# Comparative study of genetic variation in relation to social structures of animals

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# Summary

Given its importance for understanding the evolution of our own species, describing the processes that shape the wide array of animal social systems has long fascinated many researchers and the study of social behaviour is constantly being pushed in new directions. One such direction has been to add genetic approaches to answer questions on the evolution of social behavior. The recent methodological advances in molecular methods have allowed application of genetic methods to a number of natural populations of different animal species. Detailed studies based on DNA analyses now exist for a wide variety of species, and have provided insights into patterns of paternity, relatedness and dispersal, as well as to clarify how selection has shaped individual strategies.

In this thesis I used published data in comparative analyses, to see whether aspects of the social structure of animals are linked to the amount and distribution of genetic variation. This can provide a better understanding of the patterns of genetic variation within natural populations and allow inference of aspects of social structure. It also allows inferences about the selective factors that potentially have shaped the specific social structure of a species.

In the first study I analyzed patterns of average relatedness within and among social groups of wild chimpanzees. In chimpanzees males are philopatric; that is, they remain in the groups they have been born. It has therefore been speculated that the high levels of cooperation observed among chimpanzees males can be explained by kin selection. I showed that average relatedness among chimpanzee males within groups only rarely exceeds that of the females in the group, and is also similar to the relatedness of males across groups. To explain this pattern, I derived an analytical model to predict relatedness levels based on group size, reproductive skew and which sex disperses. This produced results consistent with the empirical chimpanzee data, in that the model predicts high levels of relatedness only within very small groups with high reproductive skew, and that in general relatedness among male philopatric species should be lower than among female philopatric species. This pattern was confirmed more generally with a dataset of several bird and mammalian species, clearly showing the effect of group size.

In the second study I took a closer look at the factor of variance in lifetime reproductive success (vLRS). Individuals in natural populations differ in the number of surviving offspring they produce. Since this is the basis of evolutionary change, behavioural ecologists have been trying to measure this directly, and population geneticists seek to detect resulting unusual patterns in the genome. I derived analytical approaches to derive the vLRS from the pattern of variation found at sex-specific genetic markers on a local scale. The basic premise is that if individuals differ in their reproductive success, matri- and patrilines should also differ in their sizes. Six approaches were assessed for their accuracy to detect vLRS from genetic data and robustness to potentially confounding factors by indvidual-based computer simulations. Two which proved to be suitable were applied to published data on variation at mitochondrial and Y-chromosomal genes from several populations. The results indicate that there are detectable differences between populations in the degree of vLRS, as well as between the sexes in the same population. This highlights that the social system of a species can have a large influence on the genetic diversity detected within a sample, which potentially can confound population genetic analyses.

In the last part, the two approaches were applied to published mitochondrial DNA to infer vLRS for females of several mammalian species. While many studies have looked at reproductive skew among males and its causes and consequences, differences among females and potential competition among them is less well understood. I performed comparative analyses to infer whether high or low vLRS among females are correlated with ecological, social or morphological characteristics which previously have been linked with competition among females. If resources critical for reproduction are limited so that only some females gain access, higher vLRS is expected. In fact, species in which females have a dominance hierarchy, species in which females can potentially produce a large number of offspring and species in which allonursing occurs all show higher levels of vLRS within groups as inferred from mtDNA variation. Furthermore, species in which individuals show territorial behaviour have higher levels of vLRS between social groups. This shows that in species where females show higher levels of competition there are also larger differences among them in the number of offspring they produce. While I did not detect correlation with crude measures of potential underlying ecological or social factors in this dataset, these new approaches would allow for testing of mechanisms as more detailed data becomes available.

In general, the results of this study show a clear link between the social structure animals live in and the distribution of genetic variation they carry. They highlight the usefulness of adding genetic methods to studies of social behaviour, since analyzing DNA of animals allows inference of the dispersal and breeding strategies of these individuals. In addition though, they also allow for insights into the ultimate mechanisms of these behaviours. Determining genetic relatedness is for instance essential to understand the influence of kin selection or how inbreeding avoidance shapes patterns of dispersal. While detailed studies of populations are the most direct test of selection, investigating distributions of interspecies differences in traits is a useful tool to understand the function and adaptation of these traits. The general framework of comparative studies of patterns of genetic variation developed here should prove fruitful since my results indicate that it can add to our understanding about the evolution of the amazing diversity of animal social systems.

# 1. General Introduction

## 1.1 Social structure and genetic variation

Animals do not live in a social vacuum, but regularly meet, interact or compete with other individuals of their own species. The sum of these interactions has been termed the social structure of a species. It can be described in terms of the social organization, which lists whether individuals are solitary or counts the number of females and males in groups and the dispersal among these. The next level is in the mating system, which describes who mates with whom and the distribution of offspring among individuals. Finally the social system describes the types and frequencies of interactions among individuals (apart from mating) (following Kappeler & van Schaik 2002). Approaches aiming at explaining the differences in social structure among species largely assumed that selection affecting the reproductive success of individuals has shaped this variation. The factors which have been invoked to explain the social structure of a species include: (1) ecological variables, like predation pressures and the abundance and distribution of food (e.g. MacDonald 1983), (2) social factors, primarily sexual selection (e.g. Höhner *et al.* 2007) and potential benefits from group living (e.g. Cockburn 1998), (3) demographic and life history variables (e.g. Clutton-Brock 1989), and (4) phylogenetic constraints (e.g. di Fiore & Rendall 1994).

A large number of studies have used a wide array of methods to link potential selective factors and individual properties within single populations. Ecological variables have for instance been assessed by describing habitat categories (e.g. Dunbar 1987), providing detailed analyses of the quality of foods actually ingested by the animals (e.g. discussed in Hohmann *et al.* 2006), or by measuring predator densities (Hill & Lee 1998). The behaviour of individuals has been analyzed by observing animals over periods of time and recording their interactions (Martin & Bateson 2000). Demographic and life history data can be obtained partly from captive animals, but are now also available for natural populations of animals thanks to long-term studies (e.g. Bielby *et al.* 2007). Recently, molecular genetic tools have been employed to address some of these questions. Molecular genetic tools allow description of social structure and dispersal patterns within populations, and to identify and census individuals in a population, but to also describe the genetic mating

system by assigning paternities and compare this with the mating patterns (reviewed in Freeland 2005). In addition, they are necessary for the understanding of certain aspects of social dynamics, such as the evolution of altruism through kin selection by combining direct observational data from the field with analyses of relatedness in the laboratory (Bradley & Vigilant 2002). While initially there were only few coherent studies of genetic variation in wild animal populations due to technical challenges (Taberlet *et al.* 1999), we now have genetic data aimed at particular aspects of the social system from a range of different species. The study presented here aims at extending molecular ecological studies by applying data collected for these specific questions to a comparative phylogenetic framework. As has been done with other data on ecology and behaviour (e.g. Gittleman & Harvey 1982, Rolland *et al.* 1998), comparing patterns among sets of species can test different functional explanations for the observed patterns, and by applying statistical tests identify the past action of selection.

In this study, I therefore derive analytical models to provide predictions on the amount and distribution of genetic variation expected within a specific social structure (figure 1.1), and combine these with individual-based simulations to test the predicted effects of differences in dispersal system, group size and reproductive skew on genetic variation. The new methods are applied to published data from a range of mammalian species to identify correlates between genetic structure and social and ecological factors, and to provide more insights into the factors which have shaped the variation in social systems.

## 1.2 Methods in molecular ecology

A range of specific molecular methods have been applied to answer questions in behavioural ecology (Freeland 2005). They start by obtaining suitable sample material, extraction of DNA and amplification of the genetic marker. In general, since studies in molecular ecology are aimed at providing more information about individuals, their movements and their relatedness, and therefore information about the recent past, they employ markers which are rapidly mutating and show a high degree of variation within populations (Sunnucks 2000). In the following only those methods are described which are now routinely applied to free-living populations of animals and which provide data that can easily be compared among populations.

The first step is sample collection. Recently the number of studies of wild populations has increased due to the possibility of using samples which have been collected non-invasively. Previous analysis had to rely on blood or tissue samples, and for these either had to transfer individuals to the laboratory (Birdsall & Nash 1973) or trap them (McCracken & Bradbury 1977), which limited the species to which this could be applied. By harnessing the ability of the PCR to start from the very low amounts of DNA (see below) as found in noninvasive samples (Vigilant *et al.* 1989), studies could also be extended to other species. Materials for these include plucked feathers (Taberlet & Bouvet 1991), hair (Taberlet & Bouvet 1992) and feces (Höss *et al.* 1992). These samples can be obtained without direct contact of the animals. Therefore they do not induce disturbances, but also allow collecting samples of shy and elusive species. This opened up the possibility for a broader application of genetic approaches to studies in behavioural ecology, however coherent studies initially remained limited (Taberlet *et al.* 1996). This was probably due to the perceived high costs and the need in access to expertise and an expensive set of equipment (Burke 1989). Analyses based on non-invasive samples have to account for additional difficulties and challenges due to the low amount of DNA and the degradation of the DNA, leaving only small fragments (Vigilant 2002). Different methods to store the sample have been developed to stop the degradation of the DNA even under limited field conditions (Roeder *et al.* 2004, Nsubuga *et al.* 2004). In addition, with new ways of power supply which allow having fridges at the study sites and quick transport (Roon *et al.* 2003), the reliability and success of these noninvasive samples has drastically increased.

Once suitable samples have been obtained, complete genomic DNA can be extracted. While DNA extracted from feces therefore also can be used to analyze the diet (Kohn & Wayne 1997, Bradley *et al.* 2007) or parasites found in the gut (Goldberg *et al.* 2007) to inform ecological studies, the main interest is to infer DNA sequences of the individual animal. The most important tool for this is the polymerase chain reaction (PCR). In this reaction oligonucleotide primers are added to a DNA extract, which has been heated to split the DNA into single strands. These primers have been designed to match and bind to copies of one chosen region in the genome. Beginning at these primers, an enzymatic duplication of the targeted stretch is started. The resulting double-stranded DNA is split up again by heat, and the two resulting strands now can serve as template in the next round, leading to an exponential

increase of the target region. This reaction therefore amplifies a specified fragment of the genome more than million fold by repeating the steps. Because genetic tools (DNA sequencing, restriction site analysis, microsatellite genotyping etc., see below) can be effectively applied to PCR products, this opened up the usage of samples with a low quantity of DNA. Even though PCR is an easy performable method and has therefore potential ubiquitous application, as mentioned before, the DNA in these samples is of low quality and quantity (Vigilant 2002). This makes laboratory procedures more prone to errors, like non-amplification of the target region or amplification of erroneous contaminating sequences (Pompanon *et al.* 2005). To obtain accurate information, analyses therefore have to be repeated independently several times (Taberlet *et al.* 1996, Morin *et al.* 2001), plus ideally several samples per individual should be used (Taberlet *et al.* 1999). This leads to an increase in terms of time and money investment.

The study of markers on the mitochondrial genome has dominated evolutionary genetics (Avise 2000). Since there are several mitochondrial molecules per cell, it is found in higher quantities in samples and is readily amplified from noninvasive DNA samples. The mitochondrion is an organelle within cells responsible for the majority of energy production. It has its own, circular ~16,000-17,000bp long genome. Apart from a variety of genes involved in this energy production, it contains a hypervariable region, the so-called 'D-loop', which serves as starting point for the replication of the molecule (Clayton 2000). Studies of the nucleotide variation at this and other mtDNA loci have been promoted in population genetics due several unique characteristics of this mitochondrial DNA (Avise 2000). It is only inherited along the maternal line and shows no recombination, which means that it reflects maternal relationships and the resulting gene tree therefore also allows to reconstruct recent phylogenetic relationships directly. This is additionally helped by the approximately 10fold higher mutation rate among mitochondrial than among the nuclear genes (Brown *et al.* 1979). Since the basic structure of the mitochondrial genome is rather conserved due to functional constraints, primers can easily be developed by using information from other species, and the complete sequence of the mitochondrial genome is now available from several species (e.g. Mindell *et al.* 1999). Most of these primers target the above mentioned 'd-loop', since it is assumed that substitutions in this non-coding region reflect neutral distance. Together with an inferred mutation rate, information from this locus therefore also allows to date

divergences. There are, however, limitations to the use of mtDNA in molecular ecology. The facts that it is only transmitted along the female line, and its small size in comparison to the nuclear genome, mean that a lot of information about the individuals (e.g. paternity) will be missed. Furthermore, studies limited to variation at the mtDNA and therefore to a single marker might be confounded by sampling stochasticity.

DNA sequence variation on autosomes is principally, as on the mitochondrial genome, either in the form of nucleotide substations, or changes like deletions and insertions. One special type of the last polymorphism are microsatellites. These are short 1-6 bp motifs, sequentially repeated up to 30 times in a row (Schlötterer 2000). They have a high mutation rate of ~$10^{-3}$ mutation events per locus per transmission (Weber & Wong 1993). Mutations occur as deleting or adding repeat motifs, also called slippage (but there are also other mechanisms, Ellegren 2004). These microsatellites are particularly suited for studies in molecular ecology, since they are therefore highly variable even within populations. In addition, this variation can easily be detected as simple length polymorphism by separating alleles through gel electrophoresis (Dowling *et al.* 1996). They are often rather short in length and can therefore be studied using degraded DNA as found in noninvasive samples. Even though suitable microsatellite loci can, as with mtDNA markers, be detected by having the full genome sequence or transferring this from closely related species, specific methods exist to enrich genomic DNA for specific repeat motifs and sequence the adjoining regions. This leads to the establishment of a species specific suite of unbiased markers which can be screened for variability (see Zane *et al.* 2002 for overview). Several loci have to be combined to provide detailed information about relationships among individuals, since single loci represent only one of the several possible connections. In addition, the high mutation rate combined with the special mutation type (adding or substracting one repeat) leads to a high degree of homoplasy, meaning that independent mutations have lead to the same variant. Microsatellites therefore also provide only limited information to resolve phylogenetic relationship further back in time.

Studies of variation at the sex chromosomes have only recently been applied to mammalian populations (Hellborg & Ellegren 2004). Studies of markers on the X-chromosome have not been necessary, because mtDNA can serve as an effective marker to infer female specific processes. Studies of markers on the Y-chromosome

are still limited (Lawson-Handley & Perrin 2007), mainly due to the highly complex structure (Skaletsky *et al.* 2003), which has made efficient marker detection difficult. In addition, only low levels of variation have been detected in most mammalian populations (Hellborg & Ellegren 2004). Detailed studies of natural populations are therefore limited to few species (bonobos: Eriksson *et al.* 2005; shrews: Lawson Handley *et al.* 2006; chimpanzees: Langergraber *et al.* 2007b).

### 1.3 Approaches in molecular ecology

Molecular genetic tools have been added to studies in behavioural ecology mainly to gain additional specific information on known or unknown individuals. With this information questions focusing on the movement and reproduction of individuals within social groups have been answered. The genetic approaches center on determining the kin of the specific individuals, either to understand the mating system, to test for the influence of nepotism on cooperation or to understand individual movements (Burland & Worthington Wilmer 2001, Bradley & Vigilant 2002, di Fiore 2003, Waits & Paetkau 2005) . Microsatellites have been especially applied for these questions, since they follow mendelian inheritance from both parents (Bruford & Wayne 1993), and by combining several independent loci, they allow individual identification and relatedness analysis. First, an individual genotype is assembled by determining which of the different repeat variants, the alleles, an individual carries at each of several loci (also termed 'DNA fingerprinting' Burke & Bruford 1987). If the combined number of different alleles across individuals at these loci is high enough, the chance that a second individual shares exactly the same combination is low. With knowledge on the number of alleles and their frequencies in a population the "probability of identity" can be calculated (Waits *et al.* 2001), and studies can use this information beforehand to plan the minimum number of loci necessary to discriminate all individuals within the population with high statistical certainty. This can save time and materials.

If unique genotypes have been assembled for all individuals, paternity can be assigned based on the exclusion method (Hanken & Sherman 1981). First, the genotype of an offspring is compared to that of the putative mother, which are often know from observations. Mothers are confirmed by ensuring that they share one allele at each of the loci with the offspring. The remaining allele at each of the loci is than used in comparison against all possible fathers, with (hopefully) excluding all except

one individual because they do not share one or more of the alleles. However, to obtain high power a large number of loci has to be typed. Therefore, also statistical methods based on likelihood have also been developed to identify the most likely father within a set (Marshall *et al.* 1998) in case no unique canditate is detected.

Paternity analyses have helped to understand the extent to which social and genetic mating systems can agree or differ from one another, and offer insights into the costs and benefits of sexual strategies. For instance, for socially monogamous birds (~90% if all bird species) it was found that extrapair copulations are common, less than 25% of these species are actually also genetically monogamous (Griffith *et al.* 2002). In contrast, in species where several females and males live in the group and mating is promiscuous, paternity is often significantly skewed towards one of the males siring most of the offspring (e.g. ground squirrel, Lacey *et al.* 1997; meerkats, Clutton-Brock *et al.* 2001). Understanding the number of offspring individuals sire, and quantifying the variance among these individuals, is fundamental to identify adaptation. These measures of reproductive success and reproductive skew directly relate to the fitness of individuals (Coulson *et al.* 2006). They are therefore the measure to understand to which degree specific morphological characteristics or behavioural strategies of males or females are a target of selection (e.g. Moller *et al.* 2003)

Estimation of dyadic relatedness beyond the parent offspring relationship rely on similar statistical approaches, by comparing the sharing of particular alleles among individuals to that expected under chance (Blouin 2003). Full-siblings for instance are expected to share on average one allele per locus by inheriting it directly from their parents. Several approaches have been developed which try to classify dyads into relationship categories (Weir *et al.* 2006). In addition, other estimators are more useful to apply in heritability studies (Coltman 2005). However, there are limitations in the reconstruction of relationship among individuals of similar age from genetic data. The first arises, because siblings have a 50% chance of inheriting the same versus the different copy of a gene from the common parent. This means that full sibs can either have obtained both the same copies from both their parents, just one identical, or the two different copies from each parent at any given loci. In addition, the overlap relatedness from different kinship categories, e.g. aunt-niece versus maternal half-sisters, makes exact classification of dyads difficult (Csillery *et al.* 2006). A large number of independent microsatellites are needed to reliably

discriminate related from unrelated individuals (Milligan 2003, Langergraber *et al.* 2007a).

Classifying dyads into relatedness categories has helped to understand more about the costs and benefits of social grouping (van Horn *et al.* 2004) and cooperation (Langergraber *et al.* 2007a). It has provided information on mating systems by showing the importance of inbreeding avoidance (Pusey *et al.* 1996) and differentiating models of reproductive skew (Bradley *et al.* 2006). Determining the relationship among individuals also informs about individual movements. Microsatellite data can be used to identify the population of origin for individuals (Paetkau *et al.* 1995, Bergl *et al.* 2007). In addition, by comparing the relatedness among females and males within groups, the sex bias in dispersal can be determined (Altmann *et al.* 1996).

By studying large sets of individuals to provide knowledge on the genetic relationship between dyads, genetic data with intense sampling at a local scale has now become available. With this wealth of data, there is now also the possibility to analyze the patterns of genetic variation more generally to understand more about aspects of the social structure, which would be otherwise difficult to study, and also to compare them between species. For this, one can borrow from population genetics theory (Sugg *et al.* 1996).

### 1.4 Population genetics and molecular ecology

Concepts relevant to behavioural ecology were included into population genetics theory quite early. While Fisher realized the effect of differential reproduction of individuals on gene frequencies from data of human populations (Fisher 1930), Wright developed the first analytical predictions of genetic variation at nuclear loci studying breeding populations. His approaches therefore include predictions for the effect of differences in mating systems (Wright 1921, 1965). Furthermore, Wright introduced the concept of "neighborhoods", the range of distance within which the parents of individuals can be found. In case of a philopatric group this reduces to the same location as the individuals can be found at, in case of dispersal it depends on the distance individuals move within one generation (Wright 1945). His F-statistics provide predictions for the amount of variation found within areas and the differentiation between them. However, due to the difficulties of obtaining the relevant data little actual application of these aspects of his theories was

done. Population genetics theory rather assumed the 'standard-neutral' model, describing a population of infinite size, with the same number of females and males and random mating between these (e.g. Hudson *et al.* 1987). While researchers were still aware that factors like differential reproduction would influence genetic variation (e.g. Kingman 1982 in the development of coalescent theory), tests for selection for instance were based on a comparison to the simple model (e.g. Tajima 1989).

The link between individual behaviour and distribution of genetic variation however was considered in studies on phylogeography using mtDNA (Avise *et al.* 1987, Hoelzel *et al.* 1998). Data from macaques for instance showed a clear influence of the fact that females in this species are philopatric (Melnick 1987). This principle was soon extended to compare data from genetic makers which are only transmitted along one sex and nuclear markers which are transmitted by both parents, to infer sex-specific dispersal from the different distribution of variation (Chesser 1991, summarized in Avise 2000). In addition, with the aforementioned increase in studies of natural populations of mammals the influence of demographic and social parameters on the detected genetic structure was approached again (Chesser 1983, Chepko-Sade *et al.* 1987). There were two main questions which drove this reassessment. The first aimed at understanding whether social structures of mammals were indeed caused by effects of kin selection, specifically whether group living individuals gained benefits through inclusive fitness by cooperating with relatives (Hamilton 1964). If individuals preferentially support kin, the alleles they share through common descent can spread in the population. Population genetics theory was applied to predict which combination of dispersal and breeding within groups would maximize relatedness withing groups (Chesser 1991), while minimizing inbreeding (Chesser *et al.* 1993). Combined they provided insights into the potential benefits (Pope 1990) and conflicts (Griffin & West 2002) of intragroup gene correlations, and showed how different aspect of the social structure probably coevolved (Ross 2001).

The second question aimed at understanding whether low levels of variation, combined with F-statistic values which indicated inbreeding, were indeed signs of small closed populations. In this case it was soon realized that sampling of social species has to recognize the additional structure which is imposed by the social system (Sugg *et al.* 1996), and that behaviours which indicated clear inbreeding avoidance (Emlen 1995) indeed also were reflected in the distribution of genetic variation when analyses where performed using social groups instead of populations

as the units of structure (Storz 1999). Understanding the effects of structuring into groups, sex-biased dispersal and variance in both female and male reproductive success, became especially important with the routine addition of genetic methods in the assessment of endangered species (Frankham 1996). In these cases analyses aimed at understanding whether certain species due to their structure would be more prone to the loss of genetic variation (Nunney 1994, Nunney & Elam 1994, Gompper *et al.* 1997). However, with recent increase in sample sizes and more finegrained sampling, population genetics studies try to take these factors into account (Laporte & Charlesworth 2001). This has for instance helped to provide insights into the social structure during human history (Oota *et al.* 2001, Wilder *et al.* 2004).

### 1.5 Thesis objectives

The work presented here links social structure and genetic variation in a comparative framework. It thereby aims at understanding the aspects of social structure which vary among species and identify potential selection pressures. The results also have implications for population genetics studies, since depending on the sampling and the genetic markers used different species might show different levels of genetic variation. While this could lead to misinterpretations as signal of a past demographic event, the thesis only briefly touches on these effects.

I present mathematical models to predict how changes in group size, sex-bias in dispersal and variance in lifetime reproductive success will affect variation both at sex-specific and autosomal genetic markers. I test some of the predictions using individual-based simulation and apply them to data from natural populations, both to document the predicted effect, and, by turning the analytical approach round, to infer the social parameters from the genetic data. There are two specific topics I will address with this approach, the first about relatedness within social groups and the second about variance in lifetime reproductive success.

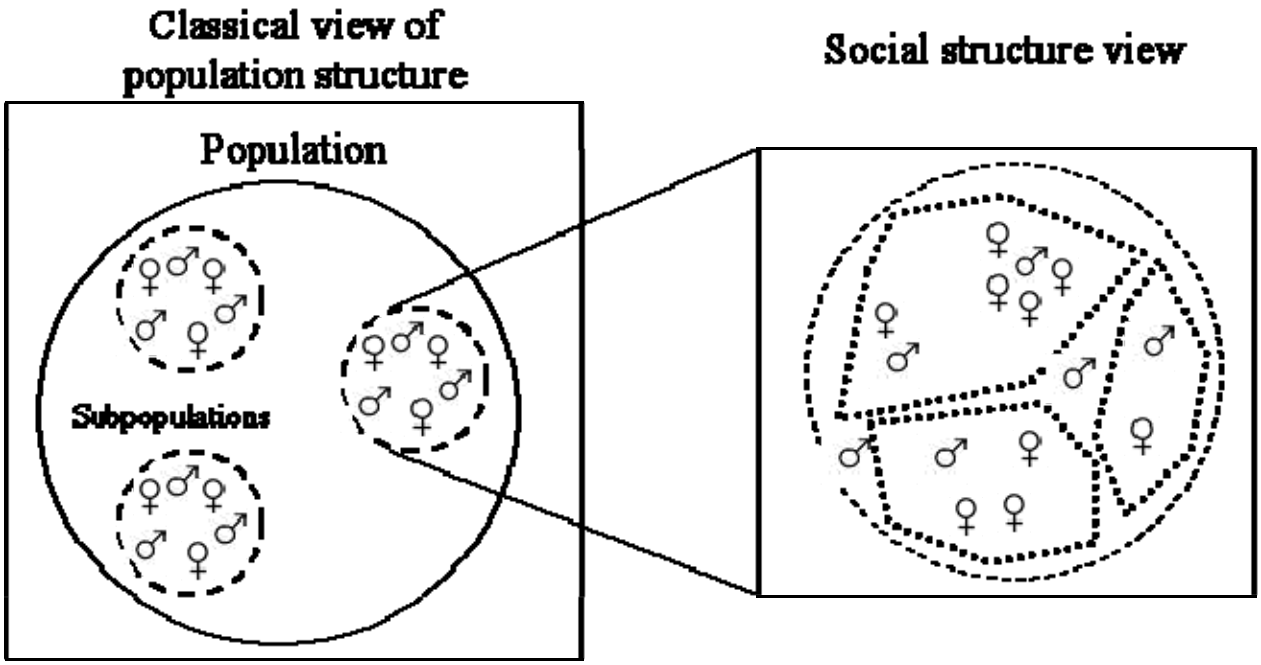
**1. Are philopatric individuals within social groups members of one large family group? Which factors of the social system lead to high relatedness among individuals within a group? Can grouping among animals be explained by the inclusive fitness benefits individuals gain through cooperation among relatives?**

In chimpanzees, males are philopatric and show high levels of cooperation. It has been proposed that this is driven by the inclusive fitness benefits males gain by cooperating among relatives. I use this specific example to analyze in detail relatedness among males and females within and between several social groups to assess whether males are in fact highly related. To understand and explain the findings I derive an analytical approach to predict relatedness levels depending on the specific social structure of a species. The results are than placed in the context of a comparative study, to assess whether grouping among philopatric individuals in general can be described as close family groups, or which social structures are needed for high levels of relatedness.

**2. Can genetic data be used to detect direct fitness differences among individuals within a population? Is there variation across species in the degree of fitness differences among females? Are there specific social or ecological situations which correlate with higher fitness differences among females?**

Studies quantifying the degree to which individuals of a population differ in the number of offspring they sire, their fitness, have been limited for mammalian species due to the need of study a large number of individuals over their whole reproductive career. However, since all genes carried by successful individuals should increase in frequency within a population, genes which are only inherited within one sex should reflect the degree of intrasexual competition. I develop predictions of how variance of lifetime reproductive success should influence genetic variation within and among social groups and analytical approaches to calculate it from a sample. These approaches are assessed in indvidual based simulations. Finally, these methods are than applied to mitochondrial data from mammalian populations to be used in a comparative study to identify whether there are social or ecological situations which correlate with higher variance in lifetime reproductive success among females.

**Figure 1.1** Comparing the classical population genetics view to one recognizing social structure. In the classical view, individuals are attributed to subpopulations containing equal numbers of males and females which mate at random and who move at random among these subpopulations. The social structure highlights that individuals are living in groups of varying sizes. In addition, it is mainly one sex which moves among these groups. Furthermore, individuals mate with specific others, with some individuals obtaining higher mating success (modified after Sugg *et al.* 1996).



# 2. General Methods

## 2.1 Overview

In this thesis, I employ analytical modeling to derive predictions and testable hypotheses for the link between the social system of a species and the distribution of relatedness or genetic variation among individuals. The derived equations are assessed for their validity and robusticity using computer simulations. They are then applied to published genetic data from a range of different species and used in cross-species comparative analyses.

## 2.2 Mathematical modeling

The most common use of math in biology is to apply established statistical models to data gathered in field studies or designed experiments, with the aim to understand the statistical relationships found among several variables. In addition however, there is also constant development of new mathematical models in all parts of biology (Peck 2004). Models in general are a formulization of theories, and thereby help to test the logic and validity of our thinking (Kokko 2007). Formulating the relationships among factors aims at explaining how something works causally and also allows the manipulation of the different factors. It thereby leads to construction of null hypothesis and competing hypotheses, which can be statistically compared with real data (Balloux 2004). This last step therefore provides a test for the underlying theory. Model formulization in ecology and genetics is driven by observation of natural populations, the supposedly relevant processes are than abstracted and solved in mathematical equations or computational simulations, and the solutions are compared to matching data (Maynard Smith 1971). The approach I choose here is not based on detailed data from within a single species, but comparative data across species. The models developed in this thesis therefore can be classified as "minimal models for a system" (Roughgarden *et al.* 1996 as cited in Grimm & Railsback 2005), like most models in ecology and genetics. These are intended to explain broad phenomena, while ignoring many characteristics of the real system in the hope they are not relevant. This is in contrast to either purely theoretical concepts or detailed simulations of all the components of a single system. The aim is

rather to seek to gain general insights by providing mathematical metaphors for broad classes of phenomena (May 1973). The approach used here is a bottom-up analysis. Actions of individuals in populations, namely dispersal and reproduction, together with rules of the interaction of these individuals, namely grouping patterns and competition over reproduction, are used as input factors to predict emerging patterns on the population level, in the form of the distribution of genetic variation. Patterns, which are clearly observable characteristics of a system, contain information on the internal organization of a system, but in a "coded" form. Specifically the question here is wether genetic data collected from social animals contains patterns in its distribution, and whether one can decode the information behind this pattern as the aforementioned individual characteristics.

## 2.3 Analytical versus simulation approaches

Generally two types of models in biology have been discriminated, with the distinction sometimes simplified into those models which can be directly solved versus those which have to be plotted using a computer (Maynard Smith 1974). However it is rather that analytical versus simulation is a definition of formulation, not implementation (Grimm & Railsback 2005) – in both cases computers can be used. Analytical approaches use mathematical language to formulate equations which can be solved by algebra or approximation. Simulations on the other hand implement complex interactions, mostly as individual-based modeling and are using computer language as formulization. The main focus of this thesis is on analytical modeling. However, individual-based simulations are implemented to assess the validity and the robustness of the derived analytical equations.

Individual-based simulations allow researchers to study how system level properties emerge from the adaptive behaviour of individuals (Grimm & Railsback 2005). There are three main reasons for why the use of IBM in an ecological context has been advocated: they allow for individual variability, local interactions and the emergence of adaptive behaviour. These three aspects are hard to deal with mathematically (Grimm & Railsback 2005). Since individual variability and local interactions can lead to stochasticity and chaotic behaviour in the system, which is sometimes impossible to predict from simple analytical approaches (May 1974), in this thesis I also apply computer simulations with individuals behaving in a virtual world. There have been previous implementations of individual-based simulations in

population genetics (Easypop: Balloux 2004, Metasim: Strand 2004). However, these specific approaches do not take the social factors specifically relevant in this study into account, so that I decided to construct a new, specific model. The aim of this individual-based modeling approach was to first see whether the individual actions in fact lead to predictable patterns in the distribution of genetic variation. In addition, they help to assess how robust the patterns is against varying additional factors which are known to influence genetic variation. Finally, they provide controlled experiments, where, by varying one factor at a time, also the performance of the analytical approaches can be assessed. Especially, if the individual-based simulations indicate that the specific signal one is interested in is robust to the stochastic effects and that it can be easily described by an analytical approach, one should try to find analytical approximation of the individual-based simulations (Grimm & Railsback 2005). Simulations allow to identify which factors are essential and which can be ignored, and thereby help to identify among a set of analytical approximations the one which captures the most information while being the simplest. Results from different studies in population genetics have for instance shown that complex demographic scenarios can, in some cases, be described using relatively simple models (Wakeley 2004). In fact, many of the analytical approaches derived in this thesis rely on previous population genetics theory. This transformation of individual-based models is useful, since analytical approaches have several advantages over individual-based models. They can, in most cases, be formulated easier. For this, they can also be communicated easier since they are writen down in the universal language of mathematics instead of in a specific computer code. The biggest advance in the context of this study is however the fact that the analytical equations can be changed so to either be used to make predictions about specific parameters, but also to estimate the parameter from data to solve for one of the predictor variables. Especially for continuous paramters like the variance in lifetime reproductive success, it would be helpful to infer the value for a given species simply by inserting some genetic variation summary statistics, instead of trying all different possibilities in the simulations to infer the most likely one. They therefore allow both the test of causality and the inferrence of the respective parameters. For both topics of this work, relatedness and variance in lifetime reproductive success, I therefore focused on analytical models. They are used to derive predictions for competing hypotheses,

which than are assessed with a reanalysis of published data in a comparison across several species.

