ABSTRACT

Title of Dissertation: FISSION-FUSION DYNAMICS IN MAMMALS: LINKING ANIMAL MOVEMENT TO GROUP BEHAVIOR

Silvia Juliana Alvarez Vargas, Doctor of Philosophy, 2017

Dissertation directed by: Dr. William F. Fagan, Department of Biology

Mammals living in groups show temporal variation in spatial cohesion and membership of groups, a behavior known as fission-fusion dynamics (FFD). Changes in cohesion depend on the movement behavior of individuals, which is influenced by their social environment, among other factors. I aimed to answer two main questions: 1) how do cognitive abilities and environmental factors explain the variation in social systems of mammals with FFD? and 2) how are FFD related to movement behavior? To answer the first question, I built a dataset on social traits of mammals with FFD from published references and used multivariate analysis to uncover the patterns of variation in social systems. Variation resulted mostly from differences in group and subgroup sizes, and differences in social traits evidenced the presence of discrete categories of social organization that might represent distinct strategies of FFD. To assess the effects of brain size and resource availability on social traits, I used generalized estimating equations as a phylogenetic comparative method. Brain size affected most social traits in marine mammals, supporting predictions of the social brain hypothesis. Resource availability was poorly correlated with social traits in all terrestrial mammals, but it had different effects for herbivores and carnivores, suggesting that environmental constraints acting on FFD differ between trophic levels. To answer the second question, I assessed the predictive power of several movement metrics characterizing tracks of orangutans on FFD, using generalized boosted regressions. Tortuosity, speed, and the number of behaviors were strong predictors of group presence and size, while temporal changes in movement behavior were correlated with changes in cohesion. These findings highlight the potential use of individual movement data to predict aspects of FFD. Lastly, I used an agent-based model to explore the influence of different levels of specificity in recognition on grouping behaviors. Model results suggest that basic social behavioral rules influence FFD, and that more complex group dynamics, such as hierarchical group structures, only emerge in scenarios with high levels of recognition specificity. Overall, the model suggests that recognition abilities, which likely correlate with cognitive skills, may play an important role in the evolution of social systems.

FISSION-FUSION DYNAMICS IN MAMMALS: LINKING ANIMAL MOVEMENT TO GROUP BEHAVIOR

by

Silvia Juliana Alvarez Vargas

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Advisory Committee:
Professor William F. Fagan, Chair
Dr. Michelle Girvan, Dean's Representative
Dr. Nathan Kraft
Dr. Katerina V. Thompson
Dr. Gerald S. Wilkinson

Preface

This dissertation includes four research chapters and an appendix. All chapters represent original work and have been formatted according to the journals to which they will be submitted for publication. The appendix contains supplementary tables and figures to each of the chapters. There is a single bibliography section at the end of the dissertation that includes all the literature cited throughout the chapters.

Dedication

A mi abuela Lucy

To my grandmother Lucy

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Chapter 1: DISCRETE TYPES OF VARIABLE SOCIAL SYSTEMS IN MAMMALS WITH FISSION-FUSION DYNAMICS

Coauthors: LIVIA BAER-BOSITIS AND WILLIAM F. FAGAN

Abstract

Mammals living in groups show different degrees of fission-fusion dynamics (FFD) that have the potential to influence their social systems. Because FFD occur under current ecological conditions to which social behavioral responses are produced, inter- and intraspecific variation is expected. This study explored the variation of social traits between and within species of mammals living in fission-fusion systems. We sought to determine if these social systems were uniformly distributed over the multidimensional space represented by social traits or were instead distributed in clusters that might indicate different strategies or types of FFD. We scanned the literature for estimates of 42 social traits to build datasets of 70 species and 368 populations, respectively. We used estimates of variation and multivariate methods to analyze the trait datasets for FFD. Community and group size traits showed higher interspecific variation than other traits. Variation was related to phylogeny in nine traits. Social systems of populations varied along two main gradients. The first gradient ranged between large and small group and subgroup sizes, and along which ungulates tended to separate from primates, cetaceans, and marsupials. A hierarchical clustering analysis suggested the presence of at least eight clusters of species that represent different social strategies in mammals with FFD. Thus, we conclude that mammals with FFD occupy a wide range of combinations of social traits but are not uniformly distributed across the range of variation. Instead, our analysis supports the presence of discrete types of social organization that may represent different strategies for social living.

Keywords: social traits, intraspecific variation, behavioral diversity, phylogenetic signal.

Significance statement

Our study explores the inter- and intraspecific variation of social traits across several mammalian orders. By doing so, we describe the multidimensional space occupied by social systems of species and of populations with different levels of fission-fusion dynamics. Despite this space being a continuum and the presence of intraspecific variation, we show evidence for discrete types of social systems shared among species of different orders. Determining the ecological and behavioral implications of fission-fusion dynamics in mammals depends on a good understanding of the diversity of their social systems, which requires understanding the relevance of common combinations of social traits across species/populations as viable responses to different selective factors.

Introduction

Many mammals aggregate into groups and form complex societies. All of these groups are characterized by a certain degree of fission-fusion dynamics (FFD), which accounts for the amount of variation in “spatial cohesion and individual membership in a group” that results from splitting and merging of group subunits or subgroups (Aureli et al. 2008; de Waal and Tyack 2009). Here, we focus on FFD that occur at temporal scales small enough to have an impact on the social system, limiting this study to dynamics with time intervals of less than a month between fission-fusion events.

The reasons for animals to form groups are, in general, well understood. Groups represent mechanisms of predator avoidance, resource and mate acquisition, offspring care, and/or homeostatic regulation (Krause and Ruxton 2002; Altizer et al. 2003; Davies et al. 2012). FFD have been framed as a strategy of group-living animals that allows them, through temporal dynamics, to maintain the benefits of grouping through fusion and to reduce the costs of group living by splitting into smaller subgroups (Lehmann, Amanda H Korstjens, et al. 2007). The spatiotemporal variation in group membership caused by FFD affects social systems by influencing opportunities for individuals to interact with one another, which leads to particular patterns of social organization (Couzin 2006). A comparison of the different social patterns in species/populations with FFD is required for a comprehensive understanding of the functions of FFD as well as of the evolution of complex social systems in mammals. From a proximate perspective, unraveling commonalities and differences in behavioral patterns across species and populations will help define hypotheses about the mechanisms involved in group formation.

Several previous studies have explored the diversity of group living and social systems in mammals. These analyses refer to traits that describe mating systems and dispersal behavior (Olson and Blumstein 2009; Lukas and Clutton-Brock 2011; Lukas and Clutton-Brock 2013). Comparative analyses of social traits in primates are more abundant than for other groups, and these studies have substantially supported the development of socioecological theory (Eisenberg et al. 1972). More recent studies of primates have started to unravel the contributions of behavioral flexibility to the evolution of social behavior (Kamilar and Baden 2014; Strier et al. 2014). However, analyses encompassing more than one order are rare, and the lack of aggregated data on the social systems of non-primate species has limited opportunities for more comprehensive analysis.

As with many other traits, variation in social behavior likely results from the variation around some defined norm (probably genetically defined) due to ecological and social drivers. In general, a low but significant phylogenetic signal in social behavior exists for mammals as a whole (Lukas and Clutton-Brock 2013), but such behavior appears much more strongly conserved phylogenetically in selected primate lineages although not across the whole order (Di Fiore and Rendall 1994; Kamilar and Cooper 2013). Differences in social systems across some equids and rodents seem to be better related to phylogenetic history than to environmental factors (Linklater 2000; Sobrero et al. 2014).

Variation in social behavior reflects different responses to functional contexts, external factors, and internal attributes, including variation in genetic and molecular traits that correspond to the phylogenetic history of organisms (Hofmann et al. 2014; Sobrero et al. 2014). Given this framework, interspecific differences of social traits across mammals is expected to be primarily explained by phylogenetic relationships, while intraspecific differences across species might originate from environmental or demographic factors. Intraspecific variation in social systems has been long recognized as an adaptive strategy to ecological, demographic and/or social correlates (Eisenberg et al. 1972; Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Lott 1991). Genetic variation, developmental plasticity, social flexibility, and entirely extrinsic factors have been proposed as drivers of intraspecific variation in social systems, and all of these can shift with environmental factors (Schradin 2013). While interspecific comparisons can be helpful to understand evolutionary processes, analyses at the intraspecific level are helpful to explore the forces behind natural selection of social traits, facilitating a review of current ideas and creating opportunities to develop and test hypotheses about the mechanisms and functions of group living.

Despite the flexibility and variation of social systems, some trait combinations are possible in nature while others have not been successful or have not yet emerged through evolution. Comparative analysis including a diverse set of animal taxa (invertebrates and vertebrates) argues in favor of discrete categories in the variation of social systems, in particular in mating systems (Rubenstein et al. 2016). The alternative perspective, in which variation in social systems exists as a continuum rather than discrete categories, is embedded in the definition of FFD and in other studies of social organization (Fuentes 2000; Aureli et al. 2008; Cantor et al. 2012).

Here, we present a general quantitative picture of the diversity of social systems in mammals with FFD .We synthesized information from diverse studies to quantify and characterize the variation in the multidimensional space defined by social traits related to demography, interactions, group organization, and group dynamics. Because of the high flexibility in social behavior observed in several species, the low phylogenetic signal reported in behavioral traits, and FFD assumed to be an adjustable process responding to resource distribution, we expected populations to be uniformly distributed over the multidimensional space represented by social traits (see also Aureli et al. 2008). The alternative possibility is that species cluster into distinct forms of social systems, in contrast to a continuum perspective, which would occur if some combinations of traits are more evolutionary stable than others. We discuss our results in the light of proximate mechanisms and ultimate functions of FFD as well as their representation within previously published conceptual models of mammal social organization.

Methods

DESCRIPTION OF DATASETS

We used literature searches to compile data on the social systems of mammals known to exhibit FFD according to previous references. We used Web of Science and Google Scholar to search online resources dated through December 2014. We first sought to identify relevant species, using “mammal” in combination with any term indicating a fluid social system (i.e., fission-fusion, group dynamics, and fluid grouping system) as query terms. For species identified using these searches, we then did species-specific searches of the literature to gather quantitative and qualitative data on 42 social variables (Table 1.1). Using the framework of Whitehead (2008), we assigned social variables into four categories that reflected different elements of social system and complexity: 1) Demographic structure, 2) Interactions and social differentiation, 3) Group/subgroup size and composition, and 4) Group stability.

We only used studies six months or longer in duration as sources for variables from Categories 2, 3, and 4. For variables from Category 1 (Demographic structure), we used any published study. Additionally, we recorded for every study the location (i.e., study area, country, and geographic coordinates), number of observed groups and subgroups, spatial criteria defining a subgroup or party, and reference details. These efforts yielded a total of 670 studies of 75 mammalian species (Online Resource 1).

We pooled data together to build global datasets at population and species levels, respectively (Fig. 1). Location metadata were used to aggregate studies to compile population-level data. Specifically, we assumed locations separated by less than 0.5 degrees (latitude or longitude) corresponded to the same population, for which we estimated values of the social traits based on the following rule. Given the differences in surveying methods, for continuous variables we calculated the median for each population after removing outliers when populations were represented by five or more studies (Zuur et al. 2010). For any discrete variable that differed among studies in a population, we assigned all values to the population. For example, if groups of a population split during foraging in one study but during resting in another study, both fission behaviors were assigned to the population.

Likewise, we built a dataset at species level by aggregating populations using the median for continuous variables and combinations of values for discrete variables when required. The number of populations representing a species varied between 1 and 35, with most species being represented by ≤5 populations. The initial species-level dataset consisted of a matrix of 75 species (Online Resource 2) and 42 variables. Of these variables, 11 (i.e., standard deviation of association rate, all nine cohesion related metrics, and social budget) were missing from more than 80% of the species, and were excluded from further analysis. Similarly, four species (*Ateles marginatus, Nyctalus lasiopterus, Chiropotes albinasus, C. satanas,* and *Tursiops* sp.) lacked data for more than 80% of variables and were removed as well. After eliminating these components, the resulting matrix included 70 species and 31 variables with 63% of entries filled. Population- and species-level datasets were archived in the Dryad repository (http://datadryad.org).

INTER- AND INTRASPECIFIC VARIATION OF SOCIAL TRAITS

Because the number of populations varied between species, we relied on weighted means and standard deviations of social traits in the estimations of the inter- and intra-specific variation of fission-fusion systems. We estimated the magnitude of intraspecific variation of each continuous trait as the mean of the coefficient of variation among populations (CV) and the mean of the relative intraspecific variation (RIV) for species represented by ≥5 populations. RIV corresponded to the ratio between the variation among populations of a species and the variation among all populations (Blanck and Lamouroux 2006). For each continuous trait, we also estimated the coefficient of variation among species as a measure of interspecific variation.

PHYLOGENETIC SIGNAL OF SOCIAL TRAITS

We estimated Pagel's λ as a measure of phylogenetic signal for both continuous and categorical traits with more than 20 observations (Pagel 1999). Estimation of λ for continuous traits included intraspecific variation as measure error and log-likelihood ratio tests were performed to determine statistical significance with the function phylosig of the package 'phylotools' for R (Ives et al. 2007; Revell 2012). For categorical variables, we compared fitted models allowing λ to range between 0 and 1 with a null model assuming λ equals zero and used AIC (Akaike Information Criterion) to select the best fitted model. To estimate λ for categorical traits, we used the function fitDiscrete of the package 'geiger' for R (Harmon et al. 2008). The tree used for estimating all analyses involving phylogenetic information was obtained from pruning a species-level supertree of mammals (Fritz et al. 2009).

MULTIVARIATE ANALYSIS OF SOCIAL TRAITS

After removing poorly represented variables (< 10% studies) and 10 highly correlated variables ($r^2 \geq 0.7$, $p \leq 0.05$), the population dataset consisted of 351 populations and 19 variables with 38% of entries filled. The quantitative variables included in this dataset were proportion of females, male/female ratio, population density, mean group size, mean subgroup size, minimum subgroup size, maximum subgroup size, subgroup size s.d., relative subgroup size, and mean fission-fusion rate. Qualitative variables corresponded to preferred association, kin association, sexual segregation, multilevel organization, subgroup composition, sexual difference in FFD, fusion behavior, fission behavior, and temporal variation in FFD.

Social systems can be described by a series of traits that likely interact with each other. Therefore, a multivariate approach to analyze the variation across different species is ideal. We applied a factor analysis of mixed data (FAMD) to explore the traits space occupied by populations with FFD and to identify key traits determining the variation in social organization. FAMD is a principal components method that can incorporate continuous and categorical variables assigning them equal influence or weight on the analysis and producing orthogonal components (Kiers 1991; Pages 2004). Considering the sparseness of the dataset, we used a regularized iterative PCA method to handle missing data (Josse and Husson 2012; Audigier et al. 2016). Although this method results in an imputed dataset, our main goal was to estimate PCA parameters and their variance and not to predict missing values. We used the functions imputeFAMD of the package 'missMDA' and FAMD of 'FactoMineR' for R to run an FAMD (Lê et al. 2008; Audigier et al. 2016).

To determine if populations were uniformly distributed over the multidimensional space represented by social traits, we estimated the probability of occurrence of combinations of social traits in the space defined by the two first principal components of the FAMD. We used a kernel density function with unconstrained bandwidth selectors. In addition, we estimated densities at the quantiles 0.5, 0.95, and 0.99. For this analysis we used the functions 'Hpi' and 'kde' of the package ks for R (Duong 2007).

We also explored the variation of social traits at the species level to identify strategies or combinations of traits that occur across different species. To avoid comparing species characterized only by different variables, we imputed missing elements of the species-level dataset. Depending on the variable type (continuous or discrete) and the level of phylogenetic signal, we used different imputation methods (Freckleton 2009; Nakagawa and Freckleton 2010). We used the most common value across congeneric species in the dataset to impute discrete variables with significant phylogenetic signal (Table 3). For continuous variables with significant phylogenetic signal we used the ‘Phylopars’ method, which reconstructs missing values based on phylogenetic and phenotypic variances estimated through maximum-likelihood (Bruggeman et al. 2009). Error estimates of Phylopars predictions were obtained from cross validation, by comparing predicted and observed values of variables. Only those variables showing low error in the cross validation test were replaced with imputed values from Phylopars.

For variables without significant phylogenetic signal or with high error from Phylopars imputation, we used multivariate imputation by chained equations (MICE) with the package ‘mice’ in R for the following three variable types. This is a multiple imputation method that allows both continuous and discrete variables to be imputed and also to be used as predictors of missing data (van Buuren 2007). We built a predictor matrix based on correlation between variables and the degree of sparseness in the data (Van Buuren and Groothuis-Oudshoorn 2011). We repeated our imputation procedure 20 times and filled in missing cells in the species matrix using the median value for each imputed continuous variable and the most frequent value for each imputed categorical variable. Thus, our final species-level dataset included both literature-derived data and data obtained through imputation.

We identified species sharing similar social traits using hierarchical clustering analysis (HCL) on the final species-level dataset. Despite the continuous multidimensional space of social organization, common patterns (not necessarily resulting from the same mechanisms) could be generalized and used to understand potential general behavioral strategies and trade-offs in social traits. We excluded demographic variables but retained variables that provided information about variation in spatial cohesion, subgroup size, and subgroup composition according to the definition of FFD (Aureli et al. 2008). We also removed variables that were significantly correlated ($r \geq 0.7$, $p<=0.05$), and all continuous variables were first scaled and centered. We ran an HCL using the average linkage method and Euclidean distances. Given the mixed dataset, we obtained Euclidean distances from multidimensional scaling based on Gower distances, which can cope with both continuous and discrete variables (Gower 1971). To evaluate robustness of the HCL output, we performed a multiscale bootstrap resampling (bootstraps=10000) with the package ‘pvclust’ in R (Suzuki and Shimodaira 2006). We selected maximum-distanced clusters with approximately unbiased p-values (AU≥0.95), which indicates significant probability of occurrence. To describe the variation of fission-fusion systems across clusters, we calculated weighted means and standard deviations of standardized continuous traits for species included in each cluster using the population-level dataset.

Results

INTER- AND INTRASPECIFIC VARIATION OF SOCIAL TRAITS

Our search identified 368 populations of 75 mammalian species (distributed across nine orders: Artiodactyla, Carnivora, Cetacea, Chiroptera, Dasyuromophia, Diprotodontia, Perissodactyla, Primates, Proboscidea) that have been described as showing FFD. Most of the social traits varied broadly between and within species. Based on the species dataset, interspecific variation tended to be higher in traits related to community and group size, population density, fission-fusion time, and minimum association rate than in other types of traits (Table 1.2). However, sample sizes in the two latter traits were small and represented only a few species. Proportion of females and males were the least variable traits. Based on the populations dataset, intraspecific variation was lower than interspecific variation for all traits. Intraspecific variation was similar among traits, except for higher values in population density and minimum association rate as well as lower values in proportions of females and males and male/female ratio. RIV values indicated that intraspecific variation accounted for most of the variation (>60%) in proportion of females, mean and maximum association rate, and community and group size traits (Table 1.2).

PHYLOGENETIC SIGNAL OF SOCIAL TRAITS

From the 28 traits for which we estimated λ, eight showed some phylogenetic signal significantly different from zero. Among continuous traits, population density and subgroup size s.d. had $\lambda > 0.5$, with the latter showing the highest signal ($\lambda = 1.0$).

Only three categorical traits (sexual segregation, multilevel organization, and subgroup composition) presented significant phylogenetic signals (Table 1.3).

MULTIVARIATE ANALYSIS OF SOCIAL TRAITS

Based on the factor analysis for mixed data, the first three principal components accounted for 66.3% of the variance across populations. The first dimension explained 42.9% of the variance and was mostly influenced ($r^2 > 0.5$) by variables related to group/subgroup size and composition (mean and maximum subgroup size, subgroup size s.d., and mean group size) and male/female ratio. Qualitative variables and other demographic variables showed low correlations with this dimension. The second dimension accounted for 18.8% of the variance. Minimum subgroup size, relative group size, proportion of females, and fission-fusion time showed high correlation with this dimension. Only fusion behavior was highly correlated with the third dimension, which accounted for 4.6 % (Table 1.4).

Within the plane defined by the first two components, we identified two gradients. A first gradient encompasses the range from large groups, large subgroups, and large variation of subgroup size (subgroup size s.d.) to those with smaller groups, smaller subgroups, and low variation of subgroup size (Fig. 1.1A along PC1). A second gradient of variation goes from populations with a larger proportion of females, lower fission-fusion rates (high fission-fusion time), smaller minimum subgroup size, and lower relative subgroup size to smaller proportion of females, higher fission-fusion rates, larger minimum subgroups, and higher relative subgroup size (Fig. 1.1A along PC2). In between these extremes of the gradients, a wide range of intermediate values exists that account for the variation in social systems among populations.

Based on the kernel density analysis, populations with FFD have a high probability of having a social system characterized by small groups and subgroups with low variation of subgroup size (s.d.), large proportion of females, and low fission-fusion rates (Fig. 1.1A). This region of high density of populations includes some representatives from all of the orders of mammals in our dataset, except for Perissodactyla (Fig. 1.1B). Despite this broad co-occurrence, some populations of some orders occupied distinctive areas of the plane. Artiodactyla and Perissodactyla (ungulates) were mostly located on the negative side of PC1 (larger groups and subgroups) while most primates, cetaceans, and marsupials (Dasyuromorphia and Diprotodontia) were on the positive side (smaller groups and subgroups). Along PC2 almost all carnivore populations were on the negative side while positive extreme values corresponded mostly to primates and cetaceans.

Of the final 70 species analyzed in the HCL, 68 sorted into significant clusters that represented distinctive types of FFD (Fig. 1.2). These species segregated into two main clusters of FFD; one of which (Cluster A) included 13 primate species that formed smaller groups (mean=78.8) but larger subgroups (mean = 21.3, minimum = 8.4, and median = 15.0). In Cluster A, CV of subgroup size was lower (mean=33%) and subgroups were not sexually segregated, which agreed with no differences in FFD between males and females. Fully 62% of the species in Cluster A formed multilevel societies, which were present in only 24% of species in the second main cluster (Cluster B). Cluster B encompassed 55 species from several mammalian orders and included species that formed smaller subgroups (mean = 5.5, minimum = 1, and median = 4). CV of subgroup size was higher in Cluster B than in Cluster A (mean=55%) and most of the species (> 73%) in Cluster B exhibited sexual segregation.

Within Cluster A, species assembled into two smaller significant clusters. Cluster A1 included both Neotropical and old-world primate species, while snub-nosed monkeys (*Rhinopithecus* spp.) formed Cluster A2. For species in Cluster A1, the minimum size of subgroups was large ($\hat{x} = 6.0$) and most subgroups corresponded to multimale-multifemale parties. In contrast, minimum subgroup size of species in Cluster A2 was smaller ($\hat{x} = 3.7$). Subgroups generally included one-male with multiple females. Species in Cluster A2 lived in some of the largest groups ($\hat{x} = 164.9$). Species in Cluster A1 fuse when resting, whereas those in Cluster A2 fuse when resting and when moving/travelling (Fig. 1.3).

Six other significant clusters occurred within Cluster B. Cluster B3 encompassed all species of antechinus shrews, a bat (*Chalinolobus tuberculatus*), and howler monkey. These species lacked sexually segregated subgroups and continuous social traits were near the average for all mammals (Fig. 1.3). The two species of kangaroo in the dataset formed Cluster B4. It was characterized by (1) little interaction between individuals (maximum association rate: $\hat{x} = 0.1$), (2) smallest overall mean subgroup size ($\hat{x} = 2.9$), (3) lowest overall CV of subgroup size ($\hat{x} = 20\%$), and (4) shortest total time interval between FF events ($\hat{x} =13$ minutes). Within this cluster, subgroups were sexually segregated and both males and females were gregarious (Fig. 1.3). Cluster B5 consisted of all species of spider monkeys, chimpanzee, bonobo, lion, and two ungulates. In general, continuous social traits for these species tended to be lower than average, except for the CV of subgroup size, which was higher ($\hat{x}$ = 67%). Time interval between FF events was the second lowest ($\hat{x}$ = 81.4). Although further hierarchical divisions within this cluster were also significant, they were excluded from further analysis because of smaller distances. Two *Equus* species formed Cluster B6, which showed the highest maximum association rates ($\hat{x}$ = 0.8) and experienced the highest CV of subgroup size ($\hat{x}$ = 150%). Subgroup units corresponded to individual males segregated from subgroups of females with young (Fig. 1.3). Cluster B7 comprised two ungulates and a primate. These species lived in the largest groups ($\hat{x}$ = 302) and split into the largest subgroups ($\hat{x}$ = 30.8). In contrast to the other clusters, species in this cluster involved subgroups that fused when resting and socially interacting. Finally, Cluster B8 consisted of four marine species, orangutan, and a bat (*Tadarida australis*), which on average showed the highest minimum association rate ($\hat{x}$ = 0.14) and least fluid dynamics (time interval between FF events: 7 days; Fig. 1.3).

Discussion

Studies on FFD have traditionally focused on the group dynamics of species with “complex” societies like elephants, chimpanzees, and spider monkeys (Archie et al. 2006; Lehmann, A H Korstjens, et al. 2007; Ramos-Fernández and Morales 2014). However, these species only represent one extreme end of the continuum of FFD (Aureli et al. 2008). The 70 species analyzed in this study expose the presence of a much broader spectrum of FFD that underlie a diversity of social systems, with substantial variation both within and among species. Intraspecific variation of social organization is a common trait of social systems and can, in general, be regarded as an adaptive strategy (Lott 1991). The processes behind this variation (i.e., genetic variation, developmental plasticity, social flexibility, and extrinsic factors) might differ between species (Schradin 2013; Kamilar and Baden 2014), although it is probably the combination of all these processes acting at different temporal scales that determines inter- and intraspecific variation in sociality. These same processes might also have an effect on FFD. For example, analyses of data from chimpanzees and orangutans found evidence for genetic variation and behavioral flexibility as mechanisms leading to local adaptation and intraspecific behavioral variation (Langergraber et al. 2011; van Schaik 2013).

