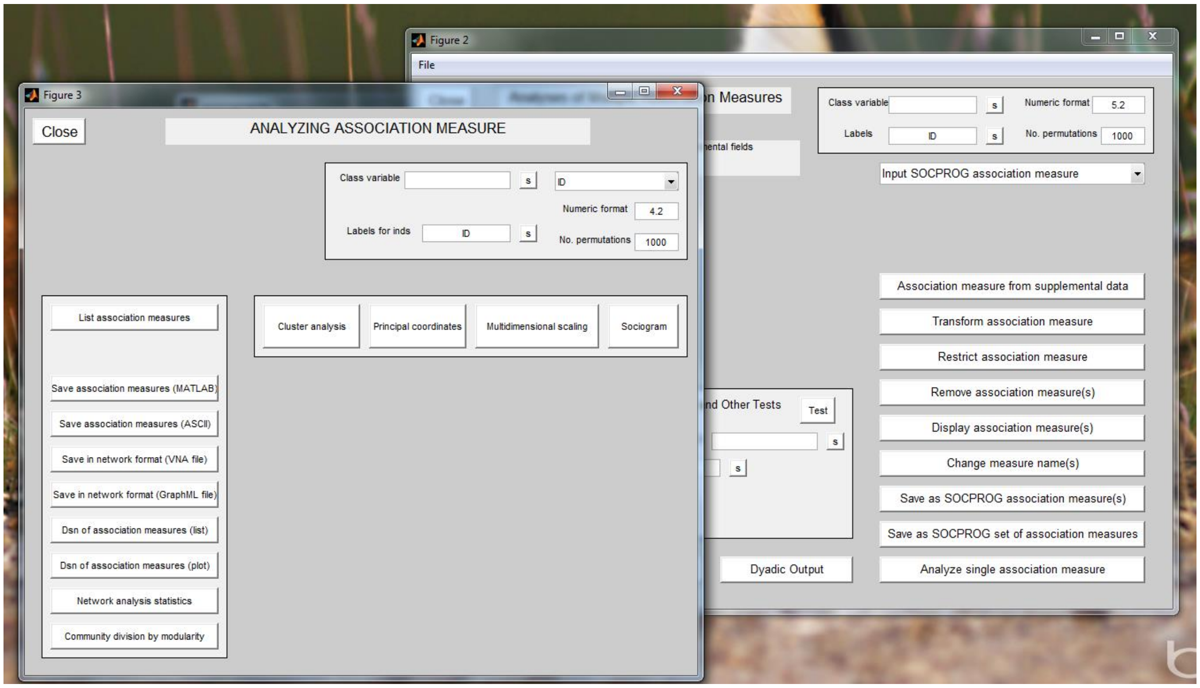


Figure 3:
Class variable: ID
Labels for inds: ID
Numeric format: 4.2
No. permutations: 1000

Figure 2:
Class variable:
Labels: ID
Numeric format: 5.2
No. permutations: 1000
Input SOCPROG association measure

Select ‘Analyze single association measure

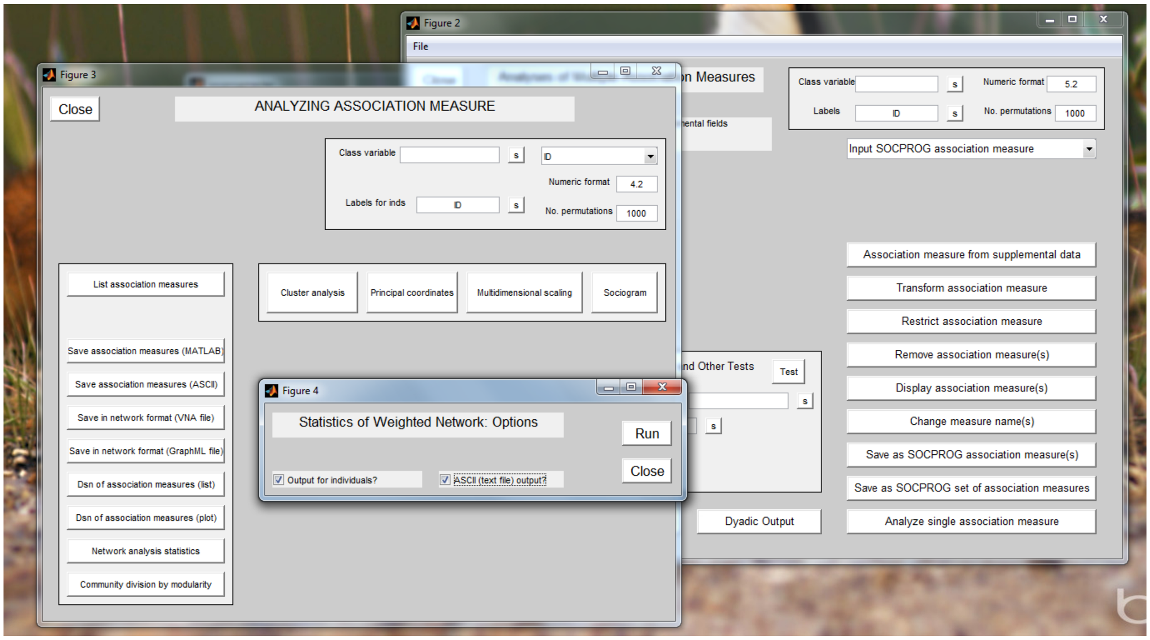


Figure 2: Class variable s; Numeric format 5.2; Labels ID s; No. permutations 1000

Figure 3: Class variable s; ID; Numeric format 4.2; Labels for inds ID s; No. permutations 1000

Figure 4: ☑ Output for individuals? ☑ ASCII (text file) output?

Select ‘Network analysis statistics’ and then make sure both boxes are checked on the box ‘Statistics of Weighted Network: Options’

Then hit ‘Run’

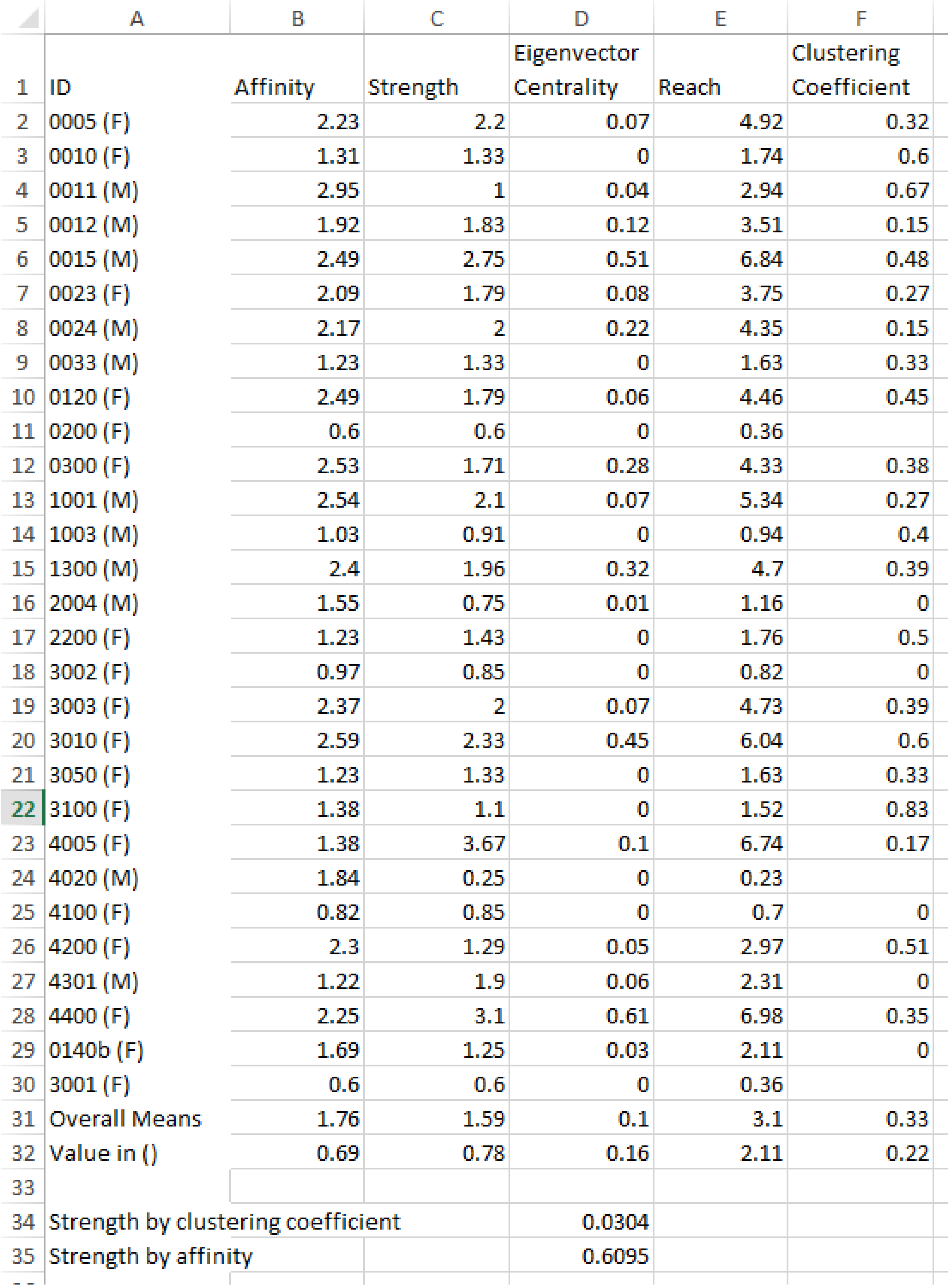
Name and save txt file.

Copy and paste data from txt file into excel.

APPENDIX D

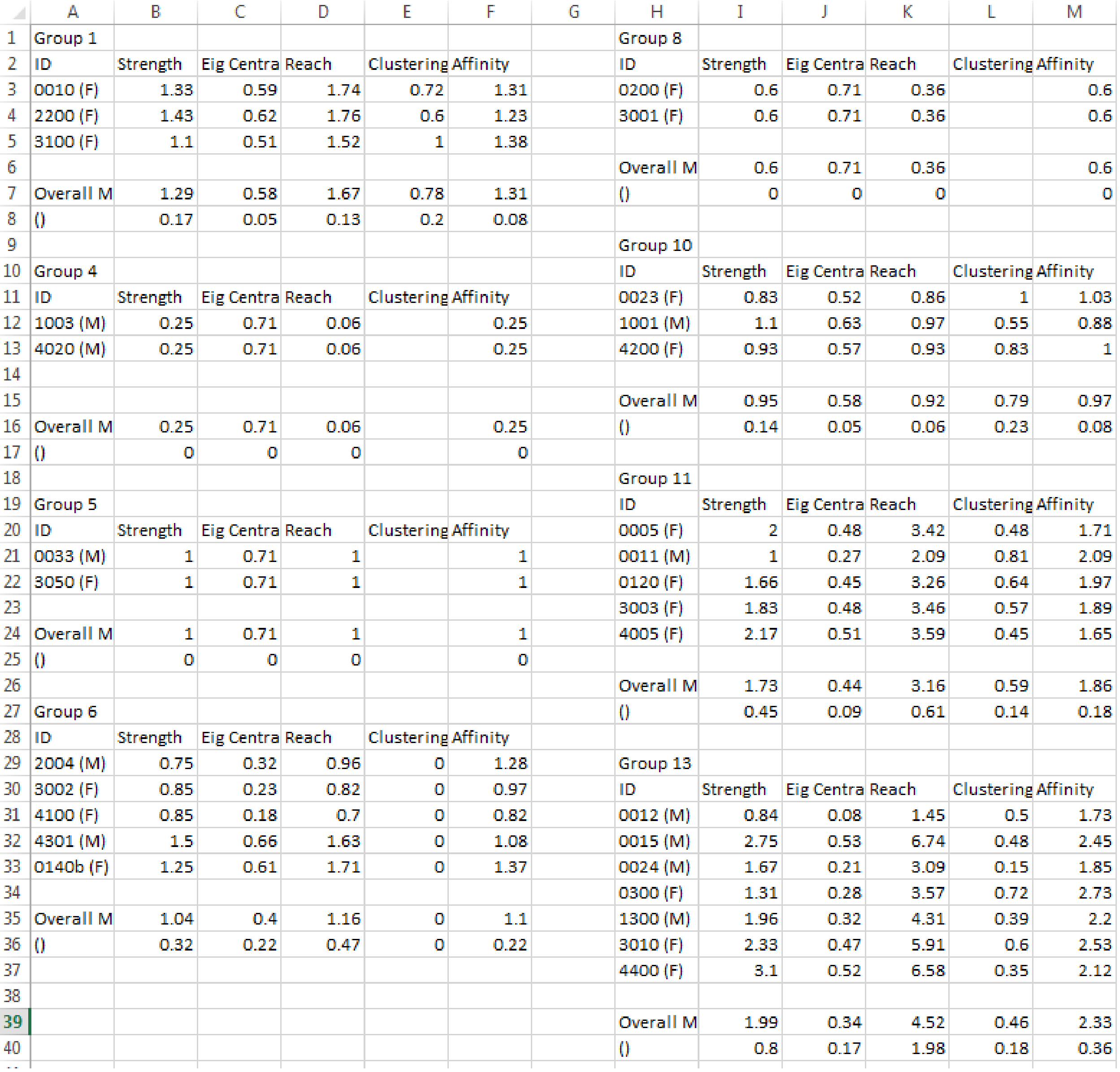
SOCPROG OUTPUTS/NETWORK DATA

2005 – Entire Population



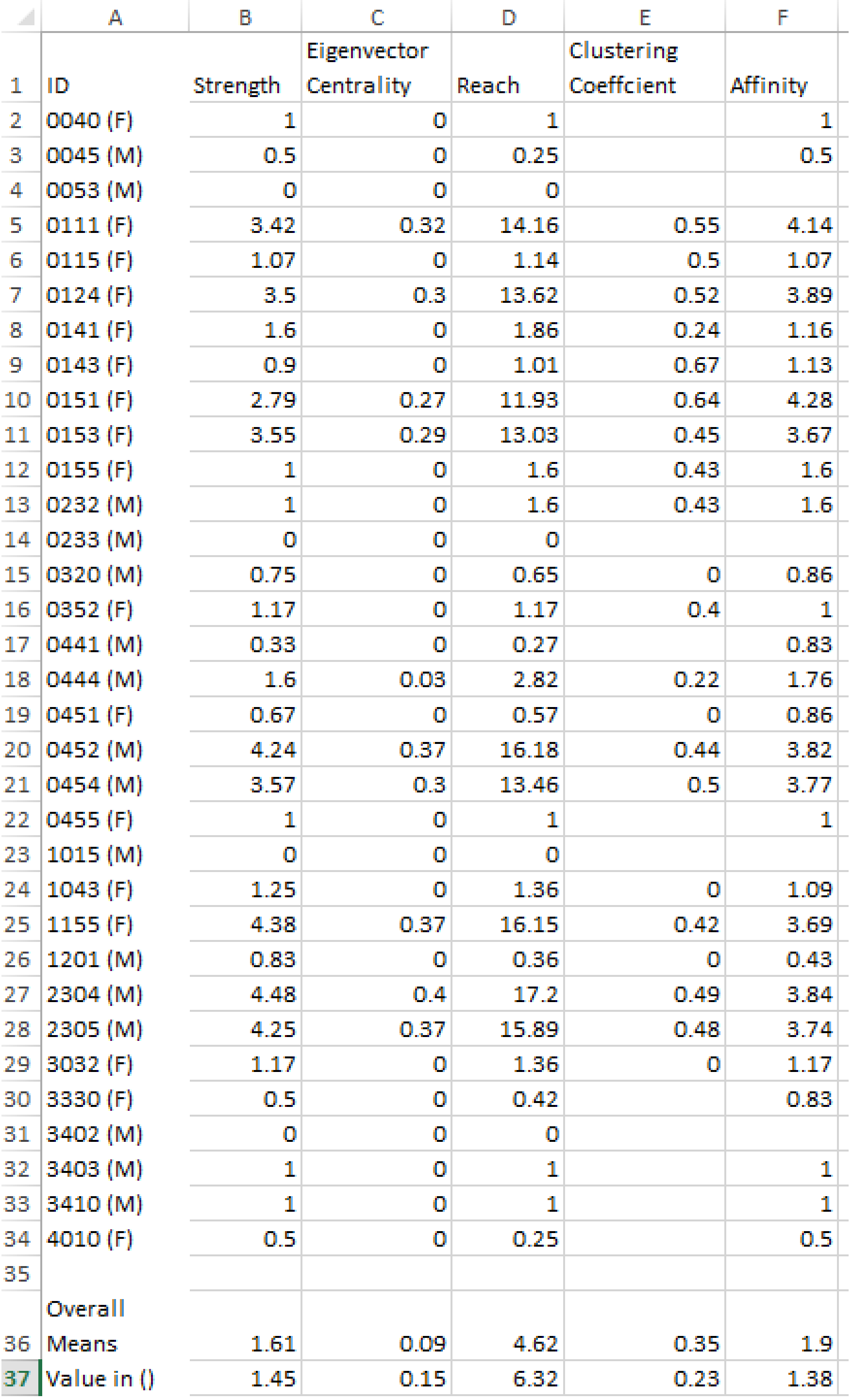
	A	B	C	D	E	F
1	ID	Affinity	Strength	Eigenvector Centrality	Reach	Clustering Coefficient
2	0005 (F)	2.23	2.2	0.07	4.92	0.32
3	0010 (F)	1.31	1.33	0	1.74	0.6
4	0011 (M)	2.95	1	0.04	2.94	0.67
5	0012 (M)	1.92	1.83	0.12	3.51	0.15
6	0015 (M)	2.49	2.75	0.51	6.84	0.48
7	0023 (F)	2.09	1.79	0.08	3.75	0.27
8	0024 (M)	2.17	2	0.22	4.35	0.15
9	0033 (M)	1.23	1.33	0	1.63	0.33
10	0120 (F)	2.49	1.79	0.06	4.46	0.45
11	0200 (F)	0.6	0.6	0	0.36	
12	0300 (F)	2.53	1.71	0.28	4.33	0.38
13	1001 (M)	2.54	2.1	0.07	5.34	0.27
14	1003 (M)	1.03	0.91	0	0.94	0.4
15	1300 (M)	2.4	1.96	0.32	4.7	0.39
16	2004 (M)	1.55	0.75	0.01	1.16	0
17	2200 (F)	1.23	1.43	0	1.76	0.5
18	3002 (F)	0.97	0.85	0	0.82	0
19	3003 (F)	2.37	2	0.07	4.73	0.39
20	3010 (F)	2.59	2.33	0.45	6.04	0.6
21	3050 (F)	1.23	1.33	0	1.63	0.33
22	3100 (F)	1.38	1.1	0	1.52	0.83
23	4005 (F)	1.38	3.67	0.1	6.74	0.17
24	4020 (M)	1.84	0.25	0	0.23	
25	4100 (F)	0.82	0.85	0	0.7	0
26	4200 (F)	2.3	1.29	0.05	2.97	0.51
27	4301 (M)	1.22	1.9	0.06	2.31	0
28	4400 (F)	2.25	3.1	0.61	6.98	0.35
29	0140b (F)	1.69	1.25	0.03	2.11	0
30	3001 (F)	0.6	0.6	0	0.36	
31	Overall Means	1.76	1.59	0.1	3.1	0.33
32	Value in ()	0.69	0.78	0.16	2.11	0.22
33						
34	Strength by clustering coefficient			0.0304		
35	Strength by affinity			0.6095		