## 2.4 Comparative method

The comparative method is based on collecting data from a range of populations to identify whether certain characteristics have evolved together (Pagel 1999). It treats data as if they were generated by replicated "natural experiments" (Doughty 1994). Since in many cases researchers cannot change specific characteristics of species (e.g. groupsize) to understand its importance and relationship to other characteristics (e.g. food competition), they can gain information by analyzing whether there are consistent correlations among species with a specific value of the one characteristic (e.g. large group size) and the other (e.g. high food competition). It therefore is one of the most applied methods to test hypotheses of adaptation (Harvey & Pagel 1991). After initial simple species comparisons, it soon became realized that phylogenetic information has to be incorporated in statistical tests of correlated evolution to avoid errors due to non-independence of data points, but also to increase the power of analyses by incorporating the distance among species as information. Closely related species will tend to resemble each other due to the recent descend from a common ancestor (Clutton-Brock & Harvey 1979), meaning that species cannot be considered statistically independent units of observation. The most common method used to deal with this problem, and also the method I apply in parts of this thesis, is the one of independent contrasts (Felsenstein 1985). In this, the phylogeny of the species is used to reveal the number of times a certain characteristics has changed in concert with the other characteristic (e.g. increase in group size and increase in feeding competition). Statistical tests can than be used to assess whether this change has happened more than expected under chance, indicating the correlated evolution. Even if one of the characteristics is flexible and potentially quickly changing (e.g. food competition depends on the amount of food present), incorporating phylogeny also corrects of the potential effect of confounding uncontrolled characteristics (e.g. closely related species will inhabit similar habitats). Furthermore, by including also the actual distances among species and a model of evolution of the character increases the power to identify a correlation (Garland *et al.* 2005). However, since most comparative analyses are correlations they do not allow to infer causality (but see e.g. Lindenfors *et al.* 2003), but should be used together

with other kind of evidence to test evolutionary hypotheses (Doughty 1994). While some of the comparative analyses performed in this thesis are also limited to simply show correlations in adaptive trait evolution, in several cases the analytical equations can be used to compare the fit of the data to alternative hypotheses to identify the most likely causal relationship. This is further supported by the simulation modeling, in which one can recreate the directed change of single factors.

There are different types of applications of the comparative method in this thesis: The first compares average relatedness within social groups and does not take phylogeny into account. In this case I derive an analytical model which predicts an immediate effect of group size on average relatedness, which cannot be inherited as such and which is not confounded by other variables. I herefore also use all observations, independent whether they are from the same or from different species, as data. The second one compares genetic variation among females within a population to that among females within another population and to the males from their own and the other population. In this case I predict that data from females of the one population is the most similar to the data from males of the other population, since they leave their natal village respectively, whereas the other sex remains. Again, no formal statistical phylogenetic corrections are applied, since I use a cross-design to control for potentially confounding factors. The last application however corrects for phylogeny by using independent contrasts to identify correlations between morphological, ecological and social characteristics of females of different mammalian species and the degree of fitness variance among them as indicated from genetic data.

# 3. Average relatedness levels within social groups

## 3.1 Summary

Chimpanzees live in large groups featuring remarkable levels of gregariousness and cooperation among the males. Because males stay in their natal communities their entire lives and are hence expected to be living with male relatives, cooperation may be explained by the inclusive fitness benefits derived from kin-biased interactions. However, I found that the average relatedness among males within several chimpanzee groups as determined by microsatellite analysis is in fact rather low, and only rarely significantly higher than average relatedness of females in the groups or of males compared across groups. To explain these findings, mathematical predictions for average relatedness according to group size, reproductive skew and sex-bias in dispersal were derived. The results show that high average relatedness among the philopatric sex is only expected in very small groups, which is confirmed by a comparison with published data. These results therefore suggests that grouping and interaction among larger number of individuals may not be primarily driven by kin selection.

## 3.2 Introduction

### 3.2.1 Philopatry and relatedness

Kin selection theory has been influential in interpreting animal behaviour by offering a framework in which high relatedness among the members of a group and the resulting inclusive fitness benefits could offset the costs associated with group living and even facilitate seemingly altruistic, cooperative activities (Hamilton 1964, Wrangham 1979). For groups of social animals, philopatry in one sex could be expected to lead to higher relatedness among members of the philopatric sex as compared to the dispersing non-philopatric sex, assuming that dispersing individuals do not move in concert with relatives. For most mammals, females are the philopatric sex, while males emigrate upon maturity (Greenwood 1980) and in general, patterns of genetic relatedness in social groups of female-philopatric mammalian species often do appear to conform to the expectation of notably higher average relatedness among females than males (de Ruiter & Geffen 1998, Surridge *et al.* 1999, Lawler *et al.* 2003). However, some recent studies have failed to find relatedness levels in accordance with expectations (guppies: Russell *et al.* 2004, wolves: Vucetich *et al.* 2004, hyenas: van Horn *et al.* 2004). In particular, a previous study on chimpanzees did not find significantly higher average relatedness of philopatric chimpanzee males as compared to females within groups (Vigilant *et al.* 2001). This was surprising because the strong social bonds between chimpanzee males within a community have previously been suggested to reflect kin associations (Morin *et al.* 1994 and references therein).

### 3.2.2 Social system of chimpanzees

In contrast to most other old world primates, but in common with humans (Ember 1978), in chimpanzees it is the females rather than the males that typically emigrate upon reaching maturity (Nishida & Kawanaka 1972; Pusey 1979; Boesch & Boesch-Achermann 2000). This reversal of the usual mammalian pattern implies that the intensity of competition among group females is even greater than that among group males, and/or that there exist factors that mitigate competition among the males. One such factor could be mutually supportive or affiliative behaviour among the males. Chimpanzees are territorial, and the adult and adolescent males of the community actively defend the community home range (Goodall *et al.* 1979; Boesch

& Boesch-Achermann 2000; Watts & Mitani 2001). The potentially lethal nature of the interactions between males of different communities underscores the potential costs of collective territory defense. This is notable as activities with high costs have been suggested as the most likely arena for the operation of kin-selected behaviour in primates (Chapais 2001). In order for male inter-community interactions to be influenced by kin selection, it is expected that the average relatedness of males within communities exceed that of males compared across communities, even though possible competition between relatives could reduce or remove potential inclusive fitness benefits (West *et al.* 2002).

### 3.2.3 Factors influencing relatedness in social groups

While patterns of philopatry and dispersal create connections between groups, empirical studies have demonstrated that reproductive skew (Altmann *et al.* 1996) and group size (humans: Brown 1991, Alvard 2003; lions: Spong & Creel 2004) influence kin-structure within groups. Male reproductive output in chimpanzees is influenced by the hierarchical dominance system, under which the highest-ranking male produces a disproportionate share of the offspring, with the relative shares influenced by factors such as the number of competing males and, to a lesser extent, the number of females simultaneously in estrous (Constable *et al.* 2001; Boesch *et al.* 2006). In addition, recent data show that a limited proportion of offspring are not sired by males of the community they reside in, but are the result of extra-group paternity or transfers as infants with their mothers (Boesch *et al.* 2006 ). Overall, the greater the extent to which a single male dominates reproduction, the greater the number of paternally-related offspring among the total number of offspring in the group. In order to understand why estimated relatedness levels within and across chimpanzee communities do not fit with pre-expectations, in this study I assess the theoretical basis of these expectations and analyze the influence of these factors on average relatedness levels. Early work by Altmann indicated that average within group relatedness could be low if multiple males sire offspring (Altmann 1979), however, her approach does not allow for assessment of the impact of factors like sex-bias in dispersal or comparison with empirical data. Therefore, I derive here a new approach to investigate the conditions under which philopatric individuals in groups are expected to be highly related.

### 3.2.4 Objectives

This study has three parts. In the first, I present a more detailed analysis of chimpanzee data in light of kin selection theory. Specifically, I employ a dataset of microsatellite markers to estimate average genetic relatedness among sets of individuals in multiple wild chimpanzee communities from two separate sites in West and East Africa. The goal is to test the following closely-linked predictions: 1) adult males within a community are more related than are adult females, 2) adult males within a community are more related than are adult males across communities, 3) cohorts of offspring are more related when few rather than many males achieve paternity. In the second part of this study, I compare these results to theoretical expectations derived from a mathematical model that reveales the effects of reproductive skew, group size and sex bias in dispersal on average relatedness levels of a group of individuals and provides values for a "chimpanzee" situation. Finally, by comparing the theoretically obtained as well as the empirical chimpanzee values to previously published relatedness estimates from a variety of species, I assess the fit and the generality of these results. This latter comparative analyses therefore also serves to understand whether grouping among social mammals is indeed driven by indirect fitness benefits.

## 3.3 Materials and methods

### 3.3.1 Genetic data of habituated chimpanzees

The genetic data of chimpanzees for these analyses were provided by collaborators, and the methods are only briefly described (for more details see Bradley *et al.* 2000; Vigilant *et al.* 2001). Noninvasive samples, primarily feces, were collected from habituated, individually-identified chimpanzees. Three communities of west African chimpanzees (*Pan troglodytes verus*) and one community of east African chimpanzees (*P. t. schweinfurthii*) were studied. The western chimpanzees were from the North, Middle and South communities in the Taï National Park, Côte d'Ivoire (Boesch & Boesch-Achermann 2000). The eastern chimpanzees were members of the Sonso community in the Budongo Forest Reserve, Uganda (Reynolds 2005). After extraction and quantification of amplifiable DNA (Morin *et al.* 2001), individuals were genotyped at a total of nine highly variable microsatellite markers. Multiple

measures to ensure accuracy as detailed in (Vigilant *et al.* 2001) were employed, the most notable being that both alleles of heterozygous genotypes were scored at least twice and depending upon template amount present in the PCR (Morin *et al.* 2001), the single allele of homozygous genotypes was scored four or more times. Genotype data of a total of 114 western and 49 eastern chimpanzees was available (Appendix 3.1).

### 3.3.2 Analyses of the chimpanzee data

For all individuals, I obtained the exact ages of individuals younger than 18, 6 and 8 years (Taï North, Middle and South, respectively) or 10 years (Sonso), while the ages of older individuals were estimates by experienced field researchers and are likely to be accurate to within 5 years. For analyses of similarly-aged cohorts, I classified individuals according to age attained in full years on January 1 of the year of interest as follows: fully adult (aged 15 years and up for males, 13 and up for females); adolescent (10 -14 for males, 10-12 for females); juveniles (5-9 for both sexes) and infants (0-4 years) (Boesch & Boesch-Achermann 2000). Since even young adolescent males father offspring (Constable *et al.* 2001; Boesch *et al.* 2006) and take part in male affiliative activities such as hunting and boundary patrolling (Boesch & Boesch-Achermann 2000; Mitani *et al.* 2002; Watts & Mitani 2002), they were considered as adult males for the purposes of all analyses.

The Queller and Goodnight estimator of relatedness (R) implemented in RELATEDNESS version 5.0.8 (http://gsoft.smu.edu/GSoft.html) was used. This particular estimator was chosen as it was designed to estimate r for the purpose of applying Hamilton's rule to natural behaviour (Queller & Goodnight 1989). Allele frequencies used in relatedness analyses of the Taï chimpanzees were based upon a subset of individuals of no known relatedness (Vigilant *et al.* 2001), and results did not vary when using allele frequencies from all individuals (data not shown). Allele frequencies from all individuals were used for the Sonso chimpanzees as the total number of individuals was too small to allow a selection of probable unrelated individuals. Thus, the relatedness values for the Sonso chimpanzees are expected to have a slight negative bias. Rarefaction analysis, whereby relatedness values were calculated after each successive inclusion of loci beginning with one locus, revealed little change in the variance of calculated relatedness values after addition of the 7th locus (data not shown). This implied that the 9 loci used here were sufficient for

robust estimates of relatedness in these populations. Standard errors of estimates of average R within and between groups of individuals were estimated by jackknifing across loci. Since standard errors are strongly influenced by the number of comparisons and so are not directly informative for comparisons between analyses using different samples sizes, instead the standard deviations of R estimates are reported as these clearly reflect the amount of scatter in the data whatever the sample sizes. However, confidence intervals cannot be directly compared because of non-independence of data. Hence, the statistical significance of differences in average relatedness values among sets of individuals was evaluated by permutation analysis (Manly 1997). For the permutations I resampled individuals by pooling all individuals in the groups to be compared, and then repeatedly drawing the same number of individuals corresponding to the original group sizes and calculating average pairwise relatedness for these randomly constituted groups. Computer programs for the permutations were programmed in Excel. All analyses were performed at the level of community-years, meaning that I compared values for each community for each of the years 1995 through 2002 (Tai Middle: 1998 through 2002). Even though the data-points within the groups are not completely independent since the majority of the individuals stays the same, this approach covers a variety of demographic conditions and allows to make statements about the general situation of chimpanzee groups. For assessing the significance of the within-group relatedness differences, in each of the 29 analyses the individuals in the group under consideration were randomly sorted into two sub-groups of sizes matching the numbers of females and males, respectively, and the difference of the average relatedness values of these random sub-groups of individuals was compared to the observed difference in average female and male relatedness. The between-group analysis was performed for the three communities at Tai, whereby I pooled all males and then randomly resorted them according to the three group sizes, calculating the relatedness within and between each of the three sub-groups and comparing it to the observed values. I conservatively considered results significant when the observed difference in average relatedness exceeded 95% of the values obtained in 5000 permutations.

Genotypic differentiation between sampled communities was studied using the program MSA (Dieringer & Schlötterer 2003). This program calculates the Weir-Cockerham estimators (Weir & Cockerham 1984) of Wright's F-statistics (Wright

1951) across loci and between population pairs, and uses permutation tests with incorporation of a strict Bonferroni correction for multiple tests to estimate the probability of departure from the null hypothesis of no differentiation.

### 3.3.3 Mathematical model

I derived an equation that describes average relatedness of a group of adult individuals remaining in their natal group as a function of reproductive skew, sex-bias in dispersal and the number of individuals. This approach to derive average relatedness estimates is similar to the path analysis used by Wright (1965) to derive the F-statistics and to the group-structured model by Chesser (1998) in that calculated values are relative to the average of the total population, and so they represent the inclusive fitness benefit of the interacting individuals compared to a random dyad. However, my approach more closely reflects the situation of a population of social animals by allowing analysis of the effect of manipulating different variables defining social structure.

The calculations assumed an idealized situation in which: 1) all the adults are of the same generation, meaning that no reproduction via parent-offspring mating occurs; 2) dispersal is completely sex-biased, meaning all individuals of one sex leave and 3) these dispersing individuals join new groups randomly, so that the relatedness among the members of the immigrating sex is 0, as is their relatedness to the resident sex, which reflects the avoidance of inbreeding. Under these conditions, individuals can be related either through sharing one or both parents or, if their respective parents are related. According to the third assumption above, the calculations only have to consider relatedness through parents of the philopatric sex. A direct parent-offspring relationship has a relatedness value (R) of 0.5 and so to connect two individuals, all parent-offspring relations are counted and the value between the two individuals is 0.5 times the number of steps. To derive the R value for any given dyad, I calculate the value for the maternal side, which the two individuals may share, as their mothers can be related or unrelated, and then add the respective value from the paternal side, again analyzing whether it is the same father, or their fathers are related or unrelated (Figure 3.1). If one parent is shared, the relatedness value is 0.25, if the parents are related the value for the dyad is 0.25 times the relatedness of those parents and if the parents are unrelated, the dyad has has a relatedness value of 0; by adding up both lines one can see that these values can range from 0 to 0.5 in the case of a full-sib dyad.

The relatedness value for a group of individuals was obtained by averaging over all dyads. The variable of lifetime reproductive skew determined the number of dyads sharing the same mother or father, while the group size variable determined the total number of dyads. Lifetime reproductive skew is expressed here for both males and females as the relative proportion of offspring of the philopatric sex per generation produced per individual. This is incorporated in the formula as ***f*** (female reproductive skew) and ***m*** (male reproductive skew) by taking the sum of the squared percentages, and because they are given in proportions, the actual value also depends upon the group size. Group size was expressed as the number of individuals ***x*** of the philopatric sex. The values used for these factors can be interpreted as averages over a population that has been stable for some generations, so that reproductive skew indicates how many adults of a given group share the same parents.

I summarized these factors in a single formula (for details of the derivation see Appendix 3.2):

$$R = \frac{(f+m)*x-2}{(3+a)*x-4} \qquad (3.1)$$

where ***x, f*** and ***m*** are the values given above, and ***a*** is either equivalent to ***f*** if females are philopatric or to ***m*** if males are philopatric. I used the formula in two ways. In the first, I set ***f*** and ***m*** to fixed values, by assuming a situation in which on average, 25% of the males of the parental generation sire 75% of the new individuals of the philopatric sex and the remaining 25% are sired by an additional 25% of the male parents. For the females I assumed that in each generation, 40% do not produce any offspring of the philopatric sex, 25% have one offspring, 25% have two offspring, and finally 10% of the females have three offspring of the philopatric sex during their lifetime. These numbers are based on the expectations for a species that like most large mammals has a limited lifetime reproductive success, and an equal chance of producing a female or male offspring at each birth. The 40% of females who do not produce any offspring of the philopatric sex include all the females who only sired offspring of the dispersing sex. Under this scenario, I calculated the group size at which average relatedness drops below the level of half-sibs (r = 0.25) or cousins (r = 0.125), respectively. Second, I compared the effects of male versus female biased dispersal, and their difference in degree of lifetime reproductive skew, upon the average relatedness. To facilitate comparison with the empirical results, I chose values

for group size to simulate a "chimpanzee" situation, with 12 philopatric individuals in the group and fixed female lifetime reproductive skew as in the calculations on group size in the first scenario (this gives for 12 individuals $\boldsymbol{f} = 0.167$), while varying male lifetime reproductive skew.

### 3.3.4 Published genetic data

I compared the chimpanzee values and the predicted values from the mathematical model with empirical data obtained from published studies. A literature search was performed in 'ISI Web of Science ®' in August 2004 using as keywords "microsatellite(s)" or "blood protein(s)" and "relatedness". Data were considered relevant if the analyses were performed at the within-group level and separately for adults of each sex. If a study included analysis of more than one group, I averaged across these values to obtain one data point per publication. Group sizes were taken as reported in the methods section of the respective papers, and I tested for the influence of this demographic factor on the relatedness values. Regression analyses were performed by taking group size as the independent and relatedness estimates as the dependent variable by assuming either a linear (relatedness = *a* times group size) or an exponential relationship (relatedness = group size to the power of *a*), or by assuming a relationship as described in the formula 1 derived above (with female and male lifetime reproductive skew as additional parameters – to reflect a biological situation they were restricted to range between 0 and 1). All analyses were performed in SPSS 11.5.2 (SPSS, Inc., Chicago IL) with iterative estimation algorithms used to derive the missing parameters.

## 3.4. Results

### 3.4.1 Relatedness within chimpanzee communities of males as compared to females

I estimated average relatedness of adult males and females for a total of 29 chimpanzee community-years. The results for males and females (Table 3.1) contrast in two ways. First, it is immediately apparent that average male relatedness levels vary greatly, with the lowest value approaching R=-0.15 (Table 3.1, Taï North) and the highest corresponding to R=0.123 (Table 3.1, Taï Middle). Average relatedness

also varied greatly within communities, as in the Taï North group that in one year through changes in group composition went from an average adult male relatedness of 0.118 in 1998 to R= –0.1268 in 1999. In contrast, average relatedness levels of adult females did not vary as much between communities and were more consistent through time. The fluctuation in the relatedness values for males across years for the Taï communities is a function of the small number of adult males present, so that the addition or loss of a single individual had more effect upon average relatedness. Composition of the relatively larger Sonso community changed very little over the time considered, which is reflected in the stable R values for both males and females.

The second notable feature of the relatedness values in Table 3.1 is the lack of consistently higher relatedness of males as compared to females. Only rarely was the average relatedness of males significantly greater than that of the females of the same group in the same year, and the range of values largely overlaps (Table 3.1). The significance of the difference between male and female average R for four years in the Tai Middle community could not be tested due to a small number of individuals, but even after leaving these four years out, the four years in which significant differences were seen (Tai South, 1995-7; Sonso, 2002) represent a minority of the 25 community years considered. The average number of adult males included in the calculation for each year was 3.9, 3.0 and 4.6 for Taï North, Middle and South, respectively and 14.8 for Sonso. The average number of females included was 11.0, 2.8, 19.5 for Taï North, Middle and South and 10.8 for Sonso. The atypically high male to female sex ratio in Sonso is attributable to lack of sampling of less-habituated females, and due to its random nature is very unlikely to lead to a bias in the relatedness results.

### 3.4.2 Relatedness among chimpanzee communities

This analysis was necessarily limited to the three adjacent communities of Taï North, Middle and South. Data on this point are limited, but it is likely that emigrating females join neighboring or at least not very distant communities (Morin 1994 and references therein). Thus, the average relatedness of females across groups should be similar or even exceed that of within-group comparisons, because of the potential inclusion of, for example, mother to adult daughter pairs across groups. The average relatedness of males within groups should exceed that of comparisons across groups.

Results generally consistent with these expectations were found, and average relatedness of adult females across groups did tend to exceed within-group values (Figure 3.2). However, average relatedness of males across the Taï communities, while lower than the values for within Taï Middle and Taï South groups, exceeded the values for most years for Taï North (Figure 3.2). I evaluated whether a significant difference in average male relatedness within and among groups was present by pooling all individuals for the year in consideration, sorting them randomly into groups of the same size as observed, and calculating the average R across groups. This analysis showed that for two of the eight years, 1998 and 2001, the average male R across groups was significantly lower than expected by chance ($p=0.036$ and 0.040, respectively).

Another way to consider the distribution of genetic variation among groups is through the use of F-statistics. I estimated genetic differentiation of the three Taï communities, using the genotypes of the adults present in 2001. I chose to use 2001 because female emigration into these habituated groups has ceased in recent years, and so a relatively recent time point might offer a greater chance to detect genetic differentiation of the groups. However, this was not the case, and the $F_{st}$ values for the pairwise comparisons of the communities were not significantly different from zero (Table 3.2). It is nonetheless interesting to note that when only females were considered, the amount of differentiation was the least and that the greatest amount of differentiation was found when considering only males, results consistent with primarily female-mediated gene flow among communities and male philopatry.

### 3.4.3 Relatedness of similarly-aged chimpanzee offspring

Since a particular male typically enjoys the reproductive advantages of top-ranking dominance status for a limited number of consecutive years, it might be possible to detect elevated average relatedness resulting from shared paternity in cohorts of similarly-aged offspring (Altmann 1979). If such a pattern was found, it would suggest that the analyses of male adults may have failed to find high average relatedness as a result of including individuals of a wide range of ages. To check this, I calculated average R for cohorts of offspring (including males and females) under five years of age for Taï North, Taï South, Sonso and across the Taï groups (Figure 3.3). Taï Middle was not considered except for the among-group calculations as only two offspring were present. It is apparent that levels of average R in offspring did not

exceed those calculated for adult males (excluding Tai Middle, Mann-Whitney U-Test, U=258, p=0.54; Fig. 3.3). Closer investigation of the patterns of shared paternity among offspring cohorts in a given year revealed that, for all three communities and for all years considered, a minimum of two males fathered the offspring, in line with results showing that reproductive skew is never complete (Boesch *et al.* 2006). Thus, although was found that average relatedness among paternal siblings was not significantly different from the expected value of R=0.25 (Vigilant *et al.* 2001), average relatedness among cohorts of offspring were reduced from that level, as evident in Figure 3.2, because of inclusion of two or more patrilines.

### 3.4.4 Values from the mathematical model

I first explored the effect of group size upon relatedness by applying a situation of fixed lifetime reproductive skew as outlined in the methods and determining the group size at which the average relatedness was still above 0.125 (cousins level) or 0.25 (half-sib level). When four individuals were present per generation, average relatedness was above 0.25 under female philopatry but below 0.25 with male philopatry. When eight or more individuals were present per generation, average relatedness values dropped below 0.125 with either male or female philopatry. In general, average relatedness values in a group will always be lower if the sex with the higher reproductive skew is philopatric, because the number of additional relatedness links between parents is higher in the sex in which individuals do not emigrate and more individuals participate in reproducing.

In the second analysis, I contrasted the effects of male and female dispersal upon average relatedness while varying male lifetime reproductive skew and keeping group size constant. With decreasing male reproductive skew towards and below the female skew, the average relatedness values decrease in both scenarios, as does the difference between the two (Figure 3.4). If a situation is assumed in which male reproductive skew is about two times greater than female, relatedness values for species with female philopatry are about 10% higher, and similarly threefold larger male skew leads to differences of about 20%.

Under the chimpanzee condition of male philopatry, average relatedness among the non-dispersing (male) sex was below that describing half-sibs (R=0.25) except for the most extreme situation in which all paternities are attributed to one male (Figure 3.4). Distribution of paternity described in actual chimpanzee

communities more closely resembles the situations of less extreme skew (***m*** < 0.35) for which the simulated relatedness values were below 0.125 (Constable *et al.* 2001; Boesch *et al.* in 2006).

### 3.4.5 Comparison with empirical data from different taxa

To compare the chimpanzee results and to assess the fit of the predicted values from the mathematical model, I used a comparative approach to assess the influence of sex-biased dispersal and group size on average relatedness values of adults of each sex in a group. Unfortunately, because most studies were limited to a small number of groups, it was not possible to use the data to make inferences about the relative degree of reproductive skew across species.

The literature search yielded a total of 22 studies reporting, for each sex, average relatedness values within social groups, 17 of which are for female philopatric species (Table 3.3). In addition, I included the data from the two chimpanzee sites. The average relatedness of the dispersing sex across these species was -0.004 (range -0.19 to 0.09), with no correlation with group size, suggesting that dispersers join groups randomly. However, as predicted from the model, average relatedness values among the members of the philopatric sex showed a clear negative trend with increasing group size for both scenarios of sex-biased dispersal (Figure 3.5). I assessed the significance of this trend by comparing the observed values in a regression to a linear and an exponential model, as well to a model based on the formula derived above. A regression for the combined data produced a less good fit then the two individual analyses. All three gave a significant fit for the two datasets (females - linear: $F=12.3$, $p=0.002$; exp.: $F=152.2$, $p<0.001$; formula: $F=158.2$, $p<0.001$; males – linear: $F=12.1$, $p=0.02$; exp.: $F=53.5$, $p<0.001$; formula: $F=62.7$, $p<0.001$), however, the model based on my new formula could explain most of the variance (for the female values the $r^2$ is 0.91, for the males 0.94). Also consistent with the new derived expectations from the model, for a given group size the relatedness values among philopatric males were always lower than those of the philopatric females (Figure 3.5).

## 3.5 Discussion

### 3.5.1 Summary of the results

Hamilton's rule predicts that the sharing of genes between individuals can facilitate the evolution of cooperative activities (Hamilton 1964). Using simulations I have shown here that high average relatedness values among individuals within social groups are only obtained if groups are small and reproduction limited to a few individuals. Even though these results are based on some simplified assumptions, such as assuming the relatedness of immigrants to be zero, these assumptions as well as the results seem well supported by published empirical data.

### 3.5.2 Relatedness among chimpanzees

In the analysis of relatedness levels in four chimpanzee groups encompassing a total of 29 group-years, I did not find consistent significantly higher average relatedness among adult community males as compared to females. This result is in contrast to that of (Morin *et al.* 1994), who used a different relatedness estimator and included individuals of all age classes (including possible parent-offspring pairs) in an examination of one community (Gombe) of chimpanzees. However, the current findings are consistent with an earlier analysis (in which age classes were also not considered) of a smaller dataset on the Taï communities as well as more recent data from Gombe (Vigilant *et al.* 2001). An interesting result from the perspective of inter-group competition among chimpanzees is that I rarely detected significantly higher relatedness among males of a community as compared to males across communities. Another approach to examining patterns of genetic differentiation among groups, $F_{st}$ analysis, also did not reveal significant differentiation among males of the different Taï communities. However, the three communities in question were close neighbors, and additional studies across broader spatial scales are needed. Finally, consideration of cohorts of similarly-aged offspring also revealed average relatedness levels only rarely approaching that of half-sibs. The fact that I considered multiple chimpanzee communities with varying demographic characteristics and histories makes it unlikely that these results are due to particularities of certain chimpanzee groups.

### 3.5.3 Philopatry and relatedness

The simulations showed that the unusual system of male philopatry, a feature of two species (chimpanzees and humans) known to have extensive repertoires of cooperative group action, reduces average relatedness as compared to a female philopatric system. This seems to contradict previous results on humans stating that groups tracing descent through the male line will have higher coefficients of group relatedness (Chagnon 1979, Hughes 1988). However, those higher coefficients only reflect the fact that the time to the most recent common ancestor is reduced in the male line due to the higher reproductive skew (e.g. humans Wilder *et al.* 2004). In contrast, my analyses considered the increase in R of a given dyad as compared to a random pair of individuals in the population, and these are higher in female philopatric species. To illustrate this result, assume the most extreme situation in which reproduction in the group is limited to one male, while several females have offspring. In the case of female philopatry, these mothers are likely to be related to some degree and the offspring therefore will in addition to being paternal half-sibs as well related maternally, while in the case of male philopatry no additional links between offspring exist. Even though my analysis assumed complete sex-bias in dispersal, which has been in some exceptional chimpanzee cases observed to be less constrained (Williams *et al.* 2002), relaxation of this factor would not change the difference in relatedness between males and females. In fact, only mating between close relatives would notably increase the average relatedness, but inbreeding avoidance seems to be prevalent in animals studied thus far (Pusey & Wolf 1996).

### 3.5.4 Reproductive skew and relatedness

In addition, the analyses highlight the roles of reproductive output and skew in creating a kin-group. Eusocial animals such as social insects or mole-rats can be seen as enlarged families, where non-reproductive offspring and siblings help (Faulkes & Bennett 2001). As previously indicated (Altmann 1979, Chesser 1998, Aviles *et al.* 2004), the low reproductive output of mammals sets a limit to the number of potentially available partners that are kin. My results converge with recent studies on single groups, which have suggested that kin selection is not the primary reason for animals to group together (Valsecchi *et al.* 2002, Russell *et al.* 2004, Spong & Creel 2004, van Horn *et al.* 2004, Vucetich *et al.* 2004), and consequently that the group size of a species is not dependent on its family size.

### 3.5.5 Structuring of relatedness within social groups

Studies in other taxa in which males affiliate have produced contradictory results on the presence of significant relatedness among clusters of males. Although an influential work on relatedness and reproductive success among affiliative male lions has been widely taken as evidence for the benefits of kin association for males (Packer *et al.* 1991), new research on multiple prides of lions suggested that relatedness among the males is not necessary for cooperative behaviour (Spong *et al.* 2002). Results for dolphins have been contradictory (no influence of kinship: Moller *et al.* 2001; influence found: Parsons *et al.* 2003). However, a recent dolphin study found significantly higher average relatedness among pairs of individuals participating in long-term alliances consisting of six or fewer individuals as compared to random pairs of individuals, but they did not find this for larger super-alliances and sub-grouping, indicating that different male strategies might explain the apparent contradictions (Krützen *et al.* 2003).