Traits differed in their levels of variation between and within species, as well as the importance of phylogeny in their variation. Among all continuous social traits, intraspecific variation of community and group size traits tended to represent a higher percentage of all variation (interspecific + intraspecific variation) than other traits (Table 1.2). These traits were important in explaining variation in social traits across populations, as they determined gradients of variation evident in the FAMD. Furthermore, these traits also varied between clusters of species and showed little phylogenetic signal (except subgroup size s.d.). Given that fission and fusion events might occur mainly as a response to ecological factors (Popa-Lisseanu et al. 2008; Smith et al. 2008), high intraspecific variation in traits related to group and subgroup size is expected when different populations reside in different ecological settings.

These results also suggest that higher flexibility in these traits of social behavior might have been selected for, in contrast with flexibility of other traits, like demographic or group stability traits. However, group size might also be constrained by morphological, physiological and cognitive aspects, which tend to be more conserved and uniform across individuals in a population and within a species (Blomberg et al. 2003). For example, cognitive skills and body mass have been shown to affect group size in primates (Clutton-Brock and Harvey 1977; Lehmann et. al. 2007). Furthermore, phylogenetic inertia has been found to influence group size in primates and dolphins (Di Fiore and Rendall 1994; Gygax 2002). However, the relevance of phylogeny as a determinant of group size in comparison to other factors might vary between taxa, and further comparative analysis within orders are needed to understand the patterns of variation in group/subgroup sizes as well as the factors generating them.

Traits related to association rate also seemed to have higher intraspecific than interspecific variation. The nature of interactions between conspecifics depends on many factors (e.g. sex, age, dominance, personality, and kinship) which together predict high levels of variation in relationships not only at the individual level, but also between individuals, groups, and populations (Kappeler et al. 2013). These interactions are further constrained by environmental cues, such as food availability and predation risk resulting in locally differentiated patterns of FFD and high intraspecific variation. Although these findings make sense in terms of the plasticity of social systems, we note that high intraspecific variation could also be a consequence of association and fission-fusion rates being sporadically reported in the literature, resulting in the small number of populations in our analysis. Moreover, such variation could also stem from differences in sampling and estimation methods between studies and populations. Rates of dyadic interactions are usually estimated through different association indices and/or based on a specific type of interaction (e.g., grooming, food sharing) that only occur in certain species, further limiting comparisons between studies or populations.

In contrast, population density was characterized by higher interspecific than intraspecific variation in addition to an intermediate-high phylogenetic signal (Tables 1.2 and 1.3). Despite the influence of environmental factors on population density that leads to intraspecific variation, intrinsic factors (e.g., body size and diet preference), which might represent ancestral states, may also constrain population density (Robinson and Redford 1986; Silva and Downing 1995). Studies on carnivores have also detected significant signals in population density and other demographic parameters such as growth rate (Lindenfors et al. 2007; Fagan et al. 2013).

Estimations of phylogenetic signal in social traits across mammals are few, potentially relying on the idea of lower signal in behavioral traits in comparison with anatomical or physiological traits (Blomberg et al. 2003). Recent studies on primates found low but significant phylogenetic signals for some social traits (Kamilar and Cooper 2013). Sexual segregation, multilevel organization, and subgroup composition tend to have very high phylogenetic signals, suggesting the presence of general patterns in the social organization among populations (e.g., males and females form separate groups). These patterns vary according to ecological conditions (e.g., different sizes of male and female groups), which can lead to the high intraspecific variation observed in subgroup size traits. Sexual segregation is common across a wide range of mammals (e.g., ungulates, carnivores) (Ruckstuhl 2007). It has been explained as a strategy to cope with differences between males and females in energetic requirements, activity budgets, and predator avoidance, all of them related to differences in body size, which is a phylogenetically conserved trait (Conradt and Roper 2000; Wolf et al. 2005). Social affinities and reproductive strategies might also be responsible for sexual segregation (Bleich et al. 1997; MacFarlane and Coulson 2009). Sexual segregation represents a particular form of FFD that contributes to the social strategy of most species in Cluster B but is absent from Cluster A. In the context of FFD, sexual segregation would allow species to reduce individual costs originating from basic differences in ecological, physiological, and social requirements of males and females.

In contrast, multilevel organization (i.e., social systems with stratification of subunits so that interactions between basal units with stable composition form a second layer or tier characterized only a few species in the dataset, including some primates and whales, elephants, zebras, and reticulated giraffe. It seems to be common to species of the same genus (e.g., *Papio* and *Equus*), which might explain the significant phylogenetic signal. In primates, multilevel systems might have evolved through different mechanisms in different groups (Grueter et al. 2012), so that its occurrence along the mammal tree could be the result of convergent evolution. FFD in populations with a multilevel organization also occur at different degrees and lead to differences in social systems, as evidenced by the presence of species with multilevel organization in both clusters A and B.

Subgroup composition describes the basic unit where most interactions occur within a group. Subgroups seem to have similar structure in terms of gender composition, but individual composition can vary in time or be fixed as in multilevel societies. Plasticity in individual composition seems to characterize most fission-fusion systems as opposed to multilevel societies, which are characteristic of fewer species. The proportion of males and females in a subgroup might be influenced by reproductive strategies, resource availability, predation, and/or infanticide risk that limit interactions between individuals of opposite or same sex (Chapman and Rothman 2009). Despite the high phylogenetic signal detected in this study for subgroup composition, intraspecific variation in subgroup composition has been observed in some species of primates (Rangel-Negrín et al. 2011; Strier et al. 2014). As more data become available, intraorder analyses might help elucidate the role of phylogeny as a determinant of group composition in different lineages.

Interestingly, despite high intraspecific variation in social systems, order –level variation is relatively muted, with diverse populations restricted within relatively narrow ranges. In particular, ungulates seem to form larger groups and split into larger subgroups than do primates and cetaceans (some bats also aggregate into very large groups but those species were not included in our study due to lack of data on their social traits; see Bradbury and Vehrencamp 1977; Betke et al. 2008; McFarlane et al. 2015). This seems to contradict the expectation based on the social brain hypothesis, in which more complex societies are expected for those species with higher cognitive abilities (Dunbar 1998). An alternative explanation is linked to predation risk, which has been identified as a factor modifying predicted group size based on cognitive abilities and might explain the larger group/subgroup sizes observed in ungulates (Shultz and Dunbar 2006; van der Bijl and Kolm 2016). However, this separation between orders is not complete, so that part of these ranges occupied by them overlapped, suggesting the presence of common patterns in social systems independent of phylogenetic relationships.

Species formed two distinct clusters (A and B), within which congeneric species tended to group together, coinciding with the high and significant phylogenetic signal detected in some social traits. We also found significant clusters including species belonging to different orders, which highlights the relevance of other factors (e.g., demographic or environmental variables) in determining social systems and providing evidence for convergence in some aspects of social systems among unrelated taxa. In addition, species from different genera that clustered together tended to do so at farther distances from each other than did species in the congeneric clusters. An exception to this pattern was the small cluster within Cluster 5 that included *Ovis canadensis* (bighorn sheep) and *Ateles chamek* (Peruvian spider monkey). Because environmental factors affecting these species are different (bighorn sheep are herbivores that live in open grassy habitats and on mountains, while spider monkeys are restricted to tropical forests), similarity between these species highlights potential convergent evolution towards highly fluid FFD and complex societies (Aureli et al. 2008).

The gradient in FFD (i.e., degree of change in cohesion and group membership over time) across mammals translates into diverse social strategies as responses, in part, to resource abundance and distribution. Clusters identified here correspond to sets of (sometimes unrelated) species that have adopted specific strategies for dealing with issues of resource availability. For example, sexually segregated subgroups (Clusters 4, 5, 6, 7) could reduce costs associated with differences in demands between males and females in a group (Ruckstuhl 2007; Hartwell et al. 2014). In mixed-sex groups, in contrast, these costs could be outweighed by increased antipredatory defense and/or enhanced mating opportunities (Neuhaus and Ruckstuhl 2002; Meldrum and Ruckstuhl 2009). However, the role of resources is not evident in all aspects of FFD. A gradient in CV of subgroup size was evident with species in Cluster 6 (*Equus* spp.), showing the highest variation, whereas those in Cluster 4 (kangaroos) showed the lowest variation. Given that both of these extremes included herbivores occupying mostly open, grassland habitats, potential drivers of this gradient could be related to demographic, social, or genetic factors instead of environmental ones.

In contrast with the gradient in variation of subgroup size, the rate of fission-fusion events was highest in Cluster 4 (kangaroos) and Cluster 5 (spider monkeys, chimpanzee, etc.) and lowest in Cluster 8 (cetaceans, orangutan, and white-striped free-tailed bat). The species at the higher end of this spectrum included some of the best studied social systems, which are commonly chosen to define and exemplify FFD and the mechanisms behind it (Aureli et al. 2008). In species with a high degree of FFD, resource distribution, predation risk, social, and demographic factors influence the rate of FF events and, consequently, the social systems that emerge (Symington 1988; Boesch 1991; Lehmann and Boesch 2004). Species with less fluid FFD have been less frequently studied, making it more difficult to understand the evolution and the role of different factors on FFD.

All things considered, variation in social systems observed in this study supports the hypothesis that social systems are influenced not only by current ecological conditions, but also by evolutionary relationships (Sobrero et al. 2014). Changing group composition, size, and cohesion through FFD might characterize an adaptive response to environmental and demographic factors that act on phylogenetically defined patterns of group size, generating the observed variation of social systems across species and populations. Moreover, we found that populations are not uniformly distributed across the multidimensional space of social systems, and species from diverse orders seem to converge to similar social systems. These results suggest the existence of a finite set of successful social strategies among mammals, highlighting the need for continued studies of the flexibility of FFD in the context of the evolution of complex social systems.

Table 1.1 Definitions of social traits used to describe the social system of mammals. * indicates variables included in multivariate analysis.

Variable	**Explanation**
Demographic structure	
Proportion of females*, males, and young	Fractions of the population size represented by females, males, and young, respectively.
Male/female ratio*	Ratio of total number of adult males and total number of adult females in the population or group as given in the literature or calculated from the number of males and females.
Population density*	Number of individuals per km^2.
Population size	Number of individuals.
Interactions and social differentiation	
Association rate (mean, s.d., min., max.)	Frequency over time of dyadic association between individuals in a group. Only indices ranging between 0 and 1 were included.
Association preference*	Presence/absence of association preference (i.e., dyadic association rates are higher than expected by chance).
Kin association*	Presence/absence of kin association (i.e., dyadic associations are more frequent between kin than

Variable	Explanation
	non-kin related individuals).
Sexual segregation*	Presence/absence of sexual segregation (i.e., males and females spend most of the time in separate groups).
Multilevel organization*	Presence/absence of multilevel or multitier organization (i.e., nested social levels of individual assemblages).
Social budget	Proportion of activity budget invested in social behaviors.
Group/subgroup size and composition	
Group size (mean*, min., max.)	Number of individuals that can interact at least over a season period.
Subgroup size (mean*, min.*, max.*, median, s.d.*, CV, range)	Number of individuals that interact at any time.
Relative subgroup size*	Subgroup size as a proportion of the group size.
Subgroup composition	Most frequent structuring of subgroups. Categories: (A) solitary males and solitary females with/without young, (B) one male with several females with young and solitary/gregarious young males, (C) multimale-multifemale subgroups, (D)

Variable	**Explanation**
	gregarious males and solitary females with young, (E) solitary males and gregarious females with young, (F) gregarious males and gregarious females with young, (G) Several adults, no sex identified, (H) Several adults with young, no sex identified,
Group stability	
Fission-fusion time (mean*, min., max., s.d.)	Time between fission and/or fusion events in minutes.
Subgroup distance (mean, min., max., s.d.)	Distance between subgroups in meters.
Sex difference*	Presence/absence of differences in FFD between males and females.
Fusion behavior*	Behavior(s) at fusion events as given in the literature or categorized into a general behavior. Categories: (1) foraging/feeding, (2) moving/traveling, (3) resting, (4) social.
Fission behavior*	Behavior(s) at fission events as given in the literature or categorized into a general behavior. See categories for fusion behavior.
Cohesion (mean, min., max., sd)	Distance between individuals in a subgroup.
Temporal variation*	Presence/absence of temporal variation in FFD.

Table 1.2 Estimates of interspecific and intraspecific variation of social traits. CV and RIV stand for coefficient of variation and relative intraspecific variation, respectively

Variable	**Species**	**Populations**	
	CV %	**CV % (n)**	**RIV %**
Demographic structure			
Proportion of females	27	21 (77)	84
Proportion of males	38	36 (77)	54
Male/Female ratio	62	37 (94)	28
Population density	334	83 (80)	45
Interactions and social differentiation			
Mean association rate	84	61 (46)	94
Min. association rate	199	136 (21)	36
Max. association rate	42	41 (25)	103
Community and group size			
Mean group size	121	56 (106)	71
Mean subgroup size	102	46 (154)	51
Min. subgroup size	122	38 (128)	80
Max. subgroup size	90	55 (130)	60
Subgroup size s.d.	197	65 (109)	88

Variable	**Species**	**Populations**	
	CV %	**CV % (n)**	**RIV %**
Subgroup size CV	257	61 (107)	93
Group stability			
Fission-fusion time	196	55 (28)	11

Table 1.3 Phylogenetic signal of social traits with signal significantly different from zero

Trait	**Pagel's λ**	**ΔAIC or p-value**
Proportion of males	0.48	$p = 0.02$
Population density	0.61	$p < 0.001$
Mean group size	0.40	$p = 0.002$
Minimum subgroup size	0.43	$p =0.07$*
Subgroup size s.d.	1.00	$p < 0.001$
Sexual segregation	0.92	ΔAIC = 9.02
Multilevel organization	1.00	ΔAIC = 28.84
Subgroup composition	0.97	ΔAIC = 39.56

Table 1.4 Influence of social traits on FAMD dimensions. Bold numbers indicate a significant effect.

Trait	**Dimension 1**	**Dimension 2**	**Dimension 3**
Proportion of females	-0.39	**-0.64**	---
Male/female ratio	**0.52**	0.44	---
Population density	0.26	---	-0.39
Mean group size	**-0.50**	-0.15	0.35
Mean subgroup size	**-0.55**	0.48	0.25
Minimum subgroup size	-0.29	**0.70**	---
Maximum subgroup size	**-0.62**	0.24	0.35
Subgroup size s.d.	**-0.53**	0.38	0.30
Relative subgroup size	---	**0.65**	---
Fission-fusion time	---	**-0.64**	0.29
Preferred association	---	0.03	---
Kin association	0.11	0.05	0.04
Sexual segregation	0.04	0.11	---
Multilevel organization	---	0.07	---
Subgroup composition	0.14	0.13	0.16
Sex difference	---	0.08	---
Fission behavior	0.12	0.08	0.15
Fusion behavior	0.30	0.07	**0.58**
Temporal variation	---	0.06	---

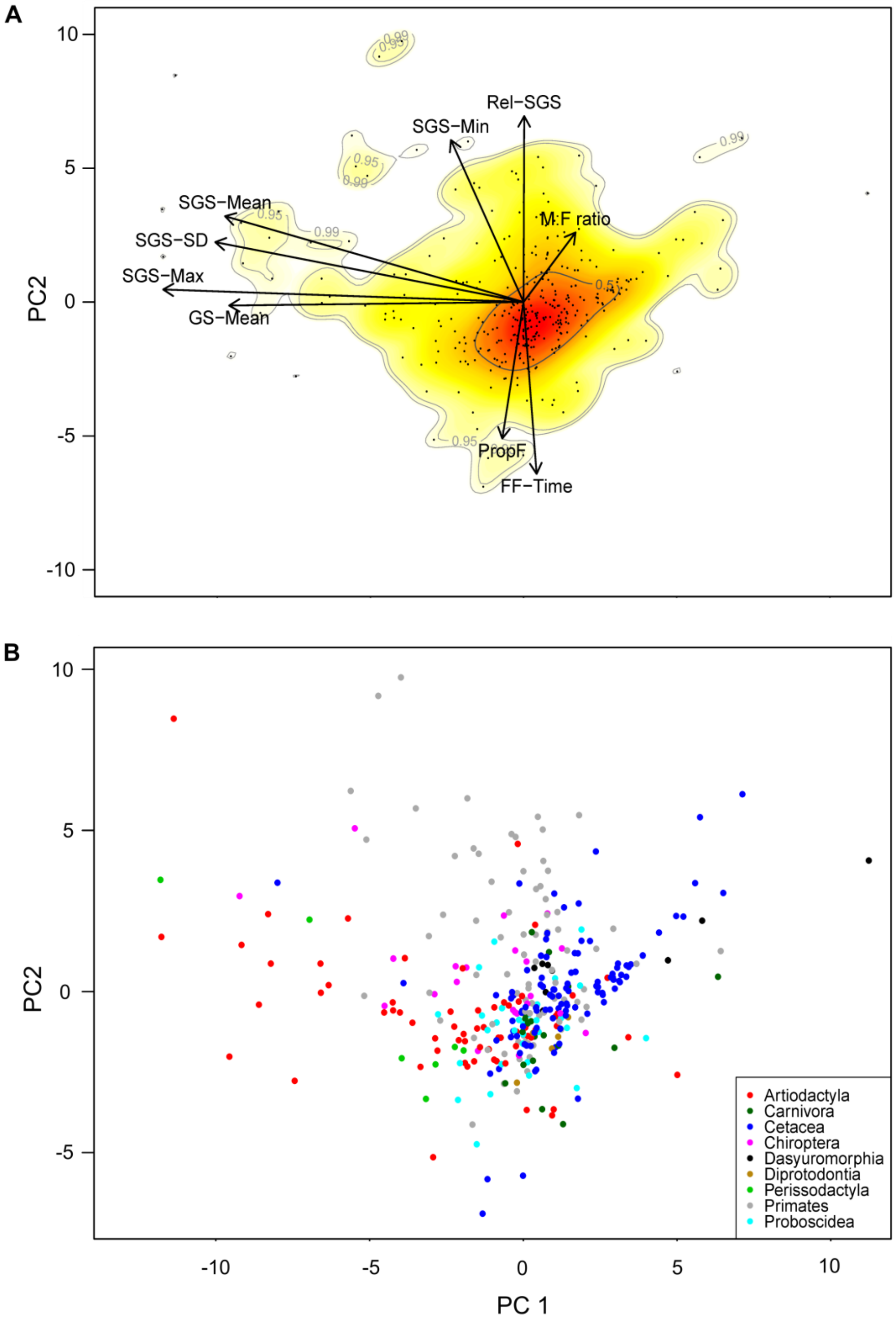

Figure 1.1. Distribution of populations and social traits in the plane defined by the first and second components of the factor analysis of mixed data (FAMD). A) Arrows represent strength and direction of the influence of traits on principal components.

Group and subgroup size influenced variation between populations mostly along the first component. Proportion of females and fission-fusion time were related to the variation along the second component. Contour curves correspond to quantiles of the density distribution of populations based on the kernel analysis. Populations are not homogeneously distributed in the social traits space. B) Distribution of populations colored by order. Ungulates (Artiodactyla and Perissodactyla) represent a different gradient of variation than Cetacean and Primates. Abbreviations in Fig. 1A: Rel-SGS = relative subgroup size; MF ratio = male-female ratio; FF-time = fission-fusion time; PropF = proportion of females; GS-mean = mean group size; SGS-max = maximum subgroup size; SGS-SD = s.d. of subgroup size; SGS-mean = mean subgroup size; SGS-min = minimum subgroup size

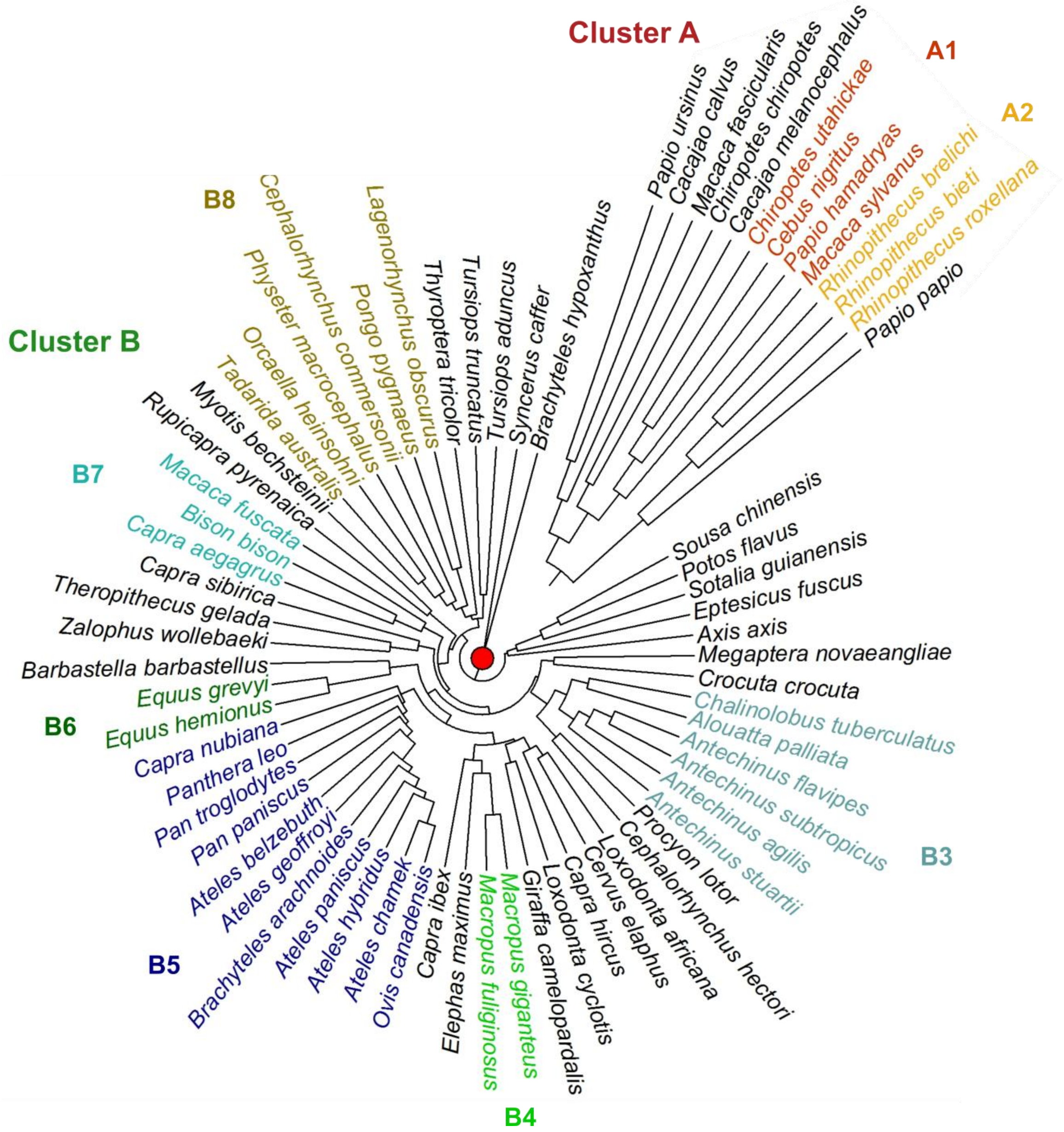

Figure 1.2. Hierarchical clustering tree of mammal species based on their social traits. Colored species names correspond to maximum distanced clusters that have a higher than 95% probability of occurrence. Species grouped into two main clusters A and B. Most congeneric species tended to cluster together.

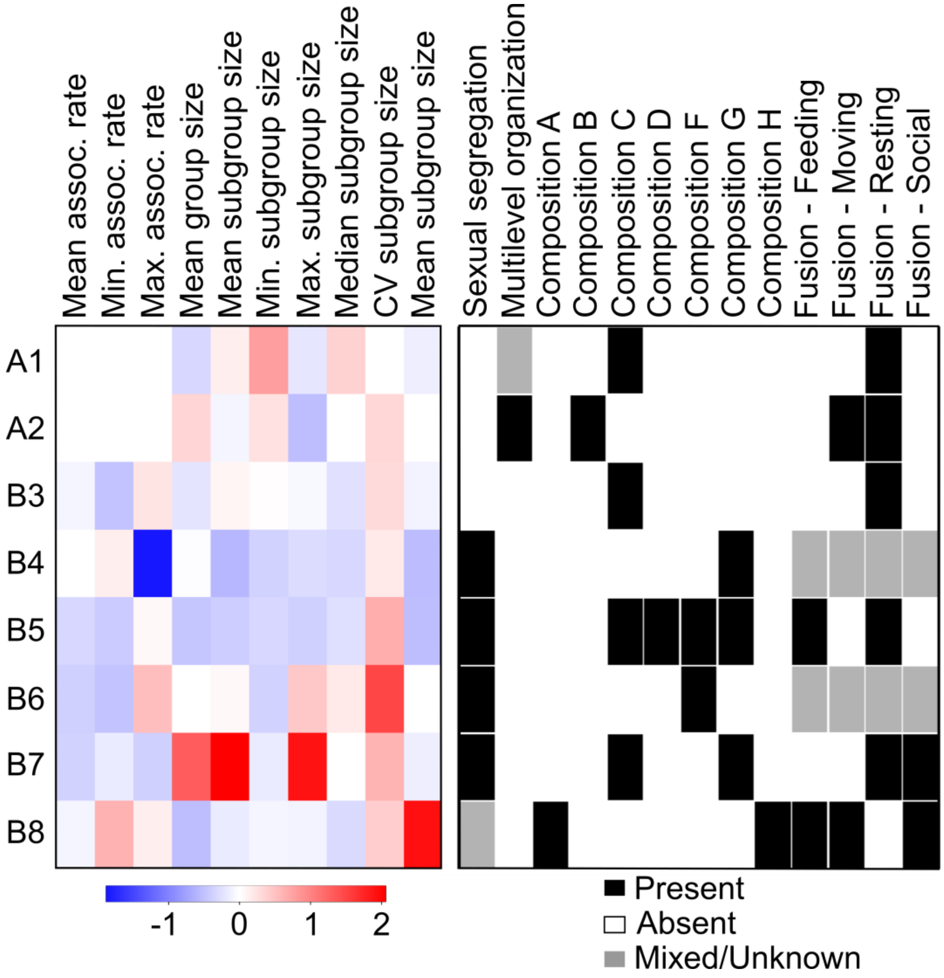

Figure 1.3. Variation of continuous and categorical social traits among clusters of species. Rows represent the identified clusters. Continuous variables were centered and scaled, so blue and red correspond to values below and above the mean, respectively. Each cluster was described in terms of a combination of values for these traits that indicated a general tendency in the social system of species within the cluster.