2005 – Group Values



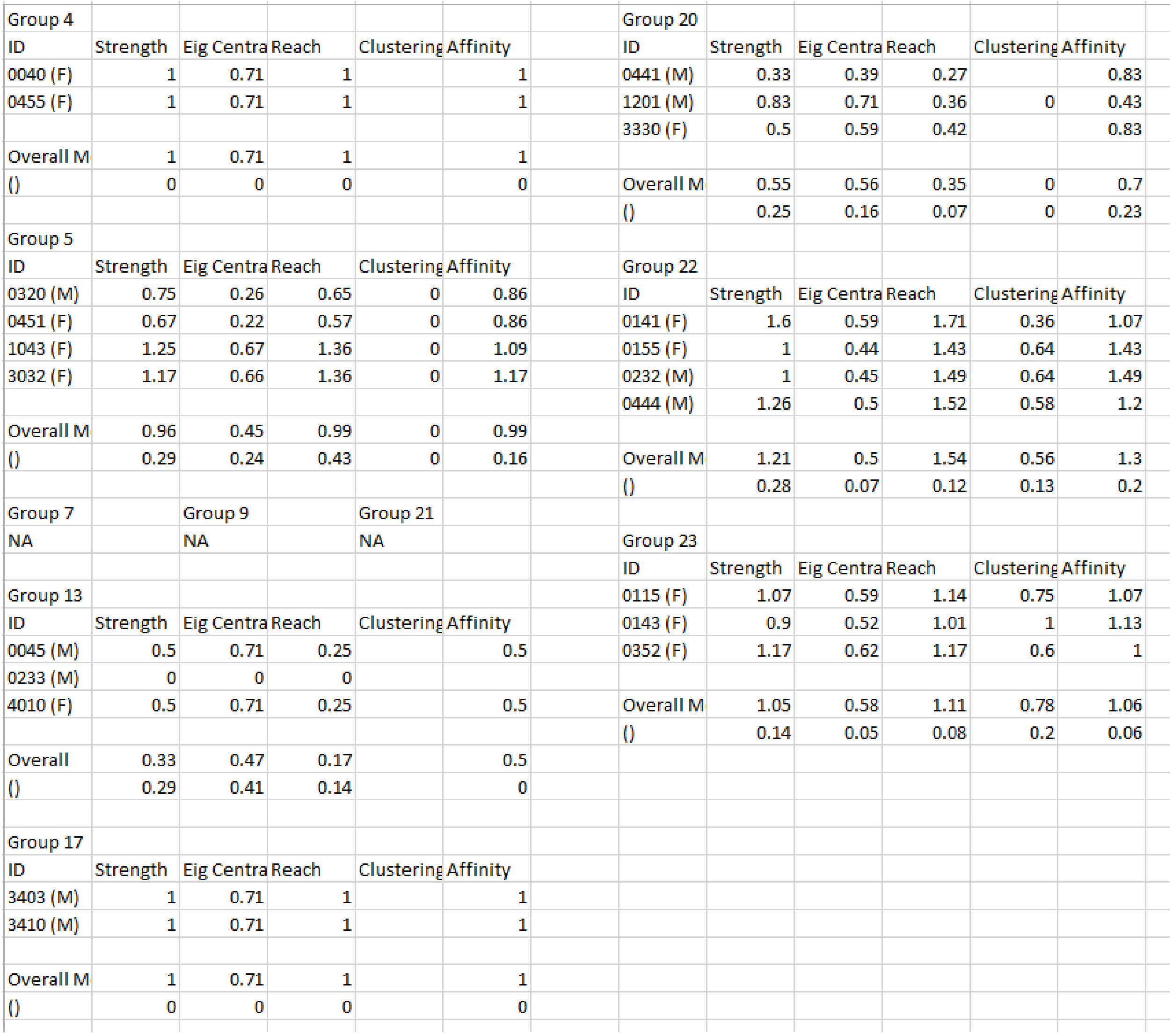
	A	B	C	D	E	F	G	H	I	J	K	L	M
1	Group 1							Group 8					
2	ID	Strength	Eig Centra	Reach	Clustering	Affinity		ID	Strength	Eig Centra	Reach	Clustering	Affinity
3	0010 (F)	1.33	0.59	1.74	0.72	1.31		0200 (F)	0.6	0.71	0.36		0.6
4	2200 (F)	1.43	0.62	1.76	0.6	1.23		3001 (F)	0.6	0.71	0.36		0.6
5	3100 (F)	1.1	0.51	1.52	1	1.38							
6								Overall M	0.6	0.71	0.36		0.6
7	Overall M	1.29	0.58	1.67	0.78	1.31		()	0	0	0		0
8	()	0.17	0.05	0.13	0.2	0.08							
9								Group 10					
10	Group 4							ID	Strength	Eig Centra	Reach	Clustering	Affinity
11	ID	Strength	Eig Centra	Reach	Clustering	Affinity		0023 (F)	0.83	0.52	0.86	1	1.03
12	1003 (M)	0.25	0.71	0.06		0.25		1001 (M)	1.1	0.63	0.97	0.55	0.88
13	4020 (M)	0.25	0.71	0.06		0.25		4200 (F)	0.93	0.57	0.93	0.83	1
14													
15								Overall M	0.95	0.58	0.92	0.79	0.97
16	Overall M	0.25	0.71	0.06		0.25		()	0.14	0.05	0.06	0.23	0.08
17	()	0	0	0		0							
18								Group 11					
19	Group 5							ID	Strength	Eig Centra	Reach	Clustering	Affinity
20	ID	Strength	Eig Centra	Reach	Clustering	Affinity		0005 (F)	2	0.48	3.42	0.48	1.71
21	0033 (M)	1	0.71	1		1		0011 (M)	1	0.27	2.09	0.81	2.09
22	3050 (F)	1	0.71	1		1		0120 (F)	1.66	0.45	3.26	0.64	1.97
23								3003 (F)	1.83	0.48	3.46	0.57	1.89
24	Overall M	1	0.71	1		1		4005 (F)	2.17	0.51	3.59	0.45	1.65
25	()	0	0	0		0							
26								Overall M	1.73	0.44	3.16	0.59	1.86
27	Group 6							()	0.45	0.09	0.61	0.14	0.18
28	ID	Strength	Eig Centra	Reach	Clustering	Affinity							
29	2004 (M)	0.75	0.32	0.96	0	1.28		Group 13					
30	3002 (F)	0.85	0.23	0.82	0	0.97		ID	Strength	Eig Centra	Reach	Clustering	Affinity
31	4100 (F)	0.85	0.18	0.7	0	0.82		0012 (M)	0.84	0.08	1.45	0.5	1.73
32	4301 (M)	1.5	0.66	1.63	0	1.08		0015 (M)	2.75	0.53	6.74	0.48	2.45
33	0140b (F)	1.25	0.61	1.71	0	1.37		0024 (M)	1.67	0.21	3.09	0.15	1.85
34								0300 (F)	1.31	0.28	3.57	0.72	2.73
35	Overall M	1.04	0.4	1.16	0	1.1		1300 (M)	1.96	0.32	4.31	0.39	2.2
36	()	0.32	0.22	0.47	0	0.22		3010 (F)	2.33	0.47	5.91	0.6	2.53
37								4400 (F)	3.1	0.52	6.58	0.35	2.12
38													
39								Overall M	1.99	0.34	4.52	0.46	2.33
40								()	0.8	0.17	1.98	0.18	0.36

2006 – Entire Population



	A	B	C	D	E	F
1	ID	Strength	Eigenvector Centrality	Reach	Clustering Coeffcient	Affinity
2	0040 (F)	1	0	1		1
3	0045 (M)	0.5	0	0.25		0.5
4	0053 (M)	0	0	0		
5	0111 (F)	3.42	0.32	14.16	0.55	4.14
6	0115 (F)	1.07	0	1.14	0.5	1.07
7	0124 (F)	3.5	0.3	13.62	0.52	3.89
8	0141 (F)	1.6	0	1.86	0.24	1.16
9	0143 (F)	0.9	0	1.01	0.67	1.13
10	0151 (F)	2.79	0.27	11.93	0.64	4.28
11	0153 (F)	3.55	0.29	13.03	0.45	3.67
12	0155 (F)	1	0	1.6	0.43	1.6
13	0232 (M)	1	0	1.6	0.43	1.6
14	0233 (M)	0	0	0		
15	0320 (M)	0.75	0	0.65	0	0.86
16	0352 (F)	1.17	0	1.17	0.4	1
17	0441 (M)	0.33	0	0.27		0.83
18	0444 (M)	1.6	0.03	2.82	0.22	1.76
19	0451 (F)	0.67	0	0.57	0	0.86
20	0452 (M)	4.24	0.37	16.18	0.44	3.82
21	0454 (M)	3.57	0.3	13.46	0.5	3.77
22	0455 (F)	1	0	1		1
23	1015 (M)	0	0	0		
24	1043 (F)	1.25	0	1.36	0	1.09
25	1155 (F)	4.38	0.37	16.15	0.42	3.69
26	1201 (M)	0.83	0	0.36	0	0.43
27	2304 (M)	4.48	0.4	17.2	0.49	3.84
28	2305 (M)	4.25	0.37	15.89	0.48	3.74
29	3032 (F)	1.17	0	1.36	0	1.17
30	3330 (F)	0.5	0	0.42		0.83
31	3402 (M)	0	0	0		
32	3403 (M)	1	0	1		1
33	3410 (M)	1	0	1		1
34	4010 (F)	0.5	0	0.25		0.5
35						
36	Overall Means	1.61	0.09	4.62	0.35	1.9
37	Value in ()	1.45	0.15	6.32	0.23	1.38

2006 – Group Values



Group 4

ID	Strength	Eig Centra	Reach	Clustering	Affinity
0040 (F)	1	0.71	1		1
0455 (F)	1	0.71	1		1
Overall M	1	0.71	1		1
()	0	0	0		0

Group 5

ID	Strength	Eig Centra	Reach	Clustering	Affinity
0320 (M)	0.75	0.26	0.65	0	0.86
0451 (F)	0.67	0.22	0.57	0	0.86
1043 (F)	1.25	0.67	1.36	0	1.09
3032 (F)	1.17	0.66	1.36	0	1.17
Overall M	0.96	0.45	0.99	0	0.99
()	0.29	0.24	0.43	0	0.16

Group 7		Group 9		Group 21
NA		NA		NA

Group 13

ID	Strength	Eig Centra	Reach	Clustering	Affinity
0045 (M)	0.5	0.71	0.25		0.5
0233 (M)	0	0	0		
4010 (F)	0.5	0.71	0.25		0.5
Overall	0.33	0.47	0.17		0.5
()	0.29	0.41	0.14		0

Group 17

ID	Strength	Eig Centra	Reach	Clustering	Affinity
3403 (M)	1	0.71	1		1
3410 (M)	1	0.71	1		1
Overall M	1	0.71	1		1
()	0	0	0		0

Group 20

ID	Strength	Eig Centra	Reach	Clustering	Affinity
0441 (M)	0.33	0.39	0.27		0.83
1201 (M)	0.83	0.71	0.36	0	0.43
3330 (F)	0.5	0.59	0.42		0.83
Overall M	0.55	0.56	0.35	0	0.7
()	0.25	0.16	0.07	0	0.23

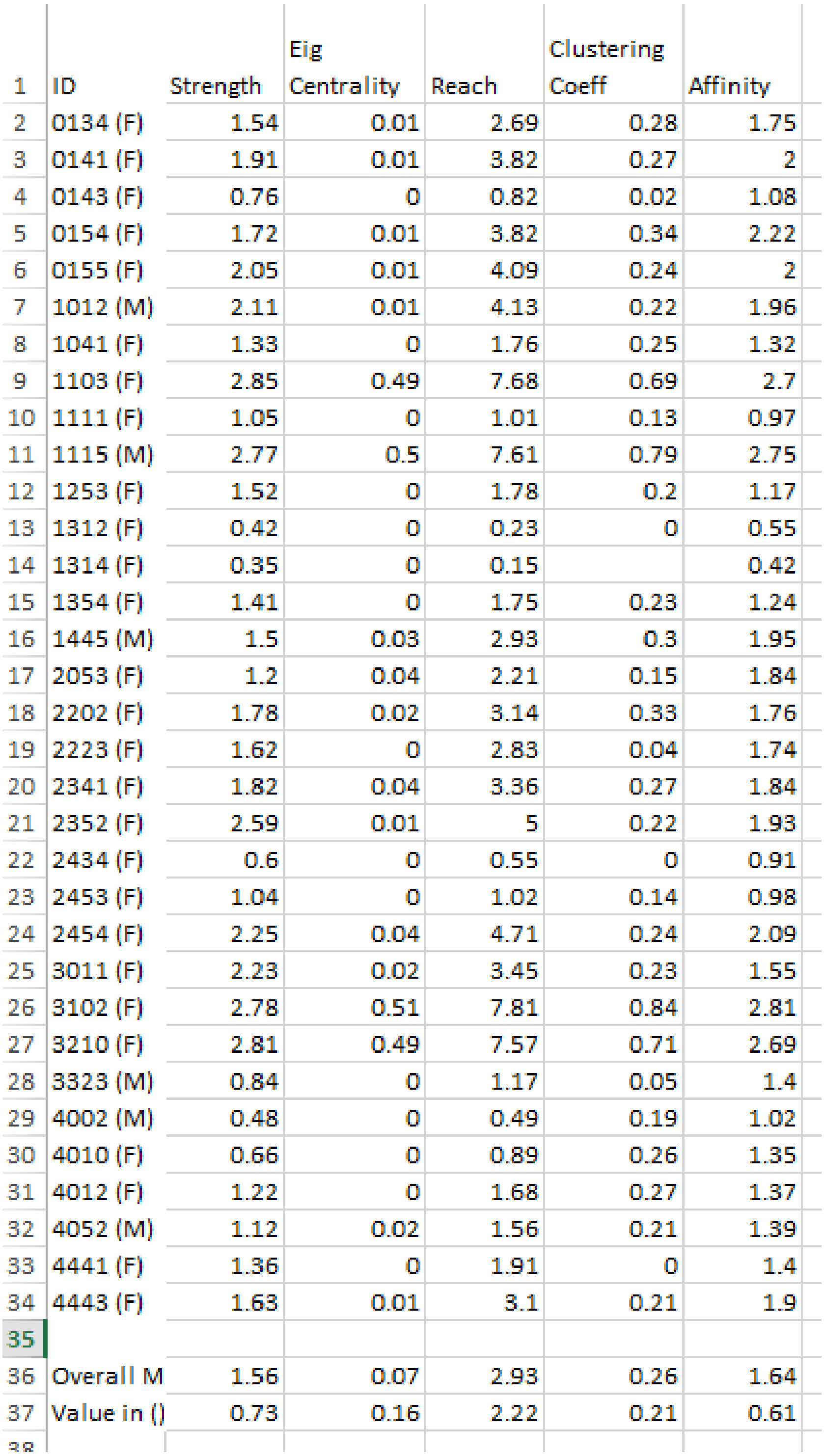
Group 22

ID	Strength	Eig Centra	Reach	Clustering	Affinity
0141 (F)	1.6	0.59	1.71	0.36	1.07
0155 (F)	1	0.44	1.43	0.64	1.43
0232 (M)	1	0.45	1.49	0.64	1.49
0444 (M)	1.26	0.5	1.52	0.58	1.2
Overall M	1.21	0.5	1.54	0.56	1.3
()	0.28	0.07	0.12	0.13	0.2

Group 23

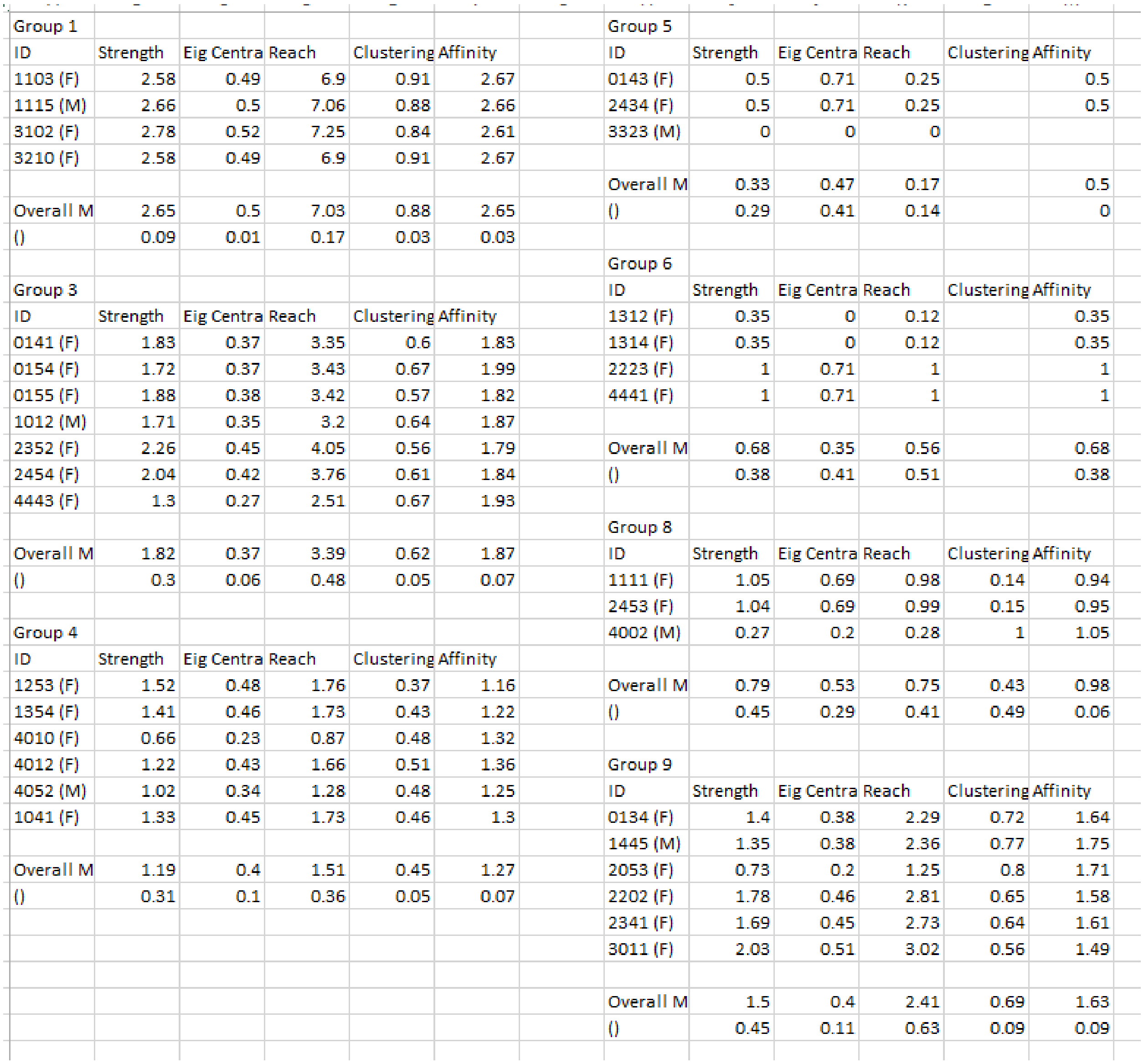
ID	Strength	Eig Centra	Reach	Clustering	Affinity
0115 (F)	1.07	0.59	1.14	0.75	1.07
0143 (F)	0.9	0.52	1.01	1	1.13
0352 (F)	1.17	0.62	1.17	0.6	1
Overall M	1.05	0.58	1.11	0.78	1.06
()	0.14	0.05	0.08	0.2	0.06