This study does not address the possibility that a large group of individuals might be substructured into clusters of related, cooperating individuals (e.g. long-tailed macaques, de Ruiter & Geffen 1998). These results show that the proportion of kin versus non-kin partners for an individual decreases with increasing group size; however, there are in all cases kin present who could be recruited as potential partners in a dyadic interaction. Some studies have highlighted the structuring of groups into matrilines and evidence showing that social behaviours are biased accordingly to favor kin (Silk 2002). And some evidence is accumulating that paternal relatedness, as indicated by age similarity (Altmann 1979), influences patterns of interaction within social groups (Widdig *et al.* 2001, Smith *et al.* 2003). More data is needed to analyze whether dyadic interactions among chimpanzee males might be influenced by relatedness. However, results thus far suggests that maternal relatives are not preferentially selected for recruitment for activities which involve only two individuals (Goldberg & Wrangham 1997, Mitani *et al.* 2002).

### 3.5.6 Relatedness and cooperation

Direct benefits from mutualism have been proposed to play a more important role than kin selection for some cooperative actions, e.g. in the evolution of cooperative breeding in meerkats (Clutton-Brock *et al.* 2002). It is also interesting that

behaviours that involve a larger number of individuals would fall into the category of complex behaviours recently suggested as less likely to be driven by kin-selection, but rather to be influenced by the relative competences of the potential partners (Chapais & Berman 2004).

A high degree of male cooperation has been suggested to be a common trait of great apes and humans (Rodseth *et al.* 1991). Genetic studies on sex-biased dispersal in humans indicate that male philopatry and female dispersal seems to be the predominant system (Oota *et al.* 2001, but see Wilder *et al.* 2004), while behavioural studies indicate flexibility on the smaller scale (Alvarez 2004). Unfortunately there seems to be very little data from humans with which to compare my analyses. Even though sociological studies have indicated that kin selection plays a role in shaping sociality, often these analyses have used the anthropological category of "kin", which does not necessarily imply recent common genetic ancestry (Rodseth & Wrangham 2004). One of the best data-sets on this topic stems from long-term study on the Yanomano people of South America. The most detailed study in the Yanomano population that uses genealogical information on kin in an analysis of 'ax-fight' shows positive kin-bias on an inter-individual level, which even overrides group membership (Chagnon & Burgos 1979). A study in Indonesia on whale-hunting, which necessitates the cooperation of relatively large number of individuals per boat, found no direct choice of kin for the cooperative action, rather just a choice of individuals from the same group, and argued that "kin selection alone cannot structure cooperation in groups larger than the nuclear family because of the ambiguous group membership it provides" (Alvard 2003). In addition, recent results from experimental economics indicate that "biological models of self-interested cooperation" which include inclusive fitness benefits through kin-selection "are rarely plausible when they involve groups of more than a few individuals" (Gintis 2004). Instead, findings on the alternative explanation, reciprocity, converge neatly with the observation in chimpanzees, that "cooperation within a group can make the group more lethally aggressive in its dealing with outsiders" (Seabright 2004). These results, and those presented here, suggest that indirect fitness benefits through gene-sharing are not necessarily the primary mechanism driving large group actions in mammals and humans.

**Table 3.1** Mean pairwise relatedness (R), and standard deviation (sd) estimates for adults (n) present each year in the four study communities. Significant p-values for the comparison between males and females of the same group in the same year are in bold. The nd indicates the test was not done as the number of possible permutations was too few.

| | males | | | females | | | p |
|---|---|---|---|---|---|---|---|
| **Tai North** | | | | | | | |
| **year** | **R** | **sd** | **n** | **R** | **sd** | **n** | |
| 1995 | -0.0697 | 0.1765 | 3 | -0.0168 | 0.2033 | 10 | 0.636 |
| 1996 | -0.0697 | 0.1765 | 3 | -0.0168 | 0.2033 | 10 | 0.636 |
| 1997 | -0.0697 | 0.1765 | 3 | -0.0375 | 0.1491 | 11 | 0.541 |
| 1998 | -0.0118 | 0.157 | 2 | -0.0375 | 0.1491 | 11 | 0.389 |
| 1999 | -0.1268 | 0.1117 | 3 | -0.0375 | 0.1491 | 11 | 0.770 |
| 2000 | -0.1392 | 0.1558 | 2 | -0.032 | 0.1045 | 7 | 0.600 |
| 2001 | -0.1392 | 0.1558 | 2 | -0.032 | 0.1045 | 7 | 0.600 |
| 2002 | -0.1392 | 0.1558 | 2 | -0.0484 | 0.1022 | 6 | 0.633 |
| **Tai Middle** | | | | | | | |
| 1998 | 0.0468 | 0.2361 | 4 | -0.0849 | 0.1048 | 3 | 0.168 |
| 1999 | 0.1232 | 0.2667 | 3 | -0.0849 | 0.1048 | 3 | nd |
| 2000 | 0.1232 | 0.2667 | 3 | -0.0849 | 0.1048 | 3 | nd |
| 2001 | 0.1232 | 0.2667 | 3 | -0.0849 | 0.1048 | 3 | nd |
| 2002 | 0.115 | 0.1978 | 2 | -0.1213 | 0.1485 | 2 | nd |
| **Tai South** | | | | | | | |
| 1995 | 0.0944 | 0.3064 | 5 | -0.0299 | 0.2247 | 20 | **0.040** |
| 1996 | 0.0944 | 0.3064 | 5 | -0.0299 | 0.2247 | 20 | **0.040** |
| 1997 | 0.0944 | 0.3064 | 5 | -0.0299 | 0.2247 | 20 | **0.040** |
| 1998 | 0.0676 | 0.2263 | 4 | -0.0299 | 0.2247 | 20 | 0.116 |
| 1999 | 0.1311 | 0.1684 | 3 | -0.0299 | 0.2247 | 20 | 0.053 |
| 2000 | -0.0206 | 0.1541 | 4 | -0.0299 | 0.2247 | 20 | 0.619 |
| 2001 | 0.0432 | 0.2315 | 5 | -0.0251 | 0.255 | 19 | 0.099 |
| 2002 | 0.0166 | 0.256 | 6 | -0.0244 | 0.2076 | 17 | 0.171 |
| **Sonso** | | | | | | | |
| 1995 | -0.0015 | 0.2164 | 15 | 0.0032 | 0.2014 | 10 | 0.172 |
| 1996 | -0.0015 | 0.2164 | 15 | -0.0188 | 0.2074 | 11 | 0.148 |
| 1997 | 0.0112 | 0.2156 | 17 | -0.0188 | 0.2074 | 11 | 0.096 |
| 1998 | 0.0112 | 0.2156 | 17 | -0.0188 | 0.2074 | 11 | 0.096 |
| 1999 | 0.0153 | 0.2186 | 15 | -0.0188 | 0.2074 | 11 | 0.113 |
| 2000 | 0.0033 | 0.2058 | 14 | -0.0188 | 0.2074 | 11 | 0.196 |
| 2001 | 0.0113 | 0.2382 | 13 | -0.0188 | 0.2074 | 11 | 0.134 |
| 2002 | 0.0422 | 0.236 | 12 | -0.0459 | 0.2005 | 10 | **0.024** |

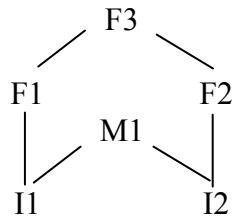
**Table 3.2** Genetic differentiation of Taï communities. Pairwise Fst values for both for all individuals, as well just for adult males are close to zero, indicating little genetic differentiation between the three neighboring communities.

| | all adults | female adults | male adults |
|---|---|---|---|
| North-Middle | 0.0004 | 0.0007 | -0.0239 |
| North-South | 0.0013 | 0.0532 | -0.00001 |
| Middle-South | -0.0072 | 0.0391 | -0.0208 |

**Table 3.3** Published relatedness data for adults of one sex within a social group. The correlation between group size and relatedness in the philopatric sex is illustrated in figure 3.5, there is no such correlation for the dispersing sex.

| common name | Number of females | R(females) | Number of males | R(males) | citation | species name |
|---|---|---|---|---|---|---|
| **female philopatric species** | | | | | | |
| redfronted lemur | **2** | **0.48** | 3 | 0.086 | Wimmer & Kappeler 2002 | Eulemur fulvus rufus |
| lion | **3** | **0.26** | 3 | 0.09 | Spong *et al.* 2002 | Panthera leo |
| grey mouse lemur | **3** | **0.36** | | | Radespiel *et al.* 2001 | Microcebus murinus |
| sifaka | **4** | **0.18** | 3 | 0.081 | Lawler *et al.* 2003 | Propithecus verreauxi verreauxi |
| rabbits | **5** | **0.24** | 5 | -0.069 | Surridge *et al.* 1999 | Oryctolagus cuniculus |
| otter | **5** | **0.18** | 11 | 0.087 | Blundell *et al.* 2002 | Lontra canadensis |
| bat | **8** | **0.02** | 2 | 0.002 | Ortega *et al.* 2003 | Artibeus jamaicensis |
| macaque | **8** | **0.14** | 4 | -0.1 | de Ruiter & Geffen 1998 | Macaca fascicularis |
| dolphins | **12** | **0.15** | 16 | 0.022 | Moller & Beheregaray 2004 | Tursiops aduncus |
| | **13** | **0.05** | 15 | -0.024 | Schulte-Hostedde *et al.* 2001 | Tamias amoenus |
| wood-rats | **14** | **0.08** | | | Matocq & Lacey 2004 | Neotoma macrotis |
| bat | **15** | **0.04** | 14 | 0.022 | Burland *et al.* 2001 | Plecotus auritus |
| bat | **23** | **0.02** | | | Kerth *et al.* 2002 | Myotis bechsteinii |
| sheep | **25** | **0.03** | 15 | -0.005 | Coltman *et al.* 2003 | Ovis aries |
| bat | **40** | **0.03** | | | Rossiter *et al.* 2002 | Rhinolophus ferrumequinum |
| baboon | **54** | **-0.02** | 10 | -0.19 | Altmann *et al.* 1996 | Papio cynocephalus |
| hyenas | **60** | **0.01** | 40 | 0.009 | Van Horn *et al.* 2004 | Crocuta crocuta |
| **Male philopatric species** | | | | | | |
| bell miner bird | 2 | -0.05 | **2** | **0.29** | Painter *et al.* 2000 | Manorina melanophrys |
| shrew | 8 | 0.05 | **2** | **0.26** | Balloux *et al.* 1998 | Crocidura russula |
| chimpanzee Tai | 12 | -0.022 | **4** | **0.07** | this study - Tai | Pan troglodytes |
| bilby marsupial | 7 | 0.005 | **6** | **0.1** | Moritz *et al.* 1997 | Macrotis lagotis |
| bonobo | 15 | -0.03 | **6** | **0.07** | Gerloff *et al.* 1999 | Pan paniscus |
| chimpanzee Budongo | 8 | -0.05 | **14** | **-0.007** | this study - Budongo | Pan troglodytes |
| red grouse | 15 | -0.013 | **15** | **-0.01** | Piertney *et al.* 1998 | Lagopus lagopus scoticus |

**Figure 3.1** This diagram illustrates how dyadic relatedness was calculated for the simulation. The numbers of steps needed to connect I1 and I2 through either the maternal or paternal side are independently counted. In this example I1 and I2 share the same mother (I1 - M1 – I2 -> 2 steps), while their fathers are paternal half-sibs (I1 – F1 – F3 – F2 – I2 -> 4 steps). For each path one takes 0.5 to the power of the number of steps and sums the two values.




I1 – I2: M: 0.5^2 = 0.25
F: 0.5^4 = 0.0625

R(I1-I2) = M + F = 0.3125

**Figure 3.2** Average relatedness (R) by year of the male and female chimpanzees, per each of the three groups at Tai and the Sonso group at Budongo, and the relatedness across the Tai communities comparing dyads of males or females, respectively, who are not in the same group.

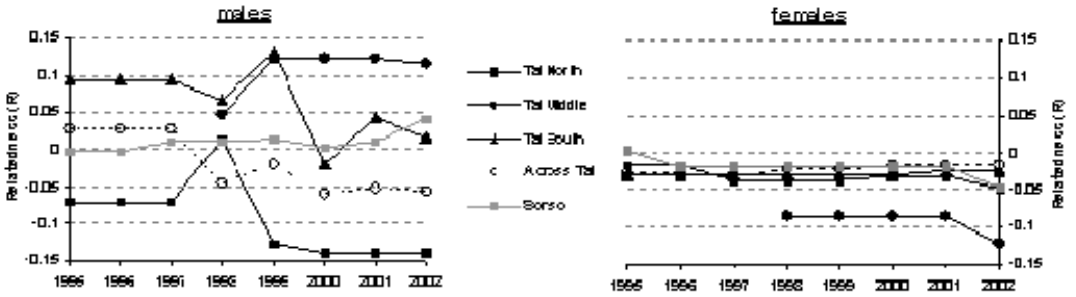


**Figure 3.3** Average relatedness (R) by year for offspring under five years of age for the three Tai communities.

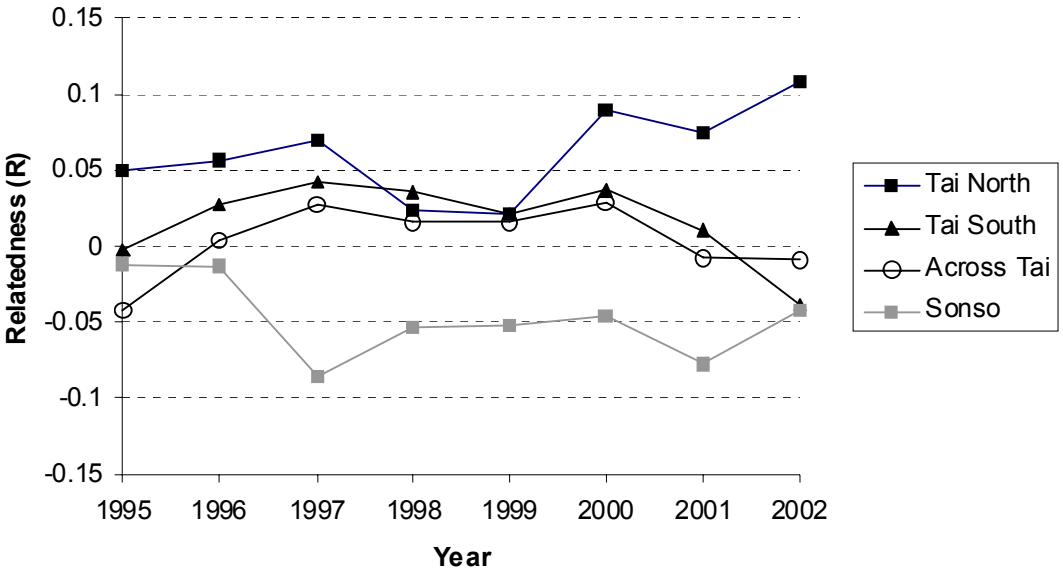


**Figure 3.4** Average relatedness (R) among members of the philopatric varies according to the identity of the dispersing sex and the level of male reproductive skew. The black bars correspond to the situation of female dispersal in chimpanzees, and thus indicate R among the males. If males disperse (grey bars), R among philopatric females is higher than it is for philopatric males (black bars) in the converse situation when females disperse and males stay. The highest category of male reproductive skew, labelled as 'high' in the figure, corresponds to one male siring all 12 offspring. The next categories are, in order: two fathers each with one and 11 offspring, two fathers with 8 and 4 offspring, two fathers each with six each, three fathers with 6, 4, and 2 offspring, four fathers with three offspring each, six fathers with two each and finally 12 fathers each have 1 offspring (labelled 'low').

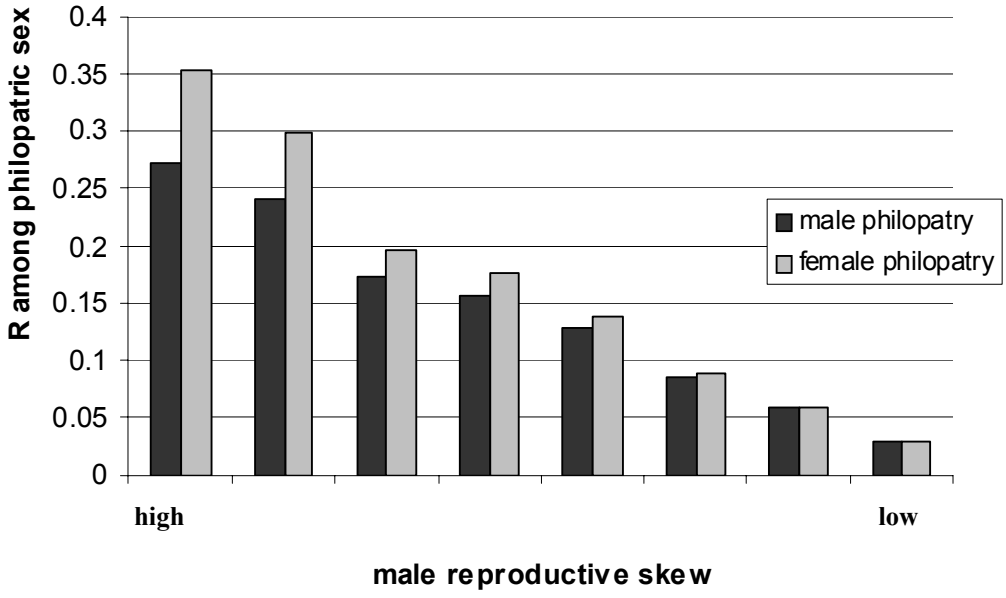
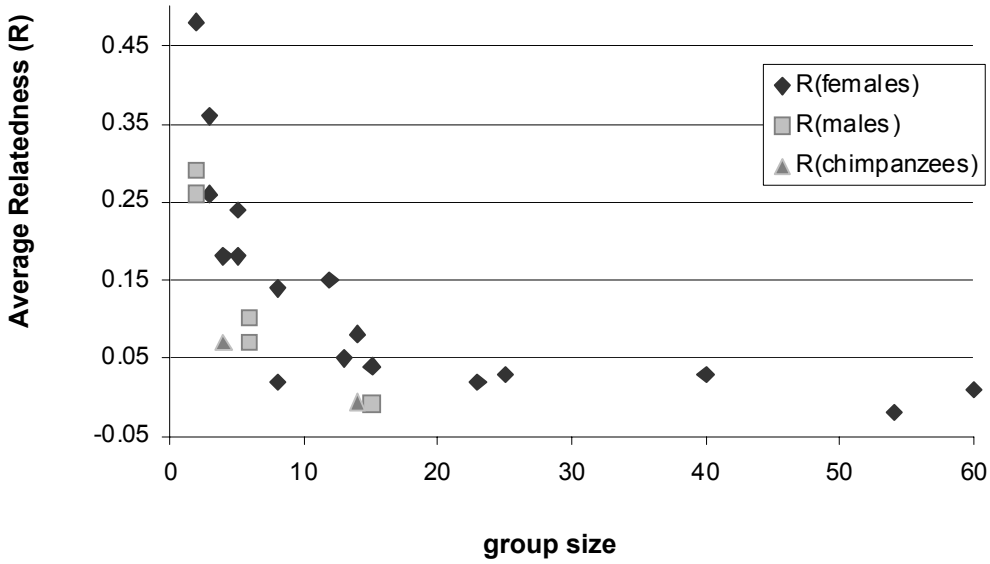


**Figure 3.5** The relationship between group size and average relatedness among the philopatric individuals, separated for species with female versus male philopatry. Relatedness values drop with larger group sizes for both scenarios, however the values for philopatric males are lower for a given group size. For details on species and publications see table 3.3.



**Appendix 3.1** List of individuals including names, sex, group, year of birth (YOB), year of death (YOD) and genotypes at 9 microsatellite loci.

| Indiv | Group | sex | yob | yod | D2s1326 | D7s817 | D5s1470 | D7s2204 | D9s910 | D2s1329 | D11s200 | 2D12s66 | vwf |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ali | North | M | 1979 | 1992 | 203/203 | 148/136 | 186/174 | 172/164 | 113/107 | 186/178 | 160/152 | 154/150 | 128/124 |
| Brutus | North | M | 1951 | 1997 | 198/194 | 132/156 | 174/178 | 152/164 | 116/107 | 178/170 | 148/160 | 158/178 | 132/132 |
| Darwin | North | M | 1969 | 1993 | 203/215 | 156/132 | 190/174 | 168/168 | 113/110 | 186/154 | 168/144 | 154/150 | 136/128 |
| Macho | North | M | 1964 | 1999 | 178/182 | 128/136 | 190/182 | 164/160 | 116/110 | 186/178 | 168/148 | 158/158 | 128/124 |
| Kendo | North | M | 1969 | 1994 | 211/215 | 124/136 | 174/190 | 168/172 | 110/113 | 154/198 | 148/148 | 150/162 | 124/128 |
| Fitz | North | M | 1975 | 1994 | 194/211 | 124/152 | 178/190 | 168/172 | 116/116 | 178/198 | 148/152 | 154/154 | 124/128 |
| Marius | North | M | 1982 | | 178/211 | 128/124 | 186/186 | 152/168 | 113/122 | 186/186 | 148/144 | 158/154 | 136/128 |
| Nino | North | M | 1988 | | 203/207 | 156/128 | 190/178 | 168/168 | 101/113 | 198/154 | 168/152 | 150/150 | 136/132 |
| Belle | North | F | 1976 | | 203/211 | 140/120 | 182/178 | 168/176 | 116/107 | 198/186 | 160/148 | 154/150 | 128/124 |
| Beye | North | M | 1999 | | 211/211 | 128/140 | 178/186 | 168/176 | 116/122 | 186/186 | 160/144 | 154/158 | 128/128 |
| Bijou | North | F | 1975 | 1994 | 178/182 | 124/144 | 182/186 | 160/172 | 113/116 | 154/178 | 144/144 | 158/158 | 124/132 |
| Bambou | North | M | 1989 | 1991 | 203/182 | 144/156 | 182/190 | 168/172 | 113/116 | 154/178 | / | 154/158 | 124/128 |
| Castor | North | F | 1976 | 1999 | 198/203 | 128/120 | 186/186 | 168/168 | 116/116 | 206/202 | 164/148 | 178/150 | 128/128 |
| Dilly | North | F | 1978 | 1999 | 198/203 | 120/152 | 182/182 | 172/176 | 110/119 | 182/186 | 160/172 | 142/158 | 128/128 |
| Dorry | North | F | 1991 | 2001 | 198/211 | 120/124 | 182/190 | 172/168 | 110/119 | 182/154 | 148/172 | 142/162 | 128/128 |
| Fanny | North | F | 1969 | 1994 | 178/223 | 128/136 | 186/194 | 168/156 | 110/122 | 186/194 | 144/144 | 150/154 | 128/136 |
| Manon | North | F | 1987 | 1992 | / | 128/124 | 186/190 | 168/172 | 110/113 | 186/154 | / | / | 128/136 |
| Fossey | North | F | 1979 | | 198/194 | 152/124 | 186/186 | 172/168 | 119/113 | 202/186 | 160/148 | 158/154 | 128/128 |
| Fedora | North | F | 1993 | | 198/211 | 124/124 | 190/186 | 172/168 | 119/116 | 202/198 | 148/148 | 154/154 | 128/124 |
| Faust | North | M | 1999 | | 182/194 | 136/152 | 182/186 | 164/172 | 110/119 | 186/178 | 148/148 | 158/158 | 124/128 |
| Goma | North | F | 1973 | 2001 | 174/186 | 148/136 | 186/174 | 164/160 | 116/113 | 186/182 | 160/144 | 154/158 | 128/128 |
| Gargantu | North | M | 1991 | 2001 | 186/198 | 156/136 | 186/174 | 164/152 | 116/116 | 186/178 | 160/144 | 158/158 | 132/128 |
| Gisele | North | F | 1996 | 2001 | 178/186 | 128/148 | 182/174 | 160/160 | 116/113 | 186/178 | 160/148 | 158/158 | 128/128 |
| Gitane | North | F | 1949 | 1994 | / | 124/120 | 182/186 | 168/176 | 116/116 | / | 144/164 | 150/158 | 116/124 |
| Hector | North | M | 1990 | 1996 | 203/207 | 136/144 | 170/190 | 156/172 | / | / | 148/156 | 162/150 | 124/128 |
| Kana | North | F | 1987 | 1998 | 178/190 | 120/136 | 186/190 | 164/172 | 116/119 | 178/182 | 152/168 | 158/158 | 128/136 |
| Lefkas | North | M | 1991 | 1999 | 194/215 | 152/136 | 190/174 | 172/156 | 113/116 | 186/154 | 148/148 | 154/150 | 124/124 |
| Leonardo | North | M | 1997 | 1999 | 178/194 | 152/136 | 190/174 | 172/164 | 113/110 | 202/178 | 164/148 | 170/158 | 128/124 |
| Loukoum | North | F | 1972 | 1999 | 194/198 | 152/148 | 178/174 | 172/156 | 113/116 | 202/186 | 164/148 | 170/154 | 128/124 |
| Mystere | North | F | 1975 | | 207/215 | 148/140 | 186/182 | 168/164 | 122/107 | 182/154 | 164/148 | 154/146 | 136/124 |
| Mognie | North | F | 1990 | | 215/215 | 124/140 | 190/182 | 168/168 | 122/113 | 198/182 | 164/148 | 150/146 | 136/128 |
| Mozart | North | M | 1995 | | 178/215 | 148/136 | 190/182 | 164/164 | 116/107 | 186/154 | 168/148 | 158/146 | 128/124 |
| Narcisse | North | F | 1983 | | 219/207 | 148/124 | 190/178 | 176/156 | 113/107 | 178/154 | 148/144 | 150/150 | 124/124 |
| Noureyev | North | M | 1997 | | 178/207 | 128/124 | 190/182 | 160/156 | 110/107 | 186/154 | 168/144 | 158/150 | 124/124 |
| Ondine | North | F | 1954 | 1992 | 182/194 | 152/140 | 178/190 | 156/172 | 119/116 | 182/206 | 144/148 | 158/158 | 124/132 |
| Sirene | North | F | 1987 | 1999 | 178/194 | 140/128 | 190/182 | 160/156 | 119/110 | 186/182 | 168/148 | 158/158 | 128/124 |
| Ovide | North | M | 1992 | 1992 | 211/194 | 136/140 | 178/190 | 156/172 | 113/116 | 154/206 | 148/148 | 150/158 | 124/132 |
| Perla | North | F | 1976 | | 178/211 | 152/144 | 174/170 | 172/168 | 113/116 | 182/182 | 152/148 | 158/158 | 128/128 |
| Pandora | North | F | 1995 | | 178/178 | 152/128 | 186/170 | 172/168 | 122/116 | 186/182 | 148/148 | 158/154 | 128/128 |
| Porthos | North | M | 2000 | | 178/178 | 128/144 | 174/186 | 168/172 | 113/113 | 182/186 | 148/152 | 154/158 | 128/136 |
| Ricci | North | F | 1963 | 1999 | 207/207 | 128/144 | 178/190 | 168/168 | 101/113 | 154/198 | 152/168 | 150/150 | 132/124 |
| Roxanne | North | F | 1994 | | 194/207 | 128/124 | 190/178 | 168/168 | 113/116 | 198/178 | 168/148 | 154/150 | 128/124 |
| Venus | North | F | 1978 | | 178/211 | 144/136 | 186/186 | 188/176 | 122/113 | 182/154 | 156/148 | 154/154 | 128/128 |
| Volta | North | F | 2002 | | 211/211 | 124/144 | 186/186 | 152/176 | 122/122 | 182/186 | 144/148 | 154/154 | 128/136 |
| Vanille | North | F | 1991 | | 211/211 | 144/136 | 190/186 | 188/172 | 122/110 | 198/182 | 148/148 | 162/154 | 128/128 |
| Violetta | North | F | 1997 | | 211/211 | 144/128 | 186/186 | 168/176 | 122/113 | 186/182 | 144/148 | 158/154 | 136/128 |
| Xeres | North | F | 1970 | 1992 | 182/203 | 124/152 | 182/186 | 172/172 | 113/116 | 186/186 | 148/148 | 150/150 | 128/136 |
| Jessica | Middle | F | 1972 | | 215/178 | 120/120 | 190/186 | 172/164 | 113/113 | 182/186 | 160/144 | 150/146 | 128/128 |
| Joanine | Middle | F | 1999 | | 215/211 | 124/120 | 190/182 | 172/164 | 113/107 | 186/186 | 160/148 | 154/146 | 128/124 |

