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Genetic Consequences of Dispersal
and Social Behavior in Lions,
Panthera leo

BY

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ABSTRACT

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This thesis combines behavioral observations of African lions (*Panthera leo*) with genetic analyses, in an attempt to clarify causes and consequences of lion group living. The numerous complex cooperative behaviors of lions present an excellent opportunity to investigate the evolution and maintenance of group living. This thesis focuses on female group living and male dispersal patterns.

Lion sociality is found to be more complex than previously thought. Short dispersal distances result in strong kinship ties among prides, creating the potential for kin selection to operate among prides. Simultaneously, some prides contained unrelated females, depriving females in such prides of inclusive fitness benefits from group living. Concurrent with short dispersal distances in both males and females, significant genetic differentiation could be detected over relatively short distances in analyses of males. Extensive behavioral observations showed that territorial behaviors were unaffected by kinship ties to intruders. Instead, favorable odds and several environmental conditions were important factors. Space use analyses showed large overlap among prides. Again, kinship did not affect degree of overlap.

Conclusively, these results show that the ultimate causes of lion sociality remain elusive, but that kin selection may be less important than generally thought. Lion sociality seems to be explicable mainly in terms of direct fitness benefits, which therefore should be given more attention.

Key words: Behavioral ecology, direct fitness, dispersal, inclusive fitness, *Panthera leo*, population genetics, sociality.

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For Elsa and Sara

This thesis is based on the following five papers, which will be referred to by their roman numerals (I-V).

I. **Spong G, Creel S, Stone J, and Björklund M.** (submitted) Genetic structure of lions (*Panthera leo* L.) in the Selous Game Reserve: implications for the evolution of sociality.

II. **Spong, G and Creel, S.** (in press) Deriving dispersal distances from genetic data. *Proceedings of the Royal Society Biological Sciences Series B.*

III. **Spong, G. and Björklund, M.** (manuscript) Genetic structure and dispersal patterns of male lions (*Panthera leo*) in the Selous Game Reserve, Tanzania.

IV. **Spong, G and Creel, S.** (submitted) Effects of kinship on inter-group conflicts in lions, *Panthera leo*.

V. **Spong, G.** (submitted) Space use in lions, *Panthera leo*, social and ecological factors.

The order of the authors reflects their involvement in each paper.

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PREFACE

The simple answer to why some animals live in cooperative groups is that it maximizes the fitness of each individual in the group. However, exactly how these fitness benefits accrue is often imperfectly understood. Some individuals forego their own reproduction to score indirect fitness points, some delay breeding in order to reap future direct fitness benefits, while, finally, others live in groups mainly because of the positive effects on direct fitness. If groups contain relatives, group living can result in an increase in both indirect and direct fitness, but the relative importance of each component is difficult to determine. Detailed knowledge of the genetic structures in and among social groups therefore is essential in order to understand the evolution of group living. By a combination of behavioral observations and genetic analyses, this work attempts to improve our current understanding of genetic structure in relation to social behavior and dispersal, using lion, *Panthera leo*, the only truly social cat, as a model.

INTRODUCTION

Cooperative behavior is a monumental step in organic evolution and one of its most intriguing results. Although our understanding of what induces and maintains cooperation has improved considerably during the last decades, new findings strongly suggest our knowledge to be far from complete. In this introduction I will briefly describe and discuss cooperation driven by; 1) kin selection, 2) reciprocity and 3) mutualism. For an excellent and exhaustive review on cooperation see Dugatkin (1997).

Kin selection

Attempting to explain altruistic behavior, Darwin (1859) concluded that selection in some cases must work on levels above the individual, i.e. the group. More than a hundred years later, this theory was revived and refined when Hamilton (1964) put forth his kin selection theory, demonstrating that behaviors with a direct fitness cost could be favored by the positive impact they have on the fitness of relatives. The theory is based on the equation $rb - c > 0$, where r is relatedness between interactors, b is the benefit to the recipient and c is the cost for the donor. A flurry of investigations into kin selection processes and its importance ensued after Hamilton's two papers. These studies often showed that individuals performing seemingly altruistic acts gained indirect benefits by helping relatives, thus promoting copies of their own genes. With the advent of relatively cheap and accessible molecular methods the scientific literature has virtually exploded with papers presenting genetic structures in natural populations that might foster kin selection.