2007 – Entire Population



1	ID	Strength	Eig Centrality	Reach	Clustering Coeff	Affinity
2	0134 (F)	1.54	0.01	2.69	0.28	1.75
3	0141 (F)	1.91	0.01	3.82	0.27	2
4	0143 (F)	0.76	0	0.82	0.02	1.08
5	0154 (F)	1.72	0.01	3.82	0.34	2.22
6	0155 (F)	2.05	0.01	4.09	0.24	2
7	1012 (M)	2.11	0.01	4.13	0.22	1.96
8	1041 (F)	1.33	0	1.76	0.25	1.32
9	1103 (F)	2.85	0.49	7.68	0.69	2.7
10	1111 (F)	1.05	0	1.01	0.13	0.97
11	1115 (M)	2.77	0.5	7.61	0.79	2.75
12	1253 (F)	1.52	0	1.78	0.2	1.17
13	1312 (F)	0.42	0	0.23	0	0.55
14	1314 (F)	0.35	0	0.15		0.42
15	1354 (F)	1.41	0	1.75	0.23	1.24
16	1445 (M)	1.5	0.03	2.93	0.3	1.95
17	2053 (F)	1.2	0.04	2.21	0.15	1.84
18	2202 (F)	1.78	0.02	3.14	0.33	1.76
19	2223 (F)	1.62	0	2.83	0.04	1.74
20	2341 (F)	1.82	0.04	3.36	0.27	1.84
21	2352 (F)	2.59	0.01	5	0.22	1.93
22	2434 (F)	0.6	0	0.55	0	0.91
23	2453 (F)	1.04	0	1.02	0.14	0.98
24	2454 (F)	2.25	0.04	4.71	0.24	2.09
25	3011 (F)	2.23	0.02	3.45	0.23	1.55
26	3102 (F)	2.78	0.51	7.81	0.84	2.81
27	3210 (F)	2.81	0.49	7.57	0.71	2.69
28	3323 (M)	0.84	0	1.17	0.05	1.4
29	4002 (M)	0.48	0	0.49	0.19	1.02
30	4010 (F)	0.66	0	0.89	0.26	1.35
31	4012 (F)	1.22	0	1.68	0.27	1.37
32	4052 (M)	1.12	0.02	1.56	0.21	1.39
33	4441 (F)	1.36	0	1.91	0	1.4
34	4443 (F)	1.63	0.01	3.1	0.21	1.9
35						
36	Overall M	1.56	0.07	2.93	0.26	1.64
37	Value in ()	0.73	0.16	2.22	0.21	0.61

2007 – Group Values



Group 1

ID	Strength	Eig Centra	Reach	Clustering	Affinity
1103 (F)	2.58	0.49	6.9	0.91	2.67
1115 (M)	2.66	0.5	7.06	0.88	2.66
3102 (F)	2.78	0.52	7.25	0.84	2.61
3210 (F)	2.58	0.49	6.9	0.91	2.67
Overall M	2.65	0.5	7.03	0.88	2.65
()	0.09	0.01	0.17	0.03	0.03

Group 3

ID	Strength	Eig Centra	Reach	Clustering	Affinity
0141 (F)	1.83	0.37	3.35	0.6	1.83
0154 (F)	1.72	0.37	3.43	0.67	1.99
0155 (F)	1.88	0.38	3.42	0.57	1.82
1012 (M)	1.71	0.35	3.2	0.64	1.87
2352 (F)	2.26	0.45	4.05	0.56	1.79
2454 (F)	2.04	0.42	3.76	0.61	1.84
4443 (F)	1.3	0.27	2.51	0.67	1.93
Overall M	1.82	0.37	3.39	0.62	1.87
()	0.3	0.06	0.48	0.05	0.07

Group 4

ID	Strength	Eig Centra	Reach	Clustering	Affinity
1253 (F)	1.52	0.48	1.76	0.37	1.16
1354 (F)	1.41	0.46	1.73	0.43	1.22
4010 (F)	0.66	0.23	0.87	0.48	1.32
4012 (F)	1.22	0.43	1.66	0.51	1.36
4052 (M)	1.02	0.34	1.28	0.48	1.25
1041 (F)	1.33	0.45	1.73	0.46	1.3
Overall M	1.19	0.4	1.51	0.45	1.27
()	0.31	0.1	0.36	0.05	0.07

Group 5

ID	Strength	Eig Centra	Reach	Clustering	Affinity
0143 (F)	0.5	0.71	0.25		0.5
2434 (F)	0.5	0.71	0.25		0.5
3323 (M)	0	0	0		
Overall M	0.33	0.47	0.17		0.5
()	0.29	0.41	0.14		0

Group 6

ID	Strength	Eig Centra	Reach	Clustering	Affinity
1312 (F)	0.35	0	0.12		0.35
1314 (F)	0.35	0	0.12		0.35
2223 (F)	1	0.71	1		1
4441 (F)	1	0.71	1		1
Overall M	0.68	0.35	0.56		0.68
()	0.38	0.41	0.51		0.38

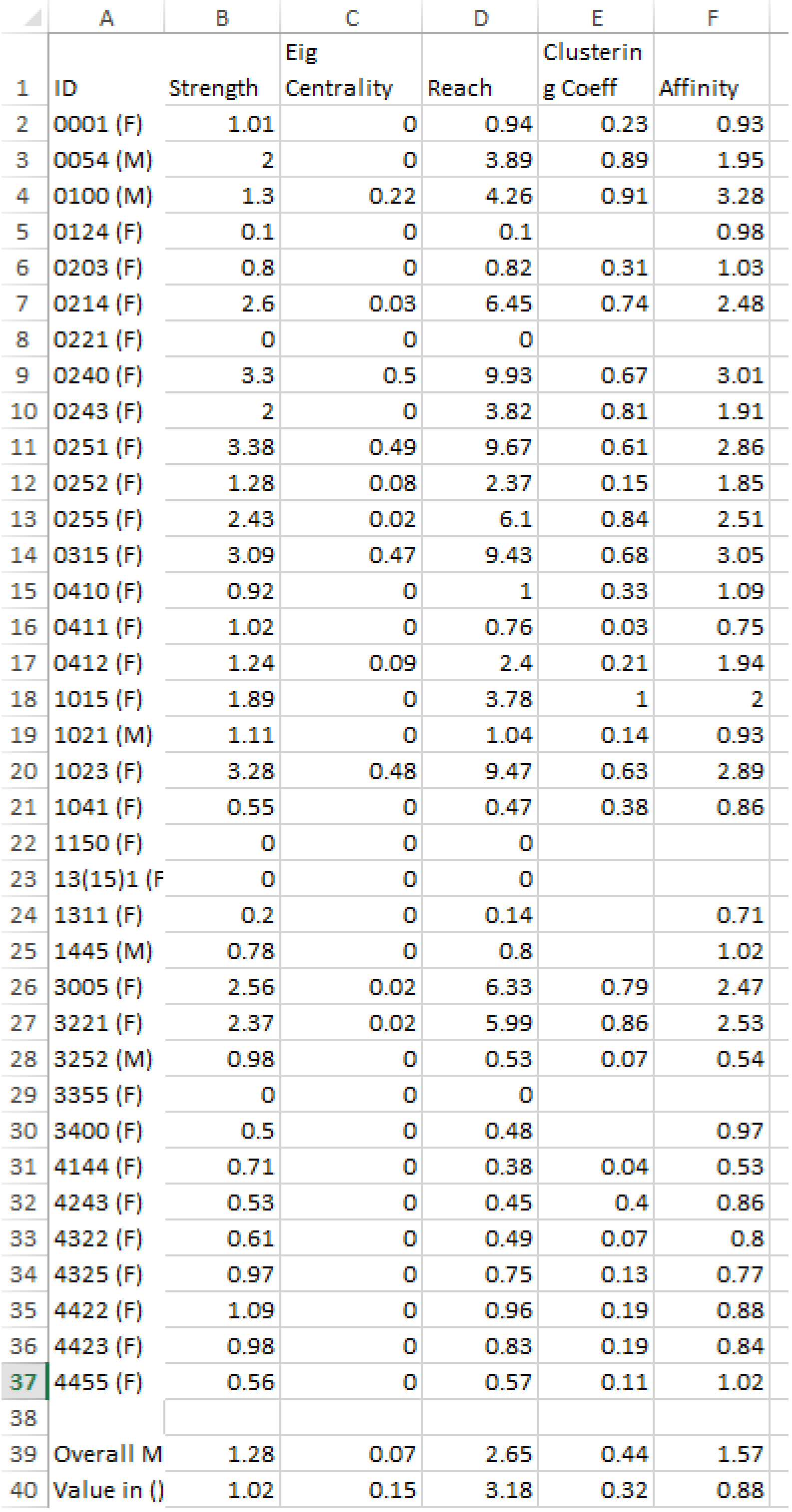
Group 8

ID	Strength	Eig Centra	Reach	Clustering	Affinity
1111 (F)	1.05	0.69	0.98	0.14	0.94
2453 (F)	1.04	0.69	0.99	0.15	0.95
4002 (M)	0.27	0.2	0.28	1	1.05
Overall M	0.79	0.53	0.75	0.43	0.98
()	0.45	0.29	0.41	0.49	0.06

Group 9

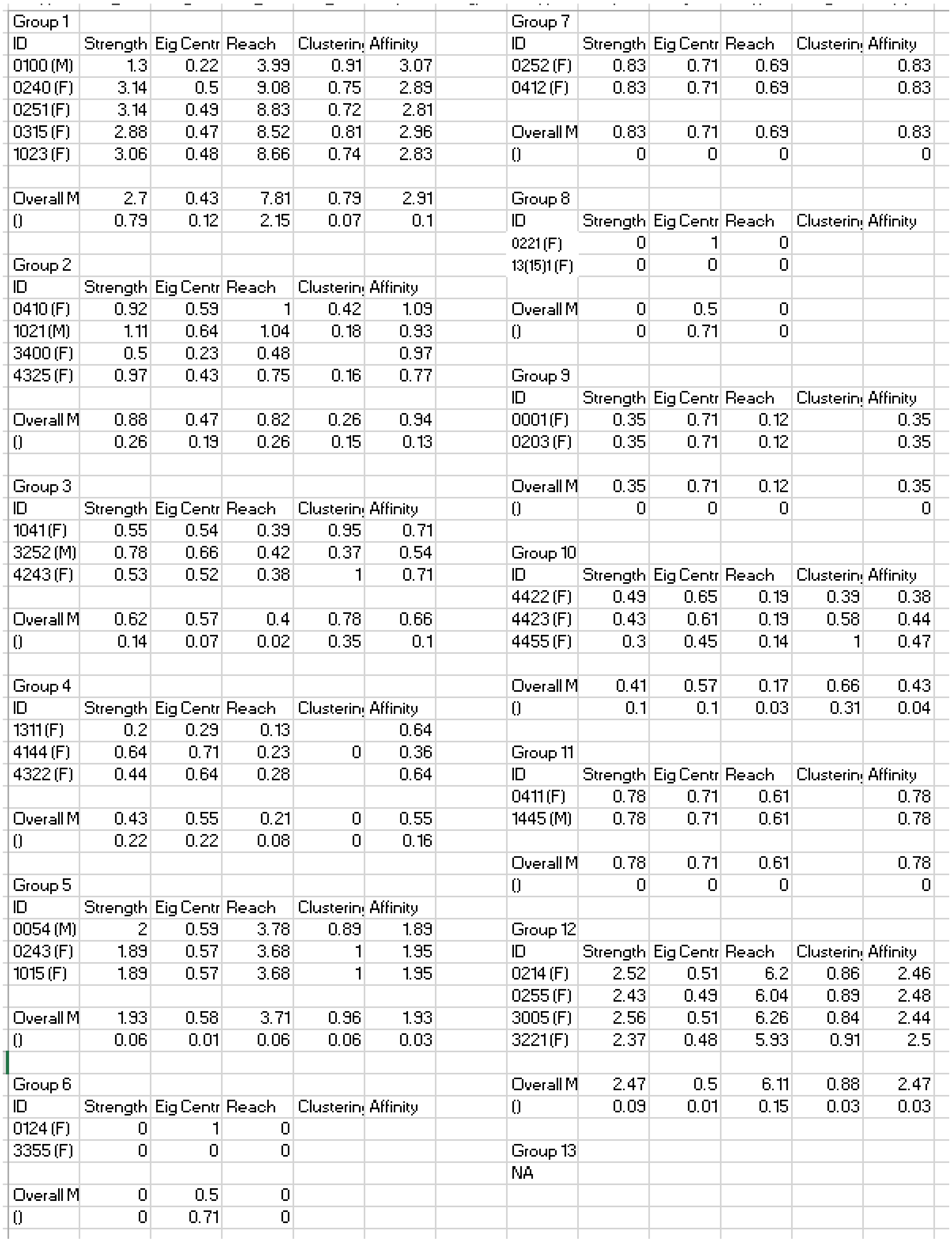
ID	Strength	Eig Centra	Reach	Clustering	Affinity
0134 (F)	1.4	0.38	2.29	0.72	1.64
1445 (M)	1.35	0.38	2.36	0.77	1.75
2053 (F)	0.73	0.2	1.25	0.8	1.71
2202 (F)	1.78	0.46	2.81	0.65	1.58
2341 (F)	1.69	0.45	2.73	0.64	1.61
3011 (F)	2.03	0.51	3.02	0.56	1.49
Overall M	1.5	0.4	2.41	0.69	1.63
()	0.45	0.11	0.63	0.09	0.09

2008 – Entire Population



	A	B	C	D	E	F
1	ID	Strength	Eig Centrality	Reach	Clustering Coeff	Affinity
2	0001 (F)	1.01	0	0.94	0.23	0.93
3	0054 (M)	2	0	3.89	0.89	1.95
4	0100 (M)	1.3	0.22	4.26	0.91	3.28
5	0124 (F)	0.1	0	0.1		0.98
6	0203 (F)	0.8	0	0.82	0.31	1.03
7	0214 (F)	2.6	0.03	6.45	0.74	2.48
8	0221 (F)	0	0	0		
9	0240 (F)	3.3	0.5	9.93	0.67	3.01
10	0243 (F)	2	0	3.82	0.81	1.91
11	0251 (F)	3.38	0.49	9.67	0.61	2.86
12	0252 (F)	1.28	0.08	2.37	0.15	1.85
13	0255 (F)	2.43	0.02	6.1	0.84	2.51
14	0315 (F)	3.09	0.47	9.43	0.68	3.05
15	0410 (F)	0.92	0	1	0.33	1.09
16	0411 (F)	1.02	0	0.76	0.03	0.75
17	0412 (F)	1.24	0.09	2.4	0.21	1.94
18	1015 (F)	1.89	0	3.78	1	2
19	1021 (M)	1.11	0	1.04	0.14	0.93
20	1023 (F)	3.28	0.48	9.47	0.63	2.89
21	1041 (F)	0.55	0	0.47	0.38	0.86
22	1150 (F)	0	0	0		
23	13(15)1 (F	0	0	0		
24	1311 (F)	0.2	0	0.14		0.71
25	1445 (M)	0.78	0	0.8		1.02
26	3005 (F)	2.56	0.02	6.33	0.79	2.47
27	3221 (F)	2.37	0.02	5.99	0.86	2.53
28	3252 (M)	0.98	0	0.53	0.07	0.54
29	3355 (F)	0	0	0		
30	3400 (F)	0.5	0	0.48		0.97
31	4144 (F)	0.71	0	0.38	0.04	0.53
32	4243 (F)	0.53	0	0.45	0.4	0.86
33	4322 (F)	0.61	0	0.49	0.07	0.8
34	4325 (F)	0.97	0	0.75	0.13	0.77
35	4422 (F)	1.09	0	0.96	0.19	0.88
36	4423 (F)	0.98	0	0.83	0.19	0.84
37	4455 (F)	0.56	0	0.57	0.11	1.02
38						
39	Overall M	1.28	0.07	2.65	0.44	1.57
40	Value in ()	1.02	0.15	3.18	0.32	0.88

2008 – Group Values



Group 1

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
0100 (M)	1.3	0.22	3.99	0.91	3.07
0240 (F)	3.14	0.5	9.08	0.75	2.89
0251 (F)	3.14	0.49	8.83	0.72	2.81
0315 (F)	2.88	0.47	8.52	0.81	2.96
1023 (F)	3.06	0.48	8.66	0.74	2.83
Overall M	2.7	0.43	7.81	0.79	2.91
()	0.79	0.12	2.15	0.07	0.1

Group 2

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
0410 (F)	0.92	0.59	1	0.42	1.09
1021 (M)	1.11	0.64	1.04	0.18	0.93
3400 (F)	0.5	0.23	0.48		0.97
4325 (F)	0.97	0.43	0.75	0.16	0.77
Overall M	0.88	0.47	0.82	0.26	0.94
()	0.26	0.19	0.26	0.15	0.13

Group 3

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1041 (F)	0.55	0.54	0.39	0.95	0.71
3252 (M)	0.78	0.66	0.42	0.37	0.54
4243 (F)	0.53	0.52	0.38	1	0.71
Overall M	0.62	0.57	0.4	0.78	0.66
()	0.14	0.07	0.02	0.35	0.1

Group 4

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1311 (F)	0.2	0.29	0.13		0.64
4144 (F)	0.64	0.71	0.23	0	0.36
4322 (F)	0.44	0.64	0.28		0.64
Overall M	0.43	0.55	0.21	0	0.55
()	0.22	0.22	0.08	0	0.16

Group 5

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
0054 (M)	2	0.59	3.78	0.89	1.89
0243 (F)	1.89	0.57	3.68	1	1.95
1015 (F)	1.89	0.57	3.68	1	1.95
Overall M	1.93	0.58	3.71	0.96	1.93
()	0.06	0.01	0.06	0.06	0.03

Group 6

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
0124 (F)	0	1	0		
3355 (F)	0	0	0		
Overall M	0	0.5	0		
()	0	0.71	0		

Group 7

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
0252 (F)	0.83	0.71	0.69		0.83
0412 (F)	0.83	0.71	0.69		0.83
Overall M	0.83	0.71	0.69		0.83
()	0	0	0		0

Group 8

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
0221 (F)	0	1	0		
13(15)1 (F)	0	0	0		
Overall M	0	0.5	0		
()	0	0.71	0		

Group 9

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
0001 (F)	0.35	0.71	0.12		0.35
0203 (F)	0.35	0.71	0.12		0.35
Overall M	0.35	0.71	0.12		0.35
()	0	0	0		0

Group 10

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
4422 (F)	0.49	0.65	0.19	0.39	0.38
4423 (F)	0.43	0.61	0.19	0.58	0.44
4455 (F)	0.3	0.45	0.14	1	0.47
Overall M	0.41	0.57	0.17	0.66	0.43
()	0.1	0.1	0.03	0.31	0.04