| Indiv | Group | sex | yob | yod | D2s1326 | D7s817 | D5s1470 | D7s2204 | D9s910 | D2s1329 | D11s200 | 2D12s66 | vwf |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Kady | Middle | F | 1966 | 2001 | 178/207 | 148/128 | 174/186 | 168/168 | 116/116 | 182/182 | 164/144 | 154/150 | 128/124 |
| Koulo | Middle | F | 1991 | 2002 | 219/207 | 148/128 | 182/186 | 168/156 | 116/116 | 182/154 | 152/144 | 154/158 | 128/128 |
| Kassiope | Middle | F | 2000 | 2001 | 174/207 | 128/148 | 170/186 | 168/196 | 116/116 | 182/186 | 164/152 | 146/150 | 124/124 |
| Nadesh | Middle | F | 1962 | | 203/190 | 128/124 | 174/170 | 172/160 | 116/113 | 186/154 | 152/144 | 158/146 | 136/124 |
| Nelly | Middle | F | 1989 | 2001 | 207/203 | 128/124 | 182/170 | 168/160 | 113/113 | 202/154 | 168/144 | 174/146 | 124/124 |
| Noah | Middle | M | 1995 | 2002 | 203/203 | 124/124 | 174/170 | 172/164 | 116/107 | 186/154 | 152/148 | 158/150 | 136/124 |
| Leo | Middle | M | 1983 | | 203/174 | 128/124 | 182/170 | 196/160 | 116/113 | 186/154 | 152/152 | 150/146 | 132/124 |
| Urs | Middle | M | 1967 | 2001 | 211/203 | 156/124 | 182/170 | 168/164 | 107/101 | 186/154 | 152/148 | 154/150 | 124/124 |
| Bob | Middle | M | 1978 | | 211/203 | 124/124 | 182/190 | 172/148 | 116/113 | 186/202 | 152/168 | 158/158 | 128/128 |
| Joe | Middle | M | 1977 | 1998 | 203/215 | 124/120 | 186/194 | 168/172 | 116/116 | 154/198 | 144/160 | 154/178 | 124/128 |
| Atra | South | F | 1981 | | 178/223 | 124/148 | 174/182 | 164/172 | 107/113 | 154/202 | 148/152 | 154/170 | 124/124 |
| Alina | South | F | 1995 | 2001 | 203/223 | 152/148 | 182/182 | 176/172 | 107/113 | 154/202 | 144/148 | 154/158 | 124/128 |
| Athena | South | F | 1999 | | 178/223 | 152/148 | 182/182 | 172/176 | 107/119 | 202/202 | 148/148 | 158/170 | 124/132 |
| Besar | South | M | 1989 | | 178/182 | 120/124 | 190/190 | 160/164 | 107/113 | 154/186 | 148/164 | 154/158 | 124/128 |
| Coco | South | F | 1980 | | 203/211 | 152/152 | 186/190 | 156/168 | 107/113 | 186/186 | 148/164 | 154/158 | 128/128 |
| Celine | South | F | 1995 | | 207/211 | 152/144 | 186/190 | 156/164 | 107/119 | 186/186 | 172/164 | 154/158 | 128/128 |
| Duna | South | F | 1974 | | 182/178 | 140/140 | 186/182 | 172/172 | 119/110 | 186/154 | 164/144 | 154/146 | 132/128 |
| Eva | South | F | 1967 | 2002 | 203/182 | 152/124 | 182/174 | 164/164 | 119/116 | 198/186 | 148/144 | 158/158 | 124/124 |
| Endora | South | F | 1991 | | 223/182 | 144/124 | 182/170 | 168/164 | 119/119 | 186/186 | 168/144 | 158/158 | 128/124 |
| Garuda | South | F | 1975 | 2002 | 207/178 | 144/120 | 190/174 | 164/156 | 119/113 | 186/182 | 172/152 | 158/154 | 128/124 |
| Gogol | South | M | 1991 | | 203/178 | 120/120 | 182/174 | 168/156 | 116/113 | 182/170 | 172/152 | 158/154 | 128/128 |
| Haraka | South | F | 1975 | 2001 | 194/194 | 124/128 | 174/182 | 172/164 | 107/113 | 182/198 | 144/152 | 158/178 | 128/128 |
| Huxel | South | M | 1996 | | 194/178 | 128/136 | 174/174 | 172/176 | 107/113 | 182/178 | 144/164 | 158/154 | 128/128 |
| Isha | South | F | 1970 | | 182/178 | 140/124 | 186/186 | 172/164 | 116/113 | 182/182 | 164/164 | 154/150 | 128/128 |
| Inousha | South | F | 1995 | | 178/194 | 124/140 | 182/186 | 156/172 | 107/116 | 178/182 | 164/168 | 150/158 | 128/128 |
| Ibrahim | South | M | 2000 | | 194/182 | 136/140 | 182/186 | 172/172 | 113/107 | 182/202 | 164/164 | 154/154 | 128/128 |
| Julia | South | F | 1970 | | 190/203 | 124/152 | 170/186 | 168/168 | 113/113 | 154/190 | 152/152 | 150/178 | 132/136 |
| Jacobo | South | M | 1998 | | 190/211 | 124/124 | 170/174 | 168/172 | 101/113 | 198/190 | 152/152 | 150/170 | 128/136 |
| Kabisha | South | F | 1977 | 2002 | 203/219 | 120/156 | 174/182 | 168/168 | 101/107 | 154/182 | 144/152 | 150/154 | 128/128 |
| Kinshasa | South | F | 1990 | | 219/219 | 152/120 | 186/174 | 172/168 | 113/107 | 182/154 | 164/144 | 158/154 | 128/128 |
| Kuba | South | M | 1996 | | 219/194 | 152/120 | 174/174 | 168/176 | 107/107 | 178/154 | 164/152 | 154/150 | 128/128 |
| Louise | South | F | 1980 | | 211/207 | 152/124 | 182/178 | 168/168 | 116/107 | 186/154 | 164/144 | 182/158 | 136/128 |
| Linus | South | M | 1993 | | 182/207 | 140/152 | 178/186 | 164/168 | 107/116 | 182/186 | 144/168 | 154/158 | 128/136 |
| Lukas | South | M | 1998 | 2002 | 207/207 | 144/152 | 170/182 | 164/168 | 119/116 | 154/186 | 144/172 | 158/158 | 128/128 |
| Mandy | South | F | 1967 | 2001 | 215/178 | 152/148 | 190/182 | 172/152 | 116/113 | 202/154 | 152/144 | 174/154 | 132/132 |
| Max | South | M | 1995 | 2001 | 178/207 | 128/152 | 190/186 | 172/172 | 116/119 | 202/186 | 152/148 | 158/154 | 128/132 |
| Margot | South | F | 1975 | 2002 | 182/203 | 152/152 | 174/190 | 168/168 | 107/113 | 182/186 | 160/168 | 150/158 | 124/128 |
| Mustapha | South | M | 1995 | | 203/182 | 152/148 | 190/182 | 176/168 | 113/107 | 202/182 | 160/144 | 158/158 | 128/128 |
| Olivia | South | F | 1973 | | 174/190 | 124/152 | 182/170 | 172/172 | 107/113 | 154/186 | 152/148 | 146/154 | 124/136 |
| Olduvai | South | M | 1994 | 2002 | 190/198 | 152/128 | 170/182 | 172/164 | 116/113 | 182/154 | 148/148 | 154/146 | 124/124 |
| Oreste | South | M | 1998 | | 174/211 | 128/152 | 182/182 | 172/176 | 116/107 | 154/198 | 148/152 | 170/154 | 124/128 |
| Rubra | South | F | 1970 | | 182/203 | 124/128 | 186/190 | 164/168 | 107/116 | 178/190 | 144/152 | 150/162 | 128/128 |
| Rebecca | South | F | 1995 | | 182/182 | 124/128 | 178/190 | 164/168 | 107/116 | 178/182 | 152/168 | 154/162 | 128/128 |
| Romario | South | M | 1999 | | 182/207 | 124/144 | 170/186 | 164/164 | 107/107 | 186/190 | 144/172 | 150/158 | 128/128 |
| Sumatra | South | F | 1965 | | 203/215 | 140/136 | 182/186 | 156/168 | 113/116 | 178/198 | 168/164 | 150/158 | 124/132 |
| Sagu | South | M | 1989 | | 215/182 | 136/144 | 186/182 | 172/156 | 116/116 | 186/178 | 164/168 | 158/150 | 124/124 |
| Settut | South | F | 1996 | | 203/207 | 128/136 | 170/186 | 168/172 | 107/116 | 178/186 | 148/164 | 158/158 | 124/128 |
| Tita | South | F | 1975 | 2000 | 194/178 | 144/128 | 174/178 | 164/168 | 116/116 | 186/186 | 148/160 | 158/150 | 136/128 |
| Taboo | South | M | 1992 | | 194/178 | 152/128 | 182/178 | 176/168 | 116/107 | 186/182 | 168/160 | 158/150 | 136/128 |
| Totem | South | M | 1992 | 1999 | 215/203 | 140/136 | 190/182 | 188/164 | 116/107 | 186/186 | 164/164 | 154/150 | 128/128 |
| Utan | South | M | 1994 | | 211/194 | 124/120 | 174/174 | 168/164 | 116/110 | 198/154 | 164/160 | 158/150 | 132/128 |
| Virunga | South | F | 1965 | | 194/194 | 148/144 | 186/170 | 168/156 | 113/113 | 198/186 | 168/160 | 178/154 | 128/128 |
| Voltaire | South | M | 1999 | | 194/215 | 144/136 | 182/186 | 156/156 | 113/116 | 186/178 | 164/168 | 154/150 | 124/128 |

| Indiv | Group | sex | yob | yod | D2s1326 | D7s817 | D5s1470 | D7s2204 | D9s910 | D2s1329 | D11s200 | 2D12s66 | vwf |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Wapi | South | F | 1970 | | 178/203 | 136/124 | 186/186 | 164/176 | 107/116 | 154/198 | 164/152 | 150/158 | 144/144 |
| Woodstoc | South | M | 1994 | | 178/194 | 136/152 | 186/186 | 164/176 | 107/116 | 154/202 | 164/168 | 158/158 | 144/128 |
| Yucca | South | F | 1970 | | 198/178 | 136/120 | 198/178 | 172/172 | 122/113 | 198/186 | 152/144 | 158/150 | 128/124 |
| Yoghiti | South | M | 1990 | 2002 | 203/198 | 136/120 | 198/190 | 160/172 | 113/107 | 198/186 | 164/152 | 158/158 | 128/124 |
| Yao | South | M | 1995 | | 194/198 | 152/136 | 182/178 | 172/176 | 113/119 | 178/186 | 148/144 | 158/158 | 132/128 |
| Zita | South | F | 1996 | 2001 | 203/194 | 136/124 | 190/174 | 172/168 | 107/107 | 186/178 | 148/144 | 154/150 | 132/124 |
| Zora | South | F | 1957 | | 203/203 | 152/124 | 190/174 | 172/168 | 113/107 | 186/154 | 168/144 | 158/150 | 124/136 |
| Zyon | South | M | 1964 | | 178/194 | 152/136 | 174/182 | 176/172 | 119/107 | 202/178 | 148/164 | 158/154 | 128/132 |
| Rafiki | South | M | 1979 | 1998 | 211/182 | 128/120 | 182/174 | 172/156 | 116/113 | 186/170 | 148/144 | 150/150 | 128/128 |
| Kaos | South | M | 1977 | | 207/207 | 144/128 | 186/170 | 172/164 | 119/107 | 186/186 | 172/148 | 158/158 | 128/128 |
| Mkubwa | South | M | 1959 | 1999 | 223/207 | 144/128 | 186/170 | 168/168 | 119/116 | 202/186 | 168/156 | 150/158 | 128/128 |
| Natan | South | M | 1960 | 1997 | 178/203 | 120/124 | 182/182 | 168/168 | 116/116 | 186/186 | 148/160 | 154/158 | 128/128 |
| Black | Sonso | M | 1975 | | 203/203 | 120/124 | 178/182 | 144/168 | 104/110 | 182/186 | 148/156 | 146/154 | 116/116 |
| Bwoya | Sonso | M | 1967 | 2001 | 190/215 | 120/140 | 174/178 | 144/184 | 104/107 | 182/190 | 152/152 | 138/154 | 120/140 |
| Duane | Sonso | M | 1965 | | 203/203 | 124/124 | 174/186 | 180/184 | 116/116 | 182/186 | 144/152 | 146/158 | 116/140 |
| Jambo | Sonso | M | 1975 | | 194/203 | 124/124 | 178/194 | 176/184 | 116/119 | 182/182 | 144/160 | 142/154 | 116/120 |
| Maani | Sonso | M | 1960 | | 203/211 | 120/124 | 178/182 | 168/184 | 116/116 | 178/186 | 140/144 | 142/142 | 116/128 |
| Muga | Sonso | M | 1976 | 2000 | 190/207 | 112/124 | 174/182 | 144/172 | 110/116 | 178/186 | 144/152 | 154/154 | 116/128 |
| Nkojo | Sonso | M | 1970 | | 190/190 | 124/124 | 178/186 | 176/180 | 116/116 | 186/186 | 144/152 | 142/142 | 116/116 |
| Tinka | Sonso | M | 1959 | | 198/211 | 120/124 | 174/186 | 184/184 | 116/116 | 186/186 | 144/152 | 150/158 | 116/120 |
| Vernon | Sonso | M | 1967 | 1999 | 198/203 | 116/124 | 178/190 | 168/184 | 116/116 | 174/182 | 144/148 | 158/158 | 116/116 |
| Kikunku | Sonso | M | 1977 | 1998 | 194/211 | 124/140 | 178/182 | 144/184 | / | 178/182 | 148/152 | 142/142 | 140/144 |
| Magosi | Sonso | M | 1972 | 1999 | 203/207 | 120/124 | 182/194 | 144/180 | 104/116 | 186/186 | / | 142/154 | 116/120 |
| Zesta | Sonso | M | 1981 | 1998 | 211/211 | 124/140 | 174/182 | 144/164 | 116/116 | 178/186 | 144/148 | 142/142 | 116/136 |
| Nambi | Sonso | F | 1965 | | / | 112/120 | 174/194 | 172/176 | 110/116 | 178/186 | 152/148 | 142/154 | 140/128 |
| Andy | Sonso | M | 1985 | 2000 | 190/211 | 120/124 | 174/178 | 172/172 | 110/116 | 178/182 | 144/152 | 142/142 | 120/140 |
| Nora | Sonso | F | 1995 | | 190/203 | 112/120 | 182/194 | 168/172 | 104/110 | 182/186 | 148/148 | 142/154 | 116/128 |
| Musa | Sonso | M | 1994 | | 190/207 | 112/120 | 174/182 | 144/176 | 104/110 | 186/186 | 148/152 | 142/142 | 116/140 |
| Kalema | Sonso | F | 1982 | | 194/215 | 116/140 | 174/178 | 144/144 | 104/116 | 182/186 | 152/152 | 142/154 | 136/140 |
| Bahati | Sonso | F | 1994 | | 203/215 | 120/140 | 174/182 | 144/168 | 104/116 | 182/186 | 152/156 | 146/154 | 116/136 |
| Kumi | Sonso | M | 1999 | | 194/203 | 124/140 | 174/178 | 144/184 | 116/116 | 182/186 | 152/152 | 142/146 | 136/140 |
| Zefa | Sonso | M | 1983 | | 190/203 | 124/136 | 174/186 | 176/180 | 110/116 | 186/186 | 144/152 | 142/142 | 116/136 |
| Shida | Sonso | F | 1990 | | 203/203 | 124/136 | 174/190 | 180/180 | 110/116 | 182/186 | 144/148 | 142/146 | 116/116 |
| Hawa | Sonso | M | 1994 | | 203/211 | 120/124 | 178/182 | 180/184 | 116/116 | 174/178 | 148/148 | 142/142 | 140/140 |
| Kigere | Sonso | F | 1966 | | 190/203 | 116/120 | 182/190 | 176/176 | 116/116 | 174/178 | 148/152 | 158/158 | 140/140 |
| Keti | Sonso | F | 1998 | | 190/203 | 116/124 | 174/190 | 176/180 | 116/116 | 174/182 | 148/152 | 146/158 | 116/140 |
| Kutu | Sonso | F | 1982 | | 203/207 | 116/124 | 182/198 | 144/172 | 116/116 | 182/182 | 152/152 | 138/142 | 116/136 |
| Kato | Sonso | M | 1993 | | 207/211 | 116/124 | 178/198 | 144/172 | 116/116 | 182/182 | 144/152 | 138/142 | 116/116 |
| Kana | Sonso | F | 1998 | | 203/207 | 116/124 | 182/198 | 144/144 | 104/116 | 182/182 | 152/156 | 142/154 | 116/136 |
| Kwera | Sonso | F | 1975 | | 198/203 | 112/124 | 178/182 | 168/180 | 116/116 | 174/182 | 144/148 | 142/146 | 116/116 |
| Kwezi | Sonso | M | 1995 | | 203/207 | 112/124 | 174/182 | 168/172 | 116/116 | / | 144/144 | 142/154 | 116/128 |
| Karo | Sonso | F | 2000 | | 198/211 | 112/120 | 178/182 | 168/168 | 116/116 | 178/182 | 144/148 | 142/142 | 116/116 |
| Ruda | Sonso | F | 1966 | 2001 | 203/211 | 120/124 | 178/182 | 172/180 | 116/116 | 178/182 | 152/152 | 154/158 | 116/128 |
| Bob | Sonso | M | 1990 | | 203/198 | 120/124 | 182/182 | 172/184 | 116/116 | 182/182 | 144/152 | 146/154 | 128/144 |
| Rachel | Sonso | F | 1997 | 2001 | 190/211 | 120/124 | 182/186 | 176/180 | 116/116 | 182/186 | 144/152 | 142/158 | 116/128 |
| Ruhara | Sonso | F | 1962 | | 203/203 | 120/124 | 178/182 | 180/180 | 116/116 | 178/178 | 148/152 | 150/154 | 116/120 |
| Rose | Sonso | F | 1997 | | 203/203 | 124/124 | 174/178 | 180/180 | 116/116 | 178/182 | 144/148 | 150/158 | 116/116 |
| Nick | Sonso | M | 1986 | | 203/207 | 120/124 | 178/182 | 144/180 | 104/116 | 178/186 | 152/152 | 142/150 | 120/120 |
| Zana | Sonso | F | 1962 | | 207/219 | 116/120 | 178/186 | 176/184 | 116/116 | 178/186 | 152/152 | 150/158 | 116/120 |
| Zalu | Sonso | M | 1995 | | 207/211 | 116/124 | 174/186 | 176/184 | 116/116 | 178/182 | 148/152 | 142/150 | 116/120 |
| Zimba | Sonso | F | 1966 | | 190/203 | 112/120 | 182/190 | 144/172 | 110/116 | 182/186 | 148/152 | 150/178 | 116/120 |
| Gonza | Sonso | F | 1989 | | 203/207 | 120/120 | 182/194 | 144/144 | 104/116 | 182/186 | 152/152 | 142/150 | 116/120 |
| Zig | Sonso | M | 1997 | | 190/207 | 120/120 | 190/194 | 144/144 | 104/110 | 182/186 | 148/152 | 142/150 | 116/120 |

| Indiv | Group | sex | yob | yod | D2s1326 | D7s817 | D5s1470 | D7s2204 | D9s910 | D2s1329 | D11s200 | 2D12s66 | vwf |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Kewaya | Sonso | F | 1983 | | 190/211 | 120/124 | 174/190 | 172/172 | 110/116 | 182/186 | 144/148 | 142/178 | 116/116 |
| Katia | Sonso | F | 1998 | | 211/211 | 120/140 | 174/182 | 172/184 | 110/116 | 178/182 | 144/152 | 142/142 | 116/140 |
| Mukwano | Sonso | F | 1969 | | 207/211 | 116/120 | 182/194 | 144/184 | 116/116 | 178/186 | 152/156 | 142/178 | 136/140 |
| Gershom | Sonso | M | 1983 | | 190/203 | 120/124 | 178/186 | 144/180 | 116/116 | 186/190 | 148/152 | 142/142 | 116/116 |
| Emma | Sonso | F | 1990 | 2001 | 203/211 | 120/124 | 174/174 | 144/176 | 116/116 | 182/182 | 144/152 | 142/142 | 116/120 |
| Bwoba | Sonso | M | 1986 | | 207/211 | 116/120 | 174/194 | 144/168 | 104/116 | 174/186 | 152/152 | 142/142 | 116/140 |
| Mark | Sonso | M | 2000 | | 194/203 | 112/124 | 190/190 | 144/172 | 110/110 | 174/186 | 152/156 | 154/178 | 124/140 |
| Janet | Sonso | F | 1998 | | 203/207 | 120/124 | 174/182 | 180/180 | 116/116 | 182/186 | 152/152 | 142/158 | 116/124 |

**Appendix 3.2**

Here I illustrate in detail how the average relatedness within one group of individuals was derived. These calculations only consider the relationship between individuals within one generation. The formula aims at deriving average relatedness in a group of individuals, so the basic approach is to analyze how many of the pairwise relationships between any two individuals in the group have a specific value.

First, individuals can be related by sharing the same parent. Per set of *n* siblings one obtains

$$\frac{n \times (n-1)}{2}$$

links. For the whole group one has to sum all these pairs *n, m,* ... and divide by the total number of possible dyads $n + m + \ldots = x$

$$\frac{\frac{n \times (n-1)}{2} + \frac{m \times (m-1)}{2} + \ldots}{\frac{x \times (x-1)}{2}}$$

$$\Leftrightarrow \quad \frac{n^2 - n + m^2 - m + \ldots}{x \times (x-1)} = \frac{n^2 + m^2 + \ldots - x}{x \times (x-1)}$$

To simplify, the actual number of siblings for each parent is replaced by his relative share $n = i \times x, m = j \times x, \ldots; 0 < i, j < 1; i + j + \ldots = 1$

$$\Leftrightarrow \quad \frac{(i \times x)^2 + (j \times x)^2 + \ldots - x}{x \times (x-1)} = \frac{(i^2 + j^2 + \ldots) \times x - 1}{x - 1}$$

This formula is based on just one sex, so one has to sum for all females (where reproductive success now is summarized by taking $f = i^2 + j^2 + \ldots; 0 < f < 1$) and for all males ($m = i^2 + j^2 + \ldots, 0 < m < 1$). In addition however, individuals who do not share a parent can be related if their respective parents are related. For this calculation, I assume the simplifying situation in which there is complete dispersal of one sex and the incoming individuals of this sex are not related among each other or

to the opposite sex. I therefore only add one term, where I take all the dyads that are not sharing the same parent and the average relatedness

$$1-\frac{\left(i^2+j^2+...\right)\times x-1}{x-1}\times R$$

.

The complete formula only aims at calculating the average relatedness of the philopatric sex (the dispersing sex has per definition a relatedness of zero), so reproductive skew in this last term is expressed as share of the offspring of the respective sex, and the reproductive success $i^2+j^2+...$ here will be termed *a* and is to be replaced by either *f* under female philopatry or *m* under male philopatry. To obtain actual relatedness values, all of the three terms have to be multiplied by 0.25, the value for half-sibs.

$$R=\frac{f\times x-1}{x-1}\times 0.25+\frac{m\times x-1}{x-1}\times 0.25+\left(1-\frac{a\times x-1}{x-1}\right)\times R\times 0.25$$

Since the R over generations is recursive, the formula is just solved for R:

$$4R-\left(1-\frac{a\times x-1}{x-1}\right)\times R=\frac{f\times x-1}{x-1}+\frac{m\times x-1}{x-1}\Leftrightarrow R\times\left(3+\frac{a\times x-1}{x-1}\right)=\frac{\left(f+m\right)\times x-2}{x-1}$$

$$\Leftrightarrow R\times\left(\frac{3\times x-3+a\times x-1}{x-1}\right)=\frac{\left(f+m\right)\times x-2}{x-1}\Leftrightarrow R=\frac{\left(f+m\right)\times x-2}{\left(3+a\right)\times x-4}$$

# 4. Variance in lifetime reproductive success and variation at sex-specific genetic markers

## 4.1 Summary

The frequencies of different variants at genetic loci is driven ultimatively by the number offspring individuals carrying certain variants sire. Population genetics has made use of this by for instance recording that in a population expansion almost all individuals can sire offspring, while during a population decline only a minority of individuals leave offspring. However, research in demography and behavioural ecology has shown that there are additional, social factors which can skew the distribution of offspring among individuals. I develop six different analytical approaches to detect and quantify this variance in lifetime reproductive success (vLRS) from the amount and distribution of genetic variation detected at a local scale at sex specific genetic markers. Their accuracy and robustness to potentially confounding factors like population size changes is assessed via individual-based modeling. Two of the approaches, one assessing vLRS within and the other between social groups of individuals of the philopatric sex, are shown to allow to quantify vLRS. These are than applied to published genetic data from natural populations and it is shown that indeed large differences in vLRS can be detected between the sexes and between different species.

## 4.2 Introduction

### 4.2.1 Factors influencing genetic variation in populations

Different factors influence the amount of genetic variation in a population. Mutation creates new variation, which depending on drift, selection, demographic changes and population structure remain in a population for different lengths of time or even get fixed. It is often difficult to disentangle the effects of these different forces in natural populations (Frankham 1995; Lawson Handley *et al.* 2006). Most approaches aim at separating aspects of selection (reviewed in Otto 2000) or past demograpic events like population size changes (e.g. Harpending *et al.* 1993) from neutral evolution. The "standard neutral theory" assumes that in a population of infinite size all individuals have the same chance of reproduction and mating occurs randomly. However, the effect of some individuals reproducing more than others, also termed genetic drift, in fact varies in extent between populations and is influenced by species characteristics. Already Fisher (1930) and Wright (1938) realized that the differential reproduction of individuals larger than chance should increase the effect of genetic drift. In populations of finite size this 'chance variation' in allele frequencies is an important factor shaping genetic diversity (Wright 1990). While studies have mentioned that the variance in lifetime reproductive success among individuals (vLRS) could influence the observed amount and structuring of genetic variation (Chesser 1991; Nunney 1993, Laporte & Charlesworth 2001), only a few attempts have been made to empirically describe the level of drift affecting the genetic variation of populations (Imaizumi & Nei 1970; Austerlitz & Heyer 1998; Turner *et al.* 2002; Helgason *et al.* 2003). Demographic studies on the other hand, which record birth patterns in populations, have shown that while some individuals never reproduce, others can produce large number of offspring (e.g. humans: Fisher 1930, deer: McLoughlin *et al.* 2006). However, the need to study a large number of individuals for their whole lifetime has largely limited getting the distribution of offspring among individuals (Coulson *et al.* 2006). Proving the effect of vLRS on genetic variation therefore would allow a better understanding of population genetics, and, in turn, being able to infer the vLRS from genetic data could prove a useful tool to possibly gain insights into the degree of competition among individuals within a population.

### 4.2.2 Levels of competition

Behavioural studies have highlighted that most of this competition over reproduction occurs on a small local scale and therefore it is important to recognize and incorporate the underlying social structure of the species in question. Individuals can either be philopatric, which means they stay at the locality or in the group they have been born, or dispersing and move away. In most mammal species there is a clear sex-bias, with nearly all individuals of one sex leaving while the others stay (Greenwood 1980). The assumption is that the individuals of the sex who benefit the most, for instance by knowing the where to find resources or from cooperative interactions, will remain in the natal area (Wrangham 1980), while the individuals of the other sex will leave to avoid inbreeding. Based upon the degree of local competition, philopatric individuals will form dominance hierarchies which are predicted to correlate with their reproductive success (Zuckerman 1932; Carpenter 1942; Dewsbury 1982). Even though the factors leading to different competition levels, like food availability, predator defense or infanticide, are still debated and difficult to quantify (König 2002), the outcome, actual differences in aggressive competition have been more clearly documented. In the case of high competition, clear despotic dominance hierarchies between individuals develop and high-ranking individuals are expected to monopolize resources and accordingly to have a higher reproductive success (e.g. birds: Arabian babblers, Lundy *et al.* 1998; mammals: gorillas, Bradley *et al.* 2005 - in the primate literature, species with a nepotistic dominance hierarchy among females within social groups have been termed as "resident-nepotistic" (RN) Sterck *et al.* 2001). I therefore expect genetic variation to be locally depleted because of high competition. In the case of more egalitarian relationships, individuals are expected to have more similar breeding success (e.g. birds: pukeko, Jamieson 1997; mammals: banded mongoose, Gilchrist 2006 – these are termed "resident-egalitarian" (RE) in the primate literature Sterck *et al.* 2001), leading to more genetic variation being retained. However, in this case higher competition between groups of cooperating individuals is expected. For species with high competition between groups I expect to see more fission of genetic lineages between different groups. Single lineages could expand while others go extinct, and this process of a natural loss of whole mtDNA lineages in female philopatric species has been described in conservation genetics studies (Gompper *et al.* 1997, Kelly 2001). In contrast, if groups are rather stable, there will be a higher retention of

variation in the population, which has been suggested in phylogeographic studies using mtDNA in female philopatric species (Avise *et al.* 1984, Hoelzer *et al.* 1998).

### 4.2.3 Objectives of this study

In this study I employ simulations to assess the specific influence of vLRS on genetic variation and ask whether is possible to quantify vLRS from a sample of genes. For this, I designed approaches to specifically estimate the variance in LRS among individuals from the distribution of genetic variation among these individuals at a local scale. The basic premise is that if within a population certain individuals produce more offspring than others, the frequency of all the genetic alleles they are carrying should increase in the population. This process should be especially pronounced for genetic markers which are perpetuated only within one sex. In mammals, mitochondrial DNA (mtDNA) is transmitted over generations only through the female line and should therefore reflect differential reproduction among females, while Y-chromosomes are only inherited through the male line and should therefore reflect the variance among the males. The approaches used here therefore aim at inferring vLRS within the sexes by studying the distribution of variation at these sex-specific genetic markers. I then apply these to genetic data from natural population to see whether species do indeed differ according to expectations based on behavioural correlates of vLRS.

This study aims to answer the following four questions: 1.) Does the variance in LRS among individuals of a population leave a discernible signal on the genetic variation? 2.) Can the distribution of variation at sex-specific markers be used to quantify the variance in LRS? 3.) Are the results of these approaches independent of sampling and demographic effects in genetic data from natural populations of mammals and birds? 4.) How do primate and human populations compare in regard to the variance in LRS for the two sexes?

To answer these questions, I first develop theoretical predictions concerning the effects of competition within and between groups on the amount and structuring of genetic variation. Based on these, I present several new approaches to summarize the amount and distribution of genetic variation. Two of these approaches analyze the branching patterns of phylogenetic trees. Another four compare the allele frequencies and genetic distances to neutral expectations based on a random (Poisson) process. Second, computer simulations are implemented to analyze the predictions of the effect

of variance in LRS on genetic variation and to assess whether the previously derived approaches are suited to quantify the effect. Finally, published data on genetic variation at sex-specific markers from mammalian populations was collected to analyze whether sex-specific markers do indeed show a signal of sex-specific processes. I tested whether genetic variation shows a signal of variance in LRS independent known changes in population size. In addition, for populations for which published data for both the mtDNA and the Y-chromosome was available, I predict that if demographic processes alone affect the amount and distribution of variation, both markers should show similar results. However, if sex-specific dispersal and variance in lifetime reproductive success influence genetic variation, divergent results within single populations are expected, but results for mtDNA in female philopatric populations should be more similar to Y-chromosome data from male philopatric populations than to mtDNA data from female dispersing species. In addition, published mitochondrial DNA data was compared for primate species in which the degree of female competition had been estimated from behavioural observations.

## 4.3 Material and Methods

### 4.3.1 Inferring variance in lifetime reproductive success

The aim here is to infer individual differences in lifetime reproductive success (LRS), which is not directly comparable to classical measures of reproductive skew, which describe the distribution of offspring among a small set of individuals within a short period of time (Kokko *et al.* 1999). The differences in LRS are estimated using one-time samples of animals from a natural population who have been typed for their genetic variation at a sex-specific genetic marker. The variance calculated based on the genetic variation reflects differences among individuals in the number of sired offspring as

$$\sigma^2 = \frac{\sum_{i=1}^{n} (x_i - \bar{x})^2}{n} \qquad (4.1)$$

with $x_i$ being the number of offspring for each individual, $\bar{x}$ the mean number of offspring and $n$ the total number of individuals. If one considers a situation in

which competition among a fixed subset of individuals (e.g. social group) is based on some individual value (e.g. strength), the variance among these individuals is not affected by the group size nor by the average number of offspring sired. This variance equals 1 for a random (Poisson) distribution of offspring (i.e. all individuals have the same competitive ability), is larger than 1 if some individuals have a disproportionate share of offspring, and smaller than 1 if individuals have a more equal distribution of offspring (0 if all have exactly the same number of daughters).

The aim is to use the distribution of the genetic variation at the sex-specific marker to infer the variance in LRS in the sex that is transmitting it. Six different approaches are presented as listed below. Two are derived to infer the population-wide variance, one is designed to infer the variance within groups for species in which the sex disperses, one to infer the variance within groups of philopatric species and two for the level of between-group variance of a philopatric sex (for a general comparison see table 4.1).

### 4.3.2 New approaches to detect vLRS from genetic data

*i) "mismatch-based"*

This approach aims to infer the within-group level variance of the philopatric sex based on derivations of Watterson 1975 and Kingman 1982. If philopatric individuals belong to a closed group, all have a recent common ancestor and they are monophyletic. Therefore, they can be treated as single closed population and their effective population size can be calculated directly from the variation found within groups. For this, the approach by Watterson 1975 was used, which predicts the frequency of pairwise differences between the sequences in a sample. The variance in reproductive success can be obtained by dividing the actual group size, ie. the number of individuals of that sex in a group, by the genetic effective population size of the group (Kingman 1982). The variance is therefore calculated as

$$\sigma^2 = \frac{2 \times \mu \times N \times Q_0}{1 - Q_0} \qquad (4.2)$$

with $\mu$ being the mutation rate, $Q_0$ the frequency of comparisons between identical haplotypes and $N$ the group size.

I calculated $Q_0$ within groups as

$$Q_0 = \frac{\left(\sum p_i^{\,2}\right) \times N - 1}{N - 1} \qquad (4.3)$$

with $p_i$ being the allele frequencies of the *i* genotypes within single groups.

*ii) "clonal-model"*

This approach aims to infer the frequency of group extinction/recolonization in the philopatric sex per generation and it is based on Maruyama & Kimura 1980. The approach was originally derived for clonal microorganisms. However, haploid sex-specific markers in a closed group of philopatric sex can be all traced back to one common ancestor, resembling clonal reproduction. The formula infers the between-group extinction/recolonization rate by using the within-group coalescence as expected rate. One assumption is that as groups go extinct, they are immediately recolonized by a single individual/lineage from one of the existing groups. This assumption seems to be valid also for social groups, where new groups are mostly formed by group fission. The extinction/fission rate λ can be calculated as

$$\lambda = \frac{\left(1 - \sum p_i^{\,2}\right) \times g + 2 \times \mu \times \left(1 - \sum p_i^{\,2}\right) \times g \times N - g - 2 \times \mu \times g \times N}{2 \times N - 2 \times \left(1 - \sum p_i^{\,2}\right) \times N - \frac{\left(1 - \sum p_i^{\,2}\right)}{\mu}} \qquad (4.4)$$

where $p_i$ is the frequency of the *i-th* allele in the total sample, $g$ is the number of groups, $N$ is the mean group size and $\mu$ is the mutation rate. To adjust for the fact that the within-group coalescence also might vary between populations the value of the mean actual group size $N$ can be replaced with the *Ne* calculate by one of the other methods for within group variance.

*iii) "variation-change"*

This approach aims to infer the within-group level of variance for females if they are the dispersing sex. In this scenario, variation at mtDNA of adult females within a single group is also influenced by dispersal distances and potential dispersal biases. Analyzing the variance found among the adult females of a group provides information on the variation that is introduced every generation. This than can be

contrasted to the variation at the mtDNA of the adult males. Since they have been born by the females of the previous generation, the difference between the two sexes indicates whether and how this variation changes due to the differential reproductive success. The variance in reproductive success therefore can be calculated as

$$\sigma^2 = \frac{\sum p_i^{\,2}(females)}{\sum p_i^{\,2}(males)} \qquad (4.5)$$

where the numerator is the sum of the squared allele frequencies among females within a group and the denominator the sum of the squared allele frequencies among males within a group. To combine data across several groups, two approaches were taken. The first is to calculate the ratio in every group and than to average the values, the second to average the sum of the allele frequencies for males and females across groups before calculating the ratio.