Chapter 2: EFFECTS OF BRAIN SIZE AND RESOURCE AVAILABILITY ON FISSION-FUSION DYNAMICS OF MAMMALS

Coauthor: WILLIAM F. FAGAN

Abstract

Mammals vary in their degree of fission-fusion dynamics, which leads to a range of levels of complexity in their social systems. Differences in cognitive abilities and ecological factors are common explanatory factors of this variation. Evolution of superior cognitive skills is favored by more complex societies. At ecological scales, complex societies necessitate high cognitive skills, but differences in resource availability could also explain intraspecific and interspecific variation. We tested the Social Brain Hypothesis (SBH) and the effects of brain size and resource availability on social traits of mammals with fission-fusion dynamics. To test the SBH we modeled brain mass as surrogate of cognitive skills in response to six selected social traits, while accounting for phylogenetic correlation. To explore the effect of cognitive abilities and resource availability on social systems, we fit models of the social traits as predicted by brain mass and proxies of primary productivity (NPP for marine species and NDVI for terrestrial species). We also compared these relationships for different trophic levels. At the species level, maximum subgroup size was the only trait correlated with brain mass. However, for marine mammals alone, a relationship between brain mass and other social traits was also found. Best fitted models involving resource availability showed stronger effects on marine than terrestrial populations. However, a comparison between trophic levels resulted in weak effects among herbivores but strong effects among carnivores. Working from a broad, multi-species comparison, these results provide evidence of the long-suspected influences of cognitive abilities and environmental factors on mammalian fission-fusion systems.

Lay summary

Previous studies covering one or a few species and patch-scale measures of ecological factors have suggested that cognitive skills and ecological variables determine social organization in mammals. We used global datasets on social traits of mammals to determine the effect of brain size and resource availability on fission-fusion dynamics. Resource availability and cognitive abilities differed in their influence on fission-fusion dynamics between terrestrial and marine species, as well as between different trophic levels.

Introduction

Many mammals aggregate into groups and form complex societies. The reasons for animals to form groups are, in general, well understood. From a socioecological perspective, social systems represent mechanisms to minimize costs (e.g., increased intraspecific competition or risk of disease transmission) while maximizing benefits (e.g., better antipredatory defense or foraging efficiency) (Macdonald 1983; Krause and Ruxton 2002; Altizer et al. 2003). All groups are characterized by a certain degree of fission-fusion dynamics (FFD), which can be defined as the temporal variation in “spatial cohesion and individual membership in a group” reflected in splitting and reshuffling of subgroup composition (Aureli et al. 2008; de Waal and Tyack 2009). FFD have been framed as a strategy of group-living animals that allows them, through temporal dynamics, to maintain the benefits of larger groups through fusion and to reduce the costs of group living through fission into smaller subgroups (Lehmann et al. 2007). The spatiotemporal variation in cohesion and group composition affects social systems by influencing opportunities for individuals to interact with one another. FFD add a layer of complexity to social systems and has been the focus of research on species considered as having complex social systems, such as chimpanzees, elephants, and dolphins (Connor et al. 2000; Archie et al. 2006; Riedel et al. 2011). Different factors may influence the degree of FFD and explain the variation in social systems across and within species with FFD. Species living in complex societies typically are expected to have more advanced or enhanced cognitive and communication skills that allow for the acquisition, processing, and use of information (Amici et al. 2008).

THE SOCIAL BRAIN HYPOTHESIS

The Social Brain Hypothesis (SBH), which was initially proposed to explain the unusually large brain size of primates, captures the relationship between the challenges imposed by social living and cognitive skills (Dunbar 1998). The hypothesis states that higher cognitive abilities, manifested in some aspect of brain size, have been selected for by the complexity in the social system of the species (Dunbar 1998).

Significant positive relationships between brain size and group size, sociality, and flexibility of social organization in primates, supports the SBH (Shultz and Dunbar 2006; Kamilar and Baden 2014). However, attempts to apply the SBH to understand the evolution of social complexity and brain size in non-primate taxa have produced mixed results. A significant positive relationship between group size and brain size or encephalization has been independently found for some carnivore, ungulate, and cetacean species (Marino 1996; Pérez-Barbería and Gordon 2005; Pérez-Barbería et al. 2007). However, negative correlations between brain size and group size or other indicators of social complexity observed in some non-primate taxa (e.g. carnivores, ungulates and birds) challenges a generalization of the SBH to all mammals and other vertebrates (Beauchamp and Fernández-Juricic 2004; Pitnick et al. 2006; Shultz and Dunbar 2006; Finarelli and Flynn 2009). Some authors suggest that the SBH should only be applicable to social groups that are "semi-permanent", while others included any groups that are not casual aggregations when testing the SBH (Byrne and Bates 2007; Shultz and Dunbar 2007). However, suitability of group size as a proxy of social complexity to test the SBH might depend on aggregation patterns of species (e.g. temporal or casual aggregations could result in large group sizes that are not cognitively demanding). This suggests that alternative measures of social complexity should be considered in comparative analysis involving the SBH.

HYPOTHESES RELATED TO RESOURCE AVAILABILITY

Socioecological theory predicts that resource availability (i.e., abundance, distribution, and diversity) influences competition; and this in turn affects social interactions and relationships between group members, and therefore, their social system (Clutton-Brock 1974; van Schaik 1999). Non-human primates, especially species with high degrees of FFD, have proved particularly useful systems to develop this theory by allowing the exploration of the effects of resource (primarily food) abundance and distribution on group size and other aspects of social organization and structure (Symington 1988; Koenig et al. 2013; Wittiger and Boesch 2013; Rimbach et al. 2014). However, most of these studies only explored the influence of resource availability on variation of social organization at the food patch scale (e.g., feeding tree, individual prey) and for single populations. There has been less attention given to the effect of abundance and temporal distribution of resources across species and larger scales (e.g., habitat types). Comparative approaches, which have explored resource availability at larger scales, did not find consistent effects of resource availability on social organization. For example, baboon troops split into small subgroups in habitats with lower food abundance (Schreier and Swedell 2012a), whereas group size of chimpanzees was not affected by habitat-wide abundance and distribution of food (Newton-Fisher et al. 2000). Among elephants, resource abundance affected group size only at the highest tiers in their multi-tiered social system (Wittemyer et al. 2005). Multispecies comparisons across different mammal orders which explore the relationship between environmental factors and social organization, while accounting for intraspecific variation, are scarce (Kamilar and Baden 2014). However, these relationships are critical for understanding selection pressures and the evolution of social systems (Strier 2009).

Several models and hypotheses have been proposed to describe the relationship between resource availability and social systems (Wrangham et al. 1993; Janson and Goldsmith 1995; Koenig et al. 2013). Based on observations of non-human primates, the ecological constraints hypothesis states that competition for resources caused by temporal variation in their availability, limits subgroup size in animals that form groups (Chapman et al. 1995). It predicts larger subgroups with increasing resource density. Similarly, the resource dispersion hypothesis was formalized to explain the association between resources and group living in carnivores (Carr and Macdonald 1986; Johnson et al. 2002). It proposes that groups will form in environments where resources are temporally and/or spatially heterogeneous. In such cases, several individuals are able to share resources if each individual can exploit them without imposing detrimental costs on other individuals (Carr and Macdonald 1986; Macdonald and Johnson 2015). This happens because in heterogeneous or patchy environments, an individual, or any other basic social unit, is expected to occupy a much larger territory than what it actually needs to satisfy its resource requirements on average. The minimum of resources expected to be available over a critical time period determines territory size. Such territories would then, on average, contain an excess of resources that other individuals could exploit (Johnson et al. 2002). This hypothesis provides explanations for the influence of resource availability on the evolution of group living. It also predicts, among other things, that larger groups should occur where resources are more heterogeneously distributed in time and/or space (Macdonald and Johnson 2015).

Ecological factors have been also hypothesized to be largely responsible for the evolution of sociality (Davies et al. 2012). However, current variation in social systems may reflect both differences in responses to environmental factors and in ancestral forms (Sobrero et al. 2014). It has long been argued that evolution of cognitive abilities sustains interspecific variation in social systems (Byrne and Whiten 1988), and brain size, a common proxy of cognitive abilities, shows a strong relationship with the phylogeny of mammals (Blomberg et al. 2003; Finarelli and Flynn 2009). Exploration into the effects of brain size and current resource availability (as an environmental factor proxy) on social traits across and within mammalian species will help elucidate the role of ancestral forms and environmental factors in the evolutionary history of social systems.

SPECIFIC APPROACH AND PREDICTIONS

In this study, we synthesized information from diverse studies to characterize the social system of mammal species and populations with different degrees of FFD. Here, we focus on FFD that occur at temporal scales small enough to have an impact on the social system, limiting this study to dynamics with time intervals of less than a month between fission-fusion events. We explored the potential association of cognitive abilities and resource availability with social systems of mammals with FFD, while accounting for intraspecific variation and phylogenetic relationships. Based on the SBH, we expected a positive correlation between complexity of social systems and cognitive abilities. We expanded the predictions of the ecological constraints and the resource dispersion hypotheses to other social traits with the expectation that abundance and heterogeneity in resource availability also affected them. Based on the conceptualization of FFD as a strategy by which animals can better exploit spatially heterogeneous resources, we hypothesized: (1) larger groups and subgroups would occur in areas with higher abundance and greater temporal variation of resources, and (2) variation in subgroup size and rate of fission-fusion dynamics would decrease with abundance and increase with temporal variation of resource availability. Because we use metrics of resource availability associated to primary productivity, we also expected these effects of resource availability to differ between groups of species occupying different trophic levels. In particular, we expected higher abundance of resources to be correlated with group size across herbivores while resource variation would mostly affect group size across carnivores. Omnivores would be less affected by resource abundance or variation than the other two trophic levels.

Methods

DATA COLLECTION

We used a global dataset containing information on social traits of 70 species and 356 populations of mammals with FFD (Appendix Table A2.1). The species dataset included data obtained from the literature and imputed values obtained through phylogenetic and multivariate imputation methods, which resulted in 20 replicated matrices differing in the imputed values (Alvarez et al. in review). As a trait that would be indicative of cognitive abilities, we gathered data on brain mass and body mass from a variety of sources (Pérez-Barbería and Gordon 2005; Marino et al. 2006; Pitnick et al. 2006; Pérez-Barbería et al. 2007; Jones et al. 2009; Boddy et al. 2012; Watson et al. 2012). To facilitate broad comparisons across mammalian groups, we used total brain mass instead of any other brain parts, such as the neocortex, which has been a common proxy in previous tests of the SBH. Data on neocortex size of non-primate species was scarce, and we assumed an allometric relationship between brain mass, brain volume, and neocortex size, as has been found for primates, to be extendable to all mammals in the data (Rilling and Insel 1999; Shultz and Dunbar 2006; Isler et al. 2008). Furthermore, in comparison to neocortex volume and other metrics, brain size seems to be a better predictor of cognitive abilities in non-human primates (Deaner et al. 2007).

As surrogates of resource availability we used different metrics for terrestrial and marine species. We used the Normalized Difference Vegetation Index (NDVI) for terrestrial systems, which has proved to be a good indicator of terrestrial net primary productivity (NPP) (Hicke et al. 2002; Pettorelli et al. 2011). Based on biweekly Advanced Very High Resolution Radiometer (AVHRR) NDVI3g data produced by NASA and covering from 1982 to 2013 (Pinzon and Tucker 2014), we estimated the annual mean, annual mean range, and mean unpredictability of NDVI (i.e., coefficient of variation for the same biweekly period across years) for the landscapes inhabited by each population. Raster resolution was 0.083 degrees (ca. 9 km on the Equator) and the average of NDVI values of the four nearest raster cells was used to characterize each population. For marine species, which included 10 cetaceans and one carnivore (Galapagos sea lion *Zalophus wollebaeki*), we used ocean NPP data that had a resolution of 0.167 degrees (ca. 18 km on the Equator) and consisted of monthly standard raster data covering the years 2003-2012 (available at http://www.science.oregonstate.edu/ocean.productivity/index.php; Behrenfeld and Falkowski 1997). We then calculated the same statistics for resource availability as for terrestrial NDVI data, again averaging values from the four raster cells nearest to each population. After inserting NDVI and NPP data, the final population dataset included 356 observations. We limited our analysis to six social traits that showed significant influence on the variation in social systems across mammals and can describe FFD (Alvarez et al. in review). These variables were the mean group size, mean, minimum, maximum, and standard deviation of subgroup size, and mean fission-fusion time (calculated as time between fission-fusion events).

TESTING THE SBH

To explore the relationship between cognitive abilities and variation of FFD, we tested the fit of models of brain size predicted by selected social traits using the species-level dataset. We included body mass as an additional covariate to account for the allometric relationship with brain mass (Freckleton 2002). Observation independence in some of these traits could be challenged by significant phylogenetic signal in some of the traits. Therefore, we relied on phylogenetic generalized estimating equations (GEE), which is a procedure to fit a generalized linear model that incorporates the lack of observation independence in the form of a correlation matrix defined by interspecific distances (Paradis and Claude 2002). This correlation matrix R, together with the expected variances of observations A and a dispersion parameter ϕ, define a variance-covariance matrix V (Liang and Zeger 1986). Estimates of regression parameters are obtained from GEEs that incorporate V:

$$\frac{\partial \boldsymbol{\mu}^T}{\partial \boldsymbol{\beta}} V^{-1}(\boldsymbol{y} - \boldsymbol{\mu}) = 0$$

where $\boldsymbol{\mu}$ and $\boldsymbol{\beta}$ are vectors of expected response values and regression parameters, respectively (Paradis and Claude 2002). This equation is solved through an iterative process using a quasi-likelihood function (Wedderburn 1974). We estimated a correlation matrix based on phylogenetic distances from a pruned tree of a species-level supertree of mammals (Fritz et al. 2009).

To account for uncertainty derived from multiple imputations, we fitted the models using each of the 20 data matrices generated through multiple imputations (Alvarez et al. in review). Coefficient means were calculated as the average of all 20 models fitted for each variable, while standard errors were adjusted to incorporate the variance within and across the fitted models for each imputed dataset (Gelman and Hill 2006).

EFFECTS OF RESOURCE AVAILABILITY AND BRAIN SIZE ON FFD VARIATION

To evaluate the effect of resource availability (i.e., mean, range, and unpredictability of NDVI or NPP) and brain size on selected social traits, we fitted GEE models to the same selected social traits as were included in the brain size models using the population level dataset. We performed separate analyses for terrestrial versus marine mammals because of the different surrogates for resource availability (i.e. NDVI and NPP, respectively). The marine dataset included 116 populations corresponding to 11 species, whereas the terrestrial dataset consisted of 240 populations that represented 59 species. Mean FF times were only modeled for terrestrial species because of the small sample size for these variables in the marine dataset. We considered 18 alternative models that included different combinations of resource availability variables and brain size, controlling also for the effect of body size (Table 2.1). In these alternative models, we assumed equal brain mass across populations of the same species (Lande 1979).

Correlation matrices for GEEs were constructed separately for terrestrial and marine species based on phylogenetic correlation matrices obtained from the species phylogenetic tree. These matrices were then expanded to accommodate multiple populations per species, preserving the original interspecific distances, i.e., we assumed populations to represent polytomies for each species in the tree. Model selection relied on (1) graphical assessment of residuals, (2) correlation tests of fitted and observed values, (3) calculation of marginal R^2 (indicating the amount of variance explained by each model), and (4) values of the quasilikelihood information criterion (QIC) of converging models, with more weight given to QIC and using mR^2 in case of ties (Hardin and Hilbe 2013).

COMPARISON OF EFFECTS OF RESOURCE AVAILABILITY BETWEEN TROPHIC LEVELS

Because responses to resource availability measured through NDVI and NPP might vary between species from different trophic levels, we fitted models to subsets of data separated by trophic levels (herbivores, omnivores, carnivores). This was only possible for terrestrial populations due to data availability. Trophic levels were obtained from panTHERIA (Jones et al. 2009). From the 18 alternative models in Table 1, we fitted the ones including mean, range, and unpredictability of NDVI, with and without brain size. Models with significant effects and significant correlation between fitted and observed values were selected. We used marginal R^2 and QIC for model selection comparing models with and without brain size that showed a significant effect of any NDVI measure.

Model fitting for each of the selected social traits was conducted using the function ‘compar.gee’ of the ‘ape’ package in R (Paradis and Claude 2002; Paradis et al. 2004). We assumed a Gamma distribution with a log link function for brain mass and all social traits. Statistical significance was defined at p-value <0.05 for all analyses. However, due to small phylogenetic degrees of freedom (DFp), statistical significance was not estimated for coefficients of some fitted models of marine mammals.

Results

TESTING THE SBH

Brain size tended to increase slightly with mean group size and was significantly positively related to maximum subgroup size and FF time (Fig. 2.1). This effect is very marked for maximum subgroup size and all imputed datasets supported these trends, which matched the small fraction of variation explained by imputation (FMI=17%). In contrast, a strong coincidence between imputations was not achieved for FF time, for which the fraction of variation explained by imputation was almost 90%. Therefore, among all variables tested, only maximum subgroup size supported the SBH.

EFFECTS OF RESOURCE AVAILABILITY ON DIVERSITY OF FFD

For both terrestrial and marine populations, resource availability, in particular range and unpredictability of resource variation, were associated with modeled social traits (Tables 2.2 and 2.3). The best fit model for all social traits in marine species included brain size as a significant predictor. In contrast, all best fit models for terrestrial species lacked brain size as covariate. Altogether, these results provided support for the effect of resource heterogeneity on grouping, and to a lesser extent for a correlation between brain size and social complexity (i.e., SBH).

In terrestrial mammals, mean group and subgroup sizes tended to increase with NDVI range. However, these models explained only 2 and 5% of the trait's variation, respectively. Models for minimum and maximum subgroup sizes together with standard deviation of subgroup size fit poorly: they even explained less of the variation than the only-intercept model. FF time decreased with NDVI range and increased with NDVI unpredictability, which explained 18% of variation in this social trait (Table 2.2).

Results from phylogenetic GEEs for marine mammals showed higher effects of NPP on social traits than those from terrestrial species. None of the variables explained the variation in mean group size and minimum subgroup size. Mean subgroup size increased with increasing brain mass, which explained 22% of this social trait variation (Table 2.3). Maximum subgroup size was influenced by NPP range and brain size, resulting in two patterns of variation. An interaction between these two covariates showed that for lower NDVI ranges, maximum subgroup size decreased with brain mass, while at higher NDVI ranges, the opposite was true (Fig.

2.2). Most observations accounted for low NDVI range values. These covariates together explained 18% of the variation in these two social traits in marine mammals (Table 2.3). Brain mass and unpredictability both had positive effects on the standard deviation of subgroup size but together they only explained 7% of the variation in this trait. Unfortunately, corrected degrees of freedom due to phylogenetic correlations (Paradis and Claude 2002) in marine mammals were too small to estimate p-values for most models. Models for FF time did not converge in most cases due to the small sample size ($n = 12$).

COMPARISON OF EFFECTS OF RESOURCE AVAILABILITY BETWEEN TROPHIC LEVELS

Variation of social traits among herbivores, omnivores, and carnivores was affected differently by NDVI metrics, contrasting also with some of the results found for all terrestrial species together. Mean group size increased with NDVI range among omnivores, but not among herbivores or carnivores. This correlation accounted for 45% of the variation. In contrast mean and unpredictability explained together 78% of the variation in mean group size among carnivores (Fig. 2.3).

Mean subgroup size was correlated with NDVI range and NDVI unpredictability in both herbivores and carnivores, although in opposite directions. In herbivores, mean subgroup size increased with these two NDVI metrics (though explaining only 3% of the variation), while it decreased with them in carnivores (explaining fully 33% of the variation) (Fig. 2.3). No effects of NDVI on mean subgroup size of omnivores were detected.

No correlation was found between minimum subgroup size and any of the NDVI metrics. Maximum subgroup size and s.d. of subgroup size were affected by mean NDVI in herbivores and carnivores, respectively (Fig. 2.3). Maximum subgroup size of carnivores slightly increased with mean NDVI, which explained 44% of the variation. In contrast, s.d. of subgroup size decreased with the mean; accounting only for 9% of the variation in herbivores. Variation in FF time was only associated to NDVI (mean and unpredictability) among carnivores (Fig. 2.3). FF time decreased with mean and increased with unpredictability, which explained 47% of this trait variation. None of these social traits was associated with NDVI in omnivores, and none of the trophic levels showed any effects of NDVI on minimum subgroup size.

Discussion

Social traits of mammals with FFD were found to be associated with both brain size and resource availability. At the species level, brain size was strongly correlated to maximum group size but not to any of the other social traits. At the population level, the association between social traits and brain size was evident in marine mammals, but not in terrestrial ones. The effects of resource availability differed between terrestrial and marine mammals, as well as between trophic levels.

BRAIN SIZE AND VARIATION OF SOCIAL TRAITS

Gradients of variation in social traits across mammals with FFD, which also indicate variation in social complexity, were significantly related to brain size in some of the fitted models. This indicates some support for the correlation between social complexity and cognitive ability hypothesized in the SBH (Dunbar 1998). Based on the species-level dataset, only maximum subgroup size was significantly related to brain size. However, group size, which is a more commonly used surrogate of social complexity in SBH studies, was poorly associated to brain mass in our study. In species with a more limited degree of FFD, group size might not capture the number of individuals that engaged in interactions regularly thus making this social trait a poor proxy of complexity (Shultz and Dunbar 2007). Because of a fluid pattern of interactions, it is possible that not all potential dyadic relationships develop, i.e., group size would overestimate dyadic relationships and social complexity (Bergman and Beehner 2015). Thus, using group size in tests of the SBH should be done carefully when species exhibit FFD. Furthermore, the relationship between group size and brain size might only be valid for some taxonomic orders of mammals and could have been masked by including species of many different orders in this analysis (Shultz and Dunbar 2007). However, separate analyses for each order were not possible because most orders were poorly represented in the dataset.

Better indicators of the number of dyadic relationships in species with FFD than group size appear to be mean and maximum subgroup size, which were substantially smaller than group size in many species. The effect of brain size on maximum subgroup size was significant and positive at the species level. However, because of high intraspecific variation in maximum subgroup size, this result needs to be interpreted with caution (Alvarez et al. in review; Ives et al. 2007). At the population level, a positive effect on maximum subgroup size was only detected for marine mammals and constrained to those species in areas with larger ranges of NPP. However, based also on the population dataset of marine species, brain size was associated with increased mean subgroup size and increased s.d. of subgroup size.

Because all but one marine population belonged to one order (i.e. Cetacea), this result accords with the positive relationship between brain size and social complexity detected in previous studies of this group (Marino 2002; Marino et al. 2007). In contrast, terrestrial mammals encompassed species from eight orders, each of which might have followed different coevolutionary pathways for fission-fusion dynamics, brain size, and social complexity (Pérez-Barbería et al. 2007; Aureli et al. 2008). Group size has been found to be largely affected by predation risk but constrained by a combination of ecological and cognitive factors in primates (Dunbar and Shultz 2007; Pollard and Blumstein 2008). Similar models integrating different factors might lie behind the high levels of social variation that we observed for other mammalian orders, but such models still need to be developed.

RESOURCES AND VARIATION OF SOCIAL TRAITS

Heterogeneity of resource availability (i.e., range and unpredictability) was significantly correlated with most selected social traits, on which resources (NDVI or NPP) seemed to have an impact. Mean group and subgroup sizes increased with range in terrestrial mammals, and together these results suggest FFD is an adaptive strategy for success in fluctuating environments, thus validating predictions of the resource dispersion hypothesis on the impact of resource heterogeneity on group size (Johnson et al. 2002; Popa-Lisseanu et al. 2008). Accordingly, our initial prediction of larger groups and subgroups occurring in more heterogeneous areas was confirmed, at least for terrestrial species. However, support for our prediction of slower FFD occurring in areas with more abundant and less heterogeneous resources appeared mixed, as mean FF time decreased with NDVI range but increased with NDVI unpredictability in terrestrial species. These NDVI metrics characterize different aspects of the temporal dynamics in resource availability, as they refer to variation across years and within a year or seasonality, respectively. Highly seasonal environments in our dataset corresponded mostly to temperate habitats or tropical dry savannas and forests. In both cases, and following the resource dispersion hypothesis, we would expect larger groups (Johnson et al. 2002), which would then utilize fission-fusion to cope with increased feeding competition (Grove 2012). Because of larger group sizes, opportunities for interaction between individuals would also be higher, which could increase group dynamics. On the other hand, unpredictability had a positive effect on mean FF time. High NDVI unpredictability in our dataset corresponded mostly to very dry areas and tropical forests, while highly seasonal environments showed lower unpredictability. A significant negative correlation between these two NDVI metrics was found. Following the same reasoning as for the effect of range on FF time, higher unpredictability might lead to smaller group sizes since it seems to be associated with environments that might have lower resource abundance or, as in the case of tropical forests, environments that can limit the formation of large groups (Barja and Rosellini 2008).