Group 11

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
0411 (F)	0.78	0.71	0.61		0.78
1445 (M)	0.78	0.71	0.61		0.78
Overall M	0.78	0.71	0.61		0.78
()	0	0	0		0

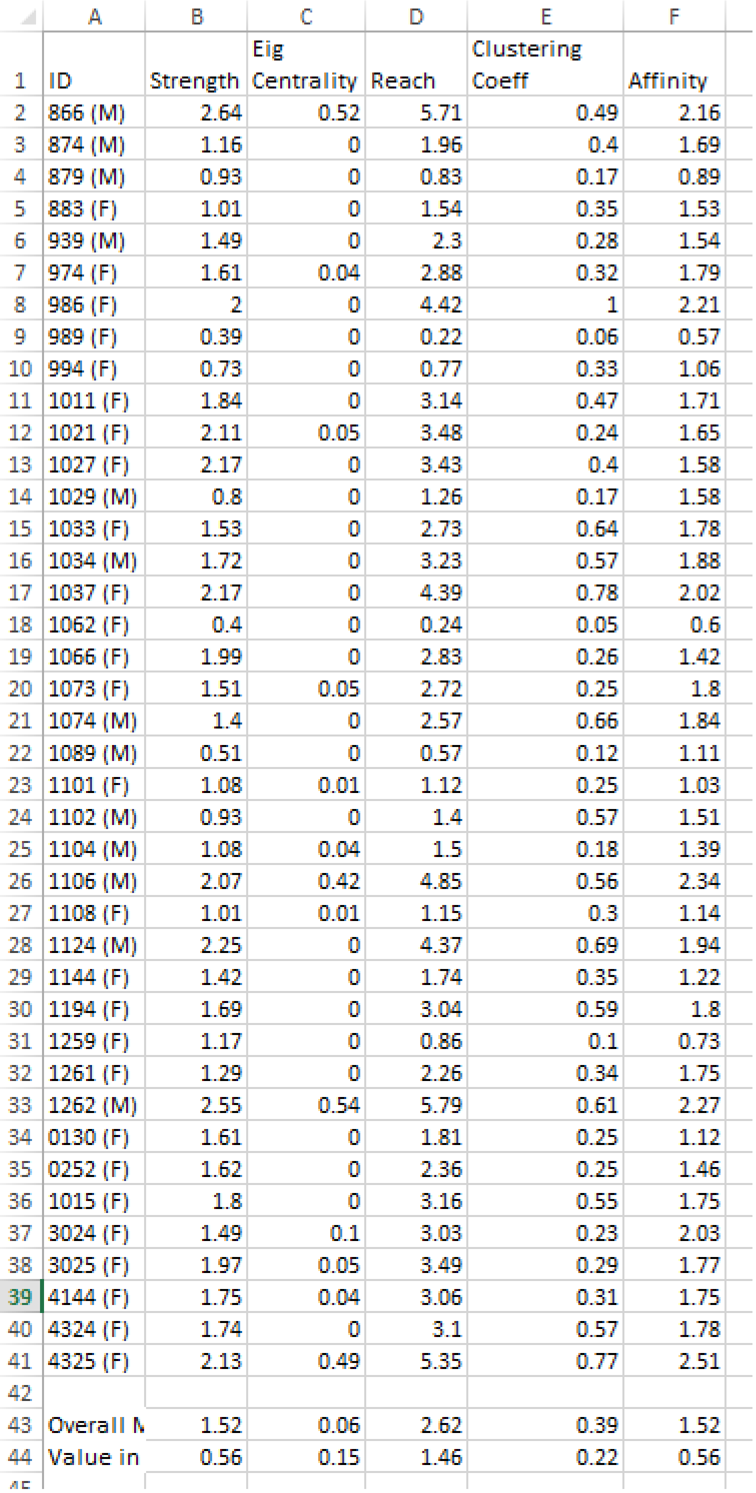
Group 12

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
0214 (F)	2.52	0.51	6.2	0.86	2.46
0255 (F)	2.43	0.49	6.04	0.89	2.48
3005 (F)	2.56	0.51	6.26	0.84	2.44
3221 (F)	2.37	0.48	5.93	0.91	2.5
Overall M	2.47	0.5	6.11	0.88	2.47
()	0.09	0.01	0.15	0.03	0.03

Group 13

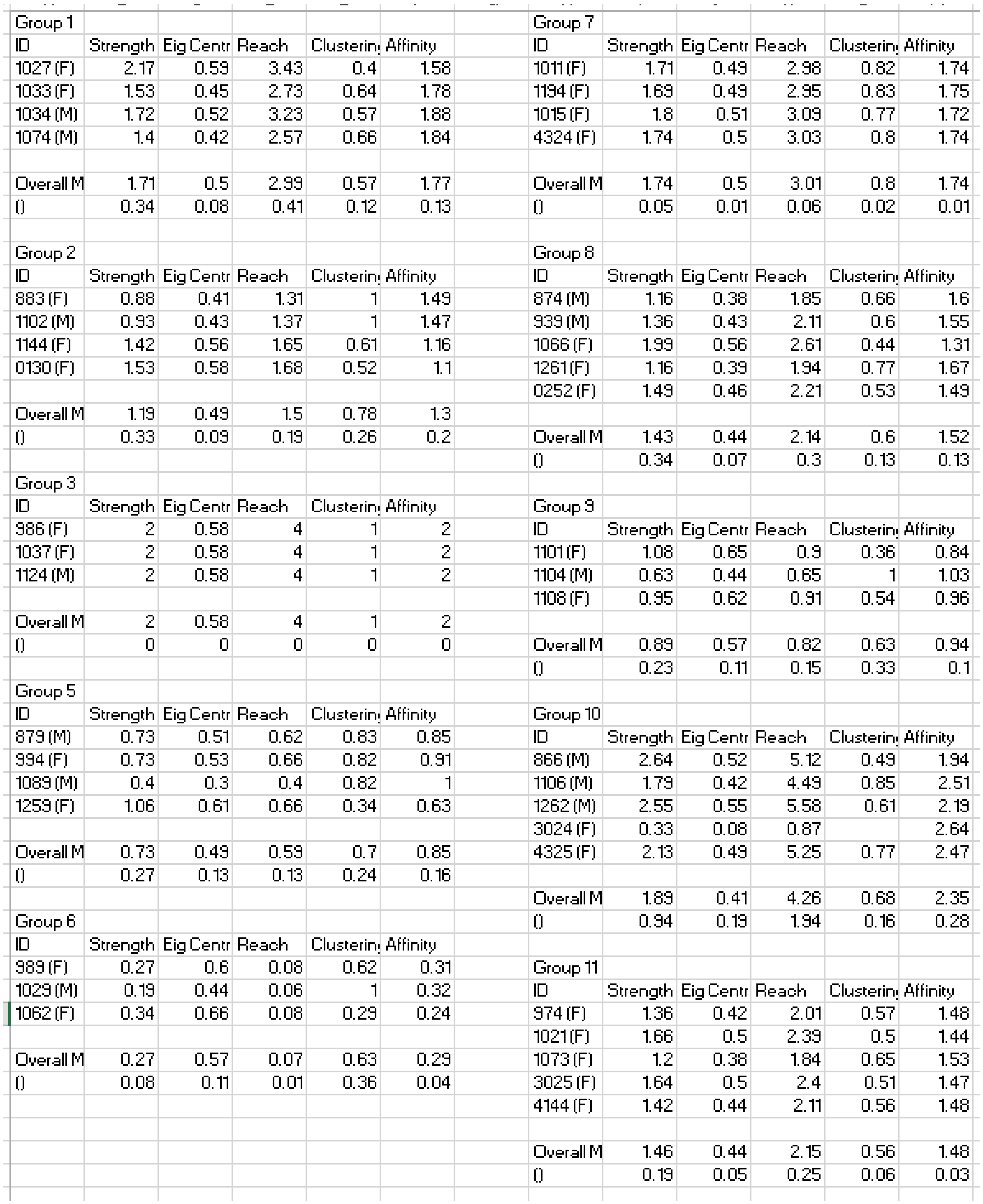
NA

2009 – Entire Population



	A	B	C	D	E	F
1	ID	Strength	Eig Centrality	Reach	Clustering Coeff	Affinity
2	866 (M)	2.64	0.52	5.71	0.49	2.16
3	874 (M)	1.16	0	1.96	0.4	1.69
4	879 (M)	0.93	0	0.83	0.17	0.89
5	883 (F)	1.01	0	1.54	0.35	1.53
6	939 (M)	1.49	0	2.3	0.28	1.54
7	974 (F)	1.61	0.04	2.88	0.32	1.79
8	986 (F)	2	0	4.42	1	2.21
9	989 (F)	0.39	0	0.22	0.06	0.57
10	994 (F)	0.73	0	0.77	0.33	1.06
11	1011 (F)	1.84	0	3.14	0.47	1.71
12	1021 (F)	2.11	0.05	3.48	0.24	1.65
13	1027 (F)	2.17	0	3.43	0.4	1.58
14	1029 (M)	0.8	0	1.26	0.17	1.58
15	1033 (F)	1.53	0	2.73	0.64	1.78
16	1034 (M)	1.72	0	3.23	0.57	1.88
17	1037 (F)	2.17	0	4.39	0.78	2.02
18	1062 (F)	0.4	0	0.24	0.05	0.6
19	1066 (F)	1.99	0	2.83	0.26	1.42
20	1073 (F)	1.51	0.05	2.72	0.25	1.8
21	1074 (M)	1.4	0	2.57	0.66	1.84
22	1089 (M)	0.51	0	0.57	0.12	1.11
23	1101 (F)	1.08	0.01	1.12	0.25	1.03
24	1102 (M)	0.93	0	1.4	0.57	1.51
25	1104 (M)	1.08	0.04	1.5	0.18	1.39
26	1106 (M)	2.07	0.42	4.85	0.56	2.34
27	1108 (F)	1.01	0.01	1.15	0.3	1.14
28	1124 (M)	2.25	0	4.37	0.69	1.94
29	1144 (F)	1.42	0	1.74	0.35	1.22
30	1194 (F)	1.69	0	3.04	0.59	1.8
31	1259 (F)	1.17	0	0.86	0.1	0.73
32	1261 (F)	1.29	0	2.26	0.34	1.75
33	1262 (M)	2.55	0.54	5.79	0.61	2.27
34	0130 (F)	1.61	0	1.81	0.25	1.12
35	0252 (F)	1.62	0	2.36	0.25	1.46
36	1015 (F)	1.8	0	3.16	0.55	1.75
37	3024 (F)	1.49	0.1	3.03	0.23	2.03
38	3025 (F)	1.97	0.05	3.49	0.29	1.77
39	4144 (F)	1.75	0.04	3.06	0.31	1.75
40	4324 (F)	1.74	0	3.1	0.57	1.78
41	4325 (F)	2.13	0.49	5.35	0.77	2.51
42						
43	Overall M	1.52	0.06	2.62	0.39	1.52
44	Value in	0.56	0.15	1.46	0.22	0.56

2009 – Group Values



Group 1

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1027 (F)	2.17	0.59	3.43	0.4	1.58
1033 (F)	1.53	0.45	2.73	0.64	1.78
1034 (M)	1.72	0.52	3.23	0.57	1.88
1074 (M)	1.4	0.42	2.57	0.66	1.84
Overall M	1.71	0.5	2.99	0.57	1.77
()	0.34	0.08	0.41	0.12	0.13

Group 2

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
883 (F)	0.88	0.41	1.31	1	1.49
1102 (M)	0.93	0.43	1.37	1	1.47
1144 (F)	1.42	0.56	1.65	0.61	1.16
0130 (F)	1.53	0.58	1.68	0.52	1.1
Overall M	1.19	0.49	1.5	0.78	1.3
()	0.33	0.09	0.19	0.26	0.2

Group 3

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
986 (F)	2	0.58	4	1	2
1037 (F)	2	0.58	4	1	2
1124 (M)	2	0.58	4	1	2
Overall M	2	0.58	4	1	2
()	0	0	0	0	0

Group 5

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
879 (M)	0.73	0.51	0.62	0.83	0.85
994 (F)	0.73	0.53	0.66	0.82	0.91
1089 (M)	0.4	0.3	0.4	0.82	1
1259 (F)	1.06	0.61	0.66	0.34	0.63
Overall M	0.73	0.49	0.59	0.7	0.85
()	0.27	0.13	0.13	0.24	0.16

Group 6

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
989 (F)	0.27	0.6	0.08	0.62	0.31
1029 (M)	0.19	0.44	0.06	1	0.32
1062 (F)	0.34	0.66	0.08	0.29	0.24
Overall M	0.27	0.57	0.07	0.63	0.29
()	0.08	0.11	0.01	0.36	0.04

Group 7

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1011 (F)	1.71	0.49	2.98	0.82	1.74
1194 (F)	1.69	0.49	2.95	0.83	1.75
1015 (F)	1.8	0.51	3.09	0.77	1.72
4324 (F)	1.74	0.5	3.03	0.8	1.74
Overall M	1.74	0.5	3.01	0.8	1.74
()	0.05	0.01	0.06	0.02	0.01

Group 8

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
874 (M)	1.16	0.38	1.85	0.66	1.6
939 (M)	1.36	0.43	2.11	0.6	1.55
1066 (F)	1.99	0.56	2.61	0.44	1.31
1261 (F)	1.16	0.39	1.94	0.77	1.67
0252 (F)	1.49	0.46	2.21	0.53	1.49
Overall M	1.43	0.44	2.14	0.6	1.52
()	0.34	0.07	0.3	0.13	0.13

Group 9

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1101 (F)	1.08	0.65	0.9	0.36	0.84
1104 (M)	0.63	0.44	0.65	1	1.03
1108 (F)	0.95	0.62	0.91	0.54	0.96
Overall M	0.89	0.57	0.82	0.63	0.94
()	0.23	0.11	0.15	0.33	0.1

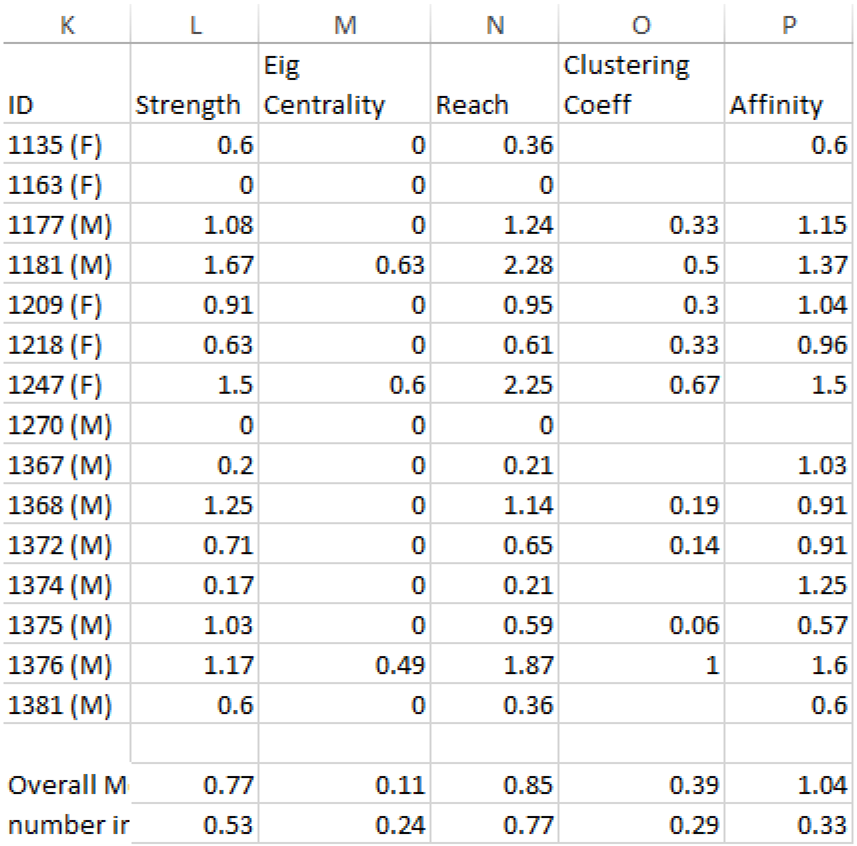
Group 10

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
866 (M)	2.64	0.52	5.12	0.49	1.94
1106 (M)	1.79	0.42	4.49	0.85	2.51
1262 (M)	2.55	0.55	5.58	0.61	2.19
3024 (F)	0.33	0.08	0.87		2.64
4325 (F)	2.13	0.49	5.25	0.77	2.47
Overall M	1.89	0.41	4.26	0.68	2.35
()	0.94	0.19	1.94	0.16	0.28

Group 11

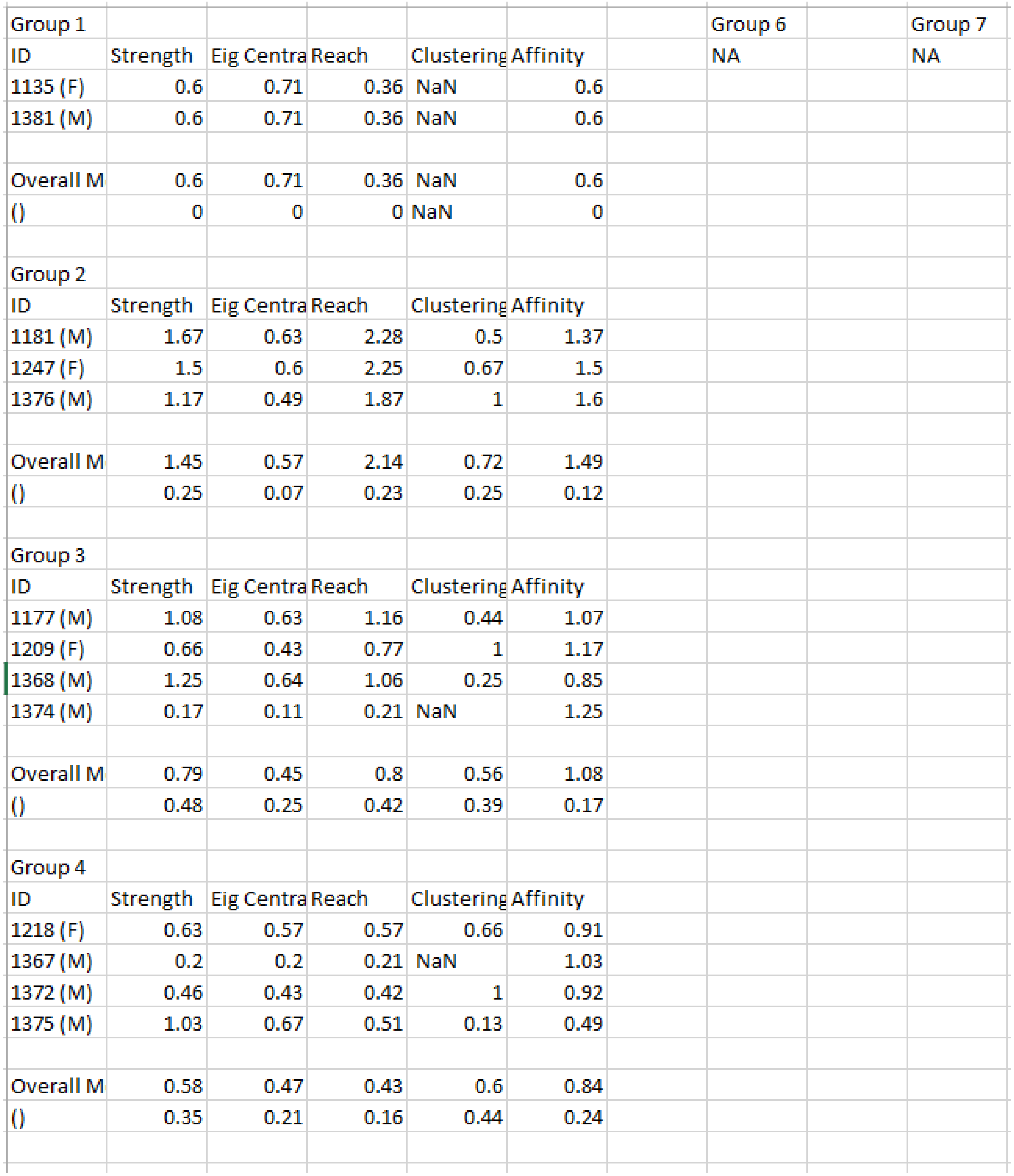
ID	Strength	Eig Centr	Reach	Clusterin	Affinity
974 (F)	1.36	0.42	2.01	0.57	1.48
1021 (F)	1.66	0.5	2.39	0.5	1.44
1073 (F)	1.2	0.38	1.84	0.65	1.53
3025 (F)	1.64	0.5	2.4	0.51	1.47
4144 (F)	1.42	0.44	2.11	0.56	1.48
Overall M	1.46	0.44	2.15	0.56	1.48
()	0.19	0.05	0.25	0.06	0.03