*iv) "two-generation"*

This approach aims to infer proportion of individuals contributing offspring per generation by inferring the change in allele frequencies in the whole population. If reproduction is not deterministic, so that every mother has exactly one daughter, the frequencies of every allele/haplotype present in the population are expected to change slightly from one generation to the next. By comparing the change in diversity observed between generations to the one expected under a Poisson distribution, this will indicate whether allele frequencies changed more than expected implying that some individuals had a higher reproductive success. The method assumes that samples from two 'generations' exist. In the context of this study this approach could be used if both infants/juveniles as well as adults have been sampled and this information would be available for the samples. Following Waples (1989), the effective population size was calculated by first estimating the variance between generations (Nei & Tajima 1981) as

$$F_c = \frac{1}{K} \times \sum_{i=1}^{K} \frac{(x_i - y_i)^2}{(x_i + y_i)/2 - x_i \times y_i} \qquad (4.6)$$

with $K$ being the number of different alleles, $x_i$ being the frequency of the *i-th* allele in the adult generation and $y_i$ the frequency of the *i-th* allele in the offspring generation.

With $S_0$ being the sample size of adults and $S_1$ the sample size of the offspring generation, and relating the calculated effective population size to the actual population size $N$ (Kingman 1982), the variance is derived as

$$\sigma^2 = \frac{1}{2 \times N \times \left[F_c - 1/(2 \times S_0) - 1/(2 \times S_1) + 1/N\right]} \qquad (4.7)$$

*v) "imbalance of phylogenetic tree":*

This approach aims to infer consistent, heritable differences among different matri- or patrilines on a population wide level, as described in Blum *et al.* 2006. The basic premise is that if there is a bias in the production of offspring along one line, there will be more tips in this line as compared to the sister line from which it split. The approach is therefore useful for population-wide analyses, but it assumes that some lineages are consistently favored for multiple generations. However, if reproductive success is not heritable and by chance different matri- or patrilines are more successful in following generations, this method will not show this. The method is based on analyzing the imbalance in the number of tips below each node. It therefore looks after each split how many haplotypes have been found on either side. Following Blum *et al.* (2006), "mean $I$" (Purvis *et al.* 1995, Agapow and Purvis 2002) was used, which computes for every node in a phylogenetic tree

$$I = \frac{B - m}{M - m} \qquad (4.8)$$

where $B$ is the size of the larger of the two daughter clades, $m$ is the minimum size of $B$ as half the number of the total number of tips below the node ($n$ / 2), and $M$ is the maximum size of $B$ as the total number of tips below the node minus one ($n$ - 1). As an adjustment for different number of tips $n$, in case of an even number of $n$ the values of $I$ are transformed by multiplying it with ($n$ - 1 / n). To analyze one summary statistic for the whole tree the mean of the values of the different nodes is calculated. For a neutral tree this will produce values of 0.5 and larger values for more unbalanced trees. Trees were constructed using the maximum likelihood method as implented in Phylip v3.5 (Felsenstein 1993) and manually analyzed. This method of tree construction was chosen because previous comparisons indicated a systematic

overestimation of the variance in lifetime LRS if simpler methods are used, probably because UPGMA and neighbor-joining do not allow multiple branching events.

*vi) "tree-splitting rate"*

This approach aims to infer the rate of group extinction/recolonization in the philopatric sex and it is based on Nee 2001 and Webster *et al.* 2003. In phylogenetic trees of sex-specific markers, haplotypes of individuals of the philopatric sex from the same group are represented as monophyletic clades. Coalescence events in the tree above the group level reflect past group relationships such as group splitting. If the habitat is saturated, extinction and splitting are coupled. Following the birth/death models applied to phylogenetic trees, the splitting rate therefore should reflect group fission events. The simplest solution therefore to derive the extinction/fission rate λ is to calculate the maximum genetic distance between two groups and divide this by the number of groups minus 1. However, this will be heavily biased by sampling. An alternative is to plot the number of lineages over time (at every split the number of lineages will increase by 1) and calculate a regression line. These estimates are rather robust to random sampling (Nee 2001), in cases where the tree has been growing according to a Moran-process (simultaneous extinction and fission). Since however in many population genetic studies sampling is not random, but extensive at several distant locations, I decided to assess the robustness of the estimate through random resampling of groups and recalculating of the slope.

### 4.3.3 Combining the results from different approaches

The last two estimators of the rate of group extinction/fission can be converted into a variance. If one assumes that the population as a whole is stable in size, than the mean reproductive success is 1. The rate of group extinction per generation, λ, reflects the chance for each group per generation to go extinct. This means that on average, a group will go extinct every 1/ λ generations. The rate of decline per generation that is needed so that a group of a given group size loses all it members can be estimated as

$$groupsize \times decline\_rate^{\left(\frac{1}{2\times\lambda}\right)} < 1 \quad \Leftrightarrow \quad decline\_rate < \left(\frac{1}{groupsize}\right)^{2\times\lambda} \tag{4.9}$$

Since I assume a stable population, half of the groups have to go extinct at twice the rate, therefore the factor of 2 x λ. The remaining groups will grow at a rate of 2 - decline-rate to have a stable population. The total variance between groups in a species where the sex of interest is philopatric can therefore be calculated as

$$\sigma^2_{BetweenGroups} = \left(1 - \left(\frac{1}{groupsize}\right)^{\lambda}\right)^2 \qquad (4.10)$$

A species value will be the combination of within- and between-group variance. If the individuals of the sex of interest disperse, local competition is expected to reflect global competition. In the case of the individuals staying in their natal group, the within- and between-group values can be combined in the following way:

$$\sigma^2_{Global} = \sigma^2_{WithinGroups} + \sigma^2_{BetweenGroups} \qquad (4.11)$$

### 4.3.4 Individual-based modeling to infer validity and sensitivity

Computer simulations were performed to assess the validity and sensitivity of these approaches. The model was constructed using Netlogo 4 (Wilensky 1999). The model, along with its code and a more detailed description is available on email request. While in recent years different simulation models to generate simulated genetic data have been developed (e.g. EASYPOP: Balloux 2001, SimCoal: Laval & Excoffier 2004, Splatche: Currat *et al.* 2004, RMetasim: Strand 2002), none of the allow changes in the variance in the number of offspring, the main parameter of interest in this study. However, the basic underlying structure is very similar.

Simulations started by generating individuals on a two-dimensional stepping-stone grid of 81 groups. All groups consist initially of the defined maximum group size. Since the approaches deal with sex-specific processes, only one sex was simulated and group size therefore refers to the number of individuals of one sex. Individuals carry at the beginning the same genotype. This resembles a situation of instantaneous expansion (Excoffier 2004) and to avoid a potential erroneous signal, simulations were run for enough generations to overcome this (e.g. in the case of dispersal enough to ensure migration of lines from one edge to the other).

To represent both types of commonly generated genetic data, genotypes are either a stretch of 300 linked basepairs ("mitochondrial sequence") or 12 linked microsatellite loci ("Y-haplotype").

For the iteration, I assumed non-overlapping generations. This approach was chosen for it easier implementation (as in most other simulation software) and is valid since in a demographically stable population (almost all simulations) the effective population size is still robustly estimated (Hill 1979). Specifically, it allows one to explicitly set the distribution of variance in LRS with no heritability among sets of individuals. Individuals in the groups were randomly assigned an exclusive dominance rank, starting with the highest rank of 1 up to values corresponding to the maximum group size. Dominance ranks are non-heritable, but assigned every generation at random within the groups. The individuals then produce a predetermined number of offspring according to their dominance rank, after which they die. For each group size five different pre-defined offspring-distributions were used to generate situations with low and high skew, as well as low and high variances. Deterministic distributions (highest-ranking individual sires X offspring) as compared to probabilistic distributions (highest-ranking individual has a chance of Y% to sire any one of the offspring) were applied, because simulations should as well include situations in which the distribution of offspring is more even than random. In addition, the deterministic distribution sets a cap on the number of offspring an individual can sire, which avoids unrealistic scenarios (especially for females), and allows more direct comparisons between different group sizes. However, to allow for variation among groups, I also included distributions in which more offspring were produced than there are parents, and offspring die off randomly. After the die-off the actual variance among individuals in the number of surviving offspring is calculated and recorded, this is the value that will be used in comparison with the estimates based on the genetic variation.

Offspring inherit the parental genotype, which however might mutate. For the sequence data, a model was used that allows every base to independently change to one of the three other bases (no substitution bias, however all the analyses of the simulated data as well assumed no model to derive the genetic distances, but just counted absolute differences). For the microsatellite locus I assumed the standard step-wise mutation model in which every locus independently increases or decreases by one repeat (Schlötterer & Tautz 1992). I choose mutation rates based on pedigree

studies (mtDNA divergence in humans, Howell *et al.* 2003; mtDNA divergence in penguins, Lambert *et al.* 2002), which are rather high. Recent analyses indicate that the divergence between the phylogenetic and the pedigree rates (Ho & Larson 2006) is due to the fact that most new mutations are lost due to drift (Zhivotosky *et al.* 2006). Since in the current approach these however could still contribute to the genetic diversity detected within a sample of a population, in which most individuals will have a recent common ancestor, similar to other genetic simulation studies, mutation rates were based on the results from the pedigree studies. For the sequence, I assumed rates of $5 \times 10^{-6}$, $5 \times 10^{-5}$ and $5 \times 10^{-4}$, per transmission per basepair and for the microsatellites $10^{-3}$, $10^{-4}$ and $10^{-5}$ per transmission per locus.

The newborn offspring could move based on three dispersal schemes: no dispersal in which all individuals stay in the group they have been born; low dispersal in which a random 5% of individuals move to one of the four neighboring groups; complete dispersal in which all individuals leave the natal group and move straight away up to three groups away, with preference for one of the four neighboring groups. After dispersal is completed, group sizes are adjusted in case any of the groups contains more than the predefined maximum number. For this, individuals are drawn at random and die.

In the case of no dispersal, whole groups could go extinct with probabilities of 0, 0.5%, 1% and 5%. In this case, groups are recolonized immediately by one individual of one of the neighboring groups (since the model only considers effects among individuals of one sex this individual can reproduce). Groups might therefore contain fewer than the maximum number of offspring, either if they just have been recolonized, or if during dispersal by chance a group does not receive enough migrants.

To test the validity of the approaches, I ran the model with different input parameters (see table 4.2) for a total of 1000 generations. For each of the combinations of group sizes and variance in reproductive success I plotted the results obtained when using the different approaches on the full sample (all simulated individuals), assuming perfect knowledge about groups.

To test sensitivity of the approaches, I first repeated the above, but added a population increase or decrease of 0.5% per generation.

To test for the effect of noise induced by sampling, different schemes aiming at replicating real sampling were used. First, I analyzed how many groups have to be

sampled to get reduce the error in the estimate to have a value close to the one from the full sample. Second, I assumed that the grouping pattern would be unknown and therefore all individuals from a small geographic area would be combined in one sample independent of their group identity. For this, I combined the individuals from four or nine neighboring groups. Third, I assumed that all individuals in an area had been typed, including therefore as well individuals of the opposite sex (typing males for mtDNA). Lastly, I assumed that studies just obtained a subset of individuals from a geographic area. For this, I randomly selected half of the individuals of the set from one area and with no knowledge of their sex.

The actual degree of variance in LRS within and between the sampled groups is continously recorded by counting the number of surviving offspring per individual. Also all the calculations for the different approaches were directly incorporated in the Netlogo model. The only exception for this is the tree-based approaches. Since one of these had been tested with simulations already (Blum *et al.* 2006) and needs a maximum likelihood algorithm for tree reconstruction, I only analyzed subsets of the data. For this, FASTA-files from the samples of the simulations were constructed, and I manually analyzed trees derived with the software Phylip. The obtained values of the different approaches were compared to the input values of vLRS, group size, mutation rate, and dispersal distance, using regression analyses in SPSS version 9.0 (SPSS, Inc., Chicago IL)..

### 4.3.5 Applying the approaches to primate and human data

Suitable studies for the comparative analysis were defined as those which had extensive sampling (at least 6 individuals) within a social group or from within a small range (locality as specified by the authors). In addition, I excluded studies in which authors had specified that related individuals had been excluded from the sample.

I created three datasets. The first was used to test whether the results of the new approaches based on data from natural populations are confounded by aspects of sampling or the demographic history of the respective species. I searched with the keyword “mitoch*” through the NCBI/Genbank database within every family of mammals (September 2005). Published sequences were cross-linked to the respective publication and checked for their suitability. I recorded the region of mtDNA used, the length of the sequence analyzed and the sample sizes. In addition, I searched the

Web of Science (ISI) with the Latin species name of the respective species and the keyword "demography" to see whether an independent study indicated a stable population, or a decline or increase in population size for the respective species.

The second dataset aimed at relating the intensity of female competition within primate species as determined by behavioural observations to the distribution of variation at mitochondrial DNA within these species. Relevant primate studies were identified by searching the Web of Science (ISI) (July 2007) for species included in the list of Sterck *et al.* (2000), using as keywords the Latin name of the species and "mitoch*".

For the last comparative dataset, studies were selected that present data on both the variation on Y-chromosomes as well as mtDNA from the same populations. Two studies on the two patrilocal *Pan* species (bonobos: Eriksson *et al.* 2006; chimpanzees: Langergraber *et al.* 2007b) were combined with studies on human populations, which were identified by searching the references of some of the global comparative studies (e.g. mtDNA vs. y: Destro-Biesol *et al.* 2004; mtDNA: Helgason *et al.* 2000; y: Pereira *et al.* 2002). Data from a total of six different human societies was available. Three of these societies have been described as matrilocal [*Greenland Inuit* (mtDNA: Saillard *et al.* 2000, Y-STR: Bosch *et al.* 2003), *African Hadza* (mtDNA and Y-STR: Knight *et al.* 2003), *Thailand Hill tribes* (mtDNA and Y-STR: Oota *et al.* 2001)] and three as patrilocal [*Central Europeans* (mtDNA: Excoffier 2004, Y-STR Pereira *et al.* 2001), *New Guineans* (mtDNA: Tommaseo-Ponzetta *et al.* 2003, Y-STR: Kayser *et al.* 2003), *Thailand Hill tribes* (mtDNA and Y-STR: Oota *et al.* 2001)]. If detailed information was available, I calculated the mismatch distributions for individuals from within single villages or localities, and report the averages.

For all three datasets, mitochondrial DNA sequences were downloaded in FASTA-format, manually aligned using BioEdit v5 (Hall 1999) and imported to a modified MEGA version 3.1 (Kumar *et al.* 2004). Given the results of the simulations (see below), I applied the "mismatch method" for these comparative tests. For both the mitochondrial DNA and the Y-chromosome data MEGA provided the actual number of differences (either state of SNPs or number of repeats for microsatellites) as reported in the papers. I did not correct for mutation models or possibly different mutation rates. The resulting matrix was imported to EXCEL, and the absolute numbers of occurrences of the sequences among individuals within groups, defined

either as social groups within the original papers or as all coming from within the same small locality, were used to calculate the frequency of pairwise sequence differences. These frequencies were calculated for 14 categories (0, <0.005, <0.01, …, <0.05, <0.06, <0.07, <1) to allow for comparison among studies using different markers and sequence lengths. I first assessed visually whether the calculated mismatch distributions are unimodal as predicted if the individuals within the group are share one common recent ancestor. In the next step, the values calculated with the mismatch approach, which aims at inferring vLRS within groups, were correlated with whether species had been classified as having a demographic history of population increase, decrease or stability. For species with female philopatry where at least three groups had been studied I also applied the clonal approach. Given the low sample size I did not perform any statistical analysis but simply present the calculated values and compare them to the range of values previously calculated for other species using demographic approaches (Gompper *et al.* 1997, Kelly 2001). Finally, I used Phylip to create maximum likelihood trees. The trees were manually analyzed for branch lengths and the occurrence of multiple branching events.

## 4.4 Results

### 4.4.1 Simulations

#### 4.4.1.1 Influence of vLRS on genetic diversity

First I assessed whether varying vLRS in the simulations influenced genetic diversity as assessed by nucleotide diversity *pi* and genetic differentiation *Fst*. Since there were no differences between the results when simulating a DNA sequence to those simulating a group of linked microsatellites, in the following only the results for the DNA sequence are presented. In a linear univariate model with group size, mutation rate, vLRS within groups and the probability of group extinction as predictor variables, the mutation rate explained the majority of the variation in *pi* within groups, while group size and vLRS within groups also explained significant amounts of the variation (all three $p<0.005$, total $R^2=0.52$). Correlations between vLRS within groups and *pi* within groups are significant when tested for the three mutation rates separately (SpearmanRho -0.18, -0.27, -0.23; all $p<0.02$). This indicates that with higher differences in reproductive success between individuals, genetic diversity within

groups declines. Similarly, in a linear univariate model with *Fst* as dependent variable using only simulations with no dispersal, mutation rate explained the majority of the variation, while group size and group extinction rate also explained significant amounts (all $p<0.01$, total $R^2=0.39$), whereas vLRS within groups was not significant. Group extinction and *Fst* were highly correlated within every group size and mutation rate combination (all $p<0.01$).

The values of *pi* when calculated among individuals within groups and *Fst* did not change if population increase was simulated as a stepwise increase in group size. However, simulating the increase by starting from a central area and expanding into new patches did decrease the value of *pi* within groups. The inverse scenario of population size decrease by letting groups at the edges become extinct however did not influence the value of pi within the remaining groups or the *Fst*. In this scenario however decreases of group sizes leads to more variance in the estimation of both *pi* and *Fst*.

In general, I observed only very little variation overall when using the lowest mutation rate even after 1000 generations (in simulations with 648 individuals less than 10 of the 300 sites showed a mutation). Diversity levels were similar to those observed in data from natural populations when using the intermediate or high mutation rates.

Variance in lifetime reproductive success, either as differences between individuals within groups or differences between groups therefore had significant and detectable influences on genetic diversity. I therefore now present the simulation results of each of the new proposed approaches, and discuss their power to provide information on the variance in lifetime reproductive success within a population from genetic variation.

#### 4.4.1.2 Performance of the different approaches

*i) mismatch for philopatry*

The mismatch approach aims at inferring the vLRS within groups for philopatric individuals by calculating the degree of haplotype sharing. In a linear univariate model with mismatch variance as dependence variable, group size, extinction rate and vLRS remained significant factors. Group size effects however dropped out when only looking at no extinction scenarios, and vLRS remained the only significant factor ($F=19$, $p<0.001$, $R^2=0.372$). On average, the values calculated

with the mismatch approach are close to the input values (figure 4.1), there are however large variances reflecting that vLRS was not fixed, but allowed to vary among groups. The effect of group size in the simulations with group extinctions is due to the way recolonization was implemented. Single individuals recolonize empty patches and immediately become dominant, so in the first generation they will have the maximum reproductive success and there is infinite variance in lifetime reproductive success in these groups. Group size also has an effect in this case, because in the transformation to the mismatch variance the actual maximum group size was used, not the potentially smaller group size which might have occurred just after recolonization. This will lead to the observed larger bias for larger groups, since they will take longer to fill up.

*ii) clonal-model for philopatry*

The clonal-model approach aims at inferring vLRS between groups of philopatric individuals by relating the variance within groups to the distance between them. Simulations with a low mutation rate did not create enough mutations to differentiate between groups. This is a particular problem for this method, since the simulations end with many groups still only having individuals carrying the initial, identical haplotype. Since in more than half the simulations the values calculated with this approach were negative and I therefore excluded all simulations with the lowest mutation rate from the further analyses. A linear univariate model with clonal variance as dependent factor and group size, vLRS, group extinction and mutation rate as explanatory variables showed significant correlations for all four factors ($F=6,5,29,154$, all $p>0.025$, $R^2=0.64$). However, in analysis only of simulations in which group extinctions actually did occur, group size no longer had a significant effect. The values calculated in the simulations with no group extinction reflect the chosen starting condition of all individuals having initially the same haplotype, reflecting one big fission event (figure 4.2). Since in groups of small size drift can happen faster, these groups will no longer show this. In addition, when I corrected the clonal measure for the vLRS within groups (as mentioned above), the latter dropped out, but the model overall has a significantly better fit (overall $R^2=0.62$ vs. 0.59). While there was a linear correlation between the corrected clonal variance and group extinction rate (e.g. doubling of extinction rate leads to doubling in clonal measure), the results including the simulations in which no extinction occurred indicated that

this measure only reflects qualitative differences. The absolute values however are determined by the time to the most recent common ancestor.

*iii) variation-change approach for dispersal*

The variation-change approach aims at inferring population-wide vLRS for dispersing individuals by comparing haplotype sharing between females and males. The values of the two-generation approach derived by averaging within groups were almost identical to those derived by combining across groups, I therefore performed the analyses only with the first. In a global model linear univariate model, only group size and vLRS are significant ($p<0.001$, $R^2=0.47$), but not dispersal radius, extinction rate or mutation rate. Mutation rate in this case drops out because it will influence the absolute amount of variation present, but not the ratio of variation change.

*iv) two-generation approach for both philopatry and dispersal*

The two-generation approach aims at inferring the populationwide vLRS by analyzing the change of allele frequencies between generations. First I compared the values obtained when using the actual population size as estimator for the number of competitors versus the values which used the sample size as estimator. Fitting population size into the calculation frequently lead to negative values of vLRS, and I therefore used the sample size estimations for the further calculations.

All factors, group size, group extinction rates, vLRS within groups and mutation rates, were significantly correlated with the variation change values in simulations with philopatry (all $p<0.001$). For the simulations in which individuals dispersed, group size, vLRS within groups and mutation rates were significantly correlated with the generational variance, while dispersal radius and group extinction were not ($R^2=0.84$). Group extinction was not significant due to the fact that in the simulations I implemented it only after migration, so it could not directly influence the reproductive success beyond the effect of group size regulation, which occurred in any case. Group size remained a significant factor, since, as mentioned, I also used it as the number of competing individuals in the formula. As shown with the population size / sample size difference, larger group / sample sizes will lead to lower values of the generational variance (one overestimates the variance because fewer individuals are plotted as competing than which actually are). This also precludes direct comparison between philopatric and dispersal situations, since the number of

competing individuals is underestimated stronger in the case of dispersal. The effect of mutation rate is in both cases due to the fact that new allelic variants are generated, which is not considered in the formula.

*v & vi) tree based approaches*

The imbalance-of-tree approach aims at inferring population-wide vLRS by analyzing the size of clades in a phylogenetic tree. The tree-splitting approach aims at inferring vLRS between groups of philopatric individuals by calculating the rate of splits group haplotypes. Both are based on the reconstruction of a phylogenetic tree and since the problems in both cases were already related to this first step, they are discussed together. In the case of low mutation rates, tree reconstruction is limited by not having enough information, leading to low bootstrap support for nodes and the presence of multiple branching events. However, tree reconstruction is also limited in the case of high mutation rates. In this case, true relationships can be lost due to multiple simultaneous branching and homoplasy leading to reticulate connections.

The imbalance approach requires a rooted tree for analysis of the branching patterns stepwise below each of the newer nodes. Many of the simulated cases produced a star-like phylogeny and a centrally rooted outgroup (I used the original haplotype from the start of the simulations for rooting), therefore tips could not be arranged this way.

For the approach based on the branching rate of groups within philopatric species, all tips have to be contemporaneous. However due to effects of rapid drift within the small, isolated social groups and long branch attraction (Anderson & Swofford 2004) due to homologous mutations in different groups, the reconstructed trees had largely differing internal branches. In addition, this method is heavily influenced by which, and how many groups have been sampled. Similar as before, combining few groups from different places leads to a starlike convergence in the tree, with all lineages directly descending from the original haplotype. Since there are therefore no informative relationships, no estimation of a linear rate of branching per time is possible. Since the number of trees output during the simulations was limited, I discuss these issues more quantitative based on the data from natural populations below.

#### 4.4.1.3 Influence of sampling

I concentrate on the approaches which showed a direct influence of vLRS not influenced by other factors, specifically philopatry clonal (between groups) and philopatry mismatch (within groups).

For the mismatch approach, I observed a decrease of the standard deviations of the calculated values with increasing group size (since groups have been sampled in whole, this is therefore identical with sample size; group size: standard deviation; 4: 0.054; 8: 0.033; 16: 0.029). This is due to the fact that haplotype sharing is measured as discrete value, and in a group of four individuals will drop from 1.0 if all individuals are identical to 0.5 if just one individual is different or 0.33 if there are twice two individuals carrying the same haplotypes. Given that these haplotype distributions are possible under different scenarios of vLRS within groups, variance in the estimation is larger for small groups. Therefore also more groups have to be sampled if groups are small to obtain a robust estimate. To have a standard error of the mean, which is smaller than the actual difference between haplotype sharing expected for situations in which the vLRS differs by 0.2, at least six groups have to be sampled.

For the clonal approach, it was more important to sample groups randomly than the actual number of groups which had been sampled. Reliable estimates were already obtained when including only four groups and the estimates where highly significantly correlated with the probability of group extinction ($p<0.001$). Increasing the sample size by two groups leads to a successive 3-4% decrease in the error.

### 4.4.2 Comparative data

Based on the above findings, I applied the philopatric mismatch method in cases where studies had sampled at least 8 individuals from a social group or within a small area, and the philopatric clonal method when this had been performed for at least three sites. Given that the latter applied only to a rather small subset of species, I only compared the values to previous published estimates of group extinction, and concentrated for the analyses of the larger datasets on the philopatric mismatch method.

Of the 14 primate species for which comparative behavioural and genetic data were available, six are considered resident-nepotistic (RN) [*Cercopithecus aethiops, Alouatta seniculus, Macaca fuscata, Papio anubis, Hapalemur griseus, Microcebus*

*murinus*], two as resident-egaliatarian (RE) [*Callithrix jacchus, Macaca sylvanus*] and six as dispersal-egalitarian (DE) [*Trachypithecus aureatus, Mirza coquereli, Lepilemur septentrionalis, Pongo pygmaeus, Papio hamadryas, Pan troglodytes*] species. For the philopatric species, mismatch distributions of sequences from within social groups are unimodal, indicating closed group which are monophyletic (figure 4.3). As expected, genetic variation within groups is lower for RE species than for RN species. Calculations based on the mismatch approach give values for the variance in LRS below 1 for egalitarian and above 1 for nepotistic species (table 4.3)

For the seven populations for which there is data both on mtDNA and Y-chromosome variation, all show clear divergence between the distribution of genetic variation at these two markers. However, they also indicate that if sampling occurs on the level of population, and therefore on a scale larger than the distance individuals normally disperse, combining individuals from several localities, the results are biased (Langergraber *et al.* 2007b). I therefore split the dataset into two subsets, the first with populations which have been sampled within a single group. For these four populations, the mismatch distribution for the philopatric sex is unimodal, with a clear peak at zero or low divergence (figure 4.4 a). In contrast, the mismatch distributions for the dispersing sex are flat, indicating large range of differences between individuals (figure 4.4 b). This is the same for dispersing sex in the dataset with the populations which have been sampled across populations (figure 4.5 b). In contrast however, the mismatch distribution of the philopatric sex in this case is bimodal, with again a clear peak at zero differences, but also a clear second peak at intermediate differences (figure 4.5 a). This indicates that the pattern not simply due to demography, which would affect both sexes equally.

MtDNA data was obtained for a total of 47 mammal species (appendix 4.1), for which it is know that females disperse. The calculated values range from 0.06 to 2.15, with an average of 0.96 (n = 47). There is no correlation between the mismatch measure and whether a species underwent a change in population size ($r = 0.277$ $p = 0.18$ $n = 25$). Values calculated with the clonal approach indicate group extinction probabilities per generation ranging from 0.5% to 18% (average 4.1%, n = 16).

Maximum likelihood trees for this dataset showed the same issues as trees generated during the simulations. Since the trees were constructed without an outgroup due to difficulties in defining these, I rooted them halfway along the largest divergence between two haplotypes. I than determined the degree to which the tips

have different total branch lengths to this root. For 65% of the trees there is at least one branch which is 25% shorter than these longest branches. Again, this would lead to difficulties in estimating a rate of divergence since haplotypes do not end up at the same estimated time period. In addition, 18% of the trees showed at least one node where a line splits into more than two descendant lines.

## 4.5 Discussion

### 4.5.1 Summary of the results

Changing the distribution of offspring numbers among individuals both within social groups and among them produced in the simulations a direct influence on the amount and distribution of genetic variation at sex-specific markers. The results of the new approaches developed here were correlated with these simulated changes, and the approaches also detected respective signals of this effect in a sample of genetic data from natural populations. As predicted, higher variance in lifetime reproductive success among individuals within groups decreased the amount of variation found at genetic sex specific markers in these. Also as predicted, higher group extinction and splitting rates lead to less differentiation in these genetic markers among the groups. While traditional methods to summarize genetic variation are influenced by this, they cannot be directly used to quantify the parameter.

### 4.5.2 Independence of signal from demographic changes

As in previous theoretical studies (Chesser 1991, Blum *et al.* 2006) my simulations also indicate that social structure produces a signal on genetic variation in populations independent of demographic history of the species. There are two reasons that this siganl can be detected even though population size changes strongly influences genetic variation. The first is that changes in group size do not bias the results because vLRS is a reflection of the difference in the number of offspring between individuals, not of the actual number. Second, there is a conceptual difference. Approaches aiming at understanding the demographic history of a population are mainly studying the rate at which genetic variation is generated and lost. If the effective population size is larger, more mutation can be generated per generation (Kingman 1982), and population size changes influence how quickly these

mutations than are lost again (Griffiths & Tavare 1998). The methods here however look at the actual distribution of genetic variation within individuals instead of summarizing it for the whole sample. In order for these methods to provide results however a standing amount of variation within the population has to be present. Variance in offspring numbers between individuals will than influence the distribution and frequencies of these different genotypes. These changes happen within very few generations (e.g. the average coalescent time for a group of six philopatric females is 24 generations (Avise *et al.* 1984)), and are therefore only little affected by population changes on a longer timescale. A pattern like this is also observed in data on y-chromosomal variation sampled within Europe. When mismatch distributions are plotted on a local scale ("countries"), they look unimodal as expected under the model proposed here and do not show any signal of population expansion. If data however were combined ("regions"), the analyses showed a clear signal of the expected population expansion (Perreira *et al.* 2001). The only potentially confounding situation could be if population expansion occurs in a wave-like frontal increase. In this case, groups at the edge will show little variation (Ray *et al.* 2003) since not enough time has passed to generate sufficient variation within these. If a sample would mainly include these outer groups, this could bias the estimates. The samples of the studies used in the comparative study however seem not biased, since they did not show an influence of past demographic history on the measure of variance in lifetime reproductive success within groups.

### 4.5.3 Mutation rates per generation

As mentioned, the approaches described here rely on genetic markers with high mutation rates. In line with this, my simulation results also indicate that in scenarios with low mutation rates calculated values are simply influenced by the chance of a whether or not a mutation recently occurred within the sampled individuals. Even in the case of a random distribution of offspring among females, more than 50% of spontaneous new mutations at the mtDNA will be lost after one generation (Avise 2000). These results therefore also go along with recent studies showing a switch from a high, short-term mutation rate to the low, long-term substitution rate (Ho *et al.* 2005). This means that even though the mutation rate per generation is tenfold higher than the one calculated based on phylogenies, implementing it in a model shows that due to rapid drift most of the generated

variation is lost and observed substition levels fall within those estimated from phylogenies (Zhivotovsky *et al.* 2006).

### 4.5.4 Problems of traditional measures of genetic diversity

Both estimates of *pi* and *Fst* show a significant influence of vLRS within social groups and group extinction rates respectively. However, neither of them allow for an easy comparison between species and studies, since there is no direct way to correct for differening group sizes. Group size, vLRS and mutation rate interact to create the diversity within groups, and the new approaches, the mismatch approach for *pi* and the clonal-approach for *Fst* are exactly extensions to account for these additional factors. In addition, *pi* is affected by both low rates of mutational changes which are not stepwise but lead to larger changes (e.g. insertions / deletions of several basepairs), and in philopatric species by low rates of migration. In both cases highly divergent genotypes would be introduced, which would change the average pairwise difference. However a low frequency of divergent genotypes would not change Qzero, the frequency of comparison among identical haplotypes, as strongly, since this is not affected by how divergent genotypes are. *Fst*, which analyzes the distribution of variation within and among groups, has large stochastic variation in case of low numbers of migrants (see also Whitlock & McCauley 1999) and in addition cannot be corrected for low variation within groups due to high vLRS.