Future analysis incorporating additional social traits as well as factors that affect group formation and social interactions, aside from resource availability, will lead to a more complete understanding of inter- and intra-specific variation in FFD and social systems of mammals. Assessment of predation and social risks in many species and populations showing FFD is needed to complement the results presented in this study.

TROPHIC LEVEL MAY PROVIDE A KEY TO UNDERSTANDING FISSION-FUSION DYNAMICS

Although we found evidence for an association between resource availability and social traits in terrestrial mammals, this may not apply equally to all mammals with FFD. Evidence for this disparity comes from the low variance explained by most models in contrast to the higher explanatory power of models fitted to trophic levels, separately (Fig. 3). These results suggest that the FFD response to environmental factors is influenced by diet. Variation of fission-fusion dynamics across omnivores seemed to be less related to resource availability than in herbivores or carnivores. It is possible that the dietary flexibility of omnivores allows them to reduce feeding competition, in which case, FFD could be more a response to social factors or to other kinds of resources (e.g., nest sites). In chimpanzees, an omnivorous species and a common example of fission-fusion societies, estrous females are the main driver of FFD (Anderson et al. 2002).

Interestingly, NDVI had a stronger impact on FFD in carnivores than in herbivores, in spite of NDVI being a strong predictor of phenology and primary productivity, which directly influences herbivore abundance and distribution (Pettorelli et al. 2011). Few studies have explored the relationship between carnivores and NDVI, although primary productivity is expected to impact all elements in the food web. Analyses of habitat selection and home-range variation in carnivores have been linked to NDVI (Nilsen et al. 2005; Basille et al. 2009; García-Rangel and Pettorelli 2013). In our study, mean NDVI explained a small fraction of the variation in s.d. subgroup size of herbivores, while range and unpredictability were slightly related to the mean group size (Fig. 2.3). In carnivores, NDVI metrics were correlated to almost all traits modeled. An explanation to this difference might rely on the divergence in territoriality and foraging behavior between these two trophic levels. In general, herbivorous mammals are non-territorial foragers, moving between depleted food patches. Their response to temporal changes in resource availability usually involves some sort of long-distance movement like migration or nomadism (Mueller and Fagan 2008; Teitelbaum et al. 2015). Individuals could also compensate for periods of resource scarcity by maintaining larger home ranges or territories, even during high-abundance periods (Lindström 1986). Such migratory and long-distance movements as well as FFD would represent different but not exclusive strategies to cope with spatiotemporal heterogeneity of resource availability in herbivores. In contrast, carnivores, which in this study included some large African species and insectivorous bats, are either territorial or have some sort of central place foraging strategy. Therefore, responses to temporal changes in resource availability might be spatially constrained, impacting social behavior. This way, group dynamics in carnivores might represent an adaptation not only to spatial, but to temporal heterogeneity in resource distribution. FFD may thus represent a convergent strategy that repeatedly appears in different taxa as a response to variation in resource availability at different temporal and spatial scales. In herbivores and omnivores, FFD might be mostly affected by short-term changes and patchy distribution of resource, while long-term temporal variation might be more influential in carnivores. Heterogeneity at larger time scales seems to limit subgroup size through similar mechanisms as those proposed by the resource dispersion hypothesis (Carr and Macdonald 1986; Johnson et al. 2002).

All things considered, variation in social systems observed in this study supports the hypothesis that social systems are influenced not only by current ecological conditions, but also by evolutionary relationships (Sobrero et al. 2014). We suggest that changes in group composition, size, and cohesion through FFD characterize an adaptive response to environmental variation that acts on phylogenetically defined patterns of group size constrained by cognitive abilities.

Table 2.1 Combinations of covariates for fitted models on selected social traits. In the equations below ‘mean’ refers to mean annual NDVI (NPP), range refers to the annual range of NDVI (NPP), and ‘unpredictability’ refers to the average coefficient of variation of biweekly NDVI (NPP) scores across years.

Model	**Predictors**
1	$\beta_0 + \beta_1\ mean$
2	$\beta_0 + \beta_1\ range$
3	$\beta_0 + \beta_1\ unpredictability$
4	$\beta_0 + \beta_1\ mean + \beta_2\ range$
5	$\beta_0 + \beta_1\ mean + \beta_2\ unpredictability$
6	$\beta_0 + \beta_1\ range + \beta_2\ unpredictability$
7	$\beta_0 + \beta_1\ mean + \beta_2\ range + \beta_3\ unpredictability$
8	$\beta_0 + \beta_1\ mean + \beta_2\ brain\ mass + \beta_3\ body\ mass$
9	$\beta_0 + \beta_1\ range + \beta_2\ brain\ mass + \beta_3\ body\ mass$
10	$\beta_0 + \beta_1\ unpredictability + \beta_2\ brain\ mass + \beta_3\ body\ mass$
11	$\beta_0 + \beta_1\ mean \times \beta_2\ brain\ mass + \beta_3\ body\ mass$
12	$\beta_0 + \beta_1\ range \times \beta_2\ brain\ mass + \beta_3\ body\ mass$
13	$\beta_0 + \beta_1\ unpredictability \times \beta_2\ brain\ mass + \beta_3\ body\ mass$
14	$\beta_0 + \beta_1\ mean + \beta_2\ range + \beta_3\ brain\ mass + \beta_4\ body\ mass$
15	$\beta_0 + \beta_1\ mean + \beta_2\ unpredictability + \beta_3\ brain\ mass + \beta_4\ body\ mass$
16	$\beta_0 + \beta_1\ range + \beta_2\ unpredictability + \beta_3\ brain\ mass + \beta_4\ body\ mass$
17	$\beta_0 + \beta_1\ brain\ mass + \beta_2\ body\ mass$
18	β_0

Table 2.2 Generalized estimating equations (GEE) output for best-fit models of selected social traits on resource availability and brain size in terrestrial mammals.

Social trait	**NDVI Mean**	**NDVI Range**	**NDVI Unpred.**	**Brain mass**	**Best model**	**ΔQIC**	**mR^2**	**r^2**
Mean group size		+			2	7.4	0.02	0.19
Mean subgroup size		+			2	8.1	0.05	0.23
Minimum subgroup size			-		10	26.2	0.01	0.12
Maximum subgroup size	-				8	13.6	<0	0.10
Standard Deviation of subgroup size					18	0	---	---
Mean FF time		-	+		6	11.8	0.18	0.45

Table 2.3 Generalized estimating equations (GEE) output for best-fitted models of selected social traits on resource availability and brain size of marine mammals.

Social trait	**NPP Mean**	**NPP Range**	**NPP Unpred.**	**Brain mass**	**Best model**	**ΔQIC**	**mR^2**	**r^2**
Mean group size					18	0	---	---
Mean subgroup size				+	17	29.6	0.22	0.47
Minimum subgroup size					18	0	---	---
Maximum subgroup size		-		-/+	12	30.0	0.18	0.43
Standard Deviation of Subgroup Size			+	+	10	46.8	0.07	0.32
Mean FF time					18	0	---	---

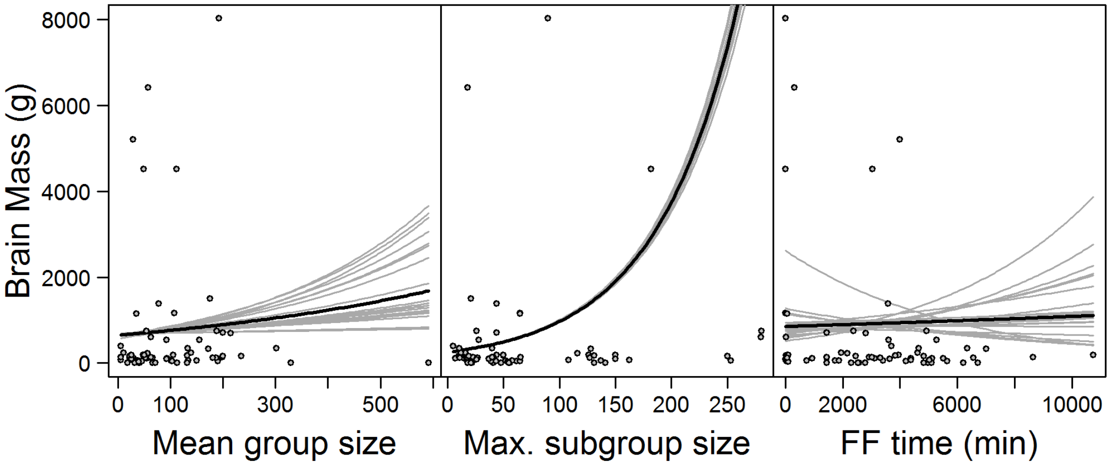

Figure 2.1 Generalized Estimating Equations (GEE) fitting results to test the SBH. A consistent positive and significant relationship was only found between brain size and maximum subgroup size. Grey lines represent fitted trends for iterations of MICE imputation; and the black line is the mean trend.

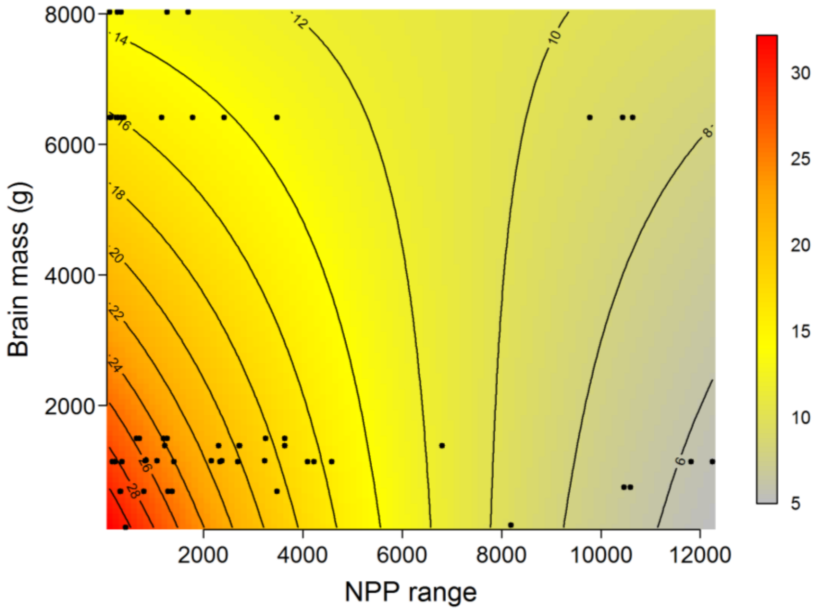

Figure 2.2 Predictive plot of the effect of NPP range and brain mass on maximum subgroup size of marine mammals. Colors in the bar represent maximum subgroup size. At smaller ranges, maximum subgroup size decreases with brain size. The opposite trend occurs at higher range values. Points represent observed population values.

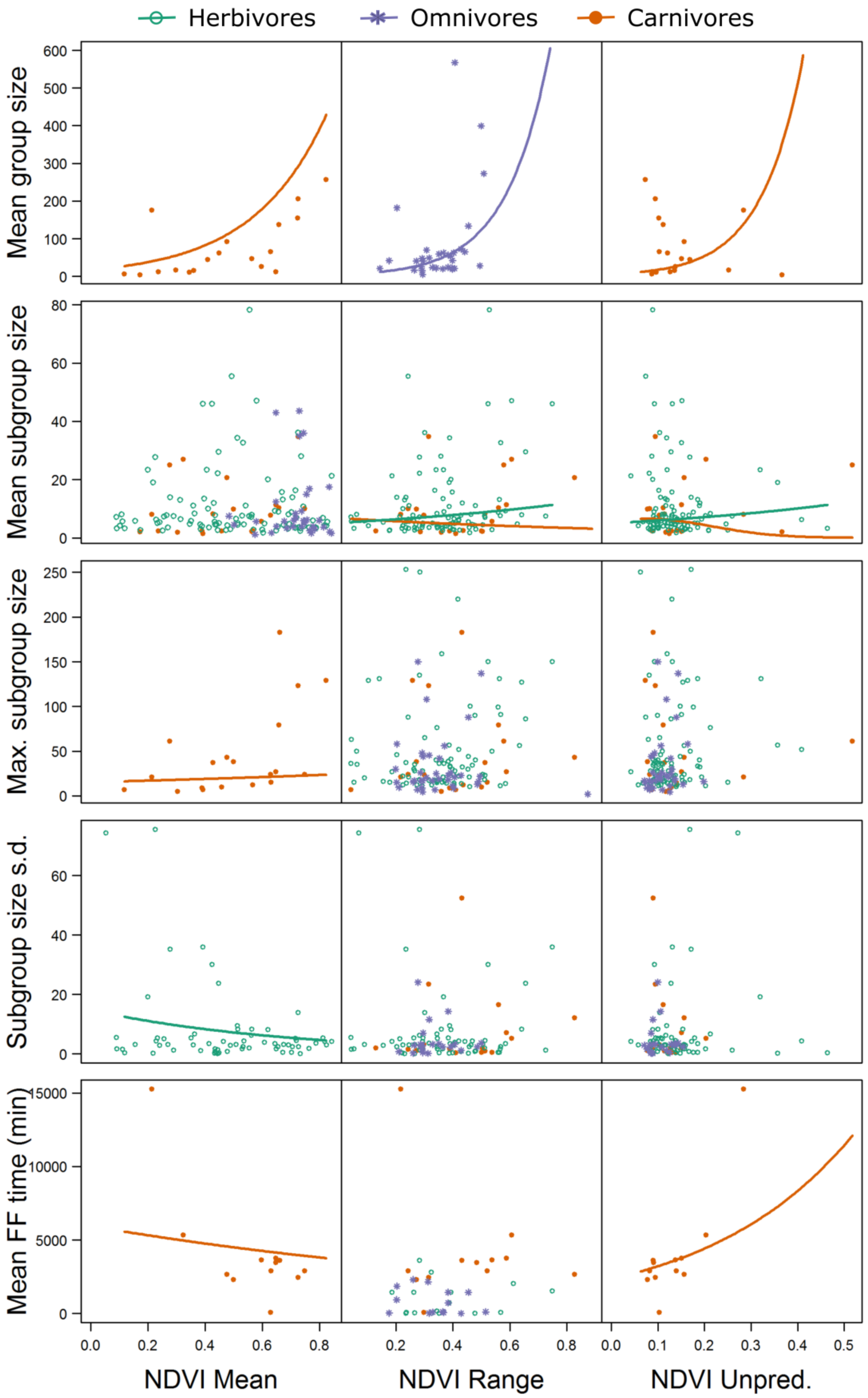

Figure 2.3 Effect of NDVI on social traits in different trophic levels. FF dynamics of omnivores were the least affected by NDVI, while the FF dynamics of carnivores

were most strongly influenced by it. Points represent observed values and lines represent significant correlations as estimated through GEE regressions.

Chapter 3: PREDICTING FISSION-FUSION DYNAMICS FROM SINGLE MOVEMENT TRACKS IN ORANGUTAN

Coauthors: SHAUHIN ALAVI, ELIEZER GURARIE, CAREL VAN SCHAIK, MARIA VAN NOORDWIJK, ERIN R. VOGEL, AND WILLIAM F. FAGAN.

Abstract

Background: Fission-fusion dynamics are widespread throughout the animal kingdom. However, studying fission-fusion dynamics in wild animals is challenging, requiring extensive and detailed datasets. To be most useful in studies of fission-fusion dynamics, movement data need to provide information on both animals' space use and their behaviors, which are influenced by environmental and social factors. Here, we used movement data of wild orangutans to infer their fission-fusion dynamics. We used generalized boosted regressions of group presence and group size to evaluate the power of movement metrics to predict attributes of fission-fusion dynamics. We also used simultaneously tracked pairs of individuals to estimate cohesion dynamics.

Results: All movement metrics provided information on group presence and group size. The probability of an orangutan being in a group was inversely related to the straightness of its movement track, and was highest at low and high numbers of behavioral phases and speed. The time scale of movement autocorrelation, the number of behavioral phases, and path straightness were strong predictors of group size. The probability of fusion increased with increasing cohesion in direction and speed between dyad members, although dyads moving in random directions also had a high probability of being together. Estimates of the time scale of autocorrelation for different behavioral phases were correlated with the degree of cohesion in direction and speed, linking temporal changes in movement to dynamics in group cohesion.

Conclusions: These results demonstrate that movement metrics alone can be used to infer attributes of the fission-fusion dynamics of orangutans, which can be complemented with analysis of dynamic interactions of simultaneously tracked individuals.

Keywords: generalized boosted regression, behavioral changes, dynamic interactions

Introduction

The way an animal moves is determined by multiple factors, including its internal state, navigational capacity, and environmental factors (Hancock and Milner-Gulland 2006, Mueller and Fagan 2008, Nathan et al. 2008). In general, a behavioral state of an individual, which is also determined by a combination of internal and external factors, is expected to be statistically different from other behavioral states based on the variation in movement parameters (Morales et al. 2004). For example, movement by herbivorous animals foraging within a food patch is often characterized by short step lengths, larger turning angles, and more frequent turns. In contrast, animals traveling between food patches will move faster and more directed, such that their movement tracks feature less frequent turns with smaller turning angles (Patterson et al. 2008). This relationship between foraging behavior and movement has been at the centre of the development of methods to model movement paths and describe behavioral changes using relocation data (Morales et al. 2004; Barraquand and Benhamou 2008; Gurarie et al. 2009; Thiebault and Tremblay 2013).

Interpretation of changes in movement parameters usually involves food resources, habitat, and/or landscape characteristics as main drivers of behavioral responses (Fritz et al. 2003; de Knegt et al. 2007; Dalziel et al. 2008). However, movement patterns of animals, and in particular movement patterns of social animals, might also be affected by the presence of conspecifics, which can affect movement decisions directly or indirectly. An alteration in conspecific interactions, for example, due to changes in group size or membership, could alter the movement pattern of an individual that needs to adjust its speed and direction to stay in or outside the group (Hoare et al. 2004; Jacobs et al. 2011). On the other hand, the presence of conspecifics can work as an indicator of habitat quality, driving movement decisions without the need for direct interactions (Donahue 2006; Kawagushi et al. 2006; Wagner et al. 2009). In theoretical scenarios, where the effect of conspecifics results from direct interaction, animals moving in groups can benefit from improved navigational performance, i.e., more directed, less tortuous movement (Codling et al. 2007; Berdahl et al. 2013). Improved navigational performance due to group formation has also been observed in homing pigeons, which traveled faster and more directed when in flocks than when solitary, although at a higher energetic cost (Dell’Ariccia et al. 2008; Usherwood et al. 2011). However, empirical studies on primates suggest that as part of the cost of grouping, individuals travel longer distances and invest more time moving when accompanied by others (Chapman et al.

1995; Gillespie and Chapman 2001). Because the benefits and costs of a selected habitat or food patch might be constrained by the presence of conspecifics (Fortin et al. 2009), it is important to understand the effects of conspecifics on movement behavior.

Mammals living in groups are characterized by a certain degree of fission-fusion dynamics, which can be defined as the temporal variation in “spatial cohesion and individual membership in a group” reflected in splitting and reshuffling of subgroup composition (Aureli et al. 2008; de Waal and Tyack 2009). Historically, studying fission-fusion dynamics has been challenging, as accurate assessments of fission-fusion behavior require extensive spatiotemporal data on the locations of all group members. However, the increasing availability of movement data, together with analytical approaches that link movements to other aspects of behavior, presents an opportunity to develop analytical methods to infer harder-to-obtain types of behavior, such as fission-fusion dynamics, from easier-to-obtain movement patterns (Cagnacci et al. 2010)**.**

Here, we evaluated whether we could predict fission-fusion dynamics from movement data of orangutans. The hypothesized relationship between movement behavior and group formation rests on the idea that detailed information from individual movement tracks can accurately indicate the grouping behavior of those individuals (i.e., whether an animal was traveling by itself or in a group, and if in a group, how big of a group). We also explored whether the temporal dynamics of group cohesion were effective descriptors of fission-fusion dynamics. We expected temporal variation in movement parameters to be correlated to temporal changes in group cohesion. Finally, we discussed two alternative hypotheses of movement performance. Namely, we asked whether movement performance improves (i.e., movements are faster and more directed) with group presence as predicted by theoretical models or whether movement performance is lower in groups as a manifestation of the cost of grouping.

Methods

FOCAL SPECIES

Orangutans (*Pongo pygmaeus)* live in semi-solitary systems with some degree of fission-fusion dynamics, where the main stable association occurs between mother and offspring (Rodman 1979; van Schaik 1999; Delgado and Van Schaik 2000). The fruit-based diet of orangutans, combined with their large body size, limit their gregariousness. As for many other species with fission-fusion systems, the distribution and abundance of food patches leads to variation in group sizes (Sugardjito et al. 1987; Utami et al. 1997). In a single day, an individual orangutan associates on average with up to 9.7 individuals, and females tend to form groups with another independent individual (Utami et al. 1997; van Schaik 1999).

Orangutan group dynamics are conditioned by the reproductive season. Subadult males can be solitary or found in groups, also including females. Non-dominant but sexually active (unflanged) male adults rarely associate with other individuals, except during the reproductive season, when they approach and force females to copulate (Fox 2002). Adult flanged males are approached by several females travelling with their infants during the breeding season, but remain mostly solitary outside this season (van Schaik 1999; Utami et al. 2002). These groups can last several days and even months (Utami Atmoko et al. 2009). Subadult females are mostly solitary, while adult females with infants can form large foraging groups (van Schaik 1999). Orangutans can form feeding parties around large food patches, but also travel together between food patches (Mitani et al. 1991; Fox et al. 2004). Group formation in orangutans plays a key role in reproduction, and may also function as a mechanism to avoid sexual harassment and provide opportunities for social learning (Fox 2002; Schuppli et al. 2016).

Movement and behavioral data on wild Bornean orangutans (*P. p. wurmbii*) were collected at the Tuanan Research Station in Borneo, Indonesia (2°09’S, 114°26’ E). The area corresponds to a peat swamp forest that is recovering from selective and illegal logging during the 1990s and 2000s (Vogel et al. 2015). Data were collected between September 2011 and June 2015 based on daily focal observations of one to five individuals following a standardized protocol (van Schaik 1999).

Movement data of 60 individuals were obtained from GPS locations recorded at 30 seconds, 1 minute, and five minute intervals by observers on the ground using hand-held GPS devices. Data with temporal resolution below five minutes were coarsened to a five minute resolution. We removed individuals followed for less than six hours or with fewer than 10 relocation points, so that the final dataset included 58 orangutans and 1365 daily tracks. We also assumed a GPS location error of five meters, clustering consecutive relocation points within that distance (Janmaat et al. 2006). In addition to relocation, observers recorded presence and number of other individuals within 50 m of the focal animal as part of a group. When possible, the identity of group members was also recorded.

MOVEMENT METRICS

We quantified a standard series of measures for characterizing animal movements from GPS data (Austin et al. 2004; Benhamou 2004; Gurarie et al. 2009; Laidre et al. 2012). Specifically, we estimated mean speed, maximum speed, mean persistence velocity, mean turning velocity, persistence index, straightness index, total displacement, and total path to characterize each track (Table 3.1). We fitted unbiased correlated velocity movement models (UCVM) to each track. These are continuous-time models that assume movement to follow an Ornstein-Uhlenbeck process without velocity correlation. They are parameterized by the mean speed value (ν) and the time scale of autocorrelation (τ) (Johnson et al. 2008; Zattara et al. 2016). We obtained maximum likelihood values for ν and τ using a Kálmán filter, which is implemented in the packages ‘smoove’ and ‘crawl’ for the R programming language (Gurarie et al. in prep.; Johnson et al. 2008).

We also estimated behavioral changes in the daily movement pattern of orangutans using a change point analysis (Gurarie et al. in prep.). In this analysis, users sweep a window across the relocation series to identify points at which the parameters of UCVMs fitted separately to data on both sides of the point differ. We identified four general movement behaviors in orangutans based on their mean speed and time scale of autocorrelation. These categories corresponded to resting ($\nu < 1$ m/min), slow-undirected movement ($1 \leq \nu < 10$ m/min and $\tau < 3$ min), slow-directed movement ($1 < \nu < 10$ m/min and $\tau \geq 3$ min), and fast movement ($\nu \geq 10$ m/min). We estimated the relative representation of each of these four behaviors in each individual track.

Every track was characterized by 16 movement metrics weighted by the duration of observation (Table 3.1). To determine if there were differences in the movement patterns of males and females, we performed Kolmogorov-Smirnov tests for each movement metric. In addition, every track was annotated at each time point with group presence or absence based on focal observation data. Group size was also assigned to each track, using the following categories: solitary for group absence, small for group sizes of 2 or 3 individuals, medium for those with 4 or 5 individuals, and large for those with 6 or more.

PREDICTION OF GROUPS BASED ON GLOBAL MOVEMENT METRICS

We used the set of 16 movement variables describing each individual track to predict the presence of individuals in groups and the size category of those groups. To implement our predictive models, we used generalized boosted regression models (GBM), which are based on a machine learning technique using regression trees and boosting methods (Friedman 2001; Elith et al. 2008). GBM is an additive stagewise method, in which regression trees are optimized by minimizing a loss function and by fitting trees iteratively to transformed residuals of the previously fitted loss function (Berk 2008). We implemented stochastic GBMs assuming Bernoulli loss and multinomial loss functions for group presence and group size, respectively (Friedman 2001; Ridgeway 2012). For group presence, we generated separate models for all individuals, all males, and all females. For all fitted GBMs, we used a shrinkage factor of 0.01 to reduce the learning speed of the algorithm and the odds of overfitting

(Friedman 2001; Berk 2008). This value was estimated after exploring reduction in prediction (error) with combinations of shrinkage values of 0.1, 0.05, 0.01, and 0.001 and 1000, 2000, 3000, 5000, and 10000 iterations (Elith et al. 2008). Likewise, we used a subsample of 50% of randomly selected observations at each iteration as an additional measure to prevent overfitting (Friedman 2002). We estimated the optimal number of iterations through cross-validation, using 70% of the observations as a training dataset. All GBMs were developed and analyzed using the package ‘gbm’ for R (Ridgeway 2012).