Reciprocity

Kin selection does not explain cooperation among non-relatives. The first attempt to explain altruism between non-kin was made by Trivers (1971). Game theory models, adopted from the field of economics, suggested that cooperative strategies based on reciprocity were vulnerable to defectors or cheaters (Axelrod and Hamilton 1981), tipping the balance further toward cooperation among kin.

Mutualism

Even in cooperative social groups consisting of relatives, direct fitness benefits, current or future, of group living often seem to outweigh the indirect fitness derived. Nevertheless, upon finding kin structures on a

small scale, many investigators have uncritically concluded that kin selection is an important factor in creating the observed patterns.

However, to be able to address these issues, the overall fitness (direct and indirect) of individuals showing natal philopatry has to be compared to the fitness of individuals who disperse. Two excellent examples of such studies include Serengeti dwarf mongooses, *Helogale parvula* (Creel and Waser 1994) and Kenyan white-fronted bee-eaters, *Merops bullockoides* (Emlen and Wrege 1989). Both studies convincingly showed that inclusive fitness benefits were important for group dynamics.

Limited dispersal can facilitate the evolution of social behaviors by allowing relatives to cooperate and thus accrue indirect fitness benefits (e.g. Kelly 1992). Indeed, natal philopatry is generally considered the first step in the evolution of carnivore social behavior (Waser 1996). However, direct fitness benefits resulting from natal philopatry would create much the same patterns. Moreover, recent work has highlighted competition among relatives as a force opposing natal philopatry. Negative effects of competition among relatives living together should be deducted from the indirect fitness gains, thus reducing the total inclusive fitness gains (e.g. Clutton-Brock in press). In line with this argument, an increasing number of empirical studies report a lack of correlation between relatedness and cooperative behaviors (e.g. Clutton-Brock *et al.* 2000; Goldbberg and Wrangham 1997; Grinnell *et al.* 1995; Schaeff *et al.* 1999). Instead, it is suggested that mutual benefits of group living maintain social and even altruistic behaviors in some species (Clutton-Brock *et al.* 2000; Kokko *et al.* 2001).

The STUDY SPECIES and METHODS

Few mammals have been as extensively studied in the wild as the African lion. Yet, our understanding of lion sociality is still patchy and suffering from a lack of consensus. Lions are highly suitable for behavioral studies since they are easy to identify individually, unwary of vehicle borne human observers, and live in rather open habitats. On the other hand, lions are active mainly at night and spend most of the light hours resting. This makes data collection difficult and often slow.

African lions form prides of related females (Gilbert *et al.* 1991; Packer *et al.* 1991; Spong and Creel in press). Throughout this summary, unless otherwise stated, pride will refer to pride females. Female offspring is usually recruited into the pride, whereas male offspring always disperse (Pusey and Packer 1987; personal observations). As males reach adulthood,

they try to attain control of a pride of females by ousting the resident males. Males may form coalitions with unrelated individuals, but coalitions are most often composed of relatives (Gilbert *et al.* 1991; Spong and Creel in press). Lions exhibit a wide range of cooperative behaviors such as communal rearing of cubs (Pusey and Packer 1994), cooperative hunting (Pusey and Packer 1994), and territory defense (Heinsohn 1997; Heinsohn and Packer 1995; Heinsohn *et al.* 1996; McComb *et al.* 1993, 1994). The females defend the permanent territory vigorously against intrusion from neighboring prides females.