### 4.5.5 Robustness of the estimators

As in other studies, the simulations here only serve to show the influence of single factors on a pattern in a population (Grimm & Railsback 2005). For this, they have to be simplified. Therefore results could be biased by the specific way life-history variables have been implemented. However, if this leads to an effect, this could already indicate limitations when applying the approaches to data from natural populations, where our knowledge about many of these parameters is often also strongly limited. Optimally, approaches should therefore be robust to deviations within certain parameters (Grimm *et al.* 2005).

Discrete generations should not have a large effect on approaches analyzing genetic variation present within a sample, since most approaches anyway assume that the detected variation is due to effects accumulated over several generations (see also Hill 1979). Overlapping generations are however a difficulty in defining samples for

the approaches which look at the variation change between generations. The sampling across two generations needed to allow strong inferences with these new approaches would allow for a more direct assessment of variance in lifetime reproductive success by directly determining parent-offspring relationships.

Many of the methods rely on comparing the number of individuals that would be needed to generate the observed genetic variation under a random distribution of offspring among them ("effective population size") to the actual number of individuals potentially siring. The latter however is in many cases difficult to know. Especially for situations in which the sex of interest disperses in the species, often detailed knowledge about the dispersal process (e.g. distance, with relatives etc.) is missing. However the results already indicate that by just using sample size as estimator qualitative comparisons between these species are possible and additional, more detailed simulations should help to clarify this aspect.

The specific way group extinction and recolonization was implemented in the model also influenced results. By allowing a single individual from one of the neighboring groups to enter and sire the maximum number of offspring in the following generation to fill up the group introduces artificially large variances in reproductive success. However, in most species group splits by fissions (Melnick 1987), so this is like a group size increase and therefore does not influence the variance calculated within groups. Combining the within and among group component of variation therefore also proved difficult. Not just the variance but also the actual total number of the lifetime reproductive success has an influence in cases where some individuals can exploit new areas.

However, I detected that for philopatric species there are two approaches which seem robust to many of the assumptions used during the simulations and which also produce consistent results when applied to genetic data from natural populations. For individuals of the philopatric sex, these allow on the one hand to estimate the variance in lifetime reproductive success among individuals within groups, and the rate of group extinctions and splits.

### 4.5.6 Group extinction rates in natural populations

The process of the loss of whole mtDNA lineages has been described in different female philopatric species (Avise *et al.* 1984, Hoelzer *et al.* 1998, Kelly 2001). The values calculated here, with a range of 0.5% to 18% (average 4.1%) fall

within the observed range of previously published rates based on demographic studies, which indicate that between 0.4% to 24% of lineages are lost per generation (average 8.8%, n = 16; Gompper *et al.* 1997). These rates indicate a large degree of change in populations, but since they also include matrilines of recent origin, which are still small and therefore prone to extinction, the numbers seem reasonable.

### 4.5.7 Genetic variation in social groups

Recently a large comparative study presented evidence that variation at the mtDNA in mammals cannot be explained by simple random processes. The unexpected low mitochondrial diversity distribution and the fact that it was not correlated with the actual population size of the species, was explained by recurrent adaptive evolution (Bazin *et al.* 2006). My model here also argues that large fitness differences among females will decrease the variability at the mtDNA, however selection does not have to act per se on the mtDNA loci. MtDNA variation is rather carried along with differences in reproductive success which might be both due to fitness differences, but also due to the social structure of the species. There have been some earlier indications that social structure influences mismatch distribution of mtDNA in human populations. Different pattern were detected for hunter-gatherer than for agricultural populations (Excoffier 2004). Similarly, in a recent study applying the tree imbalance method (Blum *et al.* 2006). In both cases the authors suggested cultural differences among the populations as explanation for the different mtDNA variation. Cultural effects on genetic variation have also been proposed for the frequency of certain alleles in small populations (Austerlitz & Heyer 1998). This process of 'cultural hitchiking' (Heyer *et al.* 2005) was also invoked for patterns of low mitochondrial DNA diversity among matrilineal whale species (Whitehead 1998). The results of my study indicate that for these pattern of variation at the mtDNA not necessarily cultural patterns have to be invoked. In socially organized species drift effects can be enhanced within potentially small groups and significantly influence genetic variation if there are large fitness differences between females. As indicated in the dataset analyzed, there seem to be species were large variance in lifetime reproductive success (vLRS) among females might exist. It would therefore be interesting to apply these new approaches to quantify the degree of vLRS across species to detect whether indeed social or ecological conditions, instead of culture, are driving this.

**Table 4.1** Comparison of the different approaches to analyze the variance of lifetime reproductive success. P-values indicate the correlation between the input parameter of vLRS either within or between social groups and the calculated value of the respective approaches. In some cases there was only a significant correlation when correcting for the respective listed factors.

| name | level of analysis | dispersal regime | approach | logic | simulation results |
|---|---|---|---|---|---|
| **i) mismatch based** | within group | philopatry | calculate genetic distance between every pair of individuals within a group | effective number of breeders is compared to group size | **$p < 0.001$ single factor** |
| **ii) clonal-model** | between groups | philopatry | calculate diversity within and divergence between groups | within-group variation is used to assess between group divergence | **$p = 0.025$ single factor** |
| **iii) variation change** | within group | dispersal | compare allele frequencies among adult females in a group to those of the adult males in the same group | philopatric males in a group reflect the variance among their mothers | *$p < 0.001$* with group size |
| **iv) two generation** | population wide | both | compare allele frequencies in total samples from two following generations | allele frequencies drift every generation | *$p < 0.001$* with group size and mutation rate |
| **v) imbalance of tree** | population wide | both | calculate whether after a split in a phylogenetic tree one lineage has more tips | more successful lineages leave more offspring | not directly applicable |
| **vi) tree-splitting** | between groups | philopatry | calculate branching rate in the phylogenetic tree based on mutation rate | with no dispersal, genetic relations between groups reflect group splits | not directly applicable |

**Table 4.2 Input parameters for the simulations**. Each of the 168 combinations was run 10 times for X generations. Group sizes are the number of individuals in each of the 81 groups. If no dispersal occurs, individuals stay in the group they are born, otherwise they move randomly out of the group to one of 12 neighboring groups. The variance of reproductive success within groups is the mean across several groups

| group size | dispersal | variance of reproductive success within groups | group extinction probability per generation |
|---|---|---|---|
| 4 | no dispersal | 0.5 | 0 |
| 8 | low dispersal - 5% of individuals move to new group | 0.8 | 0.1 |
| 16 | dispersal - all individuals move to neighboring groups, up to three groups away | 1 | 0.5 |
| | | 1.2 | 1 |
| | | 1.5 | 5 |

**Table 4.3** Variance in lifetime reproductive success among females in different primate species calculated using the mismatch approach. In species, which have been described as having egalitarian relationships among the females the values are below one, in species with dominance hierarchies among the females the values are larger than one. Number of individuals refers to either the group size, or if sampling just occurred within a locality, the total sample size.

| **Species** | **Calculated vLRS** | | |
|---|---|---|---|
| | Social System | | Number of Individuals |
| Callithrix jacchus | *RE* | **0.16** | 9 |
| Macaca sylvanus | *RE* | **0.67** | 35 |
| Hapalemur griseus | *RN* | **1.28** | 42 |
| Alouatta seniculus | *RN* | **1.35** | 26 |
| Macaca fuscata | *RN* | **1.40** | 6 |
| Microcebus murinus | *RN* | **1.44** | 88 |
| Cercophitecus aethiops | *RN* | **1.57** | 23 |
| Papio anubis | *RN* | **1.66** | 40 |

**Figure 4.1** Simulation results for the mismatch approach: On average, the mismatch approach produces values close to the input distributions. Graphs also show the 75% (box) and 95% distributions. There are large variances, which are both due to the fact that the simulated variance in lifetime reproductive success is not fixed, but a distribution, plus noise in the estimations.

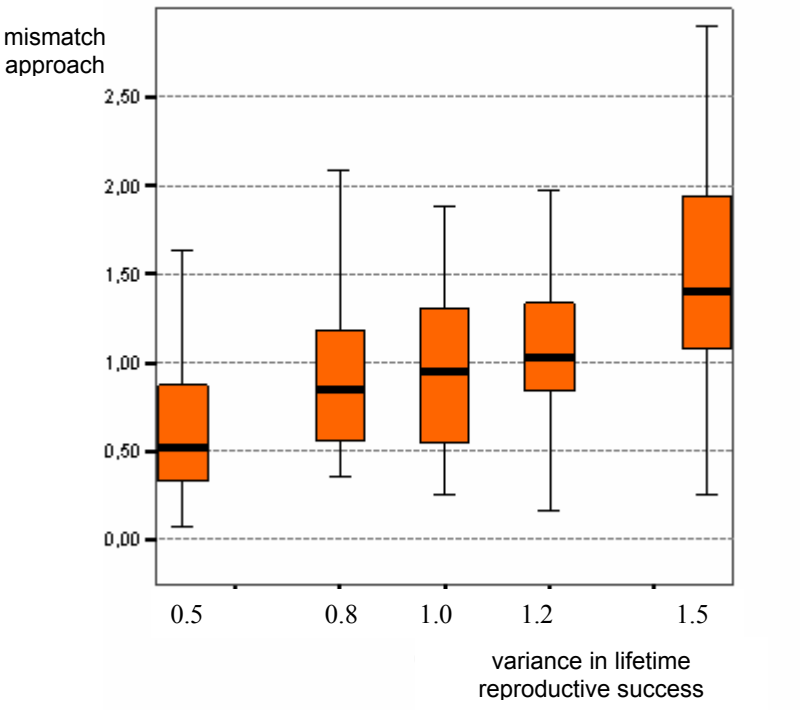


**Figure 4.2** Simulation results for the clonal approach. With increasing probability of group extinction the measured rate of group lineage fissions increases. Results are pooled for the three different group sizes, but displayed separately for the different mutation rates. The values do not start at zero since simulations started with all groups being

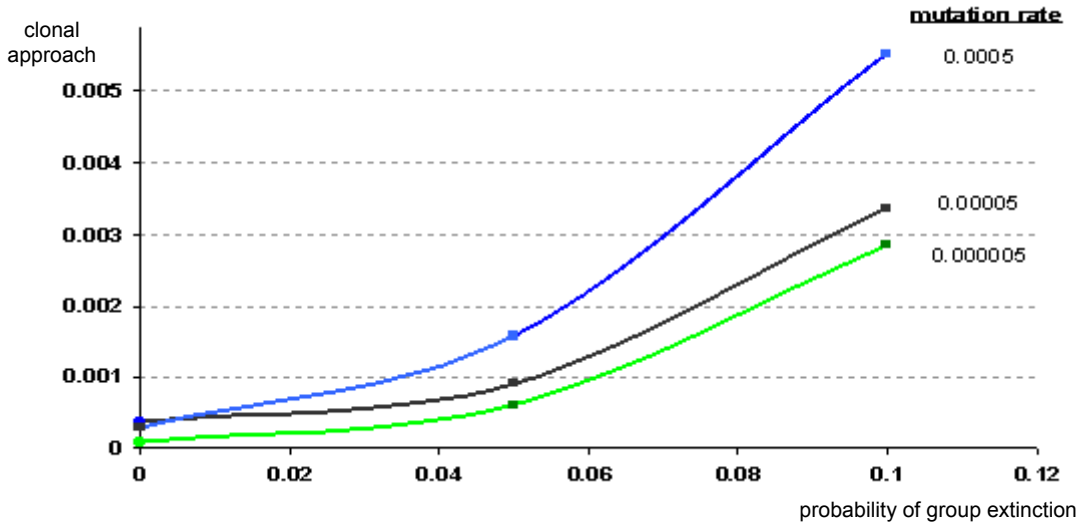


**Figure 4.3** Mismatch distributions of mtDNA of from females of a range of primate species. They are grouped by the social category they have been assigned due to behavioural studies, with DE species in which females disperse, RE species in which philopatric females are tolerant to each other, and RN species in which philopatric females compete. The latter show the highest number of comparison among identical haplotypes, whereas the DE species show a flat distribution indicating comparisons among haplotypes of a range of divergences.

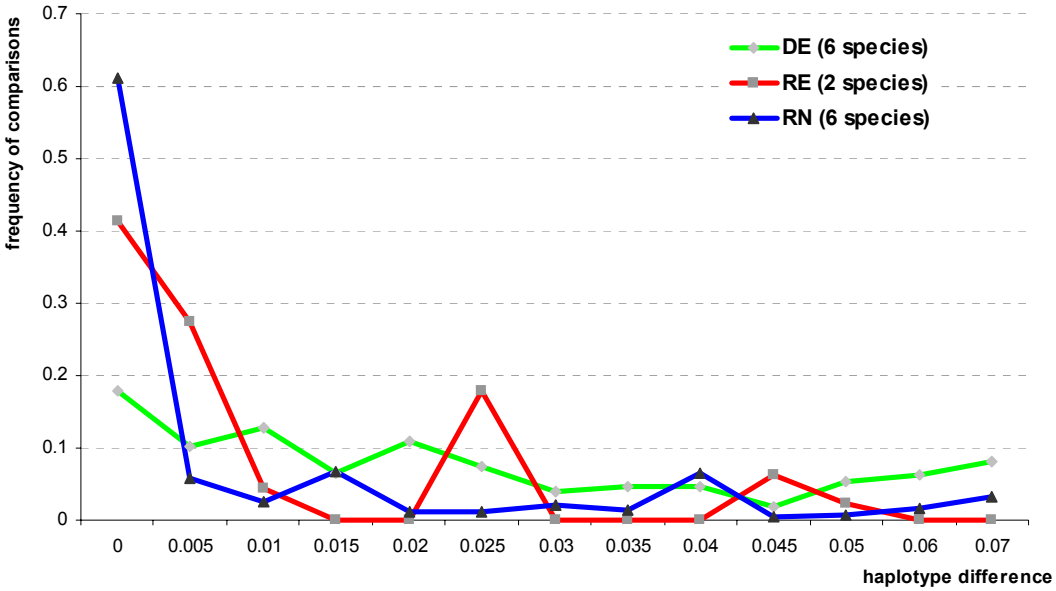


**Figure 4.4 a)** Mismatch distributions for the philopatric sex in studies with sampling across localities. The distributions are bimodal, with a first peak at zero, and a second at intermediate differences. mtDNA (red) - African Hadza and Matrilocal Thailand Hill tribes; Y-chromosome (blue) - Europeans and Patrilocal Thailand Hill tribes.

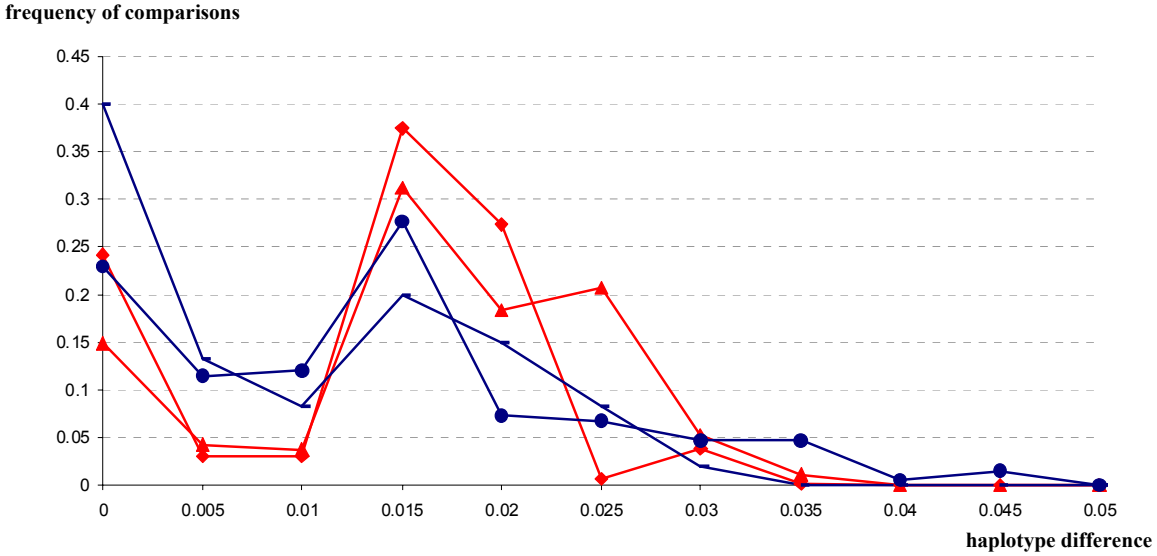



**Figure 4.4 b)** Mismatch distribution for the dispersing sex in studies with sampling across localities. The distributions are flat, with comparisons among haplotypes of various difference. mtDNA (red) - Europeans and Patrilocal Thailand Hill tribes; Y-chromosome - African Hadza and Matrilocal Thailand Hill tribes.

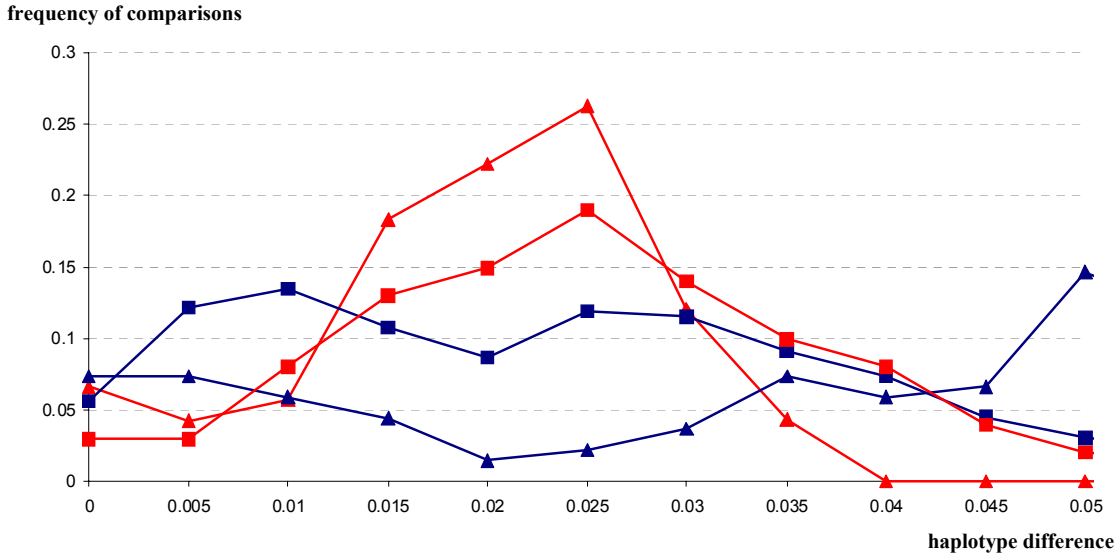


**Figure 4.5 a)** Mismatch distributions for the philopatric sex in studies with sampling within single localities. The distributions are unimodal, with a peak at zero or low divergence. mtDNA (red) - Greenland Inuit; Y-chromosome (blue) - Bonobos, Chimpanzees and New Guinean.

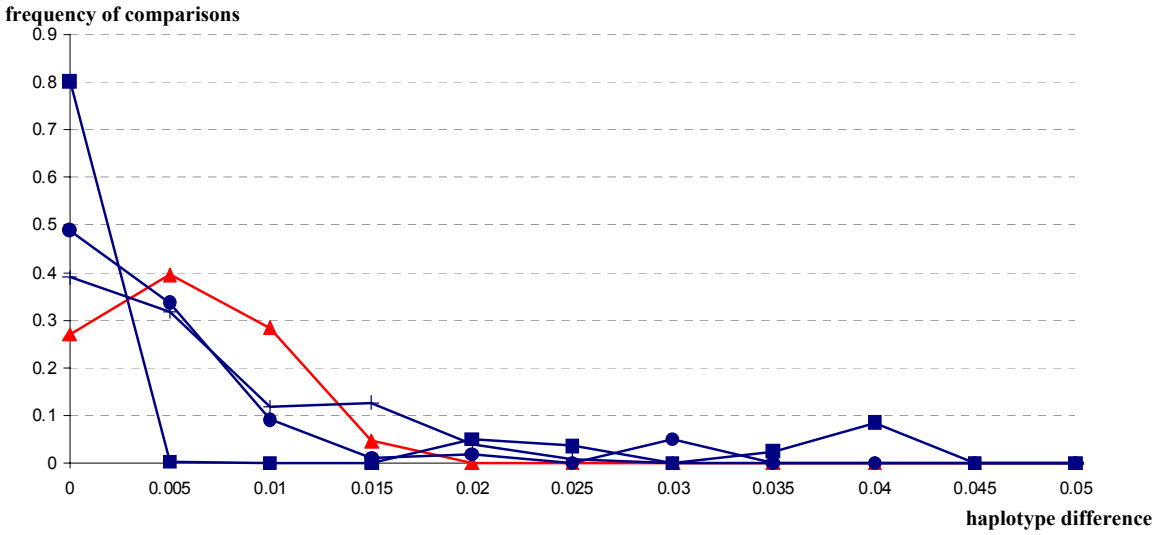
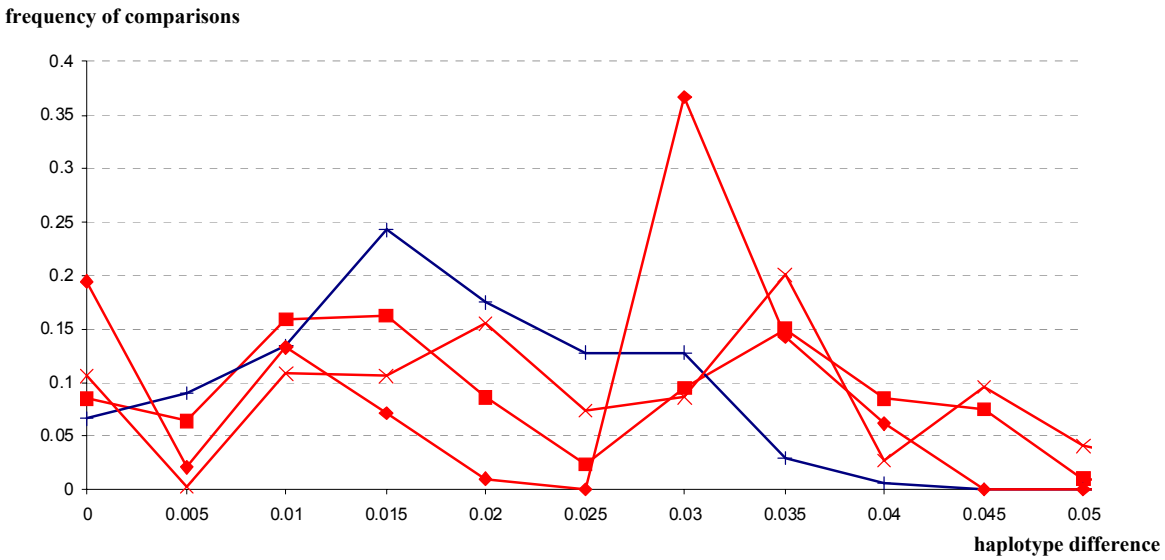



**Figure 4.5 b)** Mismatch distribution for the dispersing sex in studies with sampling within single localities. The distributions show comparisons among haplotypes with a range of divergences. mtDNA (red) - Bonobos, Chimpanzees and New Guinean; Y-chromosome (blue) - Greenland Inuit.



**Appendix 4.1** Values used in the broad comparative analyses. The 'mismatch approach' and 'lineage loss' are based on the formulas developed here. The demography classification relate to the population history of the respective species (1 = population size decline, 2 = stable population size, 3 = population size expansion). The values of the mismatch distribution are the percentage of comparisons among haplotypes with a divergence betwewen the respective categories (e.g. between 0.5% and 1% divergence).

| | mismatch approach | lineage loss | demography | actual mismatch distribution | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 0 | 0.005 | 0.01 | 0.015 | 0.02 | 0.025 | 0.03 | 0.035 | 0.04 | 0.045 | 0.05 | 0.06 | 0.07 | 1 |
| **Alouatta seniculus** | 1.35 | 0.045 | 1 | 0.67 | 0.05 | 0.10 | 0.05 | 0.00 | 0.00 | 0.10 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Cephalorhynchus hectori** | 0.59 | | | 0.44 | 0.24 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Cercophitecus aethiops** | 1.57 | | 2 | 0.72 | 0.15 | 0.00 | 0.04 | 0.04 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Clethrionomys gapperi** | 0.70 | | | 0.33 | 0.43 | 0.16 | 0.07 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Cricetus cricetus** | 0.87 | | | 0.64 | 0.16 | 0.15 | 0.04 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Crocidura russula** | 0.76 | | 1 | 0.53 | 0.14 | 0.07 | 0.25 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Ctenomys rionegrensis** | 0.78 | | | 0.61 | 0.39 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Cuon alpinus** | 1.20 | | 1 | 0.73 | 0.09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.09 | 0.09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Delphinapterus leucas** | 1.70 | | | 0.47 | 0.18 | 0.27 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Elephas maximus** | 0.99 | | 1 | 0.73 | 0.27 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Eubalaena australis** | 0.37 | | | 0.28 | 0.00 | 0.03 | 0.20 | 0.03 | 0.00 | 0.01 | 0.15 | 0.14 | 0.14 | 0.00 | 0.02 | 0.00 | 0.00 |
| **Eulemur fulvus rufus** | 0.42 | | | 0.42 | 0.36 | 0.00 | 0.21 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Hapalemur griseus** | 1.28 | | | 0.32 | 0.05 | 0.27 | 0.07 | 0.05 | 0.22 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Hippotragus niger** | 0.16 | | | 0.27 | 0.07 | 0.05 | 0.04 | 0.09 | 0.18 | 0.00 | 0.00 | 0.00 | 0.06 | 0.00 | 0.00 | 0.09 | 0.15 |
| **Hyperoodon ampullatus** | 0.42 | | | 0.41 | 0.59 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Lagenorhynchus obscurus** | 0.32 | | | 0.13 | 0.43 | 0.29 | 0.13 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Loxodonta africana** | 0.88 | 0.066 | 2 | 0.41 | 0.19 | 0.05 | 0.00 | 0.00 | 0.10 | 0.01 | 0.01 | 0.00 | 0.11 | 0.11 | 0.01 | 0.00 | 0.00 |
| **Lycaon pictus** | 1.75 | | 2 | 0.54 | 0.00 | 0.10 | 0.00 | 0.02 | 0.00 | 0.00 | 0.19 | 0.00 | 0.00 | 0.00 | 0.05 | 0.02 | 0.07 |
| **Lynx canadensis** | 0.60 | | 3 | 0.21 | 0.60 | 0.19 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Macaca fuscata** | 1.40 | | | 0.84 | 0.10 | 0.03 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Macaca sylvanus** | 0.67 | | | 0.43 | 0.31 | 0.09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.13 | 0.05 | 0.00 | 0.00 | 0.00 |
| **Megaptera novaeangliae** | 0.59 | | | 0.47 | 0.10 | 0.18 | 0.00 | 0.00 | 0.00 | 0.23 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Microcebus murinus** | 1.44 | 0.070 | | 0.24 | 0.03 | 0.00 | 0.02 | 0.01 | 0.00 | 0.03 | 0.04 | 0.04 | 0.03 | 0.01 | 0.09 | 0.19 | 0.26 |
| **Microtus oeconomus** | 0.68 | 0.006 | | 0.32 | 0.55 | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

| | mismatch approach | lineage loss | demography | actual mismatch distribution | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 0 | 0.005 | 0.01 | 0.015 | 0.02 | 0.025 | 0.03 | 0.035 | 0.04 | 0.045 | 0.05 | 0.06 | 0.07 | 1 |
| **Myotis myotis** | 0.65 | | 2 | 0.55 | 0.21 | 0.06 | 0.01 | 0.00 | 0.00 | 0.05 | 0.04 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Neotoma micropus** | 0.95 | 0.008 | | 0.22 | 0.38 | 0.35 | 0.04 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Nyctalus azoreum** | 0.22 | | 3 | 0.36 | 0.39 | 0.06 | 0.17 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Orcinus orca** | 0.67 | | | 0.47 | 0.07 | 0.19 | 0.27 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Ovis ammon** | 0.28 | 0.021 | | 0.29 | 0.39 | 0.22 | 0.00 | 0.00 | 0.08 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Ovis canadiensis** | 0.59 | 0.070 | | 0.49 | 0.06 | 0.00 | 0.00 | 0.26 | 0.19 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Panthera pardus** | 0.57 | | 2 | 0.60 | 0.24 | 0.16 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Papio anubis** | 1.66 | | | 0.61 | 0.09 | 0.02 | 0.27 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Peromyscus furvus** | 0.64 | 0.008 | | 0.49 | 0.36 | 0.11 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Phoca vitulina** | 0.75 | | 1 | 0.56 | 0.13 | 0.24 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Physeter macrocephalus** | 0.42 | | 3 | 0.33 | 0.33 | 0.31 | 0.02 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Rangifer tarandus** | 0.10 | 0.016 | | 0.28 | 0.05 | 0.05 | 0.05 | 0.11 | 0.04 | 0.05 | 0.12 | 0.06 | 0.10 | 0.05 | 0.04 | 0.00 | 0.00 |
| **Sciurus vulgaris** | 0.69 | | | 0.46 | 0.03 | 0.04 | 0.10 | 0.23 | 0.06 | 0.07 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Sorex ornatus** | 1.38 | 0.040 | 3 | 0.74 | 0.09 | 0.13 | 0.02 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Trichechus inunguis** | 0.06 | | 3 | 0.14 | 0.24 | 0.41 | 0.15 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 |
| **Ursus americanus** | 0.79 | | 3 | 0.52 | 0.22 | 0.10 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.08 | 0.01 | 0.00 | 0.00 |
| **Ursus arctos** | 1.69 | | 3 | 0.70 | 0.10 | 0.09 | 0.10 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Ursus thibetanus** | 2.15 | 0.050 | 3 | 0.54 | 0.34 | 0.10 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Varecia variegata** | 1.36 | | | 0.85 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Vulpes vulpes** | 0.10 | | 3 | 0.33 | 0.24 | 0.14 | 0.21 | 0.00 | 0.07 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Xerus inauris** | 1.22 | 0.012 | | 0.55 | 0.25 | 0.08 | 0.11 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Zapus hudsonius preblei** | 0.69 | | | 0.66 | 0.09 | 0.26 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| **Ziphius cavirostris** | 0.15 | | | 0.28 | 0.31 | 0.14 | 0.17 | 0.05 | 0.04 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

**References for mtDNA data (from top to bottom)**: Pope 2000; Pichler *et al.* 1998; Shimada 2000; Runck & Cook 2005; Neumann *et al.* 2004; Ehinger *et al.* 2002; Wlasiuk *et al.* 2003; Iyengar *et al.* 2005; O'Corry-Crowe *et al.* 1997; Vidya *et al.* 2005; Baker *et al.* 1999;Wyner *et al.* 2002; Nievergelt *et al.* 2002; Pitra *et al.* 2002; Dalebout *et al.* 2001; Cassens *et al.* 2005; Nyakaana & Arctander 1999; Girman *et al.* 2001; Rueness *et al.* 2003; Marmi *et al.* 2003; Modolo *et al.* 2006; Baker *et al.* 1998; Fredsted *et al.* 2004; Galbreath & Cook 2004; Castella *et al.* 2001; Mendez-Harclerode *et al.* 2005; Salguiero *et al.* 2004; Hoelzel *et al.* 1998; Tserenbataa *et al.* 2004; Boyce *et al.* 1999; Uphyrkina *et al.* 2001; Hapke *et al.* 2001; Harris *et al.* 2000; Stanley *et al.* 1996; Lyrholm & Gyllensten 1998; Gravlund *et al.* 1998; Barratt *et al.* 1999; Maldonado *et al.* 2001; Cantanhede *et al.* 2005; Wooding & Ward 1997; Waits *et al.* 1998; Ishibashi & Saitoh 2004; Louis *et al.* 2005; Frati *et al.* 1998; Herron *et al.* 2005; Ramey *et al.* 2005; Dalebout *et al.* 2005

# 5. Correlations of variance in lifetime reproductive success among females

## 5.1 Summary

The fact that individuals differ in the number of offspring they sire is one of the fundamental stages in Darwin's theory of natural selection. Individuals who are better adapted to specific situations are predicted to leave more offspring than others. It has however been difficult to directly assess this variation in lifetime reproductive success for animals, since it needs the detailed study of many individuals over their whole reproductive career. Here, I apply the previously derived two approaches to detect variance in lifetime reproductive success (vLRS) to published data on mitochondrial DNA from different mammalian species. The obtained values are used in a comparative analyses to detect whether specific ecological, morphological or social situations, which have been predicted to be correlated with higher competition among females, are also correlated with larger vLRS. In fact, species in which females exhibit a dominance hierarchy within social groups, in which allonursing occurs and where females can potentially sire a larger number of offspring all show higher values of vLRS among females within social groups, respectively. Species in which territorial behaviour has been recorded on the other hand show larger vLRS between social groups. However, no correlations with simple classifications of ecological categories or of competition over males were detected. These correlations indicate that females indeed seem to compete over resources, and that there are sometimes considerable differences among individuals in the number of offspring they sire allowign for future detailed studies into the mechanisms driving this competition.