2010 – Entire Population



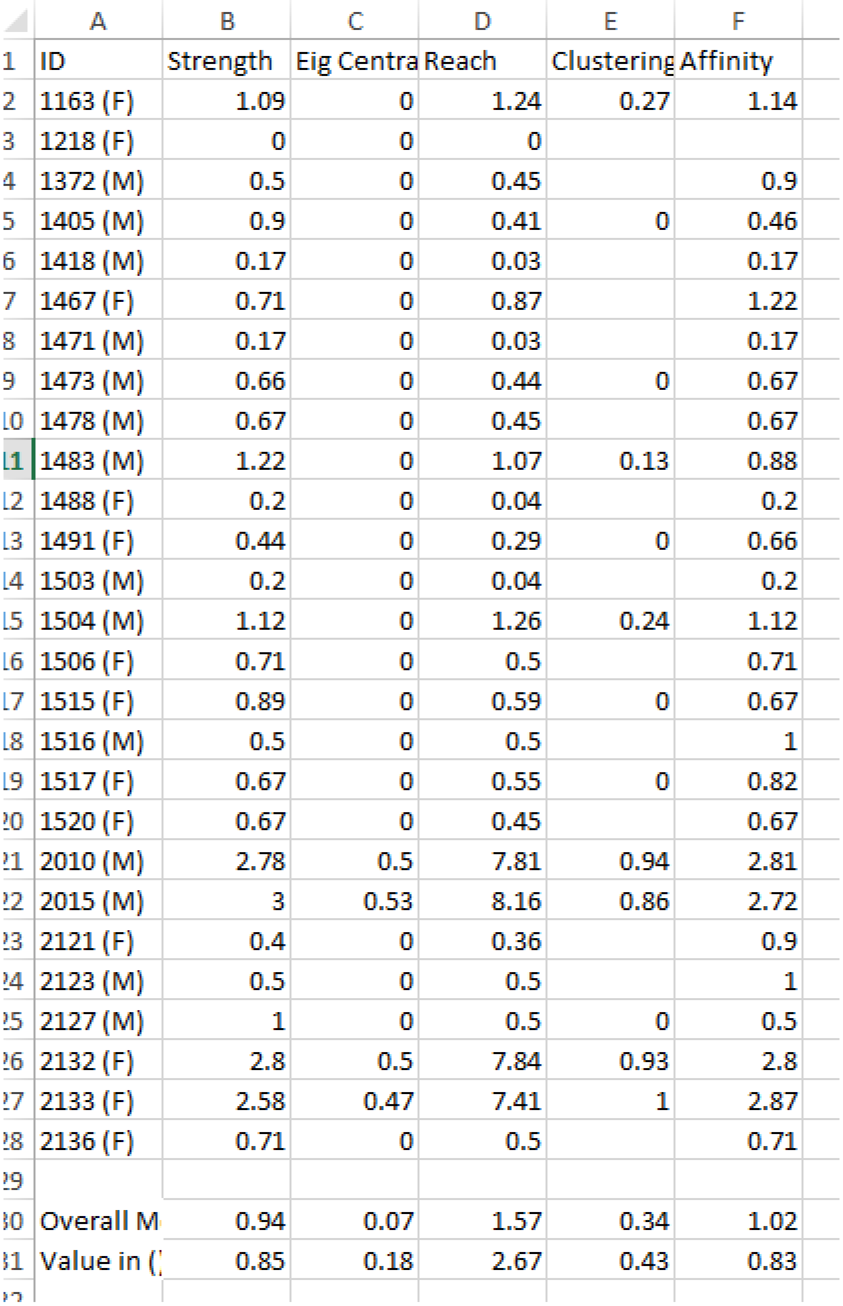
K	L	M	N	O	P
ID	Strength	Eig Centrality	Reach	Clustering Coeff	Affinity
1135 (F)	0.6	0	0.36		0.6
1163 (F)	0	0	0		
1177 (M)	1.08	0	1.24	0.33	1.15
1181 (M)	1.67	0.63	2.28	0.5	1.37
1209 (F)	0.91	0	0.95	0.3	1.04
1218 (F)	0.63	0	0.61	0.33	0.96
1247 (F)	1.5	0.6	2.25	0.67	1.5
1270 (M)	0	0	0		
1367 (M)	0.2	0	0.21		1.03
1368 (M)	1.25	0	1.14	0.19	0.91
1372 (M)	0.71	0	0.65	0.14	0.91
1374 (M)	0.17	0	0.21		1.25
1375 (M)	1.03	0	0.59	0.06	0.57
1376 (M)	1.17	0.49	1.87	1	1.6
1381 (M)	0.6	0	0.36		0.6
Overall M	0.77	0.11	0.85	0.39	1.04
number ir	0.53	0.24	0.77	0.29	0.33

2010 – Group Values



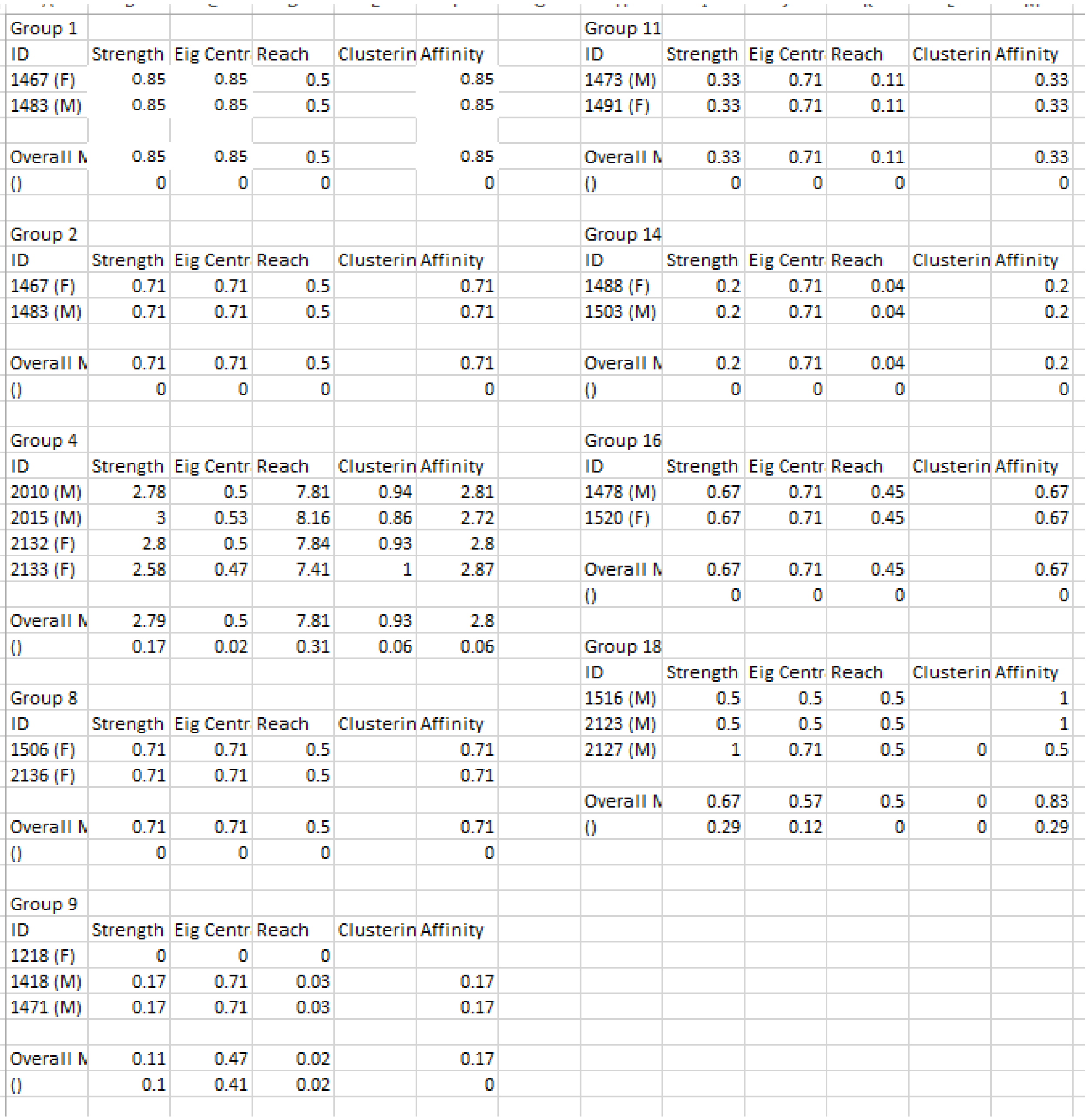
Group 1							Group 6		Group 7
ID	Strength	Eig Centra	Reach	Clustering	Affinity		NA		NA
1135 (F)	0.6	0.71	0.36	NaN	0.6				
1381 (M)	0.6	0.71	0.36	NaN	0.6				
Overall M	0.6	0.71	0.36	NaN	0.6				
()	0	0	0	NaN	0				
Group 2									
ID	Strength	Eig Centra	Reach	Clustering	Affinity				
1181 (M)	1.67	0.63	2.28	0.5	1.37				
1247 (F)	1.5	0.6	2.25	0.67	1.5				
1376 (M)	1.17	0.49	1.87	1	1.6				
Overall M	1.45	0.57	2.14	0.72	1.49				
()	0.25	0.07	0.23	0.25	0.12				
Group 3									
ID	Strength	Eig Centra	Reach	Clustering	Affinity				
1177 (M)	1.08	0.63	1.16	0.44	1.07				
1209 (F)	0.66	0.43	0.77	1	1.17				
1368 (M)	1.25	0.64	1.06	0.25	0.85				
1374 (M)	0.17	0.11	0.21	NaN	1.25				
Overall M	0.79	0.45	0.8	0.56	1.08				
()	0.48	0.25	0.42	0.39	0.17				
Group 4									
ID	Strength	Eig Centra	Reach	Clustering	Affinity				
1218 (F)	0.63	0.57	0.57	0.66	0.91				
1367 (M)	0.2	0.2	0.21	NaN	1.03				
1372 (M)	0.46	0.43	0.42	1	0.92				
1375 (M)	1.03	0.67	0.51	0.13	0.49				
Overall M	0.58	0.47	0.43	0.6	0.84				
()	0.35	0.21	0.16	0.44	0.24				

2011 – Entire Population



	A	B	C	D	E	F
1	ID	Strength	Eig Centra	Reach	Clustering	Affinity
2	1163 (F)	1.09	0	1.24	0.27	1.14
3	1218 (F)	0	0	0		
4	1372 (M)	0.5	0	0.45		0.9
5	1405 (M)	0.9	0	0.41	0	0.46
6	1418 (M)	0.17	0	0.03		0.17
7	1467 (F)	0.71	0	0.87		1.22
8	1471 (M)	0.17	0	0.03		0.17
9	1473 (M)	0.66	0	0.44	0	0.67
10	1478 (M)	0.67	0	0.45		0.67
11	1483 (M)	1.22	0	1.07	0.13	0.88
12	1488 (F)	0.2	0	0.04		0.2
13	1491 (F)	0.44	0	0.29	0	0.66
14	1503 (M)	0.2	0	0.04		0.2
15	1504 (M)	1.12	0	1.26	0.24	1.12
16	1506 (F)	0.71	0	0.5		0.71
17	1515 (F)	0.89	0	0.59	0	0.67
18	1516 (M)	0.5	0	0.5		1
19	1517 (F)	0.67	0	0.55	0	0.82
20	1520 (F)	0.67	0	0.45		0.67
21	2010 (M)	2.78	0.5	7.81	0.94	2.81
22	2015 (M)	3	0.53	8.16	0.86	2.72
23	2121 (F)	0.4	0	0.36		0.9
24	2123 (M)	0.5	0	0.5		1
25	2127 (M)	1	0	0.5	0	0.5
26	2132 (F)	2.8	0.5	7.84	0.93	2.8
27	2133 (F)	2.58	0.47	7.41	1	2.87
28	2136 (F)	0.71	0	0.5		0.71
29						
30	Overall M	0.94	0.07	1.57	0.34	1.02
31	Value in (	0.85	0.18	2.67	0.43	0.83

2011 – Group Values



Group 1

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1467 (F)	0.85	0.85	0.5		0.85
1483 (M)	0.85	0.85	0.5		0.85
Overall M	0.85	0.85	0.5		0.85
()	0	0	0		0

Group 2

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1467 (F)	0.71	0.71	0.5		0.71
1483 (M)	0.71	0.71	0.5		0.71
Overall M	0.71	0.71	0.5		0.71
()	0	0	0		0

Group 4

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
2010 (M)	2.78	0.5	7.81	0.94	2.81
2015 (M)	3	0.53	8.16	0.86	2.72
2132 (F)	2.8	0.5	7.84	0.93	2.8
2133 (F)	2.58	0.47	7.41	1	2.87
Overall M	2.79	0.5	7.81	0.93	2.8
()	0.17	0.02	0.31	0.06	0.06

Group 8

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1506 (F)	0.71	0.71	0.5		0.71
2136 (F)	0.71	0.71	0.5		0.71
Overall M	0.71	0.71	0.5		0.71
()	0	0	0		0

Group 9

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1218 (F)	0	0	0		
1418 (M)	0.17	0.71	0.03		0.17
1471 (M)	0.17	0.71	0.03		0.17
Overall M	0.11	0.47	0.02		0.17
()	0.1	0.41	0.02		0

Group 11

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1473 (M)	0.33	0.71	0.11		0.33
1491 (F)	0.33	0.71	0.11		0.33
Overall M	0.33	0.71	0.11		0.33
()	0	0	0		0

Group 14

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1488 (F)	0.2	0.71	0.04		0.2
1503 (M)	0.2	0.71	0.04		0.2
Overall M	0.2	0.71	0.04		0.2
()	0	0	0		0

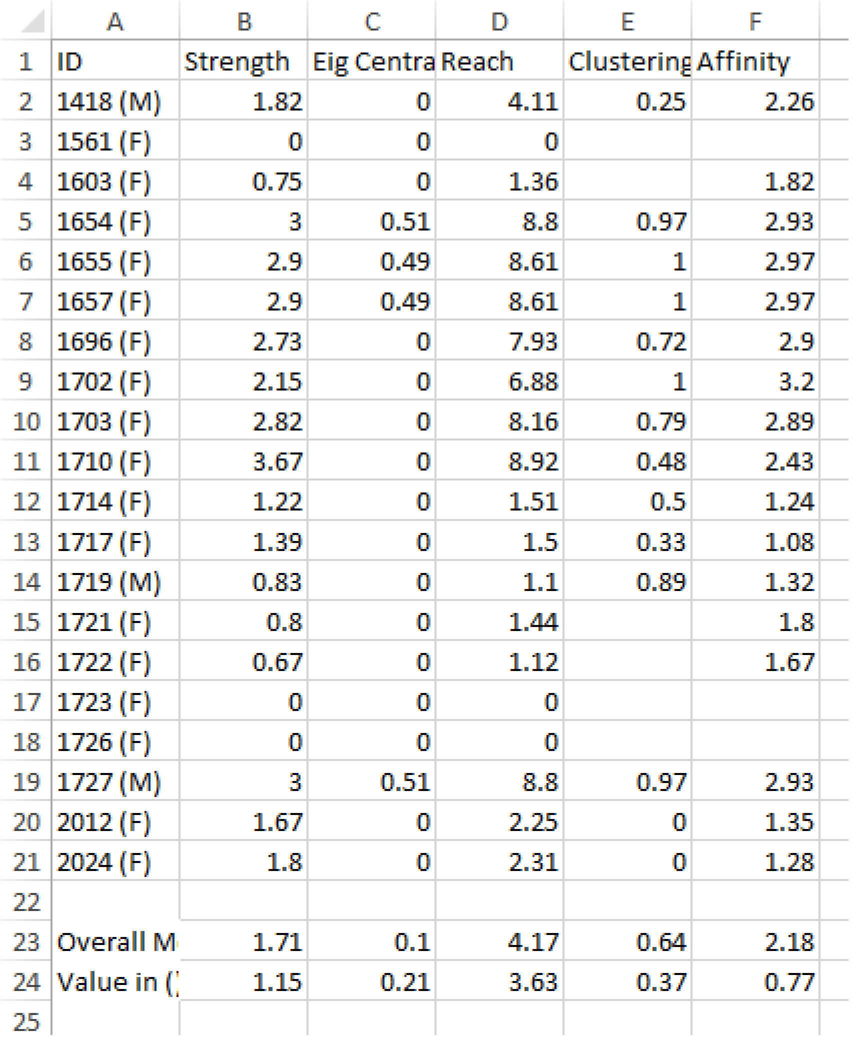
Group 16

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1478 (M)	0.67	0.71	0.45		0.67
1520 (F)	0.67	0.71	0.45		0.67
Overall M	0.67	0.71	0.45		0.67
()	0	0	0		0