To identify the most informative variables, we calculated the relative influence of each variable as the mean of the relative influence for each regression tree up to the best iteration (Friedman 2001). For the most informative variables, we produced plots of the marginal effect of these variables to explore the variation in the probability of individuals being in groups and in the different group classes (Elith et al. 2008).

Information on group behavior was available for 895 tracks. Of these tracks, 231 tracks corresponded to individuals moving alone, and the other 664 corresponded to individuals moving as part of a group. Large groups (n > 6 individuals) were underrepresented in the dataset, with only 31 tracks versus 475 tracks for small groups, which was the most frequent class. To avoid bias due to unbalanced sampling, we used a SMOTE (Synthetic Minority Over-sampling Technique) algorithm to increase the relative number of tracks in the less represented class (Chawla et al. 2002). We then applied our predictive models to equal sized (n = 180) random subsamples of each size class. We used the package 'DMwR' for R to apply the SMOTE algorithm (Torgo 2011).

FISSION-FUSION DYNAMICS BASED ON MOVEMENT OF DYADS

We used simultaneously tracked dyads (i.e., pairs of individuals) of orangutans to determine the spatiotemporal changes in cohesion (one of the dimensions defining fission-fusion dynamics, Aureli et al. 2008). We explored these changes in cohesion based on distance and correlation of movement in terms of direction and speed. For every dyad we estimated the distance between their tracks using a time threshold of three minutes to define simultaneous fixes. Of 248 dyads, 60 pairs (hereafter, "associated dyads") showed some temporal association, based on a proximity threshold of distance between individuals ≤ 50 m. These associated dyads were represented by 206 pairs of tracks. The 50m threshold for spatial association follows the definition of groups used in the sampling protocol for orangutans in the study area (van Schaik 1999).

Based on proximity, we identified periods of fission for each associated dyad when individuals were more than 50 m apart, while they were assumed to be 'fusioned' when the members of the dyad were within 50 m of each other. For each track, we estimated the duration of fission and fusion periods and the fission-fusion rate as the frequency of changes between these periods.

As an additional measure of cohesion, we calculated a dynamic interaction index (*DI*) for each dyad at a local scale (Long and Nelson 2013). This index assumes a movement track as a collection of steps, each one of them characterized by direction

(θ) and displacement (d). The product of direction and displacement interactions gives the dynamic interaction index.

At each step, direction interaction *(DI_θ)* is estimated as the cosine of the angle between directions of the dyad members. If $d = 0$, direction would be undefined. If only one of the dyad members has undefined direction, $DI_\theta = 0$. If both dyad members have undefined direction, $DI_\theta = 1$. Displacement interaction *(DI_d)* is defined as:

$$DI_d = g(d_t^1, d_t^2) = 1 - \left(\frac{|d_t^1 - d_t^2|}{d_t^1 + d_t^2}\right)^\alpha$$

where d_t^1 and d_t^2 are the displacements at time *t* of individuals 1and 2, respectively. α is a scaling parameter that determines the amount of difference allowed to define an interaction as positive (Long and Nelson 2013). If both dyad members are not moving (i.e. $d_t^1 = d_t^2 = 0$), $DI_\theta = 1$. We assumed a scaling parameter of 1 in our analysis. We used the package ‘wildlifeDI’ for R to estimate dynamic interaction values (Long et al. 2014).

To explore the relationship between dynamic interaction and fission/fusion intervals identified based on proximity, we fitted generalized linear models assuming a binomial distribution for fission/fusion. We applied different combinations of dynamic interaction, direction interaction, and displacement interaction as predictors (Table 2). We relied on the Akaike Information Criterion (AIC) for model selection.

Changes in movement parameters due to behavioral changes could be related to fission-fusion dynamics. To explore these relationships, we modeled the proximity and dynamic interaction values in response to the estimated speed (v) and time scale of autocorrelation (τ) of each behavioral phase identified in the change point analysis.

For each of these behavioral phases, we estimated the median and the mean of the proximity and dynamic interaction index, respectively, for the duration of the behavioral phase and for each individual belonging to associated dyads. We used linear mixed models with speed and time scale of autocorrelation as fixed effects and the individual orangutans as random effects. We used the package ‘lme4’ for R to fit these models (Bates et al. 2015).

Results

Orangutans move slowly through their forests. In a single day, orangutans moved at an estimated speed of 2.1 m/min based on fitted correlated velocity models. In 12 hour periods, an animal covered on average 1742 m with a total displacement of 497 m. Autocorrelation was in general low, but changes in movement behaviors indicated the presence of intervals of more directed movement (Fig. 3.1). An individual movement track was a combination of different movement patterns that could be interpreted as behavioral changes. Based on the change point analysis, orangutans had between 1.4 and 7.5 behavioral phases during a 12 hour period (average 4.1 phases ± 0.03). These phases could be grouped into four types based on the combination of autocorrelation timescale and speed parameters obtained from the fitted models (Table 3.2). Orangutans spend most of the time (76%) in slow – undirected movement, followed by slow – directed movement (19%). Complete resting/immobile and fast movement occupied only 2.5 and 1.9% of the time, respectively. There were no differences between males and females in seven of the 16 computed metrics (Table 3.3). A difference was found in maximum speed, with males reaching higher values than females. Based on persistence velocity, males also moved in a much more directed pattern than females. These differences were also reflected in higher time scale of autocorrelation, estimated speed, straightness and persistence in males. Males also traveled farther away than females (Table 3.3). Males spent more time than females using slow – directed movements and females invested more time than males in slow – undirected movement. Females were more often associated with other individuals in a group (90% of tracks) in comparison to males (56% of tracks).

PREDICTION OF GROUPS BASED ON GLOBAL MOVEMENT METRICS

Based on gradient boosting classification, all movement parameters were informative of the group status of orangutans. The most informative variables to predict presence of groups were the number of behavioral phases, straightness, and mean speed, which together accounted for 32% of the variation. The probability of group membership tended to increase with the number of behavioral phases; however, this probability drops below 0.5 at intermediate numbers of behavioral phases (Fig. 3.2A). Orangutans in groups showed less directed paths than those traveling alone (Fig. 3.2A). In terms of speed, individuals not moving or traveling fast were more likely to be in groups than those at intermediate speeds (i.e. $0.8 < \text{mean speed} < 1.5$ m/min), which were mostly solitary. Probability of groups also increased with higher persistence velocity and estimated speed (v). Individuals in groups were more likely to cover shorter distances in one day, as higher total displacement and travel path resulted in lower probability of grouping (Appendix Fig. A3.1). Including all 16 predictive variables, the accuracy of predicted presence of groups was 85%.

Predicting male presence in groups using movement parameters was difficult, with the gradient boosted classification yielding only 35% accuracy for the test dataset. In contrast, movement parameters were much better at predicting group presence for females (93%). Time spent moving fast, estimated speed, and persistence index were the most informative variables, explaining altogether 43% of the variation. Female orangutans that spent none to very little time moving fast were more likely to be in groups. For females, the probability of group presence increased with decreasing estimated speed and with increasing persistence index. Individuals in groups also tended to show higher turning velocities and more than two behavioral changes. Individuals in groups also tended to move at very low (< 1.4 m/min) or high (> 2.9 m/min) speeds, i.e., intermediate speeds were associated to solitary females. Marginal effect plots of all movement metrics are included in the appendix (Fig. A3.2).

Gradient boosted regression of group size based on movement parameters identified time scale of autocorrelation (τ), maximum speed, number of behavioral phases, and straightness as the most informative variables (Fig. 3.2B). These four variables together accounted for 35% of the variation. At smaller autocorrelation scales, orangutans were more likely in a small or medium size group, while individuals were more likely to be solitary at larger autocorrelation scales (Fig. 3.2B). At higher maximum speed values (> 43 m/min) individuals were also more probably solitary, while small and medium sized groups more likely occurred when maximum speeds were low (< 14 m/min). The probability of solitary individuals decreased with the number of behavioral phases (Fig. 3.2B). If very few behavioral phases occurred (i.e., less than four in 12 hours), orangutans were likely to be solitary or in small groups. At large numbers of phases (i.e., more than five in 12 hours), medium size groups were more probable (Fig. 3.2B). Large groups were more likely when movement paths were tortuous (straightness < 0.15), whereas straightness > 0.7 implied solitary individuals (Fig. 3.2B). Small groups were more probable than other size classes at low and high estimated speeds ($v < 0.2$ m/min and $1.6 < v < 1.9$ m/min), medium size groups at $0.2 < v < 0.7$ m/min, large groups at $1.1 < v < 1.4$ m/min, and solitary at $v < 1.9$ m/min (Appendix Fig. A3.1). Large groups occurred more likely at high positive persistence velocities (i.e. fast directed movement), but also more likely at lower persistence index values (i.e. less directed movement). Small and medium size groups tended to show more directed movement according to this index, while solitary individuals were more probable at negative persistence (i.e. individuals tending to move back and forth). At negative turning velocity values, small groups were more probable, while solitary individuals were associated with small negative and positive turning velocities. Orangutans were more likely to be in medium size groups when travel paths were longer and in small groups for shorter travel paths (Appendix A3.3). Movement parameters predicted all size classes with 78 to 88% accuracy.

FISSION-FUSION DYNAMICS BASED ON MOVEMENT OF DYADS

Based on estimates of local proximity, fission of associated orangutan dyads occurred 0.14 times/hour. These fission intervals lasted between five and 681 minutes, with a median of 90 minutes. Fusion intervals, on the other hand, were longer (median = 568.5 minutes) and occurred less often (median = 0.09 times/hour). Associated dyads spent on average 81% of the observation time fused.

Cohesion, as estimated by the dynamic interaction index, DI, was higher during fusion periods (i.e., when dyads were associated). In general, orangutans showed higher displacement interaction (DI_d) between dyad members than direction interaction (DI_θ) during both fission and fusion intervals. These two components of cohesion both predicted fission-fusion events, but DI_d had a higher effect than DI_θ (glm: $\beta_{DI.\theta} = 1.59 ***, \beta_{DI.d} = 2.42 **$). The probability of dyads fusioning exceeded 0.5 when $DI_\theta < 0.$, meaning that individuals moving at random directions from each other or slightly opposite directions could have a higher chance of being associated than separated. Individuals moving in the same direction had a high probability of being fusioned, as dyads with $DI_d > 0.4$ had a high probability of being associated (Fig. 3.3).

Results of generalized mixed models of proximity and fission-fusion dynamics as predicted by individual movement parameters during behavioral phases, showed a positive effect of the time scale of autocorrelation (i.e., degree of directedness) on DI. This tended to increase during periods with more directed movement. However, the effect of autocorrelation varied greatly among individuals (Fig. 3.4). Variations in proximity and in DI_d or DI_θ were not explained by the estimated speed and time scale of autocorrelation characterizing behavioral phases.

Discussion

Our results showed that both movement metrics and analysis of simultaneous movement tracks (i.e., associated dyads) can provide details on fission-fusion dynamics. A combination of movement metrics that accounted for speed, tortuosity, distance traveled, and behavioral changes accurately predicted the probability of a tracked orangutan being in a group and the size of the group. Temporal analysis of cohesion in associated dyads, which took into account distance and the degree of interaction in terms of direction and speed between dyad members, provided estimates of fission-fusion rates and a link between association dynamics and movement behavior.

Males and females differed in their movement patterns. In general, males travelled faster, in a more persistent direction, and moved farther than females (Table 3.3). These differences are in accord with orangutan males being able to plan their travel direction in advance, which leads them to stay moving towards a previously set goal in a more directed way (van Schaik et al. 2013). However, metrics indicative of how directed or tortuous their paths were (e.g., straightness or persistence velocity) suggest a general trend of low directedness. This apparently paradoxical result, in which males move in a planned direction but with high tortuosity, is actually to be expected in arboreal animals, where they would need to constantly change directions due to canopy connectivity (Shepard et al. 2013). The movement pattern of males also suggests that they tend to travel as individuals, because the probability of group membership decreases with straightness and the size class “solitary” was more probable with increasing autocorrelation (Fig. 3.2). Based on the different movement behaviors, we found that females spent more time than males in slow-undirected movement. This type of movement could be related to periods of feeding. Females also spent less time resting than males. Orangutan females have been found to spend more time feeding and less time resting then males in different study areas (Fox et al. 2004). These differences in time budget could be linked to costs derived from larger group sizes in females (Fox et al. 2004), which supports the alternative hypothesis that navigational performance is lower when individuals are moving in groups.

All movement metrics were informative about the presence and size of groups. The general trend of increasing probability of group presence and larger group sizes with increasing tortuosity also offered support for lower navigational performance linked to group behavior. However, other metrics were also informative of grouping behavior and should be considered when inferring details on social behavior from movement data. Group presence and size were also associated with the number of behaviors, and estimates of movement parameters of each behavioral phase helped predict temporal changes in cohesion (*DI*). Change point analysis is one valuable tool for inferring social behavior from movement data (Patterson et al. 2008; Gurarie et al. 2009; Edelhoff et al. 2016; Gurarie et al. 2016). Although researchers have previously analyzed movement data to infer foraging behavior and activity budgets in a range of species (Royer et al. 2005; Bailey et al. 2008; Fryxell et al. 2008; Breed et al. 2009), such approaches have only rarely been used to understand social behavior (Polansky et al. 2010; Pays et al. 2012). Further development of methods that incorporate changes in movement parameters and estimates of coordination or cohesiveness in movement would create additional opportunities for extracting information on behavior from movement data of social animals (Polansky and Wittemyer 2011).

Movement metrics were only weakly predictive of male membership in groups. Indeed, males moved similarly when they were in groups as when they were solitary. Such lack of predictability could arise because male involvement in groups may be restricted to associating for reproduction, except for dependent individuals (van Schaik 1999). If correct, such male behaviors would clearly limit the frequency of associative events. However, because interactions between adult males and females depends on male dominance (Fox 2002; Knott et al. 2009), different male behaviors may also have different impacts on movement patterns. For example, changes in movement due to brief interactions of a non-dominant male that harasses a female would have only minimal influence on global movement metrics. In contrast, interactions with dominant males could last longer and thus impact movement metrics in a substantial way (van Schaik 1999). However, such interactions are not frequent in orangutan populations (Fox 2002), and as a result may not be well represented in our data set. An alternative explanation is that grouping for reproductive purposes are led by the dominant male such that travel costs, and changes in movement behaviors, that are associated with grouping would only affect females.

A positive relationship between time scale of autocorrelation and dynamic interaction across behavioral phases of tracks indicates that temporal variation in the movement pattern of individuals can predict temporal dynamics. However, variation in this relationship among individual orangutans limits its predictive power, such that individual, non-simultaneous tracks would not be as useful at discriminating temporal dynamics of groups. More active female orangutans (i.e., those traveling more) associate more often with other individuals than do less active orangutans, while the tendency for males to associate with others decreases with their age (van Schaik 1999). Given the range of variation in pairwise interactions for different age-sex classes of orangutans (Watts 2012), incorporating temporal variation in movement parameters in analyses of behavioral changes and models of cohesion should be considered.

In theoretical models and empirical studies, active grouping, instead of casual aggregations, are assumed to happen when group members align their movements and stay close to each other (Bode et al. 2012). Orangutans that fused were not necessarily aligned (i.e., $DI_\theta \leq 0$ for some probabilities of fusion above 0.5) although the probability of fusion increased with increasing DI_θ (Fig. 3.3). This suggests that fusion events were also associated with foraging behaviors and not just restricted to periods of travel. The alignment condition might be valid for traveling groups, but even in those cases, arboreal individuals will be challenged to stay aligned while finding their way between trees given severe constraints on the number and location of viable arboreal paths (Cannon and Leighton 1994). Displacement interaction (i.e., moving at similar speeds) together with proximity would be more accurate as criteria to define a group in orangutans or to differentiate between active grouping and casual aggregations.

Because of the importance of reproductive seasons and sex-age classes in the grouping behavior of orangutans, analyses that consider different time frames and seasons would allow the evaluation of the effect of temporal changes in fission-fusion dynamics. Understanding the relationship between movement and group behavior also leads to a better comprehension of population dynamics (Morales et al. 2010). This has important implications for conservation. Bornean orangutans are a critically endangered species due to habitat loss and wildflife trade (Ancrenaz et al. 2016). Understanding the effects of conspecifics on movement and their implications for population dynamics can offer support for recovery and reintroduction programs (Russon 2009).

Table 3.1 Movement parameters used to characterize individual tracks of orangutan.

No.	**Parameter**	**Definition**
1, 2	Speed (*mean, maximum*)	Mean and maximum of the ratio of step length and step duration.
3	Persistence velocity	Mean of the persistence velocity, as defined by Gurarie et al. 2009. At a given step, the persistence velocity is the product of the scalar speed and the cosine of the turning angle. It indicates velocity and tendency to persist in a direction.
4	Turning velocity	Mean of the turning velocity, as defined by Gurarie et al. 2009. At a given step, the turning velocity is the product of the scalar speed and the sine of the turning angle. It quantifies the tendency to change in a direction perpendicular to the travel direction in a time step.
5	Time scale of autocorrelation (τ)	Parameter estimate obtained from fitting a movement track to an unbiased correlated velocity movement model.
6	Estimated speed (v)	Parameter estimate obtained from fitting a movement track to an unbiased correlated velocity movement model.

No.	**Parameter**	**Definition**
7	Total displacement	Euclidean distance between the start and end points of a track.
8	Travel path	Total (summed) step lengths.
9	Straightness index	The ratio between total displacement and travel path. It is a measure of path tortuosity (Benhamou 2004).
10	Persistence index	Mean cosine of turning angles across a series of steps. It indicates the level of directedness of movement (Laidre et al. 2012).
11	Behavioral phases	Number of behavioral phases identified by a change point analysis.
12	Frequency of change points	Frequency of change points between general classes of movement behavior.
13	Resting time	Total (summed) duration of resting behavior periods.
14	Undirected – slow time	Total (summed) duration of undirected – slow movement periods.
15	Directed – slow time	Total (summed) duration of directed – slow movement periods.
16	Fast time	Total (summed) duration of fast movement periods.

Table 3.2 Models fitted to predict fission and fusion intervals based on dynamic interaction metrics (DI = dynamic interaction, DI_θ= direction interaction, and DI_d= displacement interaction).

No.	**Model**
1	$F/F \sim \beta_0 + \beta_1 DI$
2	$F/F \sim \beta_0 + \beta_1 DI_\theta$
3	$F/F \sim \beta_0 + \beta_1 DI_d$
4	$F/F \sim \beta_0 + \beta_1 DI_\theta + \beta_2 DI_d$
5	$F/F \sim \beta_0 + \beta_1 DI * \beta_2 DI_d$

Table 3.3 Comparison of average ± s.e. estimates of movement metrics for males and females with results of Kolmogorov-Smirnov tests (D). Estimates were scaled to a 12 hour period.

Metric	**Males**	**Females**	**D**	**p-value**
Mean speed (m/min)	2.1 ± 0.06	2.0 ± 0.04	0.05	0.61
Maximum speed (m/min)	15.6 ± 0.87	14.5 ± 0.72	0.10	**0.04**
Persistence velocity (m/min)	0.30 ± 0.06	-0.02 ± 0.04	0.13	< **0.001**
Turning velocity (m/min)	-0.03 ± 0.02	-0.01 ± 0.01	0.05	0.63
Time scale of autocorrelation (min)	13.6 ± 0.41	12.2 ± 0.36	0.12	**0.002**
Estimated speed (m/min)	13.5 ± 0.38	12.1 ± 0.35	0.11	**0.02**
Total displacement (m)	464.5 ± 19.8	394.9 ± 14.9	0.14	< **0.001**
Travel path (m)	1778.5 ± 35.8	1714.9 ± 26.8	0.08	0.12
Straightness index	0.37 ± 0.01	0.30 ± 0.01	0.15	< **0.001**
Persistence index	0.14 ± 0.02	0.07 ± 0.01	0.12	**0.005**
Behavioral phases	4.1 ± 0.05	4.1 ± 0.05	0.06	0.54
Frequency of change points	1.1 ± 0.06	0.9 ± 0.05	0.08	0.14
Resting time (min)	18.0 ± 3.3	16.7 ± 3.0	0.02	0.99
Undirected – slow time (min)	519.6 ± 11.6	575.7 ± 9.2	0.14	< **0.001**
Directed – slow time (min)	165.3 ± 10.4	116.4 ± 8.1	0.14	**0.001**
Fast time (min)	16 ± 3.5	11.2 ± 2.5	0.03	0.99

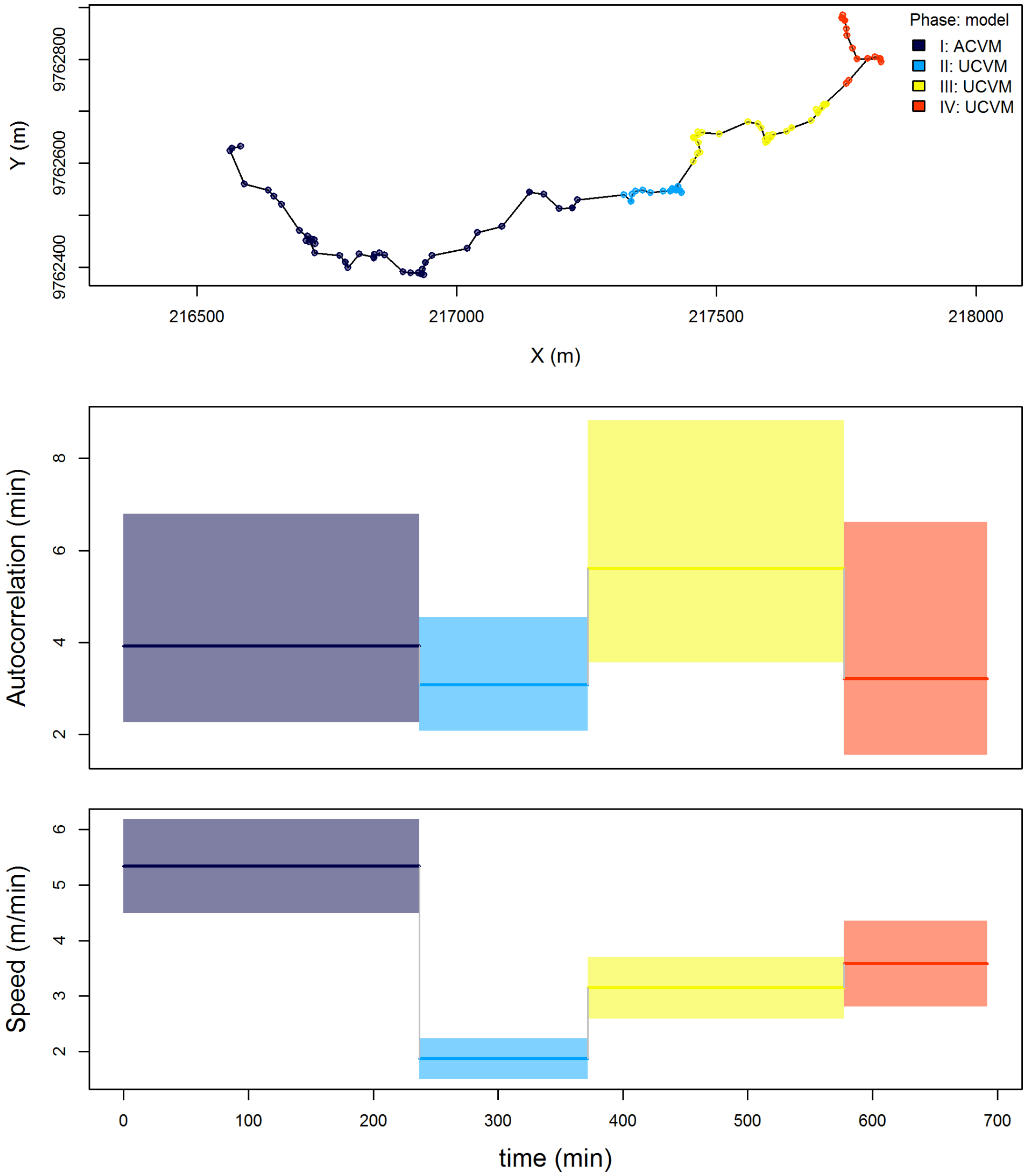

Figure 3.1 Example of a change point analysis output indicating the behavioral changes in movement in a track. Each phase is characterized by an estimated speed (v) and time scale of autorrelation (τ). In this case, the orangutan moved fast and slightly directed during the first phase (early morning hours), then changed to move very slowly for a shorter period. It increased speed and directedness in the third phase

(afternoon), which changed to a more tortuous movement by the end of the observation period (before going to the nest).