## 5.2 Introduction

### 5.2.1 Social structure of animals

Identifying the selective pressures which have shaped the variety observed in the social structure and behaviour of different animal species has been the target of a large number of studies. These mainly approach the topic by identifying potentially causal ecological, life-history and social factors. However, to ultimately show that a behavioural trait is adaptive and selected for one would need to show that the variation in the trait is linked to a variation in fecundity of the individuals, which than leads to an increase of the alleles these individuals carry. Especially the last part is difficult to address in natural populations, first because most behavioural traits are quantitative (Boake 1994), several number of genes interact to create the respective phenotype, and second because it needs the study of a large number of individuals over their entire lifetime (Coulson *et al.* 2006). It has remained somewhat unclear therefore to what degree different behaviours reflect adaptation versus drift (Hemelrijk 2000), and especially whether populations show certain traits due to phylogenetic inheritance or whether the relevant selective pressures are still acting (di Fiore & Rendall 1994). Showing that there are differences among individuals in how many genes they propagate to the next generation, and analyzing whether there are specific situations which lead to larger differences could inform about this.

### 5.2.2 Intrasexual competition among females

In the previous chapter I showed that the distribution of mammalian mitochondrial DNA variation contains information about the degree of variance in lifetime reproductive success (vLRS) of females by showing whether females sire similar or skewed numbers of offspring. These methods rely on the fact that mtDNA is only transmitted through females. While there is no direct link between the mtDNA variant a female carries and her fitness, some variants will increase in frequency in the population if they are carried by highly successful females. These previous results therefore seem to indicate to what degree females within a population differ in their reproductive success. In this study I correlate the genetic measure of vLRS with ecological and social factors which have previously been linked to female competition and adaptation. Both food and mates are seen as potentially limiting factors of female reproduction, potentially leading to competition if they are restricted in availability. This competition can be separated between what occurs among females within groups and between groups of females and different ecological correlates have been proposed

for intra and intergroup competition. If some females are more successful than others in this competition and therefore can sire more offspring, the vLRS among these females increases. In the following analyses I concentrate on mammalian species in which females are philopatric, using a broad definition which includes both species in which females stay in the groups into which they have been born (social philopatry), but also those species in which females stay in the natal area (geographic philopatry) (sensu Waser & Jones 1983). Species in which females disperse are excluded because there have been studies showing that there are fundamental differences in these species, in that female dispersal likely is driven by inbreeding avoidance (Clutton-Brock 1989) and is influenced by male strategies and their life-histories (e.g. longevity).

### 5.2.3 Objectives of this study

To assess whether there are specific ecological conditions which are correlated with higher variance in lifetime reproductive success among females, comparative analyses with a range of factors as explanatory variables are performed. If there are indeed situations in which females are experiencing selective pressures, it is expected that some females are better adapted to these and therefore sire more offspring than others. In addition to direct correlational analyses, methods which correct for phylogeny are also applied. This is because the traits analyzed here could be shared through common descent which therefore would lead to nonindependence of data points in comparative analyses. Although the behaviours underlying these new measures of vLRS are probably highly flexible and not necessarily heritable or evolving traits in mammals, they may be associated with other traits (included as variables or not) that are shared through common descent.
I make the following predictions for the factors affecting vLRS (see also table 5.1):

a) Higher variance in lifetime reproductive success (vLRS) both within and between social groups is expected in species which have a larger maximum potential lifetime reproductive success.

This is driven by the life-history of females, mainly by the number of litters per year, the number of offspring per litter and the reproductive lifespan (Kruuk *et al.* 1999). If as a result of the combination of these factors some females have the potential to sire a large number of offspring during their lifetime, there potentially can also be larger differences among females. I therefore predict a positive correlation between a higher lifetime reproductive potential and vLRS both within and between social groups.

b) Higher vLRS both within and between social groups is expected in species with more defendable food.

For this two broad classification schemes were applied to sort species. The first one just uses different dietary categories to compare among primate species. For these, it has been posed that species with higher frugivory should exhibit higher competition, since fruit trees can represent a rare, clumped and defensible resource as compared to leaves (see discussion in Snaith & Chapman 2007). I therefore test wether frugivore species have a higher vLRS within social groups than folivores. The second scheme classifies species as either having territorial behaviour or not. Actively defending a home range against intruders most likely has evolved to defend access to sparse resources (Mitani *et al.* 1979). In this case however several females could join to cooperatively defend this resource, and I therefore predict a higher vLRS between social groups in species which show territorial defense.

c) Higher vLRS within social groups is expected in species with more competition over mates.

Oestrous overlap, both due to the fact that females breed seasonally and synchronicity during the cycle, is expected to be related to female competition (Nunn *et al.* 2001). If males are limited either by the number of females they can monopolize or because of sperm depletion, dominant females might try to gain exlcusive access to these preferred males by showing estrous simultaneously with subordinate females. Since the actual degree of synchrony is however influenced by a number of different variables like seasonality in breeding, length of oestrus etc., with only limited information for most species, a simple approximation is used. The more females live in group the higher the chance that there is more than one female in estrous at a time, and with shorter interbirth intervals the number of estrous of each of these females increases (Nunn *et al.* 2001). Therefore, the number of females in group divided by the length of the interbirth interval is predicted to be positively correlated to the vLRS within social groups.

d) Higher vLRS is expected in species with a higher degree of aggressive interactions.

Three proxies are used for this. Previous results have shown that increases in canine size of female primates are correlated with broad categorizations of female agonistic interactions. I therefore predict a positive correlation between canine size corrected to for body size and vLRS both within and between social groups. In addition, species in which there is competition over resources are expected to develop a dominance hierarchy to avoid repeated

costly interactions. Therefore vLRS within soial groups should be higher in species which have a dominance hierarchy among females than those who do not. Lastly, I predict that competition is more costly for arboreal than for terrestrial species, leading to a higher vLRS both within and between social groups for the latter.

e) Higher vLRS between social groups is expected in species which show alloparental care
It has been shown before that alloparental care shortens the interbirth interval and allows for larger litters (Mitani & Watts 1997). This behaviour has also been linked to unstable environments, in which helpers are necessary to guarantee offspring survival in bad seasons. Given this environmental influence and possible differences in the number of helpers per group, I expect some social groups to perform better than others. I therefore predict a positive correlation between communal care and vLRS between groups. As for the within group level, allonursing both has been described as equally distributed cooperative behaviour and as theft by dominant females' offspring from subordinate females. The correlation in this case is therefore performed as a two-sided test, in case of a positive correlation between allonursing and vLRS within social groups indicating theft, in case of a negative correlation indicating cooperative care.

## 5.3 Materials and Methods

### 5.3.1 Data on variance in lifetime reproductive success

Suitable studies for the comparative analysis were defined as those which had sampled mtDNA sequence variation of at least 6 individuals within a social group or from within a small range (locality as specified by the authors). In addition, I excluded studies where authors had stated that related individuals had specifically been avoided during sampling.

The NCBI/Genbank database was searched for relevant studies using the keyword "mitoch" within every family of mammals. Published sequences were cross-linked to the respective publication and checked for their suitability. The sequences were then downloaded in the FASTA-format, manually aligned using BioEdit v5 (Hall 1999) and imported to MEGA v2.1 (Kumar *et al.* 2001) to calculate pairwise sequence differences as simple proportion of differing sites. The resulting matrix was imported to EXCEL and in case where haplotypes instead of individual sequences have been deposited at Genbank, the haplotype frequencies were added from the respective articles.

For the first method ("mismatch based"), which aims at inferring vLRS within social units, the absolute numbers of occurrences of the sequences in any of the population studied were used to calculate $Q_0$ , the frequency of comparisons between identical haplotypes. These distributions were first calculated for every population of a study, and than averaged across species within the study for one single entry. However, if more than one part of the mitochondrion was studied, independent entries were created. I did not combine information for one species if it stemmed from different publications. Based on this, the vLRS within groups was calculated as

$$vLRS_{within} = \frac{0.026 \times N \times Q_0}{1 - Q_0} \qquad (5.1)$$

with $Q_0$ being the frequency of comparisons between identical haplotypes and $N$ the number of competing individuals. In cases of known social structure, the number of competing individuals was set as the group size (either as reported in the respective articles from which I obtained the genetic data or as averages reported for the respective species). In cases where females stay in their natal area but are not organized into stable groups, the sample size was plotted as the number of competitors (see Chapter 4).

For the second method ("clonal model"), which aims at inferring vLRS between social units by calculating the rate of group extinction and fission, the allele frequencies in the total sample are calculated and than applied to calculated the vLRS between groups as

$$vLRS_{between} = \frac{\left(1 - \sum {p_i}^2\right) \times g + 2 \times 0.013 \times \left(1 - \sum {p_i}^2\right) \times g \times N - g - 2 \times 0.013 \times g \times N}{2 \times N - 2 \times \left(1 - \sum {p_i}^2\right) \times N - \frac{\left(1 - \sum {p_i}^2\right)}{0.013}} \qquad (5.2)$$

where $p_i$ is the frequency of the *i-th* allele in the total sample, $g$ is the number of groups, and $N$ is the mean group size.

### 5.3.2 Data on the predictor variables

For all species the following data to test my predictions (see appendix 5.1 for details and references) was collected from published studies. Most of the entries stem from previous collections in comparative analyses, however occasionally also values were entered from primary literature to increase the sample size (given that the collection of species for which I could obtain genetic data did not always overlap).

Diet was classified into different categories, primates as either folivorous, frugivorous or omnivorous. Reports from behavioural data were used to classify species into those defending its home range versus those who do not. The maximum lifespan reproductive potential was calculated by multiplying the number of offspring per litter, the number of litters per year and the length of the reproductive career (as difference between age at first birth and maximum recorded age). For estrous overlap I used a simple measure of the number of available females, calculated by dividing the group size by the interbirth interval. For canine sizes, residuals calculated from a log-log transformed regression of canine size versus body size were taken (Plavcan & van Schaik 1992). Habitat use was entered by classifying species as either arboreal or terrestrial. For allonursing, I took the categories of Packer *et al.* (1992). Given the repeatedly detected effect of body mass on some of these predictor variables, I also checked the correlation of body mass with vLRS within and between social groups.

All continuous variables were log-transformed for standardization. Classifications were treated as continuous variables, since in all cases the prediction allow for a linear ranking among them and therefore can be treated as continuous variables.

### 5.3.3 Correlation analyses

All correlational analyses were first performed applying the method of independent contrasts (Felsenstein 1985) to control for possible independence of data due to shared common ancestry among species. As underlying phylogeny the recently published mammalian supertree (Bininda-Emonds *et al.* 2007) was used. While the tree contains multiple branching events, these are treated as real polytomies, rather than unresolved nodes, and no degree of freedom subtracted in the following statistical analyses (Purvis & Garland 1993) For the calculation of the contrasts the reported branch lengths were used, but also Grafen's method (1989) of transforming branches as a function of the number of species below each node was applied, plus setting all branches to a length equal one. Contrasts were generated and plotted in bivariate regressions in the PDAP:PDTREE package (Midford *et al.* 2003) of the MESQUITE v2.0 computer program (Maddison & Maddison 2007). I also performed standard correlation analyses with using species data points as entries using Spearman's rank correlation in SPSS version 11 (SPSS, Inc., Chicago IL).

All but one of the predictions are directional, and therefore one-sided p-values are considered significant if below 0.05. Correction for multiple testing was applied within the

different predictions, by applying a strict Bonferroni-correction to change the p-value for predictions b) and e) to 0.025 and for prediction d) to 0.016.

## 5.4 Results

### 5.4.1 Variance in lifetime reproductive success in different species

I obtained suitable genetic data for a total of 39 mammalian species to calculate the vLRS among females within social groups. The calculated values range from 0.32 to 2.15 (average 0.96). Since a value of 1 indicates a random distribution of offspring among the individuals there are thus species in which the distribution of offspring is skewed among the females and species in which females are more equal than expected by chance. The vLRS between social groups could only be calculated for 29 of these, including 8 primate species, since some of the studies included only single groups. Values for vLRS between social groups ranged from 0.005 to 0.190, which would translate into up to 20% of groups/matrilines becoming extinct per generation.

### 5.4.2 Phylogenetic signal and correlation analyses

In all cases, statistical tests which do not take phylogeny into account provided a less good fit than those based on independent contrasts. In the tests correcting for phylogeny, transformation of the branch lengths did not produce different results to those which used the actual distances as given by the original mammalian phylogeny. In addition, when checking the absolute value of the contrasts against the sum of the branch lengths to detect whether these values now are in fact independent of phylogeny, the actual tree provided better correction. However, there still is a significant correlation, indicating that the vLRS within and between social groups in fact has a phylogenetic signal and that the change along the tree does not follow a simple stepwise model (at any given time step there is a certain probability that it changes by one unit). The contrast values themselves are negatively correlated with the distance among the species, meaning the longer the distance between two species, the smaller actually the divergence among them. This was true for both the values of the vLRS within social groups and the values of the maximum reproductive potential. Both variables can apparently change within very short time frames, given that most of the larger switches are among the terminal branches of the tree (figure 5.1). This indicates that changes do not follow a simple model with the amount of change dependent on the length of the branch, and makes

reconstruction of values at older nodes more uncertain. As apparently in both cases here, assuming the stepwise model in this case lead to reconstructed values tending towards the average value. If reconstructed nodes immediately below the tips however are all close to the average value, character evolution seemingly slows down along the longer, more basal branches. This is exactly what is observed with this data, with a negative correlation between absolute contrast and the estimated node height for these characters. Since the stronger changes among the terminal branches are in fact relevant and biologically more informative, this would argue for using the contrasts based on the untransformed values. However concentrating only on these terminal tip pairs leads to drastically reduced sample sizes (e.g. in the example in figure 5.1 there are only 8 comparisons including only tips) and therefore a large reduction in statistical power (see also Garland *et al.* 2005). Nevertheless, even if the perfect correction cannot be applied, correcting for phylogeny always increased the power, meaning that caution only has to be applied in interpreting the cases where no correlation is detected. Therefore I present the results of the correlations of the independent contrasts based on the original phylogenetic tree based on both the log-transformed values and on the contrasts of the original values. In addition the results of the standard correlations are indicated when significant. The calculated values for vLRS within groups do not correlate with the values for vLRS between groups in either analysis, the two approaches are therefore treated as independent.

### 5.4.3 Results for the different predictions

*a) vLRS and maximum potential lifetime reproductive output*

The correlation of vLRS within social groups and the possible maximum number of offspring shows a positive trend in the independent contrast analysis using for both the log-transformed values ($R^2 = 0.10$, $p = 0.060$, $N = 25$). It is significant when plotting the actual values in the independent contrast (figure 5.1; $R^2 = 0.27$, $p = 0.003$, $N = 25$), but not in the standard correlation. Correlations with the vLRS between social groups are not possible due to a too low sample size.

*b) vLRS and food defense*

There is no relation between diet in primates and vLRS within social groups in either analyses (independent contrasts of log-transformed values: $R^2 < 0.01$, $p = 0.46$, $N = 7$; of

actual values $R^2 < 0.01$, $p = 0.48$, $N = 7$). There is a positive relation between whether species show territory defense and vLRS, but again the log-transformed based independent contrast test does not reach significance ($R^2 = 0.21$, $p = 0.034$, $N = 16$). With the actual values, the correlation of the independent contrast is significant though ($R^2 = 0.35$, $p = 0.006$, $N = 16$), while the classical correlation is not.

*c) vLRS and competition over mates*

There is no significant correlation between vLRS within social groups and the number of females divided by the interbirth interval (independent contrasts of log-transformed values: $R^2 = 0.22$, $p = 0.10$, $N = 8$; of actual values $R^2 = 0.25$, $p = 0.17$, $N = 8$).

*d) vLRS and aggressive interactions*

For the primate species, there is no correlation between vLRS within social groups and either canine size (independent contrasts of log-transformed values: $R^2 = 0.03$, $p = 0.37$, $N = 6$; of actual values $R^2 = 0.01$, $p = 0.42$, $N = 6$) or arboreality vs. terrestriality (independent contrasts of log-transformed values: $R^2 < 0.01$, $p = 0.47$, $N = 7$; of actual values $R^2 = 0.04$, $p = 0.31$, $N = 7$). Across mammals, there is a significant correlation between vLRS within social groups and whether species have a dominance hierarchy (figure 5.2; independent contrasts of log-transformed values: $R^2 = 0.59$, $p < 0.001$, $N = 21$; of actual values $R^2 = 0.49$, $p < 0.001$, $N = 21$).

*e) vLRS and allonursing*

There is a positive, non-significant relationship between vLRS within social groups and allonursing (independent contrasts of log-transformed values: $R^2 = 0.50$, $p = 0.07$, $N = 6$; of actual values $p = 0.042$; Spearman correlation of actual values $p = 0.029$), potentially indicating that with more allonursing there is higher skew among females within groups. Again, correlations with vLRS between social groups could not be performed because of a too low sample size.

## 5.5 Discussion

### 5.5.1 Summary of the results

Differences between mammalian species in the variance in lifetime reproductive success among females are detected from the analyses of variation at mtDNA genetic markers. These differences are correlated with situations which have been predicted to be linked to higher or lower competition among females.

There is a larger vLRS among females who live together within social groups firstly if there is a clear dominance hierarchy among them. It has been predicted that high ranking individuals gain from their investment in aggressive interactions and these results clearly support this hypothesis. Second, females within groups differ more if they potentially can sire a larger number of offspring over their whole lifetime. Thirdly, there is a trend for females to have larger differences in offspring number in species which have allonursing. Given the positive relationship, this indicates that some females and/or their offspring profit more than others. This could indicate that there might be a number of species in this dataset which have milk-theft, rather than cooperative offspring care (Packer *et al.* 1992).

Higher vLRS between social groups of females is observed in species which show territorial defense behaviour. If resources are limited and it therefore pays to actively defend these, some groups of individuals might gain better access to these resources. Therefore the females in these groups could sire more offspring.

Together, the results of this study more support the importance of competition over food than that over mates, as expected from Bateman's theory (1948). Detecting the specific ecological conditions leading to higher vLRS among females however remains difficult.

### 5.5.2 Comparative analyses to detect functional explanations

While in general finding a correlation does not reveal causation, performing correlations among two or more traits across related species leads to additional problems in interpreting the relationship, as shown again in this study. For one, taking evolutionary distances among species and therefore the actual potential for evolutionary difference into account provides more power. This is the case for all the associations detected in this study. In turn, ignoring the non-independence of data points of related species could mean that the posed functional relationship between changes in two characters which both show a phylogenetic signal might be caused by shared inheritance, or, especially in cases where just one of the variables is independent of phylogeny, the correlation might have been caused by

an additional factors which has not been taken into account. For some of the characters used here I could not provide a perfect model of the evolution of the character along the tree and it remains therefore challenging to detect the actual ecological meaning behind the character (Freckleton 2000).

An additional problem is that for continuous characters a single value is entered per species. By calculating species averages, relevant and potentially informative data is neglected. Ideally, future studies should use matching data for each population studied and enter these as individual data points by using a phylogenetic tree that allows linking populations within species. In this study I simply calculated the mean of the vLRS within social groups if genetic information had been published from more than one population. In particular, this means that in many cases the genetic data has not been collected in the same population as the data on the other characters. Therefore, if there is variability within a species a measurement error is introduced. In correlations involving low samples sizes this can potentially lead to spurious results (Hormon & Losos 2005, Lindenfors & Tullberg 2006). To see whether this potentially could have affected the results, I repeated the analyses using this time the existence or absence of dominance hierarchy as dependent variable. As this is a discrete variable, measurement error is lower and it should therefore be a more stable signal across populations for a species. These tests revealed two different significant correlations. Dominance hierarchies occur more frequently in species which show higher female synchronicity ($R^2 = 0.56$, $p = 0.04$, $N = 6$) and which live longer ($R^2 = 0.28$, $p = 0.02$, $N = 17$). While again the first result is based on a very small sample, the latter result could be explained by the necessity of a long lifespan and repeated interactions to make the establishment of dominance hierarchy pay off. However, since there is no correlation between the presence of dominance hierarchies and the maximum reproductive potential (which is linked to longevity though), it seems to indicate that these different characters are in fact independent. These results therefore would support that by increasing the number of species in the analysis the effect of measurement error can be mitigated.

### 5.5.3 Defining the level of competition

The current analysis aimed at inferring the variance in lifetime reproductive success among females in species where females remain in their natal area. They show natal philopatry, which in many cases has been interpreted as having offspring in the same group in which they have been born. However, in this study this concept of living in the same group was not applied. Here also species are included, in which females might spend most of their

time solitary (following Waser & Jones 1983). Nevertheless, since all daughters remain in the same area, and close kin therefore resides together, this can lead to a "hidden" matrilineal structure (Kappeler *et al.* 2002). A social structure like this, with an organization into matrilines, seems to be shown by a range of species (e.g. bushbuck Wronski & Apio 2006; raccoons Gehrt & Fritzell 1998; squirrels Shriner & Stacey 1991; woodrats Moses & Millar 1994). For instance the Coquerel's dwarf lemur (*Mirza coquereli*), a solitary primate, for whom the term "hidden" was introduced, shows this female kin structure of related individuals occupying homeranges next to each other (Kappeler *et al.* 2002). In a sister species (*Microcebus murinus*) closely related females also aggregate in stable sleeping groups, potentially gaining benefits through heat-sharing (Wimmer *et al.* 2002). In female bears, which also forage solitary, daughters heavily overlap in their home range use with their mothers (Stoen *et al.* 2005) and might inherit the home range. There seem to be therefore also varying degrees to which this kinship structure influences social behaviour and therefore potentially also direct and cooperative competition among females. Grouping in these cases is therefore somewhat arbitrary, e.g. in case the territorial defense is by a single female deciding how many territories should be combined. While the 'mismatch approach' in principle allows detecting monophyletic clusters of females, all individuals which share one exclusive recent common ancestor, this will often be unknown during sampling. As an alternative, the variance in lifetime reproductive success could therefore be measured across a whole population. This would also allow a comparison with species which show female dispersal. While there might be confounding factors which lead to females dispersing (Clutton-Brock 1989), the degree of competition among females once they have settled could still vary in the same way as in species in which females remain in their natal range. However, these results also show that there seem to be different forces leading to local competition within social groups versus competition among groups of females. The two measures in themselves are not correlated, and show predictable correlation with different factors. Furthermore, analyzing the variance among females in more detail could provide insights into the degree of selection. The variance as measured with these methods does not allow differentiating the actual distribution of offspring among individuals. Given that different distributions can lead to similar variance values (Kokko *et al.* 1999), analyzing this at a more detailed level could provide insights into whether a large variance is caused for instance by one individual several offspring and the remaining being equal in the number of offspring, or by one group of individuals siring a few offspring and another group siring none. Therefore, a

full understanding of the selective pressures which might influence the fitness of female mammals should take the social structure into account.

### 5.5.4 Life-history traits and competition among females

Given that basic life-history traits can be easily assessed and quantitatively scored, allowing for direct comparison among species, there have been a range of studies seeking to understand the reason for the differences observable across species (e.g. Stearns 1983, Read & Harvey 1989, Geffen *et al.* 1996). In a recent, broad comparison across mammalian species two such axes were proposed to explain most of the variation among species (Bielby *et al.* 2007). The first is linked to reproductive timing, how quick offspring are produced, while the second is linked to reproductive output, how much is invested in single offspring. Based on their results, the authors concluded that individuals of a species can vary independently along those two axes of reproductive timing, for which the authors suggested interbirth interval as a proxy, and reproductive output, for which neonatal body mass could be used as proxy. For this dataset however these two factors are not correlated to the measure of vLRS. In addition, these two are also not correlated with the maximum reproductive output. This therefore indicates that there is not just one way females who are better competitors achieve a higher reproductive success. In support of this, both of the measures of vLRS are not correlated with body size, another factor which has been found to be heavily linked to life-history strategies.

These results also do not necessarily imply that higher maximum reproductive potential in itself has been selected for in these species because of increased competition. It could be that variance as calculated here is simply linked to the range of the number of offspring. Since in all species there is a natural limit at zero offspring, only species in which females can potentially sire a larger number of offspring can actually show large variance in lifetime reproductive success.

### 5.5.5 Ecology and competition among females

For females it has been suggested that the most important factor which limits reproduction is the access to resources, particularly food (Emlen & Oring 1977). Comparing ecological and specifically dietary categories across species however is difficult, e.g. a carnivore will always eat more meat than a primate. In addition, even for comparisons among related species, there have been serious doubts about simply classifying diet into types (e.g. percent herbivore vs. omnivore), without assessing the actual distribution and quality of the resource consumed by the particular species (König 2002, Harris 2006). Additionally, even if

diet is not classified, but quantified, phylogenetic comparative analyses always enter one value per species. It is therefore not surprising that no correlation was detected. However, the proxies used for competition indicate that females do compete over resources. Future studies therefore ideally would plot genetic data with detailed information on the spatial and temporal distribution of food and its nutritional qualities from the same population.

### 5.5.6 Fitness differences and evolution

These analyses indicate that there are mammalian species in which large fitness differences among females exist, but they currently do not allow to assess whether this is linked to directional selection on genetic, heritable traits. Alternatively, if high rank can be obtained by females of a certain condition, daughters of high-ranking females might have a higher chance of acquiring a dominant position themselves. Since however occasionally daughters of low-ranking females might rise in rank, a different mtDNA haplotype might be propagated to higher frequency the coming generation. Even though there would be large selection on females, this selection is not directly linked to a gene controlling a specific phenotype. In contrast to most other models of selection, there could therefore be a situation in which selection does not lead to fixation. Genetic variation would be maintained in a population if the selection is linked to non-heritable variation in fecundity. In turn, if the ecological situation leading to these fecundity differences does not change, there will always be these fitness differences among females. In the case of directional selection however the adapted phenotype would spread through the population and thereby decreasing the fitness differences among individuals. The social system of a species therefore could influence the rate of evolution in this species.

### 5.5.7 Causes of intrasexual selection

Previous studies on variance in reproductive success have concentrated on males, following the seminal papers by Bateman (1948) and Trivers (1972), which argued that males have a higher potential rate of reproduction since they invest less in offspring. However, the results of the current study indicate that, while in fact in some species females seem to be very similar in their reproductive success (even more equal than chance), in some species females might intensively compete and differ in the number of offspring they sire. This is in line with recent findings in studies which counted the number of offspring directly (e.g. Hodges *et al.* 2008). In this study however only correlations among proxies for competition were detected and it remains challenging to detect what the underlying causes for the competition among

females are (Clutton-Brock 2007). The results of my study however show that the investment into potential costly aggressive behaviours, both within groups and between groups, has a payoff for some of the females. Comparative studies could therefore also be based on this more easily available information. In addition however, the approach based on genetic variation presented here also can be directly applied to males. With the advance in sequencing technology the first data on variation of genetic markers on the y-chromosome in natural populations is becoming available (Eriksson *et al.* 2005, Handley *et al.* 2006, Langergraber *et al.* 2007b). Similarly as for the females, it will be interesting to see first what actually the degree in variance in lifetime reproductive success among males is. Most studies thus far have concentrated on reproductive skew, which only provides the distribution of offspring among individuals within a short timeframe, and it remains open for most species to what degree the sometimes observed extreme skew also can be found when analyzing the whole reproductive career. As for females, many questions remain open about intrasexual selection among males, and the approaches presented here allow a new framework to address these.

**Table 5.1** Correlation among vLRS and ecological, morphological and social factors

| **prediction** | **specific response** | **level of competition** | | **supports hypothesis** | | **tested in** | | **result** |
|---|---|---|---|---|---|---|---|---|
| | *vLRS increases with* | *within groups* | *between groups* | *competition for mates* | *competition for food* | *mammals* | *primates* | |
| food defensability | folivores < frugivores | x | | | x | | x | n. s. |
| | folivores < frugivores | | x | | x | | x | too low sample size |
| | territorial > non-territorial | | x | | x | x | | **p = 0.006** |
| potential maximum reproduction | higher number of potential offspring over reproductive lifespan | x | | x | x | x | | **p = 0.003** |
| mating competition | higher estrous overlap | x | | x | | x | | n. s. |
| aggressive interactions | larger canine size | x | | x | x | | x | n. s. |
| | terrestrial > arboreal | x | | x | x | | x | n. s. |
| | formalized dominance hierarchies | x | | x | x | x | | **p < 0.001** |
| alloparental care | non-parents care for offspring | | x | | x | x | | p = 0.042 |
| | mothers do not care for offspring other than own | x | | | x | x | | too low sample size |

**Figure 5.1** A mirrored tree depicting on the left the actual values for the measured vLRS within social groups and on the right the maximum reproductive potential of females. Both variables change within very short time frames, most of the larger switches are among the terminal branches of the tree. This makes reconstruction of values at older nodes more uncertain, and, as apparently in both cases here, will lead to reconstructed values tending towards the average value. This could explain the negative correlation between the calculated contrasts of the values and the branch length.