Group 18

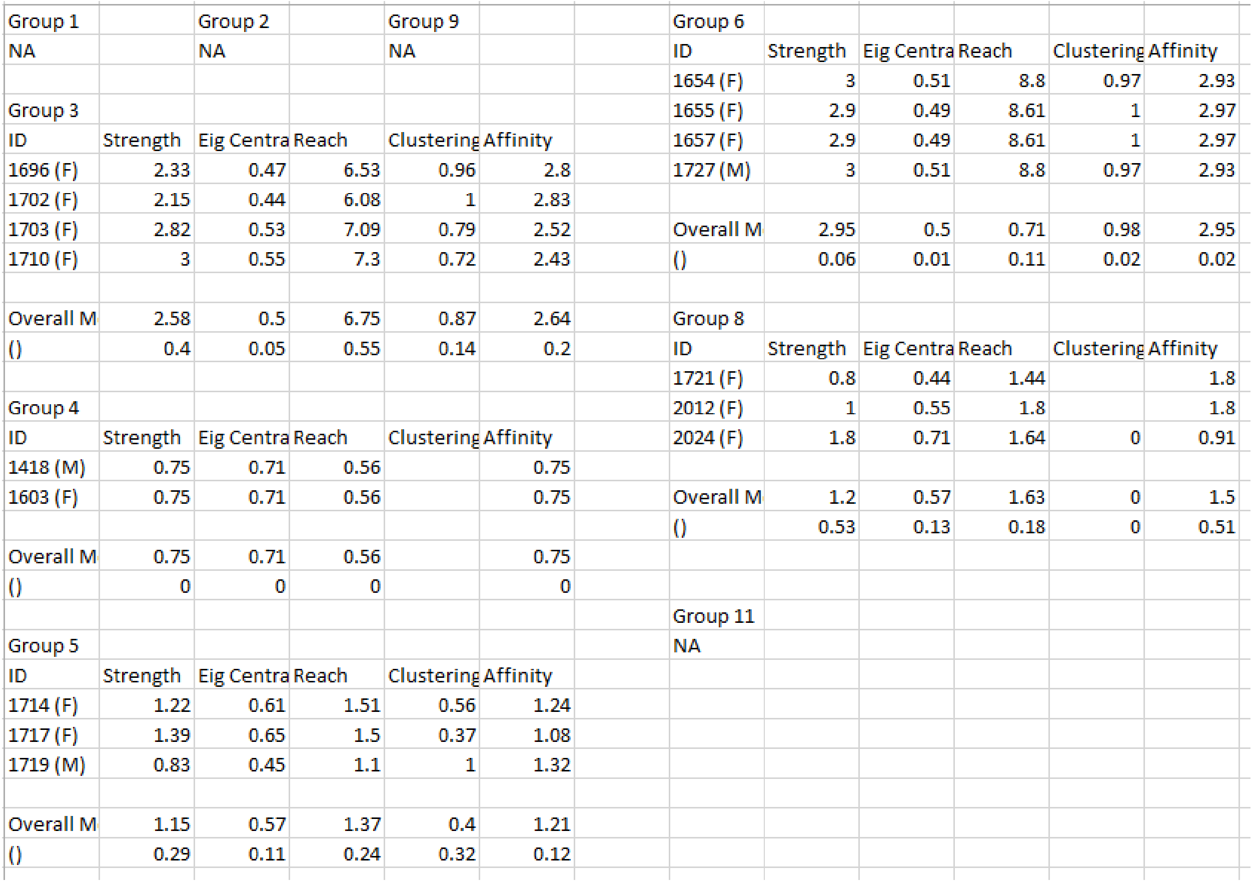
ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1516 (M)	0.5	0.5	0.5		1
2123 (M)	0.5	0.5	0.5		1
2127 (M)	1	0.71	0.5	0	0.5
Overall M	0.67	0.57	0.5	0	0.83
()	0.29	0.12	0	0	0.29

2012 – Entire Population



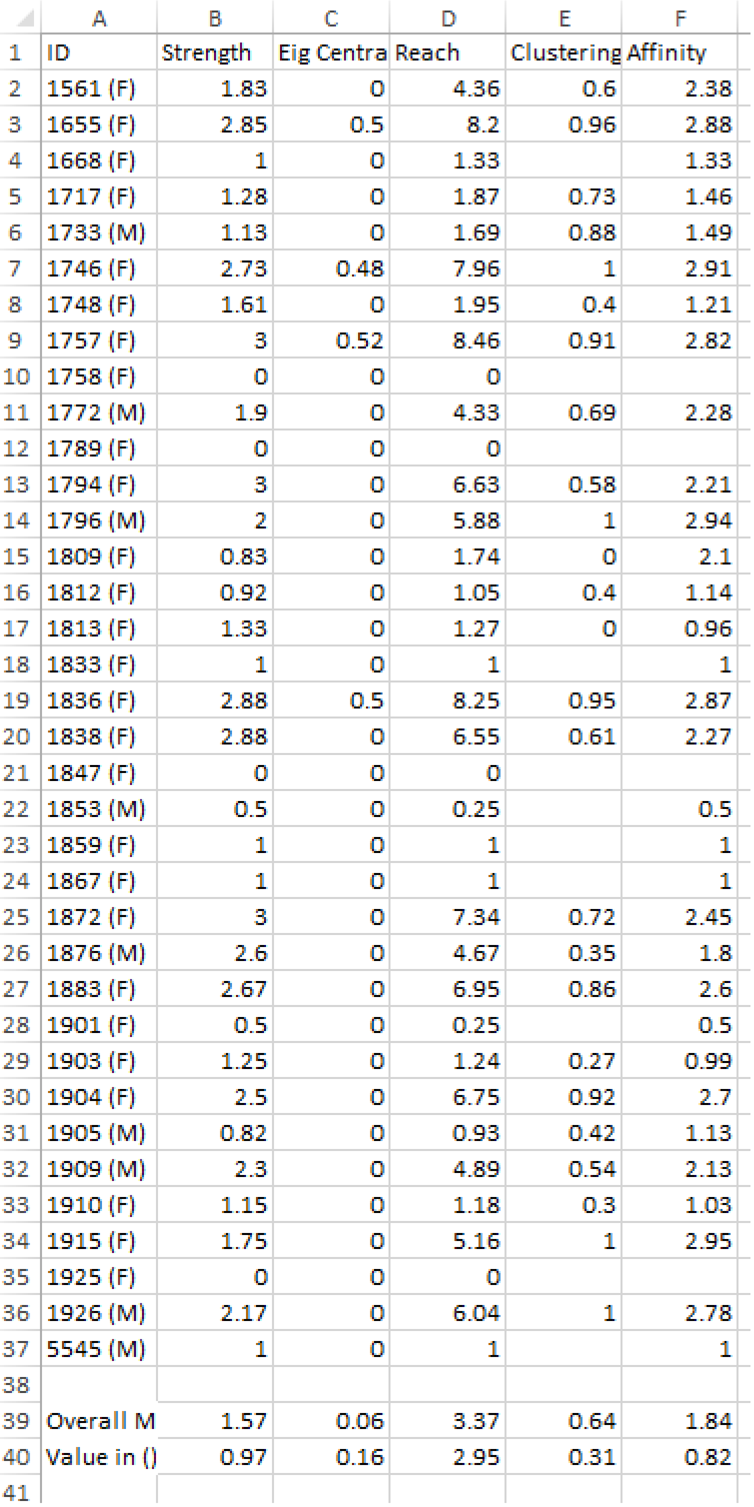
	A	B	C	D	E	F
1	ID	Strength	Eig Centra	Reach	Clustering	Affinity
2	1418 (M)	1.82	0	4.11	0.25	2.26
3	1561 (F)	0	0	0		
4	1603 (F)	0.75	0	1.36		1.82
5	1654 (F)	3	0.51	8.8	0.97	2.93
6	1655 (F)	2.9	0.49	8.61	1	2.97
7	1657 (F)	2.9	0.49	8.61	1	2.97
8	1696 (F)	2.73	0	7.93	0.72	2.9
9	1702 (F)	2.15	0	6.88	1	3.2
10	1703 (F)	2.82	0	8.16	0.79	2.89
11	1710 (F)	3.67	0	8.92	0.48	2.43
12	1714 (F)	1.22	0	1.51	0.5	1.24
13	1717 (F)	1.39	0	1.5	0.33	1.08
14	1719 (M)	0.83	0	1.1	0.89	1.32
15	1721 (F)	0.8	0	1.44		1.8
16	1722 (F)	0.67	0	1.12		1.67
17	1723 (F)	0	0	0		
18	1726 (F)	0	0	0		
19	1727 (M)	3	0.51	8.8	0.97	2.93
20	2012 (F)	1.67	0	2.25	0	1.35
21	2024 (F)	1.8	0	2.31	0	1.28
22						
23	Overall M	1.71	0.1	4.17	0.64	2.18
24	Value in (	1.15	0.21	3.63	0.37	0.77
25						

2012 – Group Values



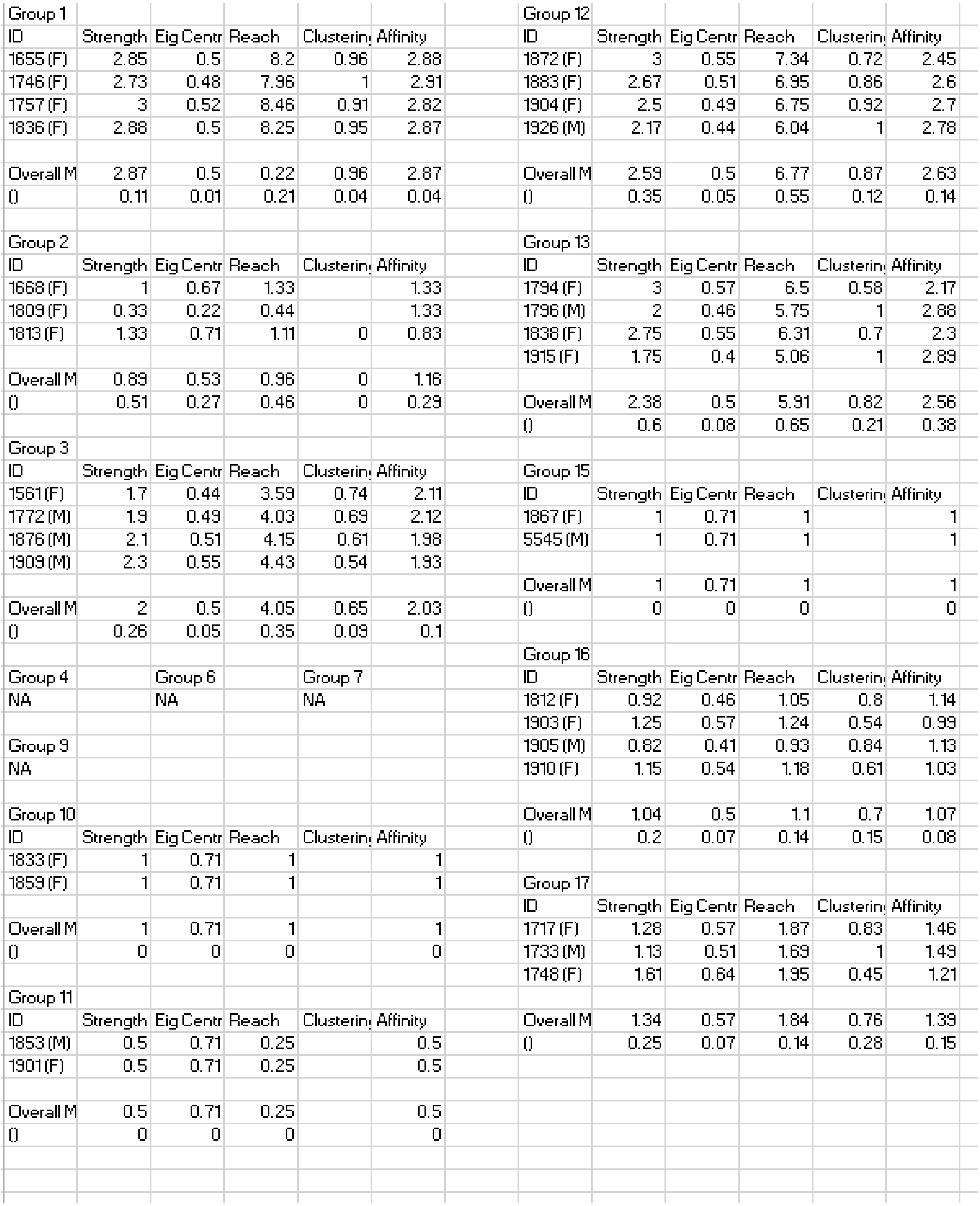
Group 1		Group 2		Group 9			Group 6					
NA		NA		NA			ID	Strength	Eig Centra	Reach	Clustering	Affinity
							1654 (F)	3	0.51	8.8	0.97	2.93
Group 3							1655 (F)	2.9	0.49	8.61	1	2.97
ID	Strength	Eig Centra	Reach	Clustering	Affinity		1657 (F)	2.9	0.49	8.61	1	2.97
1696 (F)	2.33	0.47	6.53	0.96	2.8		1727 (M)	3	0.51	8.8	0.97	2.93
1702 (F)	2.15	0.44	6.08	1	2.83							
1703 (F)	2.82	0.53	7.09	0.79	2.52		Overall M	2.95	0.5	0.71	0.98	2.95
1710 (F)	3	0.55	7.3	0.72	2.43		()	0.06	0.01	0.11	0.02	0.02
Overall M	2.58	0.5	6.75	0.87	2.64		Group 8					
()	0.4	0.05	0.55	0.14	0.2		ID	Strength	Eig Centra	Reach	Clustering	Affinity
							1721 (F)	0.8	0.44	1.44		1.8
Group 4							2012 (F)	1	0.55	1.8		1.8
ID	Strength	Eig Centra	Reach	Clustering	Affinity		2024 (F)	1.8	0.71	1.64	0	0.91
1418 (M)	0.75	0.71	0.56		0.75							
1603 (F)	0.75	0.71	0.56		0.75		Overall M	1.2	0.57	1.63	0	1.5
							()	0.53	0.13	0.18	0	0.51
Overall M	0.75	0.71	0.56		0.75							
()	0	0	0		0							
							Group 11					
Group 5							NA					
ID	Strength	Eig Centra	Reach	Clustering	Affinity							
1714 (F)	1.22	0.61	1.51	0.56	1.24							
1717 (F)	1.39	0.65	1.5	0.37	1.08							
1719 (M)	0.83	0.45	1.1	1	1.32							
Overall M	1.15	0.57	1.37	0.4	1.21							
()	0.29	0.11	0.24	0.32	0.12							

2013 – Entire Population



	A	B	C	D	E	F
1	ID	Strength	Eig Centra	Reach	Clustering	Affinity
2	1561 (F)	1.83	0	4.36	0.6	2.38
3	1655 (F)	2.85	0.5	8.2	0.96	2.88
4	1668 (F)	1	0	1.33		1.33
5	1717 (F)	1.28	0	1.87	0.73	1.46
6	1733 (M)	1.13	0	1.69	0.88	1.49
7	1746 (F)	2.73	0.48	7.96	1	2.91
8	1748 (F)	1.61	0	1.95	0.4	1.21
9	1757 (F)	3	0.52	8.46	0.91	2.82
10	1758 (F)	0	0	0		
11	1772 (M)	1.9	0	4.33	0.69	2.28
12	1789 (F)	0	0	0		
13	1794 (F)	3	0	6.63	0.58	2.21
14	1796 (M)	2	0	5.88	1	2.94
15	1809 (F)	0.83	0	1.74	0	2.1
16	1812 (F)	0.92	0	1.05	0.4	1.14
17	1813 (F)	1.33	0	1.27	0	0.96
18	1833 (F)	1	0	1		1
19	1836 (F)	2.88	0.5	8.25	0.95	2.87
20	1838 (F)	2.88	0	6.55	0.61	2.27
21	1847 (F)	0	0	0		
22	1853 (M)	0.5	0	0.25		0.5
23	1859 (F)	1	0	1		1
24	1867 (F)	1	0	1		1
25	1872 (F)	3	0	7.34	0.72	2.45
26	1876 (M)	2.6	0	4.67	0.35	1.8
27	1883 (F)	2.67	0	6.95	0.86	2.6
28	1901 (F)	0.5	0	0.25		0.5
29	1903 (F)	1.25	0	1.24	0.27	0.99
30	1904 (F)	2.5	0	6.75	0.92	2.7
31	1905 (M)	0.82	0	0.93	0.42	1.13
32	1909 (M)	2.3	0	4.89	0.54	2.13
33	1910 (F)	1.15	0	1.18	0.3	1.03
34	1915 (F)	1.75	0	5.16	1	2.95
35	1925 (F)	0	0	0		
36	1926 (M)	2.17	0	6.04	1	2.78
37	5545 (M)	1	0	1		1
38						
39	Overall M	1.57	0.06	3.37	0.64	1.84
40	Value in ()	0.97	0.16	2.95	0.31	0.82
41						

2013 – Group Values



Group 1

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1655 (F)	2.85	0.5	8.2	0.96	2.88
1746 (F)	2.73	0.48	7.96	1	2.91
1757 (F)	3	0.52	8.46	0.91	2.82
1836 (F)	2.88	0.5	8.25	0.95	2.87
Overall M	2.87	0.5	0.22	0.96	2.87
()	0.11	0.01	0.21	0.04	0.04

Group 2

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1668 (F)	1	0.67	1.33		1.33
1809 (F)	0.33	0.22	0.44		1.33
1813 (F)	1.33	0.71	1.11	0	0.83
Overall M	0.89	0.53	0.96	0	1.16
()	0.51	0.27	0.46	0	0.29

Group 3

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1561 (F)	1.7	0.44	3.59	0.74	2.11
1772 (M)	1.9	0.49	4.03	0.69	2.12
1876 (M)	2.1	0.51	4.15	0.61	1.98
1909 (M)	2.3	0.55	4.43	0.54	1.93
Overall M	2	0.5	4.05	0.65	2.03
()	0.26	0.05	0.35	0.09	0.1

Group 4		Group 6		Group 7
NA		NA		NA

Group 9

NA

Group 10

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1833 (F)	1	0.71	1		1
1859 (F)	1	0.71	1		1
Overall M	1	0.71	1		1
()	0	0	0		0

Group 11

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1853 (M)	0.5	0.71	0.25		0.5
1901 (F)	0.5	0.71	0.25		0.5
Overall M	0.5	0.71	0.25		0.5
()	0	0	0		0

Group 12

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1872 (F)	3	0.55	7.34	0.72	2.45
1883 (F)	2.67	0.51	6.95	0.86	2.6
1904 (F)	2.5	0.49	6.75	0.92	2.7
1926 (M)	2.17	0.44	6.04	1	2.78
Overall M	2.59	0.5	6.77	0.87	2.63
()	0.35	0.05	0.55	0.12	0.14

Group 13

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1794 (F)	3	0.57	6.5	0.58	2.17
1796 (M)	2	0.46	5.75	1	2.88
1838 (F)	2.75	0.55	6.31	0.7	2.3
1915 (F)	1.75	0.4	5.06	1	2.89
Overall M	2.38	0.5	5.91	0.82	2.56
()	0.6	0.08	0.65	0.21	0.38

Group 15

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1867 (F)	1	0.71	1		1
5545 (M)	1	0.71	1		1
Overall M	1	0.71	1		1
()	0	0	0		0

Group 16

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1812 (F)	0.92	0.46	1.05	0.8	1.14
1903 (F)	1.25	0.57	1.24	0.54	0.99
1905 (M)	0.82	0.41	0.93	0.84	1.13
1910 (F)	1.15	0.54	1.18	0.61	1.03
Overall M	1.04	0.5	1.1	0.7	1.07
()	0.2	0.07	0.14	0.15	0.08

Group 17

ID	Strength	Eig Centr	Reach	Clusterin	Affinity
1717 (F)	1.28	0.57	1.87	0.83	1.46
1733 (M)	1.13	0.51	1.69	1	1.49
1748 (F)	1.61	0.64	1.95	0.45	1.21
Overall M	1.34	0.57	1.84	0.76	1.39
()	0.25	0.07	0.14	0.28	0.15