Given all these social behaviors, lions present an interesting opportunity to investigate questions concerning cooperation in social animals. Some of their cooperative behaviors can be highly risky and potentially fatal, and uncooperative group members can impose dire costs on other pride members. All pride females breed with approximately equal success (Packer *et al.* 2001), thus accruing direct fitness benefits of equal size. But since most prides are composed of close relatives, indirect fitness benefits can also be substantial. Females are highly philopatric; new prides, formed by fission, invariably settle within or adjacent to their natal home range (Pusey and Packer 1987). As a result, strong kinship ties can develop among adjacent prides. On the other hand, male lions frequently form coalitions with unrelated partners (Gilbert *et al.* 1991). Thus, the pattern of lion sociality is far from straightforward.

Early attempts to explain lion group living focussed on the most spectacular of lion behavior; cooperative hunting (e.g. Schaller 1972). The importance of cooperation during group hunting in lions was later questioned by Scheel and Packer (1991). However, in a study of lion hunting behavior in Etosha, Namibia, Stander (1992) described highly coordinated and cooperative behaviors. Currently, no consensus exists on the cost and benefit of cooperative hunting in lions.

Female lions defend their cubs against infanticidal males, and larger groups of females more effectively deter males (McComb *et al.* 1993; Packer and Pusey 1983). Clearly, this is an important benefit of group living as cub mortality attributable to infanticide can be high.

Larger prides moreover dominate smaller ones in female-female encounters and thus defend their territories more successfully. Playback experiments have shown that females in the Serengeti lion population vary their behavior according to the odds and are reluctant to engage in fights when outnumbered (McComb *et al.* 1994). Additional data collection and analyses from this population found consistent individual differences among individuals in approach behavior when exposed to simulated intruders (Heinsohn and Packer 1995).

Lion Group Living; Spong

While group living in lions thus results in a number of benefits, the importance of each is unclear. Furthermore, the relative importance of direct versus indirect fitness is also unclear. Pride size and average relatedness will have important effects on adult and juvenile survival and the proportion of fitness derived from each of the two fitness paths, respectively.

The work presented in this thesis combines about 1,600 hours of behavioral observations with genetic analyses in an attempt to investigate the causes and consequences of lion sociality. Most behavioral data were collected by purely observational methods, but some behaviors were induced by playback experiments (paper IV). All data for papers I, II, IV and V were collected from a free-ranging lion population in the northern sector of the Selous Game Reserve in southeastern Tanzania (lat $7^{\circ} 35^1$ S, long $38^{\circ} 15^1$ E). Data for paper III came from biopsy samples and tissue samples collected from lions legally shot in various parts of the Selous Game Reserve by trophy hunters.

The study site covered about 1,000 km² and consisted mostly of wooded savanna, miombo and *Combretum* thickets. Data collection was initiated by Scott and Nancy Creel in 1993, and I continued this work from July 1995 until February 1999 when the project was terminated. Lions were individually recognized from external phenotypic characters aided by the use of a picture library. More than 150 lions in more than 16 prides were observed during the study. Some prides were only observed in the early stages of the study and later phased out for reasons of logistics and efficiency. Final analyses include data from 14 prides and tissue samples collected throughout the reserve. All observations were made from a vehicle at distances up to 200 meters. Some females were fitted with a radiocollar (Telonics MOD-500). When the study was terminated, collars (with two exceptions) were removed, according to a request from park authorities. No injuries occurred during these procedures.

Tissue samples were collected in the form of biopsies, using either a CapChur CO₂ pistol with custom-made darts or by hand using a scalpel during anesthesia. Tissues were stored at ambient temperatures in 95% ethanol buffer containing 100 mM EDTA in the field for up to four months. In the laboratory, samples were stored at -20°C. DNA was extracted using a standard phenol/chloroform protocol (Maniatis, Fritsch and Sambrook 1982), dissolved in water, and stored at -20°C. Fifteen flourolabeled primers (Fca001, Fca008, Fca026, Fca031, Fca045, Fca077, Fca126, Fca223, Fca272, Fca275, Fca391, Fca506, Fca567, Fca628, F115; Menotti-Raymond *et al.* 1999), were used for analyses of kinship and population

Lion Group Living; Spong

structure. Fragments were amplified in triplex PCRs and run on an ABI 310 (PE Biosystems) single capillary autoanalyzer for manual scoring.