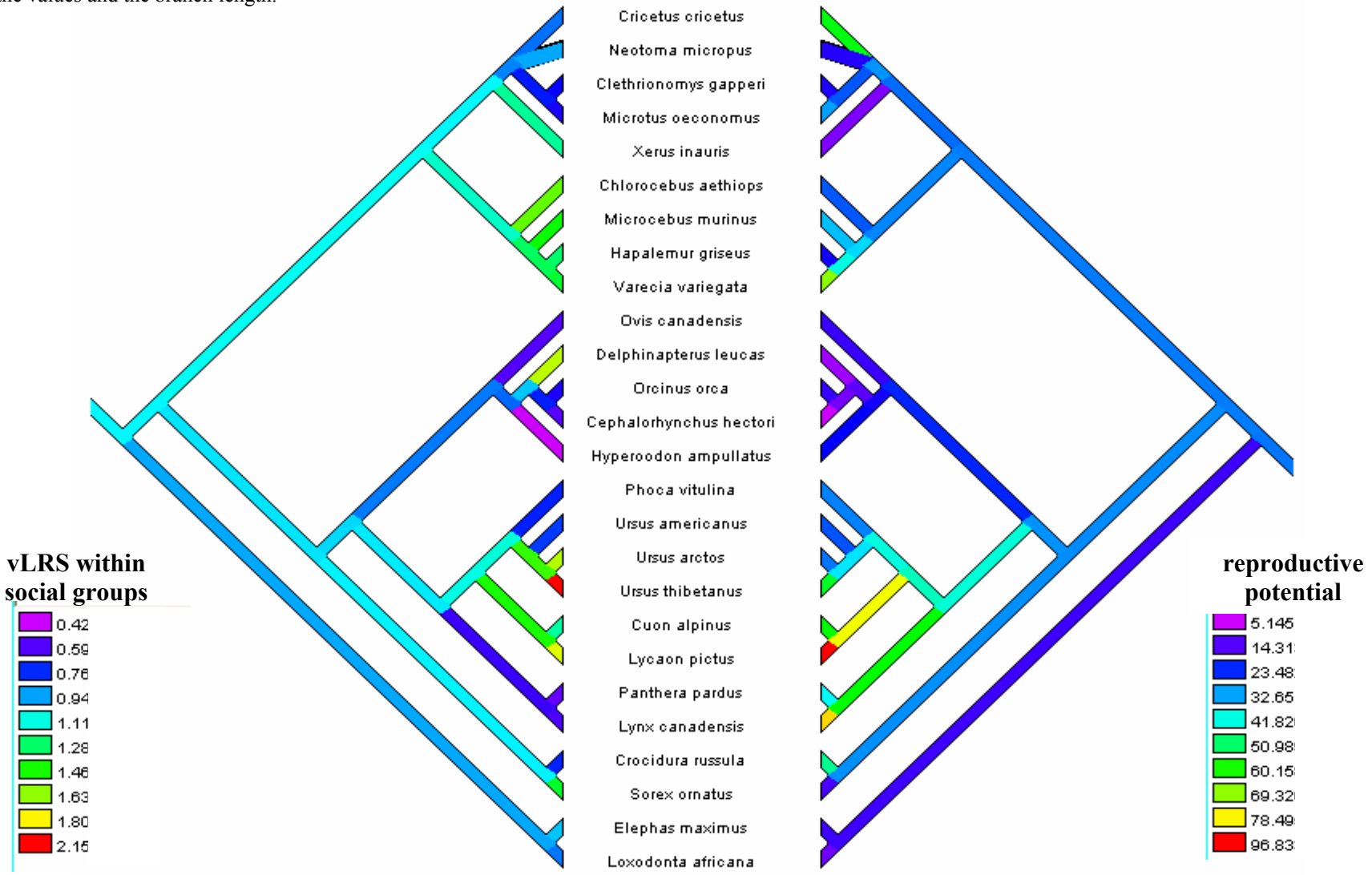
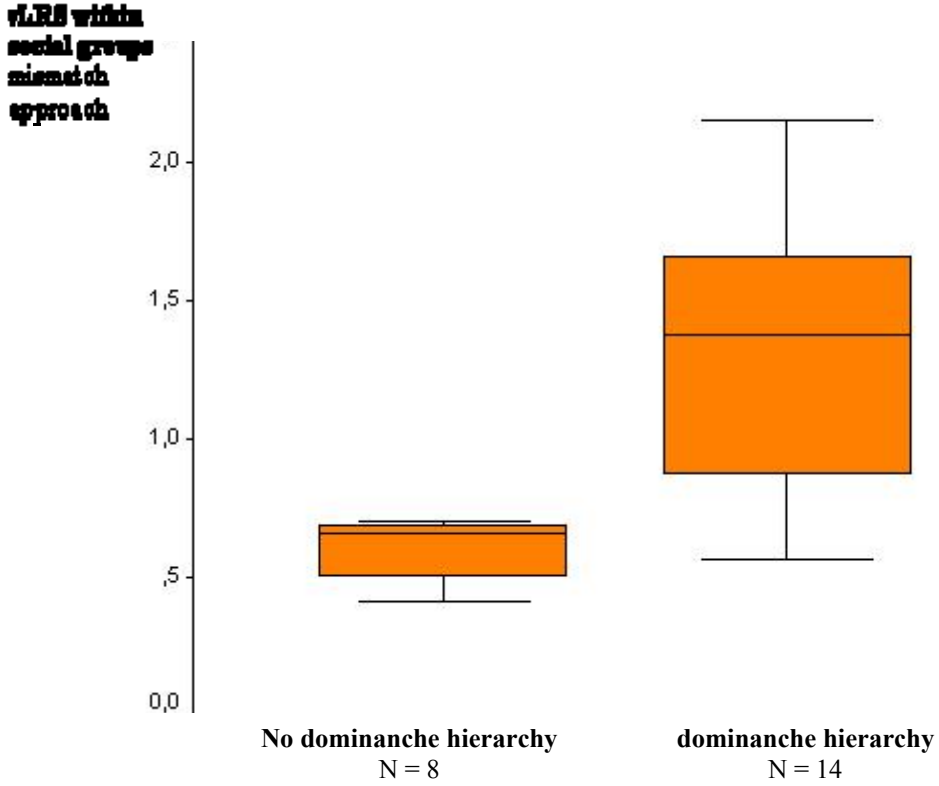


**Figure 5.2** Variance in lifetime reproductive success among females within social groups in species without and with dominance hierarchies. Boxes represent 75% intervals, and bars 95% intervals.



**Appendix 5.1** Species used in the analyses with the values for the variance in lifetime reproductive success (vLRS) calculated within and between species, based on the new approaches. In two cases the list of species analyzed here did not completely overlap with the list of species in the mammalian phylogeny (Bininda-Emonds et al. 2007), in which a closely related species was used in the phylogeny. There is also one case where the genus has been named differently. The species code is an identifier for appendix 5.2. References for the mtDNA data are given in appendix 4.1

| Species | in phylogeny | species code | vLRS within | log | vLRS between | log |
|---|---|---|---|---|---|---|
| **Alouatta seniculus** | Alouatta_seniculus | 1 | **1.35** | 0.13 | **4.50** | 0.65 |
| **Cephalorhynchus hectori** | Cephalorhynchus_hectori | 2 | **0.59** | -0.23 | | |
| **Cercophitecus aethiops** | Chlorocebus_aethiops | 3 | **1.57** | 0.20 | | |
| **Clethrionomys gapperi** | Clethrionomys_gapperi | 4 | **0.70** | -0.15 | | |
| **Cricetus cricetus** | Cricetus_cricetus | 5 | **0.87** | -0.06 | | |
| **Crocidura russula** | Crocidura_russula | 6 | **0.76** | -0.12 | | |
| **Ctenomys rionegrensis** | Ctenomys_minutus | 7 | **0.78** | -0.11 | **2.00** | 0.30 |
| **Cuon alpinus** | Cuon_alpinus | 8 | **1.20** | 0.08 | | |
| **Delphinapterus leucas** | Delphinapterus_leucas | 9 | **1.70** | 0.23 | | |
| **Elephas maximus** | Elephas_maximus | 10 | **0.99** | 0.00 | | |
| **Eubalaena australis** | Eubalaena_australis | 11 | **0.37** | -0.43 | | |
| **Eulemur fulvus** | Eulemur_fulvus | 12 | **0.42** | -0.38 | | |
| **Hapalemur griseus** | Hapalemur_griseus | 13 | **1.28** | 0.11 | | |
| **Hippotragus niger** | Hippotragus_niger | 14 | | | **18.00** | 1.26 |
| **Hyperoodon ampullatus** | Hyperoodon_ampullatus | 15 | **0.42** | -0.37 | | |
| **Lagenorhynchus obscurus** | Lagenorhynchus_obscurus | 16 | **0.32** | -0.49 | | |
| **Loxodonta africana** | Loxodonta_africana | 17 | **0.88** | -0.06 | **6.60** | 0.82 |
| **Lycaon pictus** | Lycaon_pictus | 18 | **1.75** | 0.24 | | |
| **Lynx canadensis** | Lynx_canadensis | 19 | **0.60** | -0.22 | | |
| **Macaca fuscata** | Macaca_fuscata | 20 | **1.40** | 0.15 | **1.75** | 0.24 |

| Species | in phylogeny | species code | vLRS within | log | vLRS between | log |
|---|---|---|---|---|---|---|
| **Macaca sylvanus** | Macaca_sylvanus | 21 | **0.67** | -0.17 | | |
| **Microcebus murinus** | Microcebus_murinus | 23 | **1.44** | 0.16 | **7.00** | 0.85 |
| **Microtus oeconomus** | Microtus_oeconomus | 24 | **0.68** | -0.17 | **0.55** | -0.26 |
| **Myotis myotis** | Myotis_myotis | 25 | **0.65** | -0.19 | | |
| **Neotoma micropus** | Neotoma_micropus | 26 | **0.95** | -0.02 | **0.75** | -0.12 |
| **Orcinus orca** | Orcinus_orca | 28 | **0.67** | -0.17 | | |
| **Ovis ammon** | Ovis_ammon | 29 | | | **2.10** | 0.32 |
| **Ovis canadiensis** | Ovis_canadensis | 30 | **0.59** | -0.23 | **7.00** | 0.85 |
| **Panthera pardus** | Panthera_pardus | 31 | **0.57** | -0.25 | | |
| **Papio anubis** | Papio_hamadryas | 32 | **1.66** | 0.22 | | |
| **Peromyscus furvus** | Peromyscus_furvus | 33 | **0.64** | -0.19 | **0.80** | -0.10 |
| **Phoca vitulina** | Phoca_vitulina | 34 | **0.75** | -0.12 | | |
| **Physeter macrocephalus** | Physeter_catodon | 35 | **0.42** | -0.38 | | |
| **Sciurus vulgaris** | Sciurus_vulgaris | 37 | **0.69** | -0.16 | **3.30** | 0.52 |
| **Sorex ornatus** | Sorex_ornatus | 38 | **1.38** | 0.14 | **4.00** | 0.60 |
| **Ursus americanus** | Ursus_americanus | 40 | **0.79** | -0.10 | | |
| **Ursus arctos** | Ursus_arctos | 41 | **1.69** | 0.23 | | |
| **Ursus thibetanus** | Ursus_thibetanus | 42 | **2.15** | 0.33 | **5.00** | 0.70 |
| **Varecia variegata** | Varecia_variegata | 43 | **1.36** | 0.13 | | |
| **Xerus inauris** | Xerus_inauris | 45 | **1.22** | 0.09 | **1.20** | 0.08 |
| **Zapus hudsonius** | Zapus_hudsonius | 46 | **0.69** | -0.16 | | |
| **Ziphius cavirostris** | Ziphius_cavirostris | 47 | | | **0.46** | -0.34 |

**Appendix 5.2** Species values for the correlations with the vLRS. The species code is depicted in appendix 5.1. Explanations of the variables: ln(mass): natural logarithm of the body mass in kg; AFR(mo): age at first reproduction for females in months; max. life (mo): maximum recorded lifespan in months; litter size: number of offspring per birth; litters/year: number of litters which can be sired by a female during one year; max reproduction: the potential maximum number of offspring a female can sire, calculated as the maximum lifespan minus the age at first reproduction times the litter size times the number of litters per year; dominance: females of this species are reported to have (1) or not have (0) a dominance hierarchy; canine size: residuals of the female canine size from a regression with body mass; num fem: number of females in a group; IBI: interbirth interval in days; synchron: degree of female estrous overlap, calculated as the number of females per group divided by the length of the IBI; arboreality: species recorded to be mainly arboreal (0) or terrestrial (1); diet: species recorded to be mainly folivore (0) or frugivore (1); nursing: milk received from non-offspring nursing is 0% (0), less than 10% (1), less than 50% (2), or more than 50% (3); defense: species does not show territorial defense behaviour (0) or does (1).

| species | ln (mass) | *AFR(mo)* | *max. life(mo)* | *litter size* | *litters/year* | max reproduction | dominance | canine size | *num fem* | *IBI* | synchron | arboreality | diet | nursing | defense |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 8.81 | *54.96* | *?* | *1.20* | *0.80* | ? | 1 | -0.32 | *2.2* | *461.16* | 0.0048 | 0 | 0 | 0 | 0 |
| 2 | ? | *93.00* | *240* | *1.00* | *0.42* | 5.15 | ? | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 3 | 8.98 | *47.37* | *372* | *1.00* | *1.00* | 27.05 | 1 | -0.01 | *7.7* | *377.5* | 0.0204 | 1 | 1 | 1 | ? |
| 4 | ? | *4.00* | *20* | *5.04* | *2.71* | 18.21 | 0 | ? | *?* | *17* | ? | ? | ? | ? | ? |
| 5 | ? | *3.34* | *48* | *7.73* | *2.00* | 57.54 | ? | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 6 | ? | *4.34* | *38* | *4.88* | *3.50* | 47.91 | ? | ? | *?* | *28.5* | ? | ? | ? | ? | ? |
| 7 | ? | *?* | *?* | *?* | *?* | ? | ? | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 8 | ? | *11.50* | *186* | *4.13* | *1.00* | 58.65 | ? | ? | *?* | *365* | ? | ? | ? | ? | ? |
| 9 | ? | *56.21* | *360* | *1.02* | *0.33* | 8.52 | ? | ? | *?* | *1004* | ? | ? | ? | ? | ? |
| 10 | ? | *126.53* | *960* | *1.00* | *0.23* | 15.97 | 1 | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 11 | ? | *108.00* | | *1.00* | | ? | ? | ? | *?* | *?* | ? | ? | ? | 0 | ? |
| 12 | 7.65 | *?* | *?* | *1.10* | *0.80* | ? | ? | 0.13 | *3.5* | *456* | 0.0077 | 0 | 1 | ? | ? |
| 13 | 6.80 | *28.93* | *204* | *1.20* | *1.09* | 19.08 | 1 | -0.25 | *1* | *335* | 0.0030 | ? | ? | ? | ? |
| 14 | ? | *24.51* | *267* | *1.00* | *1.00* | 20.21 | 1 | ? | *?* | *365* | ? | ? | ? | 0 | 1 |
| 15 | ? | *117.38* | *444* | *1.00* | *0.75* | 20.41 | 0 | ? | *?* | *?* | ? | ? | ? | ? | ? |

| species | ln (mass) | *AFR(mo)* | *max. life(mo)* | *litter size* | *litters/year* | max reproduction | dominance | canine size | *num fem* | *IBI* | synchron | arboreality | diet | nursing | defense |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 16 | ? | | | *1.00* | *0.42* | ? | ? | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 17 | ? | *147.51* | *840* | *1.02* | *0.21* | 12.36 | 1 | ? | *?* | *1825* | ? | ? | ? | 1 | 1 |
| 18 | ? | *25.25* | *204* | *6.99* | *0.93* | 96.83 | 1 | ? | *?* | *376.19* | ? | ? | ? | 3 | ? |
| 19 | ? | *17.60* | *321* | *3.19* | *1.00* | 80.65 | ? | ? | *?* | *365* | ? | ? | ? | ? | ? |
| 20 | 9.41 | *55.02* | | *1.33* | *0.50* | ? | 1 | -0.37 | *17.5* | *443.37* | 0.0395 | 1 | 1 | ? | 0 |
| 21 | 9.38 | *49.81* | | *1.50* | *0.55* | ? | 0 | ? | *7* | *802.5* | 0.0087 | 1 | 1 | ? | ? |
| 22 | ? | *64.28* | *924* | *1.01* | *0.50* | 36.18 | ? | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 23 | 3.85 | *12.90* | *186* | *2.41* | *1.00* | 34.76 | 1 | 0.06 | *1* | *312* | 0.0032 | 0 | 1 | ? | 0 |
| 24 | ? | *0.94* | *21* | *5.76* | *3.38* | 32.55 | 0 | ? | *?* | *23* | ? | ? | ? | ? | 1 |
| 25 | ? | *?* | *?* | *?* | *?* | ? | 0 | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 26 | ? | *4.48* | *40* | *2.51* | *2.40* | 17.83 | ? | ? | *?* | *?* | ? | ? | ? | ? | 0 |
| 27 | ? | | | *2.00* | | ? | 0 | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 28 | ? | *138.22* | *1080* | *1.00* | *0.21* | 16.48 | 1 | ? | *?* | *1825* | ? | ? | ? | ? | ? |
| 29 | ? | *11.67* | | *1.20* | *1.00* | ? | 0 | ? | *?* | *365* | ? | ? | ? | ? | 0 |
| 30 | ? | *30.00* | *192* | *1.20* | *1.00* | 16.20 | 0 | ? | *?* | *?* | ? | ? | ? | 0 | 0 |
| 31 | ? | *34.10* | *276* | *2.38* | *0.83* | 39.82 | 1 | ? | *?* | *588.94* | ? | ? | ? | ? | ? |
| 32 | 10.65 | *?* | *?* | *1.03* | *0.33* | ? | 1 | ? | *17.5* | *1122.5* | 0.0156 | 1 | 1 | ? | ? |
| 33 | ? | *?* | *?* | *?* | *?* | ? | ? | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 34 | ? | *46.51* | *408* | *1.00* | *1.00* | 30.12 | 1 | ? | *?* | *365* | ? | ? | ? | ? | ? |
| 35 | ? | *?* | *?* | *?* | *0.29* | ? | 0 | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 36 | ? | *23.93* | *242* | *1.20* | *0.91* | 19.84 | 1 | ? | *?* | *365* | ? | ? | ? | 1 | ? |
| 37 | ? | *9.52* | *144* | *5.10* | *2.22* | 126.88 | ? | ? | *?* | *91* | ? | ? | ? | ? | 1 |
| 38 | ? | *12.00* | *18* | *5.00* | *3.00* | 15.00 | ? | ? | *?* | *?* | ? | ? | ? | ? | 1 |
| 39 | ? | *36.00* | *150* | *1.00* | *1.00* | 10.00 | ? | ? | *?* | *?* | ? | ? | ? | 1 | ? |

| species | ln (mass) | *AFR(mo)* | *max. life(mo)* | *litter size* | *litters/year* | max reproduction | dominance | canine size | *num fem* | *IBI* | synchron | arboreality | diet | nursing | defense |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 40 | ? | *40.71* | *372* | *2.54* | *0.38* | 26.65 | ? | ? | *?* | *799.56* | ? | ? | ? | ? | ? |
| 41 | ? | *60.01* | *472* | *2.36* | *0.36* | 29.17 | 1 | ? | *?* | *913.75* | ? | ? | ? | ? | ? |
| 42 | ? | *31.33* | *432* | *1.67* | *1.00* | 55.76 | 1 | ? | *?* | *365* | ? | ? | ? | ? | 0 |
| 43 | 8.16 | *24.28* | *396* | *2.23* | *1.00* | 69.08 | ? | 0.22 | *3* | *365* | 0.0082 | 0 | 1 | 1.5 | ? |
| 44 | ? | *9.76* | *144* | *4.34* | *0.91* | 44.18 | ? | ? | *?* | *365* | ? | ? | ? | 3 | ? |
| 45 | ? | *11.32* | *72* | *2.18* | *1.00* | 11.02 | 0 | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 46 | ? | *?* | *?* | *?* | *?* | ? | ? | ? | *?* | *?* | ? | ? | ? | ? | ? |
| 47 | ? | *?* | *432* | *1.00* | | ? | ? | ? | *?* | *?* | ? | ? | ? | ? | ? |

**References for the species values in appendix 5.1**

*Values taken from comparative studies:*
ln mass (Isaac et al. 2005); AFR (mo), max. life (mo), litter size, litters/year (Ernest 2003); canine size (Plavcan et al. 1995); num fem (Nunn & Barton 2000); IBI (Bielby et al. 2007); arboreality, diet (Nunn & van Schaik 2001); nursing (Packer et al. 1992)

*Values taken from primary literature*
dominance:
Alouatta seniculus (Grant et al. 1992); Clethrionomys gapperi (Ostfeld 1985); Hippotragus niger (Grant et al. 1992); Loxodonta africana (Laursen & Bekoff 1978); Macaca fuscata (Grant et al. 1992); Microcebus murinus (Grant et al. 1992); Microtus oeconomus (Andreassen et al. 1998); Neotoma micropus (Hansteen et al. 1997); Ovis ammon (Shackleton & Shank 1984); Ovis canadiensis (Ruckstuhl 1998); Peromyscus furvus (Haigh 1987); Sciurus vulgaris (Wauters et al. 1995); Sorex ornatus (Owen & Hoffmann 1983); Ursus thibetanus (Izumiyama & Shiraishi 2004); Xerus inauris (O'Shea 1976); Ziphius cavirostris (McSweeney et al. 2007); Varecia variegata (Geissmann & Mutschler 2006); Rangifer tarandus (Stuart-Smith et al. 1997)

territory defense:
*primates (*Sterck et al. 2001); Alopex lagopus (Strand et al. 1999); Clethrionomys gapperi (Perrin 1981); Crocidura russula (Balloux et al. 1998); Cynopterus brachyotis (Burland & Worthington Wilmer 2001); Delphinapterus leucas (Ruckstuhl & Neuhaus 1999); Hippotragus niger (Thompson 1993); Lycaon pictus (Creel et al. 1997); Microtus oeconomus (Andreassen & Ims 1998); Myotis myotis (Twenter 1955); Nyctalus azoreum (Burland & Worthington Wilmer 2001); Orcinus orca (Conner et al. 1998); Ovis canadiensis (Boyce et al. 1999); Panthera pardus (Mizutani & Jewell 1998); Phoca vitulina (Sullivan 1982); Physeter macrocephalus (Richard et al. 1996); Rangifer tarandus (Holand et al 2004); Sciurus vulgaris (Lurz et al. 1997); Tursiops truncatus (Krützen 2002); Ursus americanus (Swenson et al. 1998); Ursus arctos (Stoen et al. 2005); Ursus thibetanus (Gende & Quinn 2004); Vulpes vulpes (Doncaster & MacDonald 1991); Xerus inauris (Waterman 2002); Zapus hudsonius preblei (Meany et al. 2003)

# 6. General Discussion

## 6.1 Summary of the findings

### 6.1.1 Social structure and genetic variation

Evolution can be described as the change of allele frequencies in the gene-pool of a population (Stearns & Hoekstra 2001). Understanding the processes that lead to this change will inform us about the selective pressures which shape the diversity of life. In this study, I have presented new approaches to analyze the distribution of genetic variation to infer information about the social structure of animals. I thereby concentrate on particular aspects of the social system, namely sex-bias in dispersal, group size and variance in lifetime reproductive success. Through the use of mathematical analytical models and individual-based simulation I aim at understanding how these influence the amount of genetic variation within social groups and its distribution within individuals. In cross-species analyses using published genetic data these models are tested and it is shown these new approaches in fact allow quantying these aspects of the social system. The so gained information is applied to test questions on the importance of inclusive fitness benefits for cooperation and on the correlations of variation in fitness among females.

### 6.1.2 Relatedness within social groups

In the first part I show that inclusive fitness benefits through cooperation among kin are limited to small family clusters and are unlikely to explain grouping of more than very few individuals. Given that most animals can only sire a limited number of surviving offspring, the number of siblings as potential cooperation partners will be low. Average relatedness will therefore drop quickly with increasing group size, since the chance increases that a random partner will be from a different family line. In addition, average relatedness within groups is influenced by which of the sexes is philopatric. In case males disperse, relatedness can be higher, because there are a higher number of additional relatedness links among mothers. While individuals therefore reside with kin and dyadic interactions still could be influenced by kin-relationships, in most species the majority of partners in the group are not closely related to each other, excluding indirect fitness benefits as explanation for these larger scale associations and cooperations.

### 6.1.3 Variance in lifetime reproductive success and variation at sex-specific genetic markers

In the second part, sex-specific effects on genetic variation are analysed in more detail by specifically focusing on the patterns of distribution of variation at sex-specific genetic markers. Different approaches are developed to infer variance in lifetime reproductive success within the sexes from these patterns. While most of the proposed new approaches show a fit to simulated data, two of them, which analyze these patterns within the philopatric sex, are particularly robust. When these are applied to published data, the results show that, in addition to demographic effects, the social pattern indeed influences the distribution of genetic variation. There are differences between the two sexes on the local scale linked to both which sex disperses, but also to the particular social structure.

### 6.1.4 Comparative study of variance in lifetime reproductive success among female mammals

In the last part, the new approaches are applied to a dataset of mitochondrial DNA of several mammalian species to infer vLRS for females. It is shown that considerable fitness differences among females exist in certain species, potentially as high as among males. Phylogenetic comparative analyses show that there are species specific patterns which coincide with high or low fitness differences among females. There is higher vLRS among females within social groups in species who potentially can sire a larger number of offspring, and in those species which have a dominance hierarchy. Species which show territorial behaviour have a higher vLRS between social groups. While these analyses did not reveal any correlation with ecological conditions, the results indicate that the new approaches have the potential to identify underlying causes which lead to the differences in social system among mammalian species.

## 6.2 Future possible additions

### 6.2.1 Reliance on published data

As with most cross-species comparative studies, published data was mused for most of the analyses in these studies. The sampling design therefore often does not specifically fit the need of the approaches developed here. This was particularly a problem when trying to extend the approaches to data from human populations. All the approaches developed here aim,

directly or indirectly, at detecting individuals which share a common ancestor within the last few generations. However, population genetic studies of human populations are mainly interested in broad phylogeographic questions and want to detect all the different variants within a population to relate them to another (Jobling *et al.* 2004). Therefore, they reduce the laboratory work by specifically excluding related individuals. This however is the main source of information to describe the social structure. However, with the decreasing costs and effort involved in obtaining genetic information and therefore the increase in sample sizes, it will be interesting to see to what degree relatedness and competition over resources among individuals also shape the social structure also of humans.

Studies of natural population of animals on the other hand are often limited by not encountering all the animals and therefore as well have no information about how their sampling is in relation to the social structure, e.g. if the sampled individuals are from a single or several groups and whether all individuals have been sampled. However, again due to the decreasing costs, genetic analyses are more routinely added to studies of behavioural ecology. This will increase the availability of data for comparative studies. For instance, a search in ISI Web of Science with the keywords “relatedness” and “microsat*” shows a constant increase in the number of publications, with each year 10% more papers published than the previous year. Furthermore, ideally these approaches could than be applied to different groups from the same species, to more precisely detect the correlation between genetic variation and social structure. As potential new, additional strategy, samples could be collected from the same group from consecutive generations. For one, this would allow to infer how quickly genetical variation and therefore the inferred signal can change and in turn how many generations back it reflects. In addition, it would allow more causal inferences by identifying the sequence of change among the correlated factors.

Not only sampling is a limiting factor though, also the choice and number of genetic markers. For the relatedness analyses many studies still rely on a limited number of microsatellite markers. There is therefore a large sampling variance in the estimates (Csillery *et al.* 2006). Two advances should allow more precise description of the relatedness structure and its influence on social behaviours. The first will be the possibility to construct genealogies based on the direct paternity and maternity data (e.g. Kerth *et al.* 2002), when field studies continue to be performed long enough. The second is the possibility to use novel techniques to amplify a larger number of markers to reduce the error in the estimates (e.g. Bellemain *et al.* 2005, Langergraber *et al.* 2007a). Both of these advances will allow to describe in more detail which types of relationships are present in a population (Widdig 2007)

and whether and how they influence cooperative behaviour (Langergraber *et al.* 2007a). For the information on the variance in lifetime reproductive success it would be interesting to see whether data from autosomal markers could also be added and thereby reducing the stochastic error associated with analyzing a single genetic marker. However, as with the relatedness, with the continuation of long-term studies of specific populations, also for the vLRS more direct data will become available in the form of maternity and paternity data. Using these in a comparative framework as described here should further allow to understand difference in social structure among animal species.

### 6.2.2 Correlations are not causations

Comparative phylogenetic analyses aim to infer whether across several species certain characters always occur together. They normally do not allow to infer the causal relationship between the character though. While new approaches have been developed which for instance look at the sequence of changes (Lindenfors *et al.* 2004), these might not necessarily be used for some of the social behaviours analyzed here. The information of these stepwise sequential changes could be limited, given that some of the behaviours can change quickly, varying even within species. In these cases future studies based on population genetics data from several species could be based on meta-analysis. For this, data addressing a common hypothesis for a set of evolutionary related species is combined (Schino 2001). Meta-analysis tests for the overal pattern in significance and strength of the association and is an appropriate tool for identifying general patterns. However, given that again the species or populations under examination are not phylogenetically independent, also here new approaches which aim to derive a phylogenetic independent framework for meta-analysis should be considered (Adams 2007).

### 6.2.3 Philopatric versus dispersing sex

While there are not just methodological, but probably biological reasons for differentiating among species in which females versus males disperse, this obviously misses on relevant information if the aim is to understand the evolution of social systems. Also in the case of dispersal relatedness could nevertheless influence the interaction of individuals (e.g. Bradley *et al.* 2007). In the case of fitness differences, if the distribution of a certain resource is relevant for reproductive success, this should also influence the competition among associated females/males even if they come from different natal groups. However, comparing across all species in all situations does not provide the general explanation for the variation in

social structures, but allows addressing different questions, elucidating different aspects. As shown in the case of the vLRS within versus between social groups of philopatric females, different factors seem to influence the competition on these different levels. Since certain factors only will be detected by analyzing the right part of the social structure, information addressing these questions on the different levels should therefore be combined.

## 6.3 Outlook

### 6.3.1 Comparative studies of population genetics of social animals

Even with the aforementioned limitations, in all the analyses significant correlations were detected. While in the first study on relatedness this correlation is only between the mathematical model and the actual data, thereby allowing to test hypothesis, in the second part the correlations are between different characters of the natural populations. Comparative analyses, based on specific predictions, can therefore be a powerful tool to understand more about the evolution of social systems using genetic data. Together, these results indicate that the social system of an animal species creates an additional level of structure below the level of populations which influences the amount and distribution of genetic variation and therefore can confound population genetic analyses. More specifically however, these approaches allow to infer information on aspects of the social structure from one-time samples of genetic data, which would otherwise be difficult to obtain for most mammals. Especially information on vLRS, the quintessential measure of fitness, normally needs the study of a large number of individuals over their whole lifetime. Analyzing genetic data in this way therefore allows to understand a specific population in more detail, but especially to standardize across populations to perform comparative analyses, which provide additional insights. This therefore also open up new directions of understanding which factors lead to fitness differences, and have or are still acting as selective forces.

### 6.3.1 Kin selection theory

Kin selection theory has been influential in explaining cooperation of individuals due to its intuitive concept and the support from a number of different species. However, recently studies began to challenge it as the general explanation for all types of cooperation observed. For one, it became clear that cooperating individuals, even if they seemingly pay a cost, indirectly or directly also might gain benefits themselves (Clutton-Brock 2002). For

cooperative breeders for instance it has been found that helpers might pay rent to stay within a home range, given that there is nowhere to go, that they might learn valuable skills or wait to inherit the territory. Since individuals will stay within the area they have been born, they in turn will help their relatives. Whether inclusive fitness benefits are the driving force behind the evolution of certain cooperative behaviours or whether it is rather that there is a direct benefit of the cooperation, and than, if available, related individuals are selected as partners therefore remains to be clarified for many cases. This might actually be the case for chimpanzees. A recent study shows that, as predicted from the results of my first study, cooperation among chimpanzees in the majority of cases occurs between unrelated dyads. However, maternal brothers show significantly elevated levels of cooperation (Langergraber *et al.* 2007a). Those results indicate that more detailed studies on the actual kinship composition, rather than average relatedness levels, combined with direct behavioural information on the related dyads, can help us to understand the influence of inclusive fitness benefits on social behaviours. Furthermore, kin structures however also influence other aspects of the social system. Inbreeding avoidance seems to be a major factor leading to the clear-sex bias in dispersal observed in most species (Pusey *et al.* 1996). But also competition among kin can potentially influence interactions of individuals (Griffin & West 2002). Data on the actual costs and benefits of the behaviour, combined with the genetic information on the availability of partners of different genetic relationships, will help to clarify also these patterns in more detail.

### 6.3.2 Fitness measures from genetic data

From a genetics viewpoint, ultimatively the goal would be to detect the genes that underly these behavioural differences. More detailed description of individual behaviours could allow for association studies. In its simplest form, the approach presented here could be extended to see whether there are consistent differences between individuals of successful, frequent, versus unsuccessful, rare mtDNA or Y-chromosome lineages. While this could lead to the identification of certain phenotypes, it seems more difficult though to pinpoint the genetic variants. Only in some rare cases differences at single genes are leading to phenotypic differences in behaviour (e.g. Pedersen *et al.* 1992, Lim *et al.* 2004). It is quite likely that many of the behavioural characters are complex traits, with many genes contributing relatively little. For most natural population of animals it will remain challenging to obtain the relevant sample sizes to detect the the small effect of a genetic variant for behavioural variation (Plomin 1990). In addition, characteristics like attaining a dominant position is

likely also influenced by ecological factors and also feedback mechanisms (e.g. offspring of dominant mothers get more food). Identifying instead of the genes the social and ecological conditions underlying functional species differences, as approached in this study, will therefore be the more promising step in the near future. Coming from a genetics viewpoint though emphasises that to understand the actual success of a behavioural strategy it is important to study individuals for their whole reprodutive career. Many studies of male strategies for instance focus on reproductive skew by analyzing the distribution of offspring among males within one situation. If however males who are competitively successful during a breeding season have a higher mortality, other strategies might in fact be more adaptive. Given that fitness is a relative measure, so that the traits of those individuals will spread in a population who sire more offspring than the others, it is important to assess their lifetime reproductive success. There is still a lot to learn about the evolution of social systems, and, based on the results, the framework developed in this study should prove fruitful to gain insights into some of factors behind this.

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# Declaration of independence

I herewith declare that I, Dieter Lukas, have conceived and written this dissertation, entitled "Comparative study of genetic variation in relation to social structures of animals", without any inadmissible help and/or material that has not been explicitly indicated. This dissertation has not been submitted elsewhere, either inside or outside of Germany. I have not previously attempted to complete this or any other PhD thesis

Dieter Lukas
Leipzig, 22. Januar 2008

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