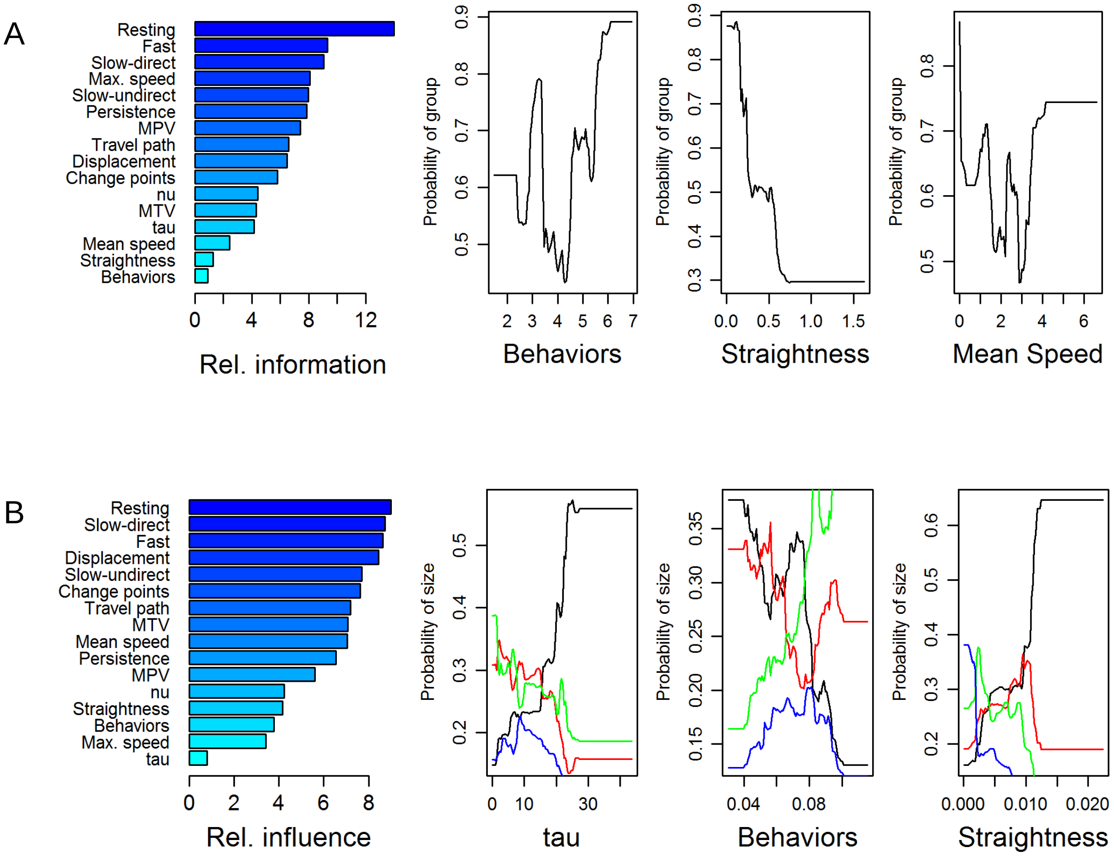

Figure 3.2 Results of gradient boosted regressions for (A) group presence and (B) group size including all individuals. Barplots show the ranking of movement metrics based on relative influence. MTV and MPV stand for mean turning and mean persistence velocity, respectively. Line plots are marginal effect plots of the most informative variables. In (A), the probability of group presence is lowest at intermediate numbers of behaviors, decreases with increasing straightness, and is lowest at intermediate mean speed. In (B), the probability of solitary individuals is highest at large time scale of autocorrelation (τ) and straightness, while the probability of large groups is highest at large numbers of behaviors (black = solitary, red = small, green = medium, blue = large).

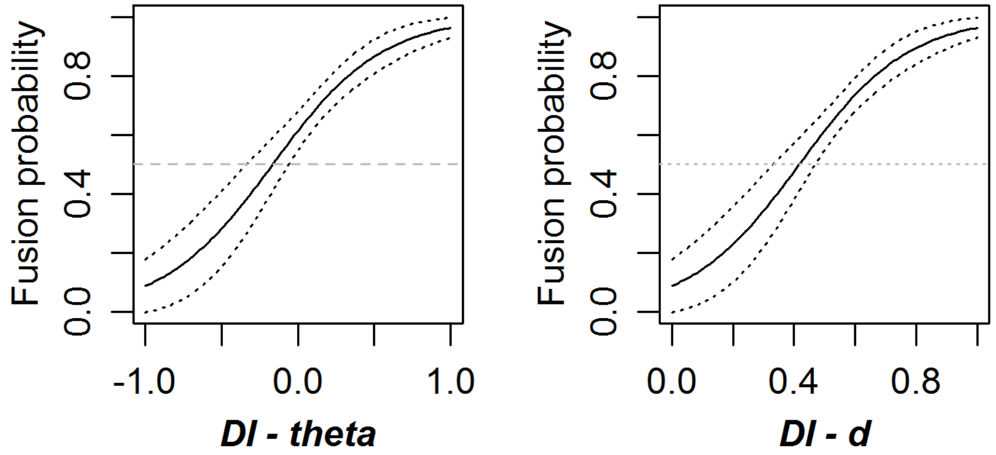

Figure 3.3 Generalized linear model prediction of fusion probability in response to the components of dynamic interaction: direction interaction (DI_θ) and displacement interaction (DI_d). Black dashed lines indicate 95% confidence intervals and the grey horizontal line marks 0.5 probability. Fusion probability increases with increases in both components of dynamic interaction.

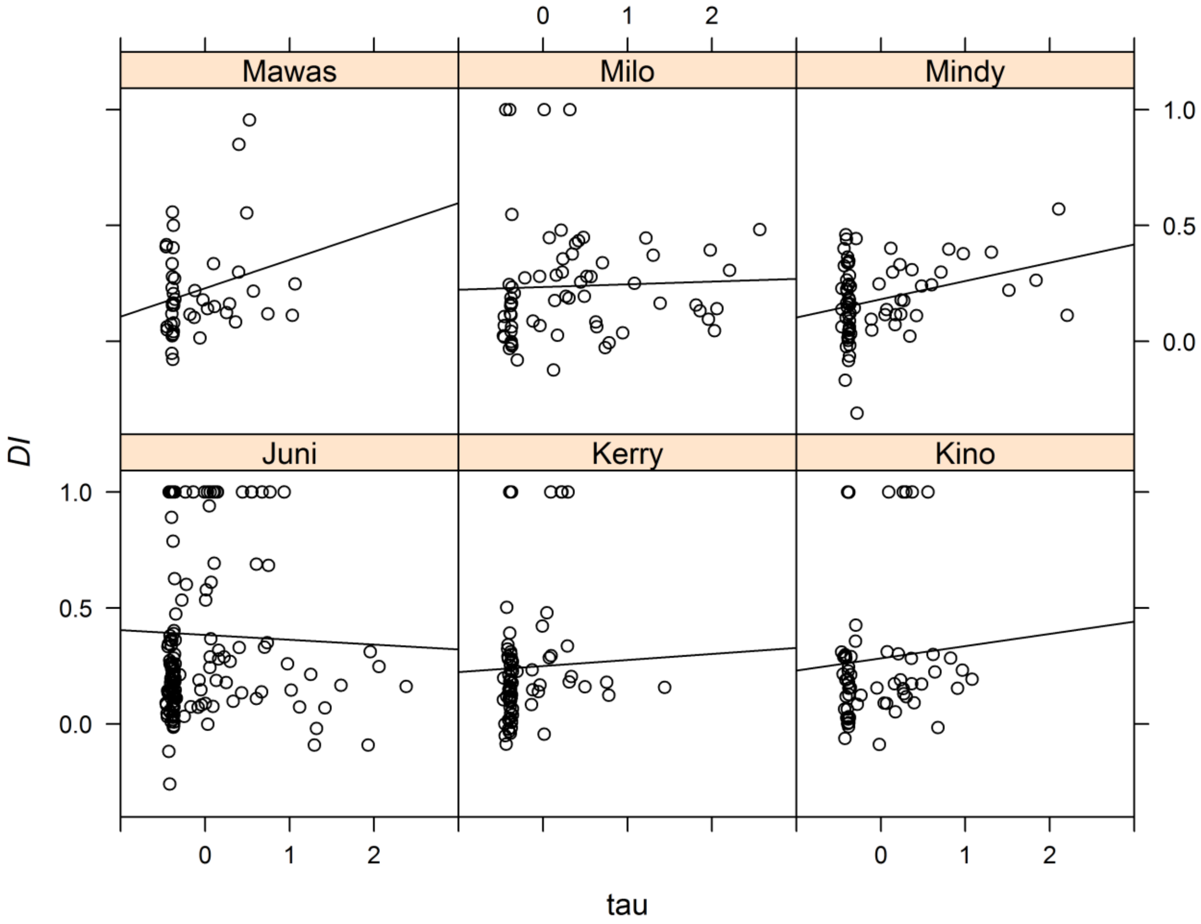

Figure 3.4 Linear fit of dynamic interaction (*DI*) in response to time scale of autocorrelation (*tau*) for six representative individual orangutans. There is a trend towards *DI* increasing with *tau*, but this is not consistent across all individuals.

Chapter 4: RECOGNITION AS A DRIVER OF COMPLEXITY IN GROUP DYNAMICS

Coauthor: WILLIAM F. FAGAN

Abstract

Recognition of conspecifics is essential for social life, as it mediates behavioral responses and social interactions. Such recognition can occur at different levels, from nest or neighborhood conspecifics to individual status, leading to different aggregation patterns that differ in their complexity. Using an agent-based model, we investigated the effects of different mechanisms of recognition acting at different levels of group association. We hypothesized that more complex systems would emerge with more complex recognition systems and used comparisons of network communities and group temporal dynamics to test this idea. We considered four nested levels of recognition (i.e., species, neighborhood, kin, and individual). Species and neighborhood recognition relied on a signal detection system, while kin and individual recognition levels utilized phenotypic matching and a memory-based system, respectively. We explored the effects of these recognition mechanisms in terms of how they influenced group structure and dynamics at three levels of group association: number of groups, group sizes, and cohesion of emergent aggregations. Variation of the recognition criterion at the species and neighborhood levels had a larger impact on grouping patterns than the difference in signal with other species or neighborhoods. Individuals aggregated into fewer, better aligned groups when they were able to quickly memorize individual identities and forget them slowly. Across the four levels of recognition, more complex grouping systems emerged when the recognition mechanisms allowed for increasing detail. The mechanism with the greatest detail, individual recognition, drove the formation of a grouping system resembling multilevel fission-fusion systems observed in wild populations of elephants or baboons. Our model demonstrates how basic rules mediating social behavior determine grouping patterns and suggests that more complex social systems can evolve with more complex systems of recognition.

Key words: signal detection theory, agent-based model, phenotype matching, individual recognition, multilevel organization

Introduction

Animals form different kinds of groups, ranging from casual aggregations around resources to stable groups with complex social structures. Living in social groups requires cognitive skills that allow individuals to constantly gather and process information about their social environment and confront that knowledge with individual needs to make decisions that would ultimately benefit their own fitness. A core element of an individual's social environment is its ability to identify other animals and then appropriately classify them based on distinctive features derived from a learned pattern. This classification process is also known as recognition (Mateo 2004; Shettleworth 2010). Because animals can be recognized at different levels (e.g., based on familiarity or kin), a variety of recognition mechanisms can occur across species or individuals (Stuart and Herbers 2000; Ward et al. 2009).

Recognition is a basic process required for social behavior. It consists of the interaction between a receiver and a signaler, in which the receiver assigns an identity to a signaler based on a matching process of cues emitted by the signaler with templates owned by the receiver (d'Ettorre, 2008; Shettleworth, 2010). The characteristics of the signal and the matching mechanism define the level at which an individual can be recognized. A signaling individual can be recognized by a receiver as a distinctive individual or as belonging to a class (e.g. offspring, mate) (Sherman et al. 1997). Most social organisms, however, not only rely on group recognition but also on more sophisticated levels of recognition, such as kin and individual recognition, where clear individual preferences for other individuals are established. For example, individuals of an ant colony will rely on nest mate or group recognition to effectively defend their nest from ants belonging to other nests (d'Ettorre & Lenoir, 2010). Within a colony, ants may recognize classes of individuals based on the task they perform, caste, age, reproductive status, and/or kin relationship (Wilson 1985; Cuvillier-Hot et al. 2001; Greene and Gordon 2003). Some ants have also been shown to recognize individuals (d'Ettorre & Heinze, 2005). Some birds are able to learn who their neighbors are, and given these recognition abilities, can direct energy and time to repel new arrivals but not their neighbors, which also increases time available for foraging and other activities (Shettleworth 2010).

Furthermore, particular species may exhibit more than one level of recognition, which can result in different patterns of association or grouping systems (e.g., casual aggregations or stable social units). For example, female chacma baboons (*Papio hamadryas*) typically associate in family units, but may form casual aggregations during periods of high resource abundance (Schreier and Swedell 2012b). Likewise, many species aggregate into very large groups during migration while maintaining small social units at local foraging scales (Henzi et al. 2009; Guttal and Couzin 2010). Understanding the mechanisms behind different recognition levels can help reveal some of the processes involved in the emergence of sociality.

Incremental increases in the level of detail necessary for recognition would also require improved cognitive skills to process the information, therefore increasing the cost of recognition. From an evolutionary perspective, selection will favor recognition mechanisms that would balance the cost-benefit involved in effective discrimination of other individuals. Benefits of recognition emerge through inbreeding avoidance, social learning, avoidance of brood parasitism, and decreased harassment of neighbors in territorial species, among others (Lyon 2006; Tibbetts and Dale 2007). Furthermore, recognition also facilitates the development of nepotistic or reciprocal altruistic social behaviors and the establishment of dominance hierarchies (Barnard and Burk 1979; Mateo 2002; Lehmann and Keller 2006).

In general, group dynamics are locally controlled, and grouping patterns emerge from the behavioral response of individuals to their neighbors and/or environmental cues. In this paper, we focused on the role of social responses to neighbors based on differential use of recognition systems, thereby linking social behavior to spatiotemporal dynamics. We aimed to determine the effects of recognition mechanisms and specificity of recognition on the structure and complexity of aggregations. Because higher specificity in recognition requires better cognitive skills, which have been related to more complex social systems (Croney and Newberry 2007; Dunbar and Shultz 2007), we hypothesized that greater specificity in recognition also leads to more complex social systems. Consequently, we expected group size to decrease when we increased the specificity of recognition from species, to neighborhood, kin, and individual. Similarly, we expected cohesion to decrease and dynamics (i.e., group size and composition turnover) between groups to increase with increasing specificity of recognition.

Methods

To determine the effect of social recognition on group formation and dynamics, we developed an individual based model with four scenarios of nested recognition levels (species, neighborhood, kin, and individual). Our model represented two populations of two species (e.g., ungulates). Each population consisted of 50 individuals moving in an open, homogeneous 2-D environment with unlimited resources (i.e., resources or competition had no influence on individual movement decisions). The environment was defined as a 500 x 500 units bounded polygon (i.e., individuals were not able to move beyond edges). To ease explanation of the model, we will use meters as the spatial units, but this is arbitrary and could be adjusted to other scales. Animals started at random locations $\boldsymbol{c_i}$with a random direction $\boldsymbol{v_i}$ (unit direction vector) and moving at a constant speed of 6 m/min.

RECOGNITION AND MOVEMENT RULES

The presence of others affected the movement behavior of individuals following a repulsion-alignment-approach model of collective motion (Couzin et al. 2002).We assumed each animal was surrounded by a circular perception field of 70 m radius (r_a) with a blind angle of 60° behind the animal. Additionally, an area of repulsion was defined around each animal at radius $r_r = 2$ m and an area of alignment at radius $r_l = 50$ m. Time was assumed as discrete and at each time step every animal would assess the presence of other individuals within its perception field and adjust its direction. Assessment of the *N* individuals within the perception field consisted of a discriminatory process that resulted in the recognition of those to which an animal would align to or approach ($n = N - u$, where u is the number of missed or correctly rejected individuals) based on the recognition level and parameters.

The most basic level of recognition in our model was species recognition, for which we relied on signal detection theory, an idea borrowed from electronic engineering and applied to understand optimization and evolution of communication in animals (Wiley 2006; Bogaardt and Johnstone 2016; Wiley 2016). Signal detection theory focuses on the effect of noise (e.g., another signal) on a receiver's performance, which can lead to errors in signal reception and affect behavioral responses (Shettleworth 2010). The theory states that an individual is exposed to a signal with an intensity coming from a given probability density function (PDF) that partially overlaps with the PDF of background noise. A threshold value or criterion for discriminating between signal and noise defines the probability of the individual correctly detecting the signal (i.e., correctly recognizing the sender of the signal).

Selection would favor receivers that can minimize detection errors (i.e., false alarms and false negatives) and maximize correct detections (Wiley 2006). In the context of our recognition models, all individuals of Species 1 were characterized by a signal intensity, s, randomly obtained from the PDF for the species signal $S_1 \sim N(\mu_1, \sigma_1^2)$. Individuals of Species 2 would also produce a signal coming from $S_2 \sim N(\mu_2, \sigma_2^2)$ (Fig. 1). We assumed $\sigma_1 = \sigma_2$, $\mu_1 < \mu_2$, and no temporal changes in S_1 and S_2 or in individual signal values. Individuals were also characterized by a recognition threshold or criterion (β_1 or β_2), which was equal for all individuals of the same species and estimated through the quantile q of the PDF. We simulated different scenarios of species recognition by varying values of $\beta_1$and μ_2 (Table 1), i.e., changing the degree of overlap between the PDFs of Species 1 and 2, thereby changing the probability of correct detection of a Species 1 sender by a Species 1 receiver (and vice versa). We used a 0.01 quantile for β_2, which corresponded to a 0.99 probability of correct detection (Fig. 4.1). At every time step of the simulations, an individual would compare the signal of other individuals within its perception field to the recognition criterion, in order to discriminate between those it would interact with and those it would not.

A second level of recognition contemplated the presence of neighborhoods and was an extension of the species recognition level, where individuals of Species 1 were distributed into two neighborhoods (e.g., nesting regions) while Species 2 remained as a single neighborhood. Each of these neighborhoods had its own PDF from which signals were randomly assigned to individuals and a constant, neighborhood-wide recognition criterion. We varied recognition criteria for both

Species 1 neighborhoods and signal difference between Species 1 neighborhood PDFs among simulated scenarios (Table 4.1). However, we maintained a large signal difference ($\Delta\mu$) between Species 1 and Species 2 ($\mu_2 = 15, \sigma_2 = 0.5$) and high recognition criteria ($\beta_1 = \beta_2 = 0.99$) for both species throughout the simulations of neighborhood recognition to minimize the effects of species recognition. At each time step, Species 1 individuals would first discriminate between species, and then between neighborhoods, to define which individuals to interact with. At all levels of recognition, Species 2 is limited to species recognition.

For kin recognition we added a phenotypic matching mechanism for Species 1, following the assumption that phenotypic similarity represents genetic relationship (Lacy and Sherman 1983; Mateo 2010). The probability of recognizing another individual as kin, $p(k)$, was a negative exponential function ($p(k) = e^{-l\Delta s_{ij}}$) where l is the rate of decay in recognition probability as a function of the signal difference between individuals i and j, Δs_{ij}. The parameter l varied among simulations, while parameters of species and neighborhood recognition were kept constant at values that maximized the probability of correct recognition at those levels (Table 4.1). In this scenario, each individual of Species 1 could now discriminate between individuals in its perception field based on species, neighborhood, and kin at every time step, to define the individuals to interact with.

To incorporate the most specific level of recognition, identification of individuals, for Species 1, we assumed that individuals were able to memorize the identity of individuals they associated with according to processes of memorizing (gaining memory) and forgetting (losing memory) (Shettleworth 2010). The probability of an individual memorizing another individual, $P(m)$, increased with the number of interactions k and the rate of memorizing g following $P(m) = 1 - e^{gk}$. We stipulated that an interaction occurred whenever two individuals were closer to each other than the alignment radius; thus *k* counted the number of times that individuals were in proximity to one another. The parameter g represented an intrinsic cognitive capacity of the species to memorize an individual per encounter.

An individual would also forget a previously memorized individual with a given probability, $p(f)$, depending on the time since last interaction t_l and a rate of forgetting h, following $p(f) = e^{-ht_l}$. We varied g and h between simulations, while using fixed parameter values for species, neighborhood, and kin recognition (Table 1). We also varied the number of individuals memorized at each time step, assuming an individual could only memorize its nearest neighbor or the closest six individuals (Ballerini et al. 2008; Herbert-Read et al. 2011). At every time step, individuals would discriminate between species, neighborhood, kin, and finally between individuals based on the probability of remembering it ($p(m) * p(f)$). Only the maximum level of recognition (i.e. individual) was possible in this scenario, with no probability of individuals preferring others based on kin or other lower levels of recognition.

If a focal animal detected one or more individuals, n_r, within its repulsion radius r_r, the focal animal's expected direction for the next step, $\boldsymbol{d_r}$, would be 180 degrees from the mean direction towards the set of detected individuals. If $n_r = 0$, and there were individuals, n_l, within the alignment radius r_l but not at distances $>$ r_l, the focal animal would attempt to align its direction to n_l so that the expected direction for the next step, $\boldsymbol{d_l}$, would be the mean direction of the n_l. If all detected individuals were outside r_l , then the focal animal would set its expected direction, $\boldsymbol{d_a}$, to the mean of the directions to those individuals, $n_{a.}$If $n_l > 0$ and $n_a > 0$, the expected direction would be $(\boldsymbol{d_l} + \boldsymbol{d_a})/2$. In those cases where there were no individuals within the perceptual field r_a , the expected direction of the focal individual would be set to its current direction $\boldsymbol{v_i}$. We also assumed a maximum turning speed of 40° every time step.

Simulations accounting for different combinations of parameters for each recognition level were run 20 times for 10,000 time steps each. The output of each iteration (i.e., snapshot with the position of individuals) was analyzed every 300 steps starting at 4200 steps, after the model had reached a dynamically stable state in terms of grouping. We used NetLogo 5.2.1 to develop our model (Wilenski 1999).

EFFECTS OF RECOGNITION CRITERION AND SIGNAL DIFFERENCE ON GROUPING

We used the results of the species and neighborhood recognition levels to explore the effects of variation in the main parameters defining the recognition mechanism. We estimated the variation in number of groups, group size, and alignment as functions of the recognition criteria β_1 and the signal difference $\Delta\mu$ during the last snapshot. To estimate the number of groups, we used a distance-based hierarchical clustering method with a distance threshold equal to the alignment radius ($r_l = 50m$) and calculated the number of groups considering the two species and Species 1 separately. We estimated the number of mixed groups (i.e., groups including both Species 1 and Species 2 indviduals and the proportion of Species 1 individuals participating in those groups. Similarly, we estimated the extent of neighborhood mixing for Species 1 by recording the fraction of Species 1 groups that included individuals from both neighborhoods, *A* and *B*. At the species recognition level, we used generalized linear models to determine the effect of $\beta_1$and $\Delta\mu$ on the number of groups, number of mixed groups, mean group size, and maximum group size. For neighborhood recognition, we used ANOVA to compare these group descriptors across different $\Delta\mu$ values, and for different combinations of the Species 1 neighborhood recognition criteria, β_{1A} and β_{1B}. The combinations of β_{1A} and β_{1B} considered were: 1) different criteria (opposite values, e.g. $\beta_{1A} = 0.05$ and $\beta_{1B} = 0.95$), 2) equal large criteria ($\beta_{1A} = \beta_{1B} \geq 0.75$), and 3) equal small criteria ($\beta_{1A} = \beta_{1B} < 0.75$).

The degree of alignment was estimated through polarization (i.e., similarity in movement direction; Couzin et al. 2002), calculated for the population and also as the average of polarization of all groups, where polarization $p_{group} \in [0,1]$. To determine the effect of $\beta_1$and $\Delta\mu$ on polarization we used beta regressions at the species recognition level and ANOVA at the neighborhood recognition level.

EFFECTS OF PHENOTYPIC MATCHING ON GROUPING

We analyzed the effects of different decay rates of the phenotypic matching function (Table 4.1), on group behavior of Species 1. As for species and neighborhood recognition, we estimated the number of groups, group size (mean and maximum), and polarization for simulation outputs of different phenotypic matching functions. We fitted non-linear regressions of the form $y \sim a/(1 + b * e^{-cl})$ for number of groups and $y \sim a * e^{-cl}$ for group size, where *l* represented the decay rate in recognition probability and *a, b,* and *c* were estimated constants. For polarization across all individuals and by group, we used beta regressions.

EFFECTS OF MEMORY ON GROUPING

Simulations of individual recognition accounted for variation in the rates of memory gain and loss, *g* and *h, respectively,* as well as the two scenarios for the number of individuals memorized every step, $m \in \{1,6\}$. We estimated the effects of these parameters on the number of groups, group size, and polarization for Species 1, by comparing group metrics for different combinations of memory abilities. We used ANOVA to determine differences among these memory combinations, and we compared group metrics between *m* values using Kolmogorov–Smirnov tests.

EFFECTS OF RECOGNITION ON GROUP DYNAMICS

We evaluated the effect of increasing complexity in the recognition system by comparing estimates of grouping patterns and dynamics across recognition systems using approaches from network analysis. We analyzed and compared simulation outputs corresponding to high species and neighborhood recognition with all recognition criteria equal to 0.99. We assumed a moderate level of kin recognition , determined by *l*=0.5, while individual recognition relied on the memory rates *g*=0.5 and *h*=0.1. We considered the two *m* values separately.

For each of 5 recognition levels (i.e., species, neighborhood, kin, individual (*m*=1), and individual (*m*=6) we obtained unweighted, undirected networks for each iteration and time step (400 networks each), with edges occurring between individuals located less than $r_l = 50$ m apart. For every simulation, we also estimated weighted networks based on the frequency of time steps an edge occurred during the simulation time. We used an edge-betweeness-based algorithm to identify the community structure of weighted networks (Girvan and Newman 2002). This method unveils the hierarchical structure of a network based on the iterative removal of edges with highest betweenness, leading to hierarchical splits (Newman 2010). We compared estimates of community sizes and modularity between recognition levels using ANOVA.

To analyze temporal dynamics, we built temporal networks for each iteration of all recognition levels and estimated edge density and rates of edge formation and disappearance from networks. We used the packages ‘igraph’ and ‘tsna’ for R to perform all network analysis.

Results

A model with individuals incapable of any kind of recognition but following repulsion-alignment-approaching rules resulted in a single mixed group of species 1 and 2 clustered together. This aggregation resulted in a fully-connected network, with a modularity of 0 (i.e., no subgroups) and without changes in connectivity through time. Polarization fluctuated in time between 0.46 and 0.62 (i.e., individuals moderately aligned with each other), with no difference between species. These values provided a baseline for determining the effects of the different levels of recognition on group behavior.