APPENDIX E

STATISTICAL PROGRAMMING CODE (SAS)

SAS Code and Outputs for All Individuals

```
data PCOSxAffinity;
input year$   GS    PCOW                        SN1;
cards;

;
proc mixed;
class year;
model PCOW= SN1 GS SN1*year GS* year year/cl;
LSmeans year / adjust=tukey pdiff;
run;
quit;
```

PCOW x Strength

```
Type 3 Tests of Fixed Effects

Effect      Num DF   Den DF   F Value   Pr > F

SN1         1        38       1.84      0.1831

GS          1        38       0.30      0.5846

SN1*year    8        38       0.80      0.6090

GS*year     8        38       0.59      0.7799

year        8        38       1.33      0.2603
```

PCOW x Eigenvector Centrality

```
Type 3 Tests of Fixed Effects

Effect      Num DF   Den DF   F Value   Pr > F

SN1         1        38       1.86      0.1802

GS          1        38       0.87      0.3577

SN1*year    8        38       0.75      0.6438

GS*year     8        38       1.61      0.1542

year        8        38       1.03      0.4306
```

PCOW x Reach

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	38	0.59	0.4488
GS	1	38	0.88	0.3555
SN1*year	8	38	0.64	0.7378
GS*year	8	38	0.57	0.7994
year	8	38	0.96	0.4831

PCOW x Clustering Coefficient

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	23	1.13	0.2992
GS	1	23	5.36	**0.0299**
SN1*year	8	23	0.99	0.4664
GS*year	7	23	1.54	0.2043
year	8	23	1.42	0.2400

PCOW x Affinity

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	36	0.91	0.3469
GS	1	36	0.25	0.6208
SN1*year	8	36	0.84	0.5756
GS*year	8	36	0.78	0.6206
year	8	36	1.27	0.2902

PCOS x Strength

Solution for Fixed Effects

Effect	year	Estimate	Standard Error	DF	t Value	Pr > |t|	Alpha	Lower	Upper
SN1*year	2005	-2.0326	1.0644	38	-1.91	0.0637	0.05	-4.1874	0.1221
SN1*year	2006	0.6993	1.2901	38	0.54	0.5909	0.05	-1.9124	3.3110

Solution for Fixed Effects

Effect	year	Estimate	Standard Error	DF	t Value	Pr > |t|	Alpha	Lower	Upper
SN1*year	2007	0.02658	0.4924	38	0.05	0.9572	0.05	-0.9703	1.0235
SN1*year	2008	-1.8503	0.5063	38	-3.65	**0.0008**	0.05	-2.8752	-0.8253

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	38	0.07	0.7946
GS	1	38	0.57	0.4536
SN1*year	8	38	2.43	**0.0314**
GS*year	8	38	0.89	0.5340
year	8	38	1.16	0.3456

PCOS x Eigenvector Centrality

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	38	0.04	0.8487
GS	1	38	0.14	0.7076
SN1*year	8	38	1.13	0.3661
GS*year	8	38	0.95	0.4886
year	8	38	1.20	0.3248

PCOS x Reach

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	38	0.07	0.7936
GS	1	38	0.15	0.7052
SN1*year	8	38	1.52	0.1828
GS*year	8	38	0.47	0.8701
year	8	38	0.45	0.8799

PCOS x Clustering Coefficient

```
Type 3 Tests of Fixed Effects

Effect      Num DF  Den DF  F Value  Pr > F

SN1         1       23      0.00     0.9792

GS          1       23      0.02     0.8792

SN1*year    8       23      0.79     0.6144

GS*year     7       23      1.02     0.4415

year        8       23      0.92     0.5164
```

PCOS x Affinity

```
Type 3 Tests of Fixed Effects

Effect      Num DF  Den DF  F Value  Pr > F

SN1         1       37      0.63     0.4315

GS          1       37      3.01     0.0913

SN1*year    8       37      1.09     0.3904

GS*year     8       37      0.48     0.8590

year        8       37      1.19     0.3331
```

SAS Code and Outputs for Females Only

```
data PCOSxAffinity;
input year$   GS    PCOW            SN1;
cards;

;
proc mixed;
class year;
model PCOW= SN1 GS SN1*year GS* year year/cl;
LSmeans year / adjust=tukey pdiff;
run;
quit;
```

PCOW x Strength

```
Type 3 Tests of Fixed Effects

Effect      Num DF  Den DF  F Value   Pr > F

SN1              1      24     1.36  0.2552
```

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
GS	1	24	0.10	0.7504
SN1*year	6	24	1.89	0.1247
GS*year	6	24	0.87	0.5296
year	6	24	1.36	0.2713

PCOW x Eigenvector Centrality

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	24	2.46	0.1295
GS	1	24	1.82	0.1903
SN1*year	6	24	0.57	0.7523
GS*year	6	24	1.37	0.2675
year	6	24	0.67	0.6747

PCOW x Reach

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	24	0.23	0.6378
GS	1	24	0.61	0.4421
SN1*year	6	24	0.69	0.6576
GS*year	6	24	1.76	0.1503
year	6	24	1.85	0.1308

PCOW x Clustering Coefficient

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	13	1.82	0.2002
GS	1	13	2.01	0.1800
SN1*year	5	13	0.26	0.9258

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
GS*year	5	13	1.43	0.2787
year	5	13	1.57	0.2367

PCOW x Affinity

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	22	0.00	0.9551
GS	1	22	0.93	0.3457
SN1*year	6	22	0.26	0.9498
GS*year	5	22	1.04	0.4193
year	6	22	1.05	0.4194

PCOS x Strength

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	24	0.01	0.9242
GS	1	24	0.96	0.3364
SN1*year	6	24	0.72	0.6344
GS*year	6	24	0.39	0.8784
year	6	24	0.07	0.9985

PCOS x Eigenvector Centrality

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	24	0.82	0.3739
GS	1	24	0.49	0.4915
SN1*year	6	24	0.34	0.9082
GS*year	6	24	0.54	0.7723

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
year	6	24	0.26	0.9496

PCOS x Reach

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	24	0.31	0.5807
GS	1	24	2.56	0.1229
SN1*year	6	24	0.88	0.5276
GS*year	6	24	0.61	0.7162
year	6	24	0.33	0.9126

PCOS x Clustering Coefficient

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	13	0.01	0.9426
GS	1	13	4.15	0.0625
SN1*year	5	13	0.70	0.6342
GS*year	5	13	0.98	0.4683
year	5	13	0.94	0.4875

PCOS x Affinity

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
SN1	1	22	0.06	0.8020
GS	1	22	4.31	**<u>0.0499</u>**
SN1*year	6	22	0.89	0.5183
GS*year	5	22	1.43	0.2524
year	6	22	1.14	0.3741

APPENDIX F

STATISTICAL PROGRAMMING CODE (R)

R Code Sample

```
#########
######### Mixed model analysis script
#########
# DESCRIPTION OF VARIABLES IN OBJECT data
#
# Response variables modeled
# PCOW: offspring
# offspring.fall: offspring next fall
#
# Predictor variables
# mean.alim, cv.alim, Females, etc
#
# random factor: sampling year


library(nlme)

SNdata =read.csv("C:/Users/xmv694/Desktop/Thesis/cvs for R females only 11.13.csv", sep=",", head=T)

m0<-gls(PCOW~1,data=SNdata,na.action=na.omit,method="ML")

### intercept model only for offsping in fall, with no grouping variable
m0a<-gls(offspring.fall~1,data=SNdata,na.action=na.omit,method="ML")

### null models for PCOW and offsping in fall using year as grouping factor
m1<-lme(PCOW~1,random=~1|as.factor(year),na.action=na.omit, method="ML",data=SNdata)
summary(m1)
m1a <-lme(offspring.fall~1,random=~1|as.factor(year),na.action=na.omit, method="ML",data=SNdata)
summary(m1a)

#### OBJECT NAMES ASSIGNED TO MIXED MODELS. COMBINATIONS REPRESENT MODELS AT THE
LOWEST LEVEL

##############################################################################
##### Model PCOWxFoodxfemales
PCOWxFoodxfemales <-lme(PCOW~mean.alim*females+cv.alim*females,
                random=~1|as.factor(year),na.action=na.omit,method="ML",
                data=SNdata)
summary(PCOWxFoodxfemales)

##### Model offspringxFoodxfemales
```

```
m2b<-lme(offspring.fall~mean.alim*females+cv.alim*females,
        random=~1|as.factor(year),na.action=na.omit, method="ML",
        data=SNdata)
summary(m2b)
####################################################################################
##Clust.Coeff
##### PCOWxFoodxClust.Coeff
PCOWxFoodxClust.Coeff <-lme(PCOW~mean.madr*Clust.Coeff+cv.madr* Clust.Coeff,
                        random=~1|as.factor(year),na.action=na.omit, method="ML",
                        data=SNdata)

summary(PCOWxFoodxClust.Coeff)

##### offspringxFoodxClust.Coeff
offspringxFoodxClust.Coeff <-lme(offspring.fall ~mean.madr*Clust.Coeff+cv.madr*Clust.Coeff,
                             random=~1|as.factor(year),na.action=na.omit,method="ML",
                             data=SNdata)

summary(offspringxFoodxClust.Coeff)
####################################################################################
```

APPENDIX G

OUTPUTS FROM STATISTICAL PROGRAMMING (R)

Table G1. Models used to examine the influence of yearly mean and variance (based on CV) in ecological conditions on the relationship between strength and either per capita offspring weaned or per capita offspring surviving to reproductive age. Only significant models are included. A list of all models is included in Table G2.

Source of variation	**Estimate**	**SE of estimate**	**DF**	**t-value**	**p-value**
Model 2: modulating roles of food abundance on the relationship between strength of all adult group members and per capita offspring weaned					
Intercept	5.87	1.70	56	3.46	0.0011
Strength	-0.88	1.19	56	-0.74	0.4622
Mean food abundance	-0.02	0.01	6	-1.42	0.2066
CV food abundance	4.98	1.74	6	2.86	0.0290
Mean food abundance*strength	0.01	0.01	56	2.02	0.0478
CV food abundance*strength	-3.91	1.73	56	-2.26	0.0277
Model 6: modulating roles of food abundance on the relationship between strength of adult female group members and per capita offspring weaned					
Intercept	7.36	2.0	34	6.14	0.0000
Strength	-1.02	1.19	34	-0.86	0.3949
Mean food abundance	0.00	0.01	4	0.07	0.9414
CV food abundance	-8.30	3.55	4	-2.33	0.0256
Mean food abundance*strength	-0.00	0.01	34	-1.04	0.3034
CV food abundance*strength	8.10	3.62	34	2.26	0.0319
Model 18: modulating roles of burrow density on the relationship between strength of all adult group members and per capita offspring weaned					
Intercept	6.70	3.02	56	2.22	0.0304
Strength	-1.17	2.48	56	-0.47	0.6384
Mean burrow density	-18.37	20.86	6	-0.88	0.4125
CV burrow density	5.99	2.03	6	2.95	0.0255
Mean burrow density*strength	16.29	17.27	56	0.94	0.3497
CV burrow density*strength	-5.19	2.31	56	-2.25	0.0286

Model 27: modulating roles of predator abundance on the relationship between strength of all adult group members and per capita offspring surviving to reproductive age					
Intercept	3.37	0.98	50	3.46	0.0011
Strength	-1.87	0.79	50	-2.36	0.0221
Mean predator abundance	-0.08	0.08	5	-0.99	0.3644
CV predator abundance	-1.34	0.47	5	-2.87	0.0349
Mean predator abundance*strength	0.12	0.08	50	1.37	0.1771
CV predator abundance*strength	0.91	0.36	50	2.52	0.0149
Model 34: modulating roles of soil hardness on the relationship between strength of all adult group members and per capita offspring weaned					
Intercept	-30.58	18.98	56	-1.61	0.1129
Strength	23.47	12.38	56	1.90	0.0631
Mean soil hardness	0.01	0.01	6	1.94	0.1001
CV soil hardness	7.40	2.30	6	3.21	0.0183
Mean soil hardness*strength	-0.01	0.00	56	-1.96	0.0553
CV soil hardness*strength	-6.67	2.61	56	-2.56	0.0133
Model 38: modulating roles of soil hardness on the relationship between strength of adult female group members and per capita offspring weaned					
Intercept	17.81	15.07	34	1.18	0.2455
Strength	-22.37	15.26	34	-1.47	0.1518
Mean soil hardness	-0.59	0.83	4	-0.71	0.4840
CV soil hardness	-84.77	44.14	4	-1.92	0.0632
Mean soil hardness*strength	1.14	0.84	34	1.135	0.1856
CV soil hardness*strength	107.37	44.55	34	2.41	0.0215
Model 43: modulating roles of precipitation on the relationship between strength of all adult group members and per capita offspring surviving to reproductive age					
Intercept	-3.67	2.34	56	-1.57	0.1225
Strength	2.36	1.90	56	1.25	0.2175
Mean precipitation	0.08	0.02	6	4.37	0.0047

CV precipitation	2.53	1.95	6	1.29	0.2437
Mean precipitation*strength	-0.06	0.01	56	-3.85	0.0003
CV precipitation*strength	-1.04	1.55	56	-0.68	0.5019
Model 61: modulating roles of ectoparasitic flea intensity (EFI) on the relationship between within group strength of adult female group members and per capita offspring weaned					
Intercept	3.76	5.03	28	0.75	0.4612
Strength	2.22	3.83	28	0.58	0.57
Mean EFI	0.29	0.24	2	1.21	0.3498
CV EFI	-0.07	5.22	2	-0.016	0.9894
Mean EFI*strength	-0.39	0.19	28	-2.07	0.0473
CV EFI*strength	0.50	4.01	28	0.12	0.9021
Model 64: modulating roles of ectoparasitic flea intensity (EFI) on the relationship between within group strength of all adult group members and per capita offspring surviving to reproductive age					
Intercept	1.19	1.96	44	0.61	0.5476
Strength	-1.17	1.25	44	-0.94	0.3527
Mean EFI	0.29	0.11	4	2.57	0.0620
CV EFI	-3.52	1.97	4	-1.78	0.1501
Mean EFI*strength	-0.16	0.07	44	-2.20	0.0334
CV EFI*strength	3.10	1.33	44	2.34	0.0241
Model 65: modulating roles of ectoparasitic flea intensity (EFI) on the relationship between population level strength of all adult group members and per capita offspring surviving to reproductive age					
Intercept	0.95	2.22	44	0.43	0.6706
Strength	-0.90	1.29	44	-0.70	0.4882
Mean EFI	0.35	0.12	4	2.83	0.0473
CV EFI	-3.85	2.27	4	-1.70	0.1649
Mean EFI*strength	-0.20	0.08	44	-2.50	0.0163
CV EFI*strength	3.01	1.38	44	2.20	0.0338
Model 68: modulating roles of ectoparasitic flea intensity (EFI) on the relationship between population level strength of adult female group members and per capita offspring surviving to reproductive age					
Intercept	3.45	2.47	28	1.40	0.1729
Strength	-2.16	1.39	28	-1.55	0.1315

Mean EFI	0.16	0.14	2	1.17	0.3635
CV EFI	-4.27	2.28	2	-1.87	0.2026
Mean EFI*strength	-0.07	0.08	28	-0.87	0.3914
CV EFI*strength	3.00	1.33	28	2.26	0.0320

Table G2. Models used to examine the effect of mean and coefficient of variation (CV) of ecological variables on the relationship between social network metrics and per capita offspring weaned (PCOW) and the relationship between social network metrics and per capita offspring surviving to reproductive age (PCOS). Models were examined for both all adult group members (A) and adult female group members (F) based on trapping overlap. Bold type indicates best fit models based on decreasing AIC values and significant p-values. Hypothesis supported indicates whether mean (harsh) ecological conditions, CV (variable) of ecological conditions, both mean and CV of ecological conditions, or neither mean nor CV of ecological conditions were significant in the model. Models 1-68 correspond to models examining strength and models 69-76 correspond to models examining eigenvector centrality. Models for EFI were examined for both within group (WG) strength and population level (PL) strength.

Model Number	Source of variation	All Adults (A) or Females (F)	Direct Fitness Correlate	AIC	Hypothesis Supported
1	*Null*	A	PCOW	317.8180	
2	**Food Abundance**	**A**	**PCOW**	**304.3481**	**Both**
3	Degu Density	A	PCOW	305.0116	Neither
4	Food Abundance x Degu Density	A	PCOW	305.8600	Neither
5	*Null*	F	PCOW	194.3667	
6	**Food Abundance**	**F**	**PCOW**	**181.9357**	**Variable**
7	Degu Density	F	PCOW	192.3009	Neither
8	Food Abundance x Degu Density	F	PCOW	187.9537	Neither
9	*Null*	A	PCOS	175.1417	
10	Food Abundance	A	PCOS	178.8810	Neither
11	Degu Density	A	PCOS	174.8335	Neither
12	Food Abundance x Degu Density	A	PCOS	181.0343	Neither
13	*Null*	F	PCOS	114.3182	
14	Food Abundance	F	PCOS	115.6589	Neither
15	Degu Density	F	PCOS	118.1938	Neither
16	Food Abundance x Degu Density	F	PCOS	120.6647	Neither
17	*Null*	A	PCOW	317.8180	
18	**Burrow Density**	**A**	**PCOW**	**303.9374**	**Variable**
19	Predator Abundance	A	PCOW	276.4828	Neither
20	Burrow Density x Predator Abundance	A	PCOW	280.5329	Neither
21	*Null*	F	PCOW	194.3667	
22	Burrow Density	F	PCOW	189.3690	Neither
23	Predator Abundance	F	PCOW	172.5700	Neither
24	Burrow Density x Predator Abundance	F	PCOW	172.6019	Neither
25	*Null*	A	PCOS	175.1417	
26	Burrow Density	A	PCOS	178.5085	Neither
27	**Predator Abundance**	**A**	**PCOS**	**156.2027**	**Variable**
28	Burrow Density x Predator Abundance	A	PCOS	158.2723	Variable

29	*Null*	F	PCOS	114.3182	
30	Burrow Density	F	PCOS	120.2991	Neither
31	Predator Abundance	F	PCOS	107.7124	Neither
32	Burrow Density x Predator Abundance	F	PCOS	114.1267	Neither
33	*Null*	A	PCOW	317.8180	
34	**Soil Hardness**	**A**	**PCOW**	**300.2612**	**Variable**
35	Monthly Precipitation	A	PCOW	300.3701	Neither
36	Soil Hardness x Monthly Precipitation	A	PCOW	300.9658	Neither
37	*Null*	F	PCOW	194.3667	
38	**Soil Hardness**	**F**	**PCOW**	**185.4810**	**Variable**
39	Monthly Precipitation	F	PCOW	190.5321	Neither
40	Soil Hardness x Monthly Precipitation	F	PCOW	190.0278	Variable
41	*Null*	A	PCOS	175.1417	
42	Soil Hardness	A	PCOS	177.7651	Harsh
43	**Monthly Precipitation**	**A**	**PCOS**	**162.9760**	**Harsh**
44	Soil Hardness x Monthly Precipitation	A	PCOS	166.5473	Harsh
45	*Null*	F	PCOS	114.3182	
46	Soil Hardness	F	PCOS	114.4831	Neither
47	Monthly Precipitation	F	PCOS	115.5260	Neither
48	Soil Hardness x Monthly Precipitation	F	PCOS	114.6463	Neither
49	*Null*	A	PCOW	317.8180	
50	Temperature	A	PCOW	311.5103	Neither
51	*Null*	F	PCOW	194.3667	
52	Temperature	F	PCOW	192.1340	Neither
53	*Null*	A	PCOS	175.1417	
54	Temperature	A	PCOS	169.6826	Neither
55	*Null*	F	PCOS	114.3182	
56	Temperature	F	PCOS	113.1700	Neither
57	*Null*	A	PCOW	238.0259	
58	Ectoparasite Flea Intensity (WG)	A	PCOW	232.1658	Neither
59	Ectoparasitic Flea Intensity (PL)	A	PCOW	233.2664	Neither
60	*Null*	F	PCOW	157.1688	
61	**Ectoparasite Flea Intensity (WG)**	**F**	**PCOW**	**154.6643**	**Harsh**
62	Ectoparasitic Flea Intensity (PL)	F	PCOW	157.1688	Neither
63	*Null*	A	PCOS	139.8505	
64	**Ectoparasite Flea Intensity (WG)**	**A**	**PCOS**	**138.3267**	**Both**
65	**Ectoparasitic Flea Intensity (PL)**	**A**	**PCOS**	**137.506**	**Both**
66	*Null*	F	PCOS	93.45992	
67	Ectoparasite Flea Intensity (WG)	F	PCOS	93.33148	Neither
68	**Ectoparasitic Flea Intensity (PL)**	**F**	**PCOS**	**92.01377**	**Variable**
69	*Null*	A	PCOW	238.0259	

70	Ectoparasitic Flea Intensity	A	PCOW	238.5218	Neither
71	*Null*	F	PCOW	157.1688	
72	Ectoparasitic Flea Intensity	F	PCOW	163.8251	Neither
73	*Null*	A	PCOS	139.8505	
74	Ectoparasitic Flea Intensity	A	PCOS	141.8681	Neither
75	*Null*	F	PCOS	93.45992	
76	Ectoparasitic Flea Intensity	F	PCOS	96.11983	Neither

APPENDIX H

MATHEMATICAL DESCRIPTION OF THE MODEL BUILDING APPROACH (EBENSPERGER ET AL. 2014)

The following information (Appendix H) was published as supplementary material in a previous study (Ebensperger et al. 2014).