EFFECTS OF RECOGNITION CRITERION AND SIGNAL DIFFERENCE ON GROUPING

The mean number of groups formed varied between 1.0 and 42.9 across all simulated combinations of recognition criterion and signal difference ($\Delta\mu$) at species level. When all individuals were analyzed together regardless of the species, $\Delta\mu$ had a small significant effect on the number of groups. Increasing the criterion towards more inclusive values strongly decreased the number of groups (Fig 4.2A). Similarly, the number of groups including only Species 1 tended to increase with signal difference ($\gamma_{\Delta\mu}$=0.23±0.06, df=1280, p<0.001) but decreased with increasing criterion (γ_{β_1}=-10.08±0.06, df=1280, p<0.001). Individuals formed fewer mixed groups with increasing $\Delta\mu$ and β_1, but only for $\Delta\mu > 2$, i.e., at small $\Delta\mu$ values there was no effect of β_1 (Fig. 4.2B). Across all simulations, group size was most strongly affected by β_1 when considering both species together and Species 1 separately. For the latter, individuals aggregated into small groups of less than 10 individuals when $\beta_1 < 0.7$ and into larger ones with over 20 individuals when $\beta_1 > 0.9$ (Fig. 4.2C). Individuals aligned slightly better with others at higher criteria (γ_{β_1}=0.20±0.02, df=1280, p<0.001) and larger signal differences ($\gamma_{\Delta d}$=0.03±0.00, df=1280, p<0.001).

With neighborhood recognition, the number of groups was lower and the number of mixed groups was higher when the two signal PDFs completely overlapped (i.e., d_1' =0), in comparison to other signal differences (Fig 4.3). Individuals aggregated into fewer groups when both β criteria were equal and large ($\beta \geq 0.75$) or when one of the neighborhoods had $\beta \geq 0.75$, individuals also formed fewer groups than when both β_{1A} and β_{1B} < 0.75 (Fig. 3A). Groups were larger when the signal PDFs of the two species completely overlapped than when those PDFs differed. Individuals formed small groups when the β criteria were equal and small and formed larger groups when the two species had equal large β criteria (Fig. 4.3C). Based on polarization estimates, alignment across all individuals varied greatly among simulations with significant differences between combinations of recognition criteria (F=335.0, df=2, p<0.001). Individuals aligned better when the β criteria were large and equal for both neighborhoods (p=0.48±0.01), whereas they aligned poorly when the β criteria were equal but small (p=0.26±0.00). However, alignment within groups was very high (p=0.93±0.00) with no difference between combinations of recognition criteria. Complete overlap in signals between the two neighborhoods resulted in poor alignment compared to larger signal differences (F=7.45, df=5, p<0.001).

EFFECTS OF PHENOTYPIC MATCHING ON GROUPING

A faster decay in the probability of recognizing another individual as kin based on phenotypic matching (i.e., successful recognition requires small differences between signaler and receiver) resulted in more and smaller aggregations (Fig. 4.4A, B). All individuals also tended to be better aligned at slower decay rates, although variation among simulations was also higher (Fig. 4.4C). Polarization at the group level also tended to decrease with increasing decay rate, however, this effect was very small (r^2=0.01, p<0.001), and overall, groups were highly aligned across the whole gradient of recognition decay.

EFFECTS OF MEMORY ON GROUPING

Individuals memorizing six individuals (m=6) every time step clustered into fewer groups than when individuals could memorize only one individual (m=1) (D=0.71, p<0.001). However, these two scenarios followed a similar pattern when comparing different combinations of memorizing and forgetting rates. Individuals memorizing and forgetting slowly (g=h=0.01), or memorizing slowly and forgetting fast (g=0.01, h > 1), formed more groups, while those memorizing fast and forgetting slowly (g > 1, h=0.01) clustered into the fewest groups (Fig. 4.5A). Mean and maximum group size were smaller for m=1 than m=6 (D=0.67, p<0.001 for mean group size; D=0.62, p<0.001 for maximium group size). As with variation in number of groups, mean and maximum group size were highest at high memorizing and low forgetting rates (g > 1, h=0.01) and lowest when both memorizing and forgetting rates were high (g = h > 1) or when the memorizing rate was low and the forgetting rate high (g = 0.01, h > 1; F=451.6, p<0.001 for mean; F=167, p<0.001 for maximum). Polarization ranged widely over all individuals. However, it was highest for high memorizing and low forgetting rates than for any other combination of rates when m=1. For m=6, polarization was higher for high memorizing and low forgetting rates, high memorizing and forgetting rates, and moderate memorizing and forgetting rates (g = h = 0.1) than for the other two combinations (Fig. 4.5B). At the group level, polarization also differed between combinations of memorizing and forgetting rates. When memorizing rates were high and forgetting rates were low, individuals aligned better then when these rates were equal or memorizing rates were low.

EFFECTS OF RECOGNITION ON GROUP DYNAMICS

Based on the community detection analysis, individuals of Species 1 clustered differently based on their specificity of recognition (Fig. 4.6). Except for species-level recognition, Species 1 segregated into groups, and an even more complex hierarchical structure emerged at the individual recognition level. Mean group size tended to decrease with increasing specificity of recognition (F=39.01, p<0.001), confirming our initial group size hypothesis. Species and kin recognition resulted in fewer interactions between groups, while neighborhood and individual recognition resulted in more between-group interactions (Fig. 4.6). Based on modularity estimates, association between group members was less dense at the individual recognition level but similar across the other levels (F=99.1, p<0.001), partially supporting our cohesion hypothesis.

Temporal dynamics also differed between recognition levels. Changes in association occurred by single individuals changing their association in only one of the clusters formed in neighborhood recognition, while the other cluster was mostly stable (Fig. 4.7). In contrast, changes in association at the kin and individual recognition levels occurred mostly as groups of individuals followed the same temporal pattern. These groups were smaller (2-3 individuals) for individual recognition when m=1. At this level, dynamics due to single individual changes were also present (Fig. 4.7). Based on edge density, the average proportion of edges (i.e., associated dyads) present at any given time was highest for individual recognition with m=6 and lowest for species recognition (F=13.16, p<0.001). The rate of formation of new edges also varied among recognition levels (F=4.10, p=0.004). New associations were formed and dissolved at a higher rate for species level recognition (0.36 ± 0.06) and individual recognition (0.30 ± 0.03) than for the intermediate levels of recognition.

Discussion

Recognition ability strongly influenced group dynamics. We observed impacts of recognition ability on several group metrics, including number of groups, group size, and alignment among individuals. These metrics responded both to parameter variation at a given level of recognition specificity and to changes in the level of recognition that was possible. In particular, the more specific recognition mechanisms (kin and individual) resulted in the formation of smaller groups that interacted with each other forming temporary larger units. Put another way, hierarchical group structure emerged when individuals were capable of more specific recognition. Our model and results provide one approach to exploring how recognition, a basic mechanism of social behavior that mediates interactions between individuals, can affect movement and group behavior. Demonstration of this link between recognition ability and group dynamics allows for the development of new hypotheses regarding the mechanisms driving group behavior and social evolution.

Our basic model underlying species and neighborhood recognition relied on signal detection theory, which, when applied to animal communication systems, predicts the presence of some inevitable error in the recognition process. In this signal detection framework, animals should try to optimize their recognition process by reducing the error (Rodríguez-Gironés and Lotem 1999; Wiley 2006). In species recognition, it is crucial that the error gets minimized for individuals to interact with their own species. In our model, mixed-species groups were only absent for very high values of the recognition criterion, which suggests that the mechanism behind species recognition follows the predictions of the signal detection theory.

Signal detection theory applied to species recognition might also explain the occurrence of mixed-species groups. Mixed-species groups are common in a diversity of animal groups, e.g. fish, birds, and mammals (Schlupp and Ryan 1996; Stensland et al. 2003; Sridhar et al. 2009). Mixed groups may form to improve access to resources or predatory defense (Heymann and Buchanan-Smith 2007; Sridhar et al. 2009). In mixed groups these benefits may have favored the evolution of a lower or a more flexible, context-dependent recognition criterion, which could be adjusted based on assortment preference or environmental conditions, such as resource availability (Ward et al. 2009). In future work, incorporating resources or another environmental factor into the model would help to identify the conditions under which more flexible recognition systems are favored.

Comparing across recognition systems, we found only partial support for our initial hypothesis that group complexity should increase with more complex recognition systems. Group size tended to decrease as recognition abilities became more specific (Fig. 6), and cohesion was higher for individual recognition and lower for species recognition. However, other recognition levels showed no differences in cohesion, and group dynamics did not systematically change across recognition levels. Switches in edges between individuals were more frequent for species and individual recognition, but evidence suggests that the mechanisms responsible for these switches differed between the two extreme recognition scenarios we considered. For species recognition, switches were probably related to intra-group changes in interactions driven by repulsion-alignment-attraction forces acting on larger groups. Polarization was lower in larger groups, while it was usually above 0.8 for smaller groups, increasing the chance of changes in spatial positions, which could translate into edge switches within the network. In contrast, for individual recognition, switches in edges between individuals likely resulted from temporal associations between highly aligned groups.

Some fission-fusion dynamics occurred at all levels of recognition; however, more complex grouping systems resembling multilevel systems only emerged when recognition was more specific (i.e., kin- or individual-based). Animals with multilevel fission-fusion systems, such as African elephant (*Loxodonta africana*) or Hamadryas baboons (*Papio hamadryas*) have tighter or more permanent connections to few individuals while also associating into larger units with fixed composition at different scales for brief periods (Wittemyer et al. 2005; Schreier and Swedell 2009). This particular kind of fission-fusion system seems to emerge at the level of individual recognition with m=6, when all individuals in smaller clusters temporally interacted with other clusters, but composition within clusters barely changed over time. Future analysis looking at the community structure for different modularity values (instead of just the maximum values we explored here) could help uncover these patterns in more detail. It is also possible that, at a given time, an animal that is capable of recognizing a signaler’s identity might only act in response to its neighborhood or kin status, which would result in different group formations (Starks et al. 1998; Ward et al. 2009). This flexibility in the recognition pattern could also explain the emergence of multilevel systems, and our model could also be adapted to explore the contexts (e.g. population density, resource availability) under which which one type of organization is favored over others.

Our model focused on the receiver's side of the recognition process. However, a more complete understanding of the role of this process on structuring groups would result from simultaneously considering variation in the signaler's side. If recognition is beneficial for signalers, selection would favor behaviors of actively cueing on their status or identity, which could lead to more frequent unique signals (Tibbetts and Dale 2007). Which recognition mechanisms would work best under a variable signal scenario, and how receivers would optimize reception in such a context, might result in a contrasting perspective of recognition than the one based on the receiver's function. Furthermore, because different types of signals would likely have different ranges over which they could be perceived, differences in the types of cues used as signals (e.g., visual vs. olfactory) or the types of cues used to indicate different status, could also affect the probability of recognition and group dynamics.

Our model could also be applied to explore questions related to cooperation, which is expected to evolve and be maintained when individuals cluster in space due to non-random social interactions (Nowak and May 1992; Sachs et al. 2004). Crucial to understanding evolution of cooperation is the identification of mechanisms that drive assortment (Croft et al. 2015). Recognition in our model led to assortment of individuals into clusters, and the characteristics of these clusters varied depending on the specificity of recognition that was possible. This idea could be developed further by assigning attributes of cooperative behavior and incorporating a cost-benefit function associated to the recognition process and grouping behavior.

The model developed here connected the basic social process of recognition to the spatiotemporal movement dynamics of individuals. It provides a tool for further exploration of the mechanisms behind recognition and the evolution of social systems.

Table 4.1 Parameter values for simulations of different recognition levels.

		Recogntion level			
Parameter	**Symbol**	**Species**	**Neighborhood**	**Kin**	**Individual**
Signal mean of PDF for Species 1	μ_1	1	1	1	1
Signal mean of PDF for Species 2	μ_2	1-7	15	15	15
Signal mean of PDF for neighborhood A	μ_{1A}	---	1	1	1
Signal mean of PDF for neighborhood B	μ_{1B}	---	1-6	3	3
Recognition threshold for Species 1	β_1	0.01 – 1	0.99	0.99	0.99
Recognition threshold for Species 2	β_2	0.99	0.99	0.99	0.99
Recognition threshold for neighborhood A	β_{1A}	0.1 – 1	0.01-1	0.99	0.99
Recognition threshold for neighborhood B	β_{1B}	0.99	0.01-1	0.99	0.99
Decay rate of phenotype matching	l	---	---	0-30	0.5
Memory gain rate	g	---	---	---	0-70
Memory loss rate	h	---	---	---	0-100

		Recogntion level			
Parameter	**Symbol**	**Species**	**Neighborhood**	**Kin**	**Individual**
Number of memorized neighbors	m	---	---	---	1, 6

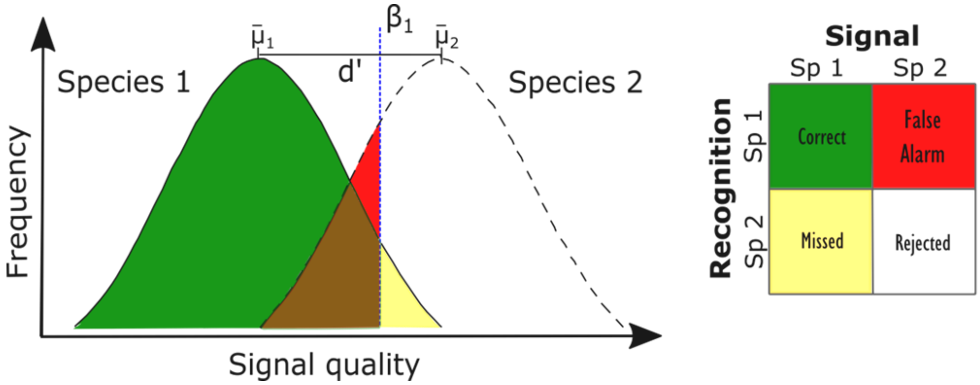

Figure 4.1 Recognition mechanism based on signal detection theory (Shettleworth 2010). Any individual of a kind (e.g. Species 1) produces a signal with a quality s_1, where $S_1 \sim N(\mu_1, \sigma_1^2)$. An individual receiving the signal recognizes it as a member of its own kind based on a criterion value or threshold β_1. Signals produced by individuals of a different kind (e.g. Species 2) may overlap, affecting the probability of the receiver correctly recognizing a signaler. The difference between the distributions of signals produced by Species 1 and 2 (d') and (β_1) determine the probabilities of correctly recognizing, missing, correctly rejecting or producing a false alarm in the interaction between signaler and receiver.

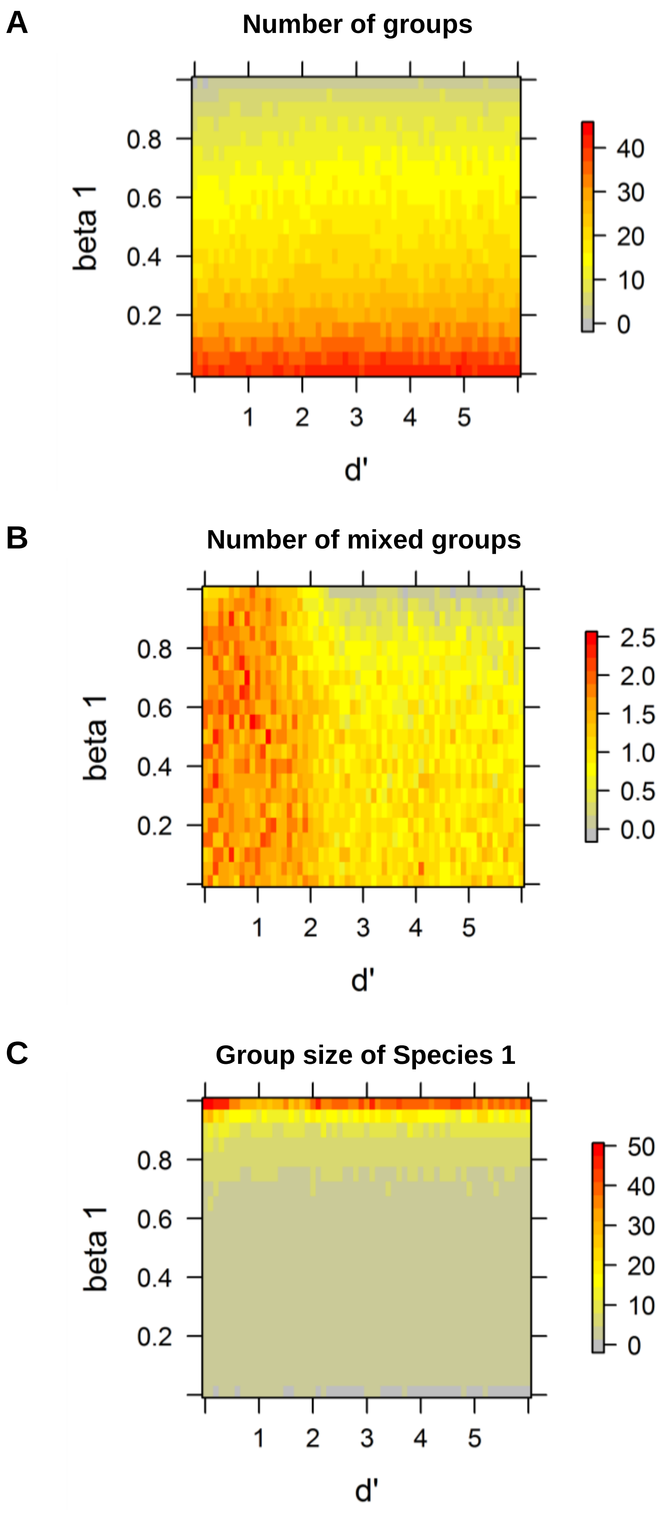

Figure 4.2 Effects of recognition criterion β_1 and signal difference d' on group metrics: A) number of groups, B) number of mixed groups, C) group size of Species

1. Overall, $\beta_1$has a larger effect than $\Delta\mu$ on all group metrics. Number of groups increased with β_1 (γ_{β_1}=-9.96±0.06, df=1280, p<0.001) and $\Delta\mu$ ($\gamma_{\Delta\mu}$=0.55±0.06, df=1280, p<0.001). Mixed groups were more frequent at higher values of β_1, but only for $\Delta\mu > 2$ ($\gamma_{\Delta\mu * \beta_1}$=-0.09±0.08, df=1280, p<0.001). Independent of signal difference, very high values of $\beta_1$were needed for the formation of large groups (γ_{β_1}=-0.48±0.01, df=1280, p<0.001). In all cases, the total number of individuals was fixed at 100.

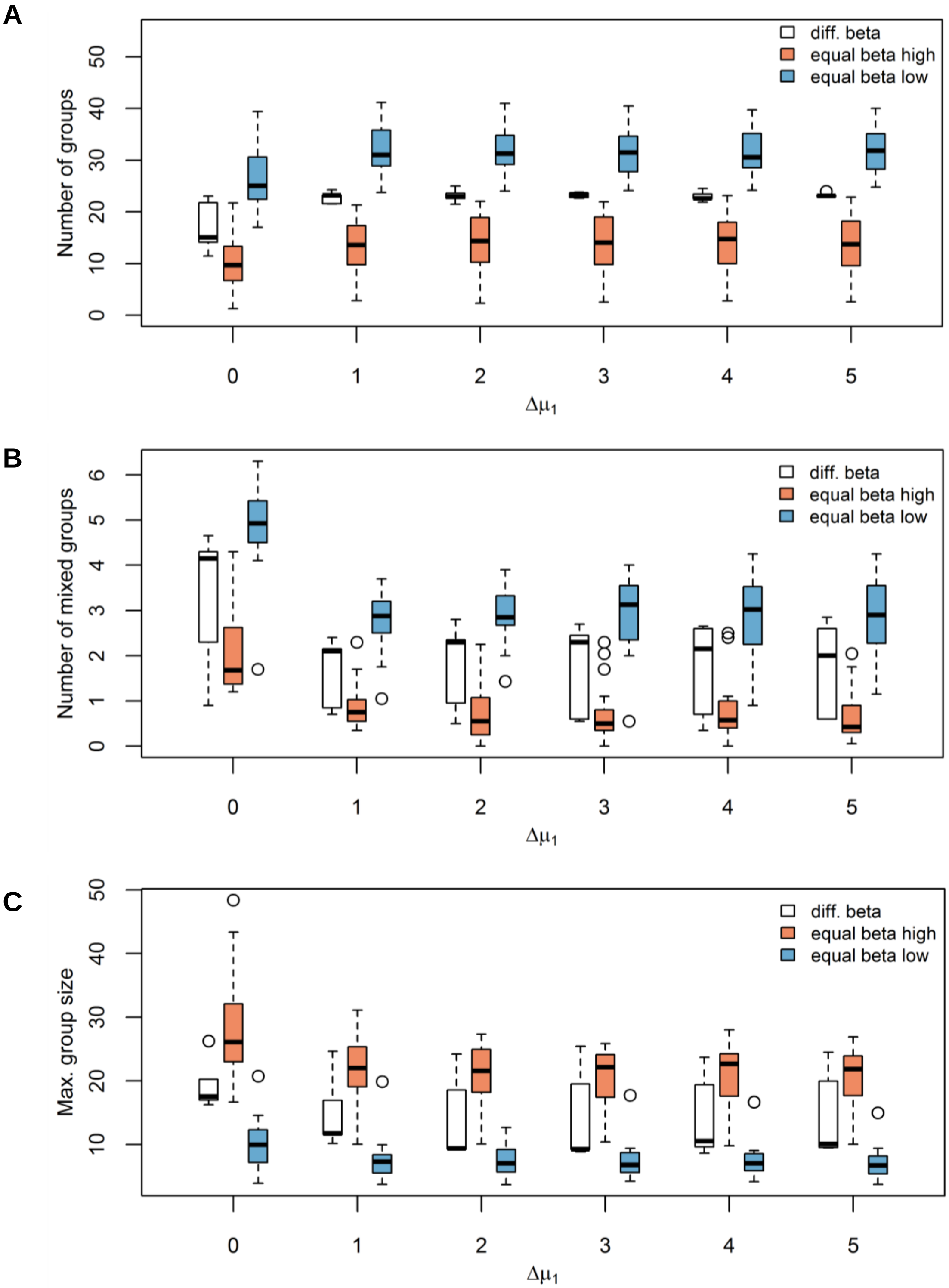

Figure 4.3 Effects of group recognition criteria β_{1A}, β_{1B}, and signal difference $\Delta\mu$ on group metrics of Species 1: A) number of groups, B) number of mixed groups, C) maximum group size. Individuals clustered into fewer groups (F=11.19, df=5,

$p<0.001$) but more mixed groups ($F=34.31$, $df=5$, $p<0.001$) when signal difference was absent. They formed more groups when criteria of neighborhoods was equal low ($F=770.4$, $df=2$, $p<0.001$). Groups were larger at $\Delta\mu_1 = 0$ ($F=4.64$, $df=5$, $p<0.001$) and when criteria were both high ($F=89.76$, $df=2$, $p<0.001$). In all cases, the total number of individuals was fixed at 100.

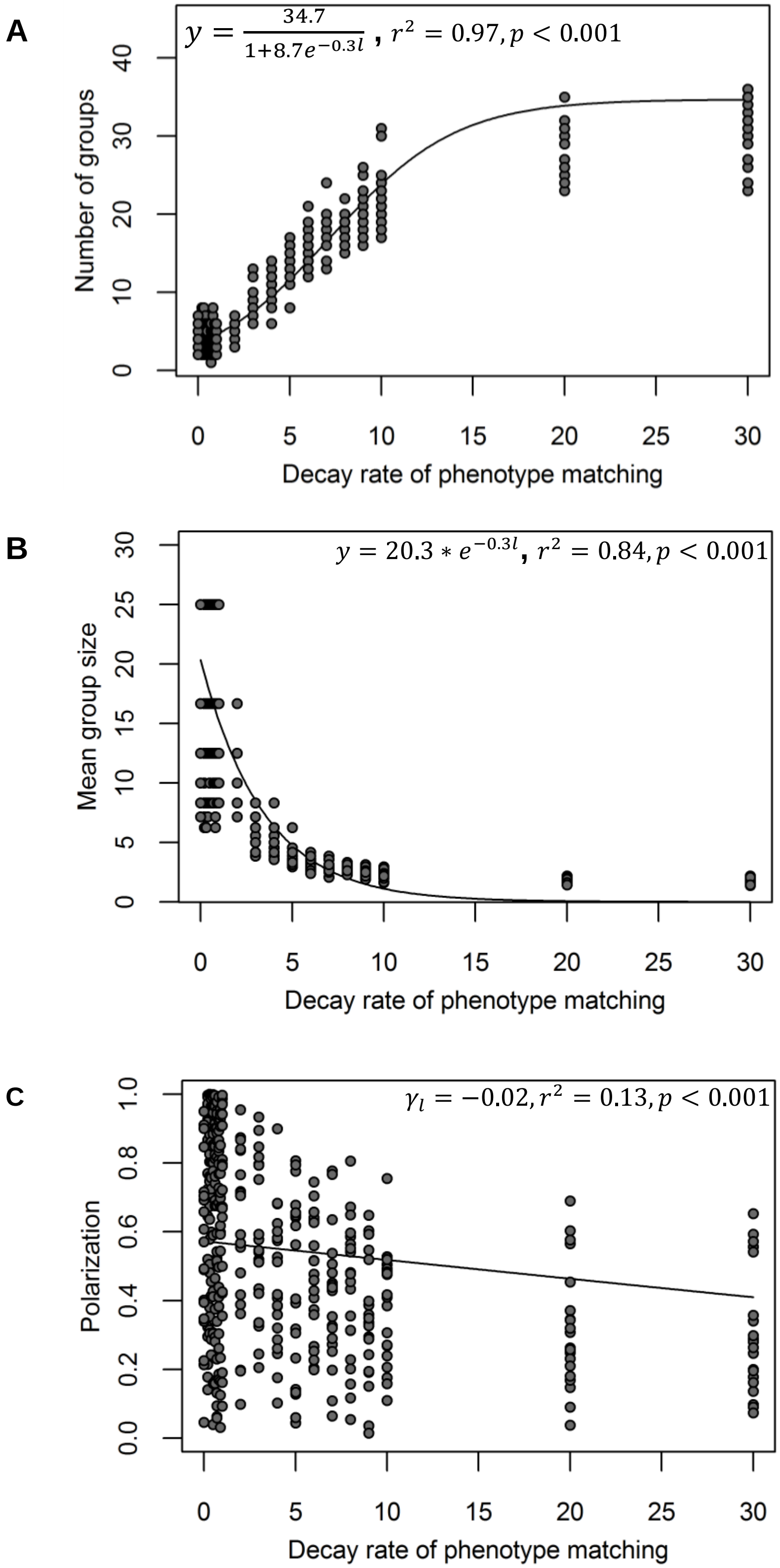

Figure 4.4 Effect of phenotypic matching on group behavior of Species 1. A) The number of groups formed increased asymptotically with increasing the rate of decay l.

B) Group size and C) polarization and variation in polarization decreased with increasing *l*. At small *l* values, a large difference in signal Δs_{ij} defines kin while at large *l* values, small Δs_{ij} defines kin. In all cases, the total number of individuals in Species 1 was fixed at 100.

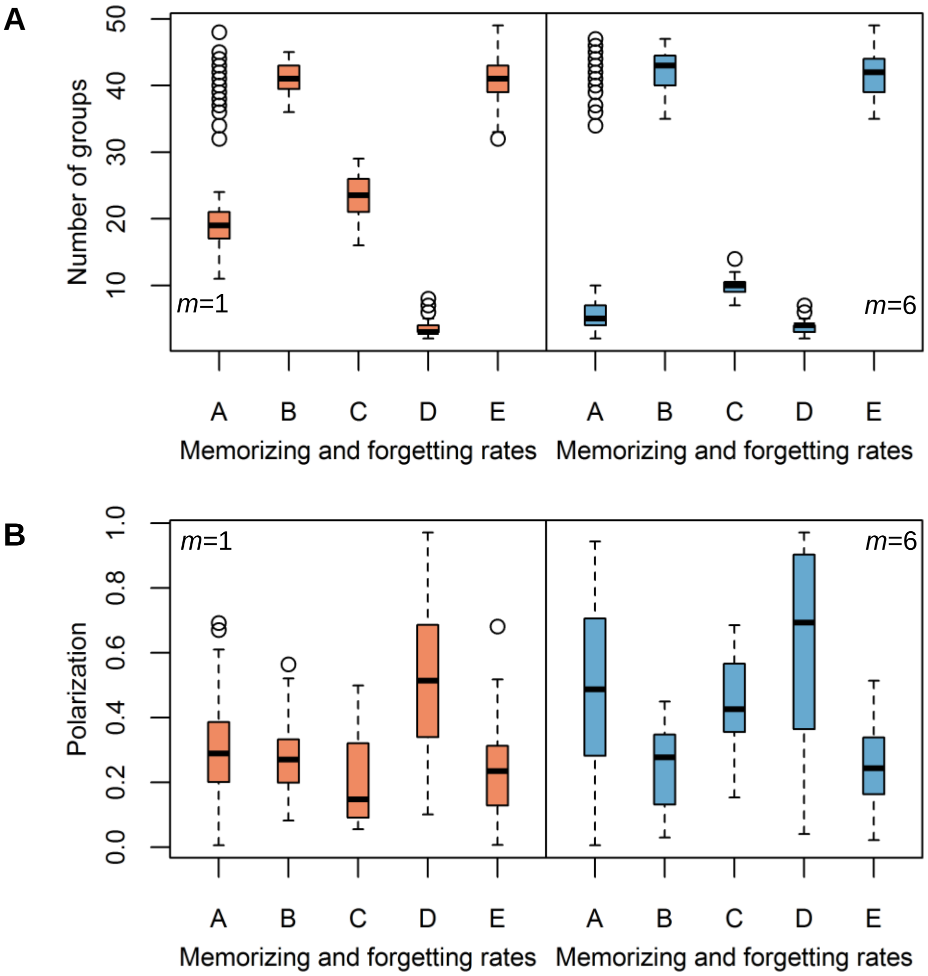

Figure 4.5 Comparison of A) number of groups, and B) polarization across all individuals, between rates of memorizing g and forgetting *h* (A: $g = h > 1$; B: $g = h = 0.01$; C: $g = h = 0.1$; D: $g > 1$, $h = 0.01$, $g = 0.01$, $h > 1$). Fewer groups were formed when $g > 1$ (*F*=495.1, p<0.001). Polarization also differed between rates (*F*=33.1, p<0.001) and was higher when *m*=6 (*D*=0.28, p<0.001).

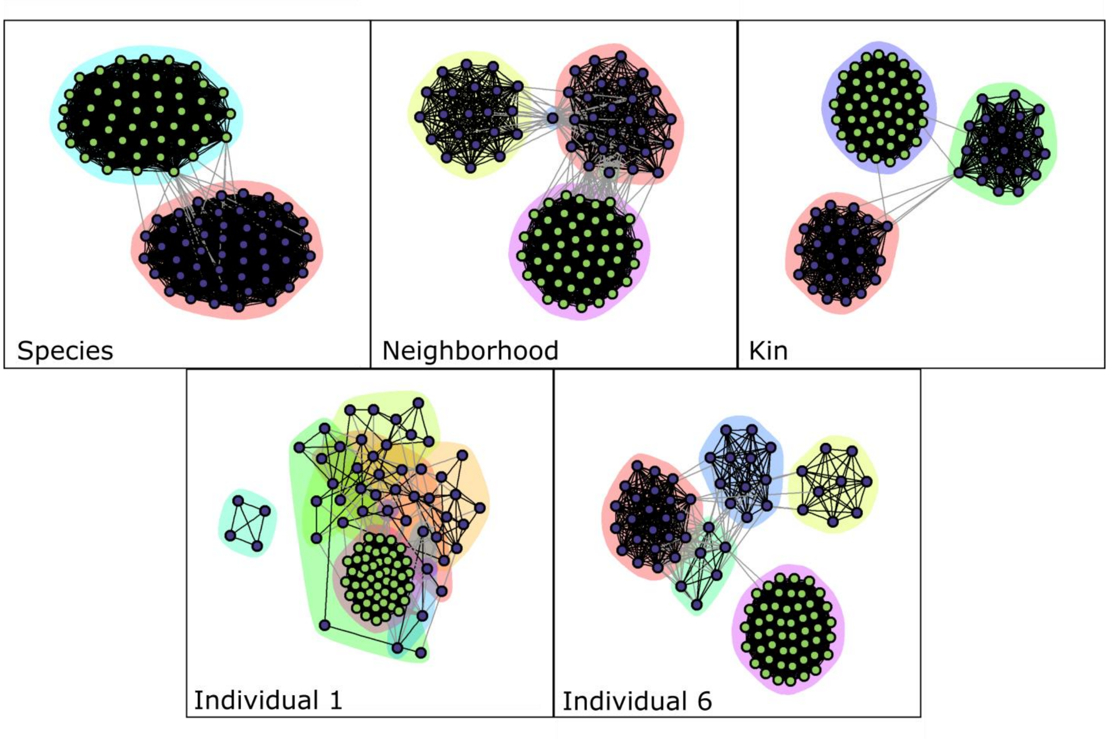

Figure 4.6 Examples of community structure for different recognition levels. Background colored areas mark different communities. Black and grey edges represent connections within and between communities, respectively. Species 1 fragments into communities at all recognition levels, except species. A hierarchical structure emerges with individual recognition. In all cases, the total number of individuals was fixed at Species 1 = 50 and Species 2 = 50. Node colors: blue=Species 1, green= Species 2.

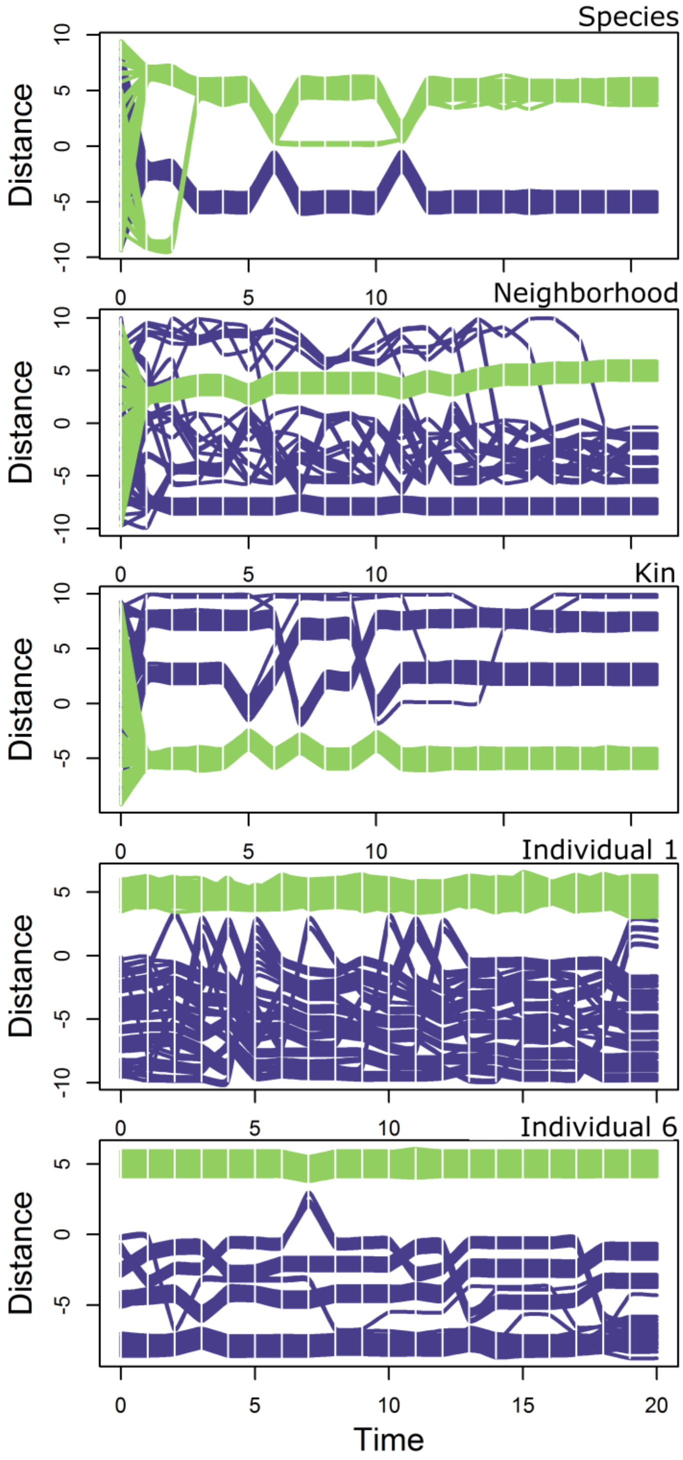

Figure 4.7 Timelines representing temporal dynamics of networks for each recognition level. Lines represent nodes or individuals distributed based on the

geodesic distance (shortest path as defined by the number of edges between nodes) between them projected into one dimension using a multidimensional scaling (MDS) analysis. Dynamics occurred by changes in the network position within groups (which occurred more commonly for neighborhood and kin recognition) and by changes in distances between groups (which occurred more commonly for kin and individual recognition). Node colors: blue=Species 1, green= Species 2.

Appendices

Table A2.1 Mammal species and number of populations with fission-fusion dynamics.

Order	**Species**	**# Populations**
Artiodactyla	*Axis axis*	8
	Bison bison	6
	Capra aegagrus	3
	Capra hircus	4
	Capra ibex	2
	Capra nubiana	3
	Capra sibirica	1
	Cervus elaphus	12
	Giraffa camelopardalis	11
	Ovis canadensis	4
	Rupicapra pyrenaica	2
	Syncerus caffer	12
Carnivora	*Crocuta crocuta*	7
	Potos flavus	1
	Panthera leo	8
	Procyon lotor	4
	Zalophus wollebaeki	1

Order	**Species**	**# Populations**
Cetacea	*Cephalorhynchus commersonii*	4
Cetacea	*Cephalorhynchus hectori*	6
	Lagenorhynchus obscurus	7
	Megaptera novaeangliae	36
	Orcaella heinsohni	1
	Physeter macrocephalus	15
	Sousa chinensis	9
	Sotalia guianensis	9
	Tursiops aduncus	7
	Tursiops truncatus	22
Chiroptera	*Barbastella barbastellus*	2
	Chalinolobus tuberculatus	4
	Eptesicus fuscus	11
	Myotis bechsteinii	1
	Tadarida australis	1
	Thyroptera tricolor	2
Dasyuromorphia	*Antechinus agilis*	4
	Antechinus flavipes	2
	Antechinus stuartii	3

Order	**Species**	**# Populations**
	Antechinus subtropicus	1
Diprotodontia	*Macropus fuliginosus*	4
	Macropus giganteus	1
Perissodactyla	*Equus grevyi*	3
	Equus hemionus	4
Primates	*Alouatta palliata*	4
	Ateles belzebuth	4
	Ateles chamek	3
	Ateles geoffroyi	8
	Ateles hybridus	3
	Ateles paniscus	1
	Brachyteles arachnoides	1
	Brachyteles hypoxanthus	1
	Cacajao calvus	2
	Cacajao melanocephalus	2
	Cebus nigritus	2
	Chiropotes chiropotes	2
	Chiropotes utahickae	1
	Macaca fascicularis	5

Order	**Species**	**# Populations**
	Macaca fuscata	8
	Macaca sylvanus	3
	Pan paniscus	3
	Pan troglodytes	10
	Papio hamadryas	2
	Papio papio	1
	Papio ursinus	5
	Pongo pygmaeus	2
	Rhinopithecus bieti	2
	Rhinopithecus brelichi	2
	Rhinopithecus roxellana	1
	Theropithecus gelada	2
Proboscidea	*Elephas maximus*	7
	Loxodonta africana	19
	Loxodonta cyclotis	7

*excluded from analysis

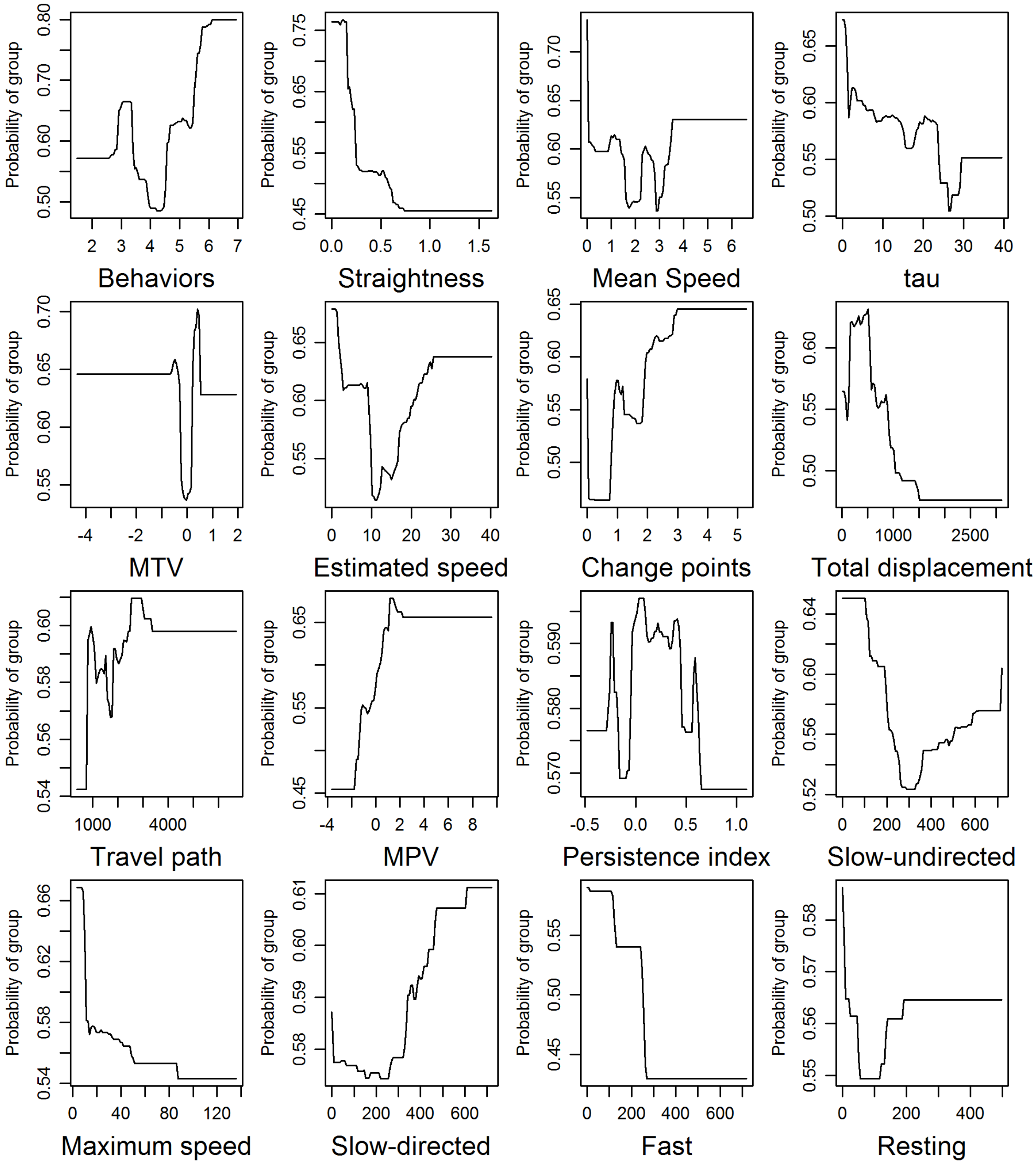

Figure A3.1 Marginal effect plots for all movement metrics as predictors of group presence in all orangutans (males plus females). MTV and MPV stand for mean turning and mean persistence velocity, respectively. Variables are ordered from left to right and top to bottom based on their relative influence.

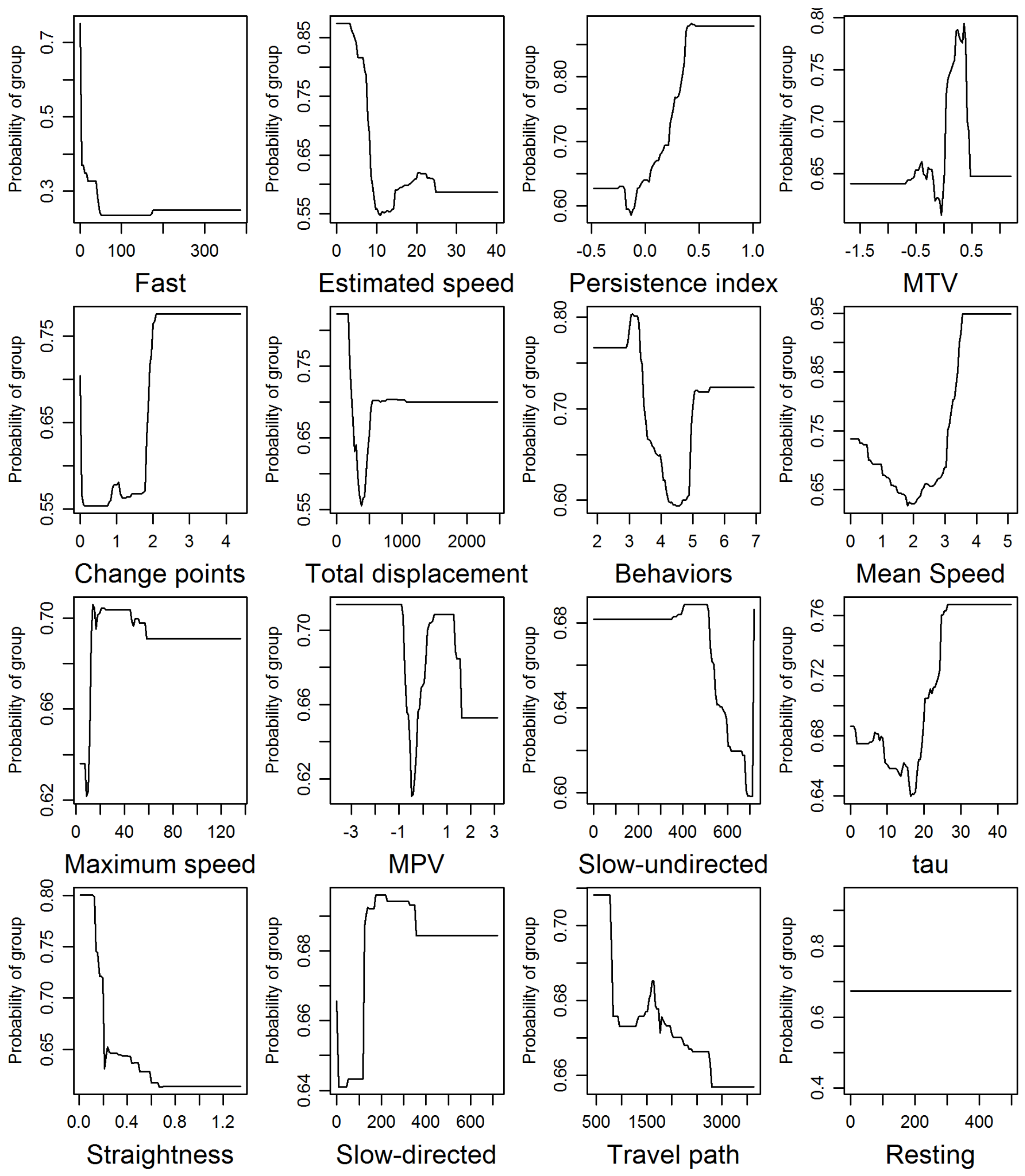

Figure A3.2 Marginal effect plots for all movement metrics as predictors of group presence in female orangutans. MTV and MPV stand for mean turning and mean persistence velocity, respectively. Variables are ordered from left to right and top to bottom based on their relative influence.

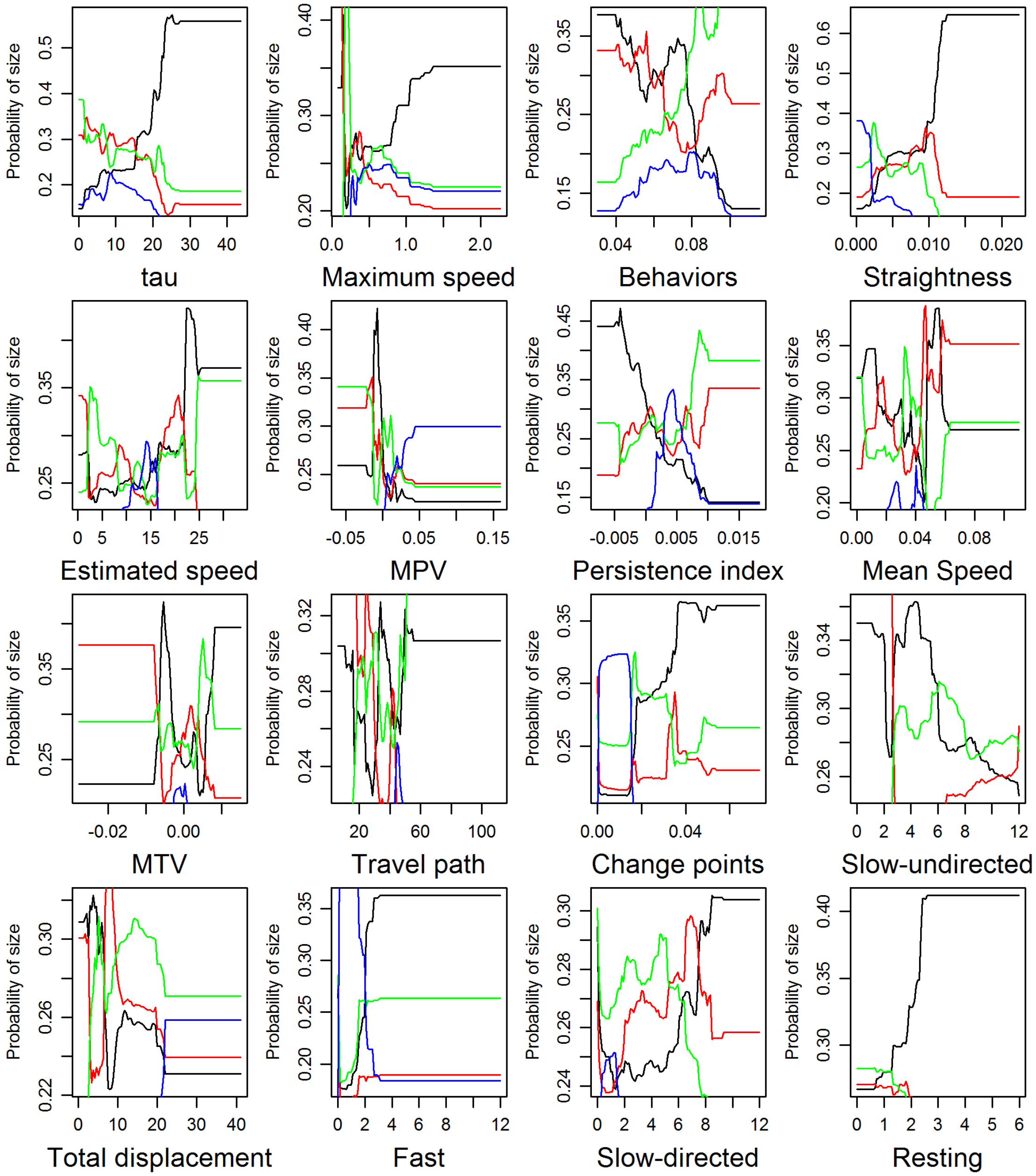

Figure A3.3 Marginal effect plots for all movement metrics as predictors of group size (black = solitary, red = small, green = medium, blue = large) in orangutans. MTV and MPV stand for mean turning and mean persistence velocity, respectively. Variables are ordered from left to right and top to bottom based on their relative influence.

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