Herein, we illustrate the general approach used to analyze our Degu Database. For the sake of simplicity we provide the mathematical formulation that includes two ecological predictors. The mixed effect model used for a two level hierarchy takes the following form:

(Eq. 1) $$y_{ij} = \beta_{0j} + \beta_{1j}\,(x)_j + \varepsilon_{ij}$$

(Eq. 2) $$\beta_{0j} = \gamma_{00} + \gamma_{01}\,(\bar{z}_1)_j + \gamma_{02}\,(\bar{z}_2)_j + \mu_{0j}$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11}\,(\bar{z}_1)_j + \gamma_{12}\,(\bar{z}_2)_j + \mu_{1j}$$

Where Eq. 1 represents the relationship between the *i*-th fitness observation of variable *y* (i.e., per capita offspring produced, or per capita offspring that survived to breeding age) and a sociality measurement *x* (i.e., group size, or number of females) grouped at the *j*-th sampling year. This simple linear regression was declared at level-1 of the model hierarchy, whose subscripts allowed us to model independently its intercept β_{0j} and slope β_{1j} as functions of environmental and ecological variables measured al level-2 in the model hierarchy (Eq. 2). Thus, Eq. 2 allowed to model level-1 regression parameters as a function of mean values for the set of $\bar{z}$ variables measured every *j*-th sampling year. As a result, the effects of ecological variables on fitness were assessed on a single modeling step without sacrificing degrees of freedom.

Combining Eq. 1 and Eq. 2 give us the mixed effects model,

(Eq 3) $$y_{ij} = \gamma_{00} + \gamma_{01}\,(\bar{z}_1)_j + \gamma_{02}\,(\bar{z}_2)_j + \gamma_{10}(x) + \gamma_{11}\,(\bar{z}_1)_j(x)_j + \gamma_{12}\,(\bar{z}_2)_j\,(x)_j + \mu_{0j} + \mu_{1j} + \mu_{1j}(x)_j + \varepsilon_{ij}$$

Note that this model formulation appropriately isolate the error terms ε_{ij} , μ_{0j} and μ_{1j} , reducing the probability of committing type-II errors.

Eq. 3 specifies that the effects of mean ecological conditions $\bar{z}$ over fitness response y are propagated through sociality variable x. Accordingly, their ecological relevance can be statistically assessed using parameters γ_{11} and γ_{12} accompanying the 1 and 2-level interactions terms. If more than two $\bar{z}$ variables were modeled, their respective interaction terms can be used to test these effects.

APPENDIX I

SOCIAL NETWORK MAPS (2007-2013; NETDRAW)

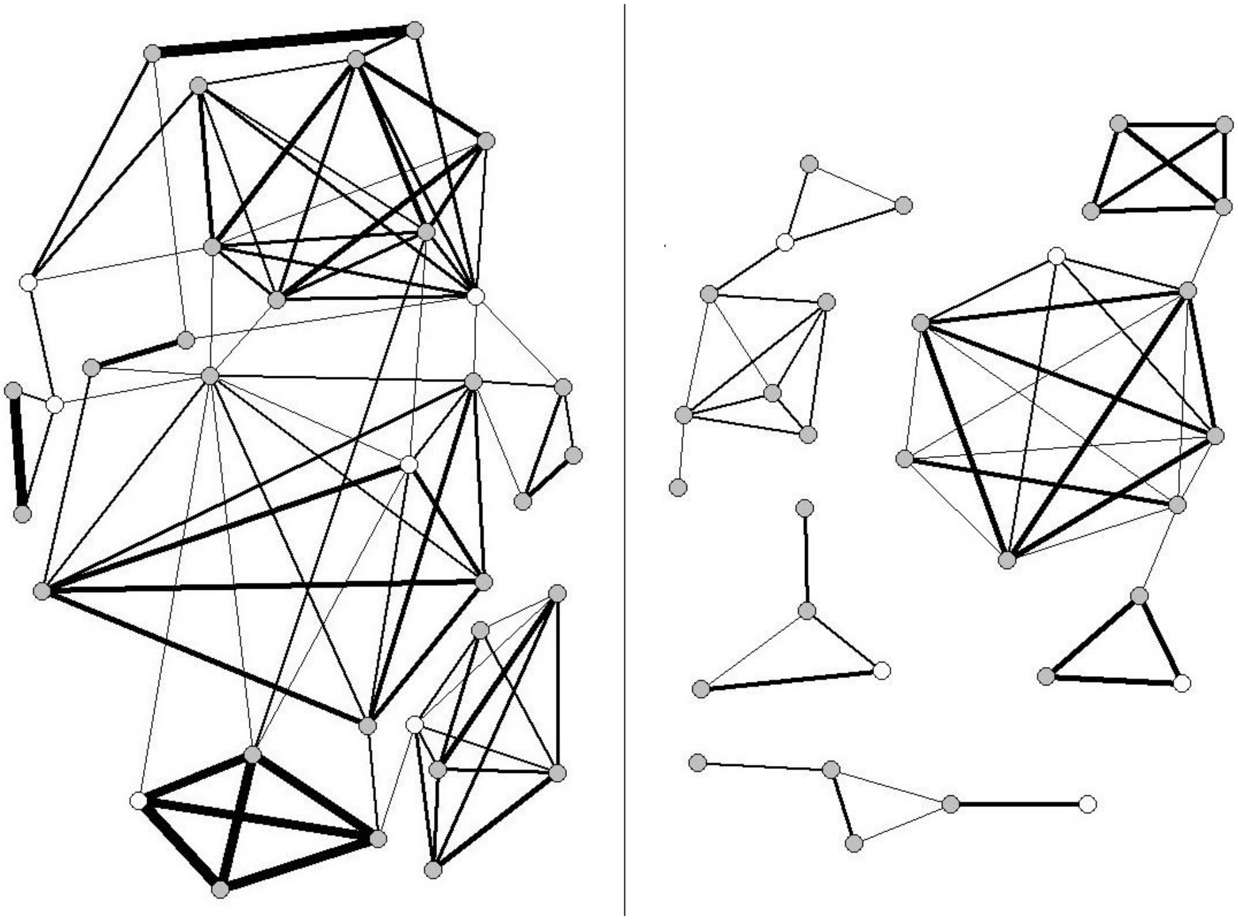


Figure I1. Representative social network maps from 2007 (left) and 2008 (right) showing all individuals assigned to a social group. Males are represented by white circles, females by grey circles, and the thickness of the lines indicates the amount of trapping overlap between any two individuals. There were 7 social groups in 2007 and 13 in 2008. There was one solitary adult females (no trapping overlap with any other individuals) in 2008 that is not shown in the network map.

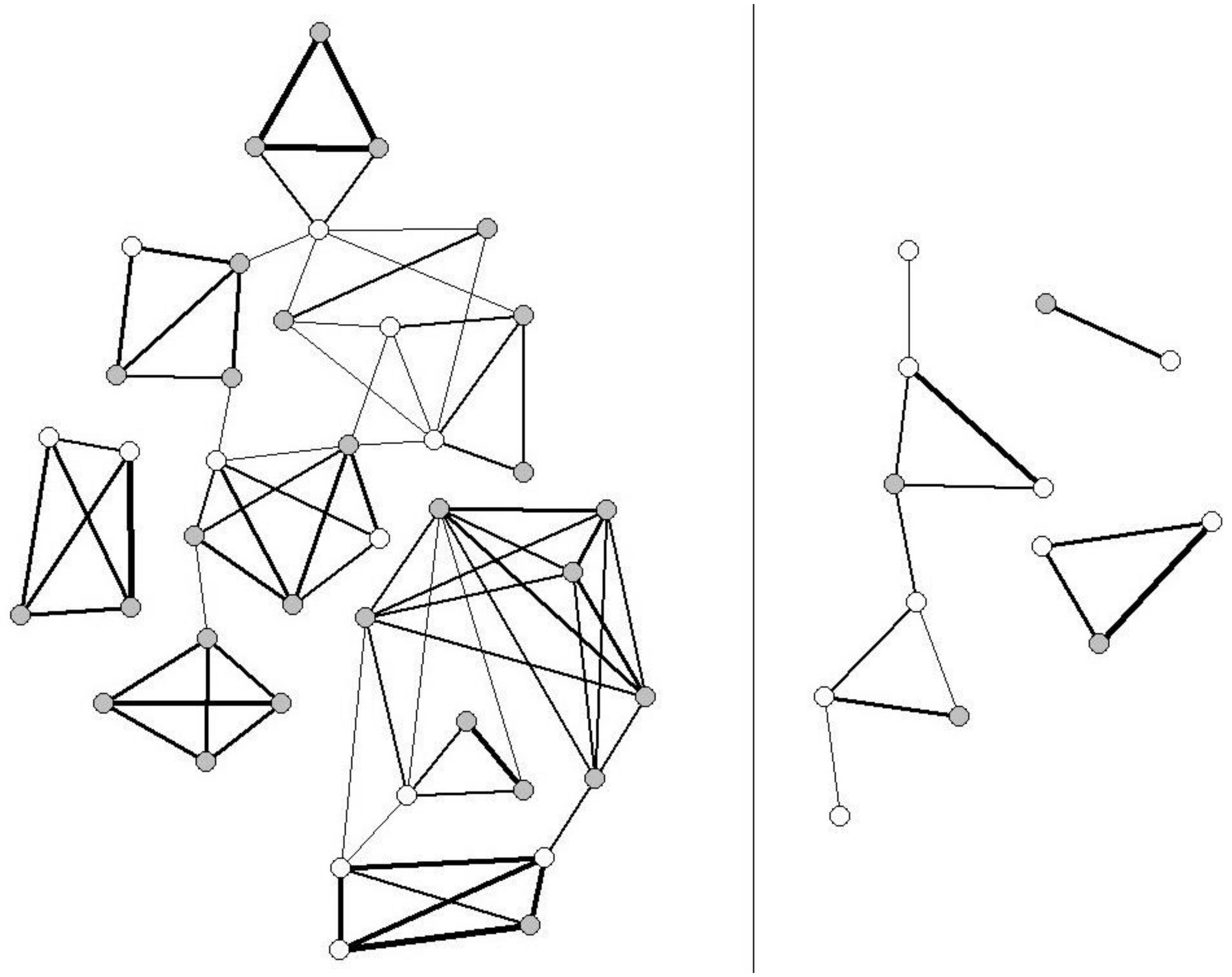


Figure I2. Representative social network maps from 2009 and 2010 showing all individuals assigned to a social group. Males are represented by white circles, females by grey circles, and the thickness of the lines indicates the amount of trapping overlap between any two individuals. There were 10 social groups in 2009 and 6 in 2010. There were 2 solitary adults (no trapping overlap with any other individuals; one male and one female) in 2010 that are not shown in the network map.

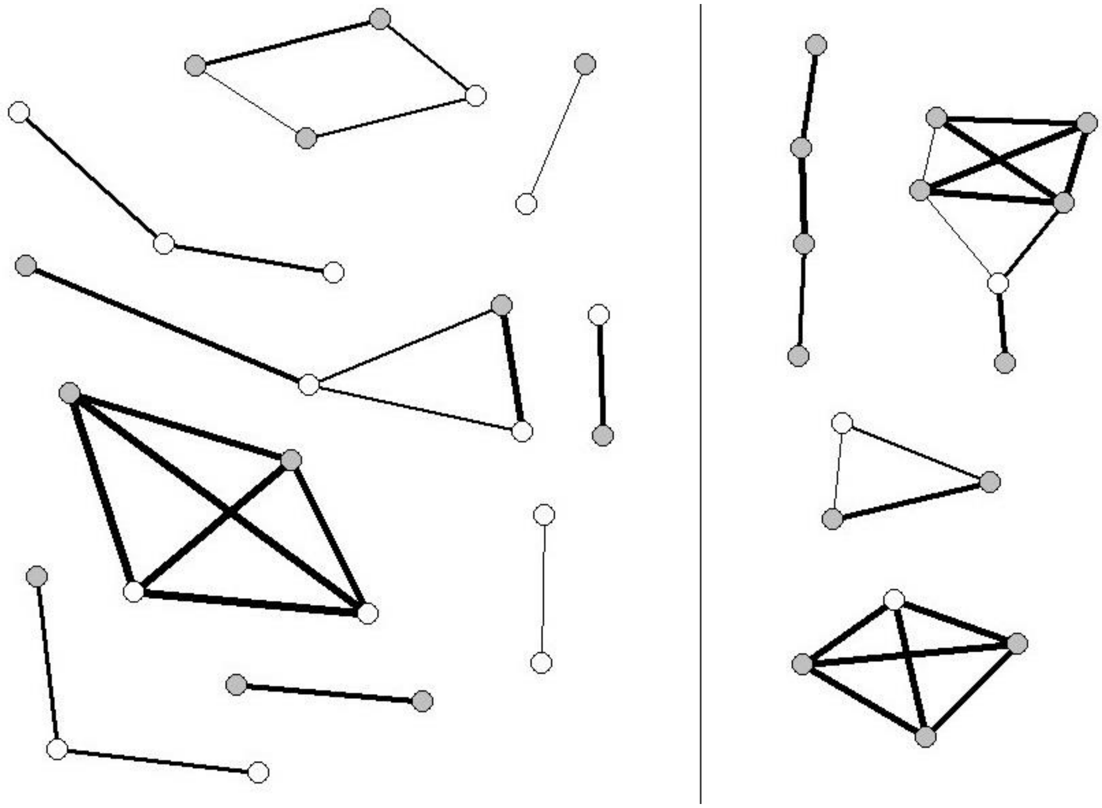


Figure I3. Representative social network maps from 2011 (right) and 2012 (left) showing all individuals assigned to a social group. Males are represented by white circles, females by grey circles, and the thickness of the lines indicates the amount of trapping overlap between any two individuals. There were 11 social groups in 2011 and 9 in 2012. There were 4 solitary adult females (no trapping overlap with any other individuals) in 2012 that are not shown in the network map.

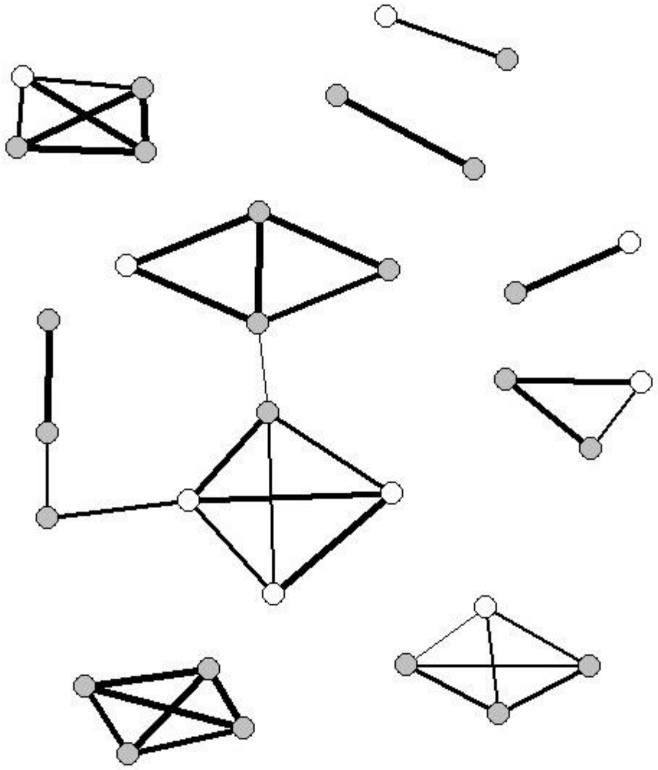


Figure I4. Representative social network maps from 2013 showing all individuals assigned to a social group. Males are represented by white circles, females by grey circles, and the thickness of the lines indicates the amount of trapping overlap between any two individuals. There were 13 social groups in 2013. There were 4 solitary adult females (no trapping overlap with any other individuals) in 2013 that are not shown in the network map.

VITA

Kathleen Carroll was born in Mesa, AZ, to Timothy and Angela Carroll. She received two undergraduate degrees one in wildlife ecology and one in marine biology with high honors from the University of Maine at Orono in 2013. During her four years at the University of Maine, Kathleen conducted research in the United States, South Africa, Mozambique, Canada, and Ecuador. She wrote and defended an undergraduate thesis on the natural history of twenty-six vertebrate species in the Galapagos Islands for her degree in Marine Biology. Additionally, she wrote a capstone on habitat use by the short-tailed weasel (*Mustela erminea*) for her degree in Wildlife Ecology. Kathleen conducted research in a national park in Chile before graduating with a Master's of Science degree in Environmental Science at UTC in May 2016. She is planning on continuing her education in the fields of conservation and behavioral ecology by pursuing a Ph.D. in the future. She recently accepted a laboratory position at the Alexander Lab at Virginia Polytechnic Institute and State University (Virginia Tech), which focuses on human-wildlife disease dynamics in Chobe, Botswana. She will be beginning an Appalachian Trail thru-hike in May of 2016.