Replicates of triplexes occasionally (fewer than 20 replicate runs) showed inconsistent genotypes. Sixteen of these inconsistencies could be explained by mistakes during pipetting steps (i.e. human error; tubes were mixed up). By rerunning the correct genotype could be confirmed. Four samples misprinted and were run repeatedly to minimize the risk of an incorrect genotype. These samples were from biopsies that yielded only hair and thus extracts contained very little DNA. For the vast majority of samples, replicates matched perfectly. Negative controls failed to show contamination to be a factor.

RESULTS and DISCUSSION

Social group genetic structure (Paper I)

The genetic structure within and between social groups is of vital importance for the understanding of the evolution and maintenance of sociality. The fact that many, if not most, social groups are composed of relatives creates the possibility that kin selection is an important component of benefits derived from group living.

In this paper we use behavioral and demographic data (table 1) in combination with genetic data derived from 14 microsatellite markers (table 2), to investigate the genetic structure of the lion population under examination. Both F-statistics (figure 1) and estimates of relatedness (r ; figure 2) were used, allowing a more detailed view of the genetic processes in the population.

Table 1. Pride composition in early 1999. Numbers within parentheses indicate number of individuals included in molecular analyses.

Pride	# of females	# of males	# of cubs	Total adults
Sand River	5(4)	2	5(4)	7
Tagalala	2(2)	3(3)	-	5
Selous Mdogo	3(1)	2	-	5
Selous Grave	7(7)	1(1)	9(1)	8
BehoBeho	3(2)	2	2	5
Beho Mdogo	1(1)	3	-	4
Shortcut	5(4)	4(3)	4(1)	9
Shortcut North	2(2)	?	-	2
Manze	4(3)	0	-	4
Nzerakera	5(3)	4(4+1) ^{1, 2?}	11(6)	9
Mbuyuni	3(3)	4(4+1) ^{1, 2?}	1(1)	3
Siwando 2	2(2)	1(1)	2	3
Siwando	3(3)	2(2) ²	5	5
Mzizimia	3(2)	2(2) ²	4(3)	5
Mean±SD	3.4±1.6	2.4±1.0	5.3±3.2	5.3±2.1

¹⁾ two different coalitions.

²⁾ these males held tenure in both prides.

Lion Group Living; Spong

Table 2. Summary statistics of the 14 loci used in the analysis.

Locus	# of ind.	# of alleles	H _{exp}	H _{obs}
Fca001	70	14	0.80	0.80
Fca008	66	6	0.56	0.72 ¹
Fca026	66	9	0.69	0.84
Fca031	70	9	0.68	0.70
Fca045	66	4	0.41	0.67
Fca077	68	10	0.72	0.77
Fca126	63	10	0.71	0.78
Fca272	60	7	0.61	0.63
Fca275	70	7	0.60	0.79
Fca391	70	8	0.64	0.75
Fca506	68	14	0.80	0.83
Fca567	61	6	0.56	0.70 ¹
Fca628	70	5	0.48	0.58
F115	69	16	0.83	0.87
Mean±SD	66.9±3.5	8.9±3.6	0.65±0.12	0.75±0.08

¹) Significantly deviating from HW.

These results largely confirmed previous genetical and observational work on lions (Gilbert *et al.* 1991), but revealed some important differences. First, prides were found to form clusters of related prides in the population. Even though the structure was relatively weak, it was significant (table 3), and its importance tested in papers IV and V. Second, some prides were found to be composed of unrelated females.

Table 3. F-statistics allowing for the social structure of the population. The first row lists F-statistics when including all pride members. The second includes adult females and dependent young, and the last row includes only adult females.

	F _{IL}	F _{IT}	F _{LC}	F _{ZT}
All pride members (n=70)	-0.11***	-0.02 ns	0.07***	0.02 ns
Excluding males (n=55)	-0.12***	-0.02 ns	0.07***	0.02 ns
Adult females only (n=34)	-0.20***	-0.01 ns	0.11***	0.05**

*) p<0.05, **) p<0.01, ***) p<0.001 based on randomization (1023 permutations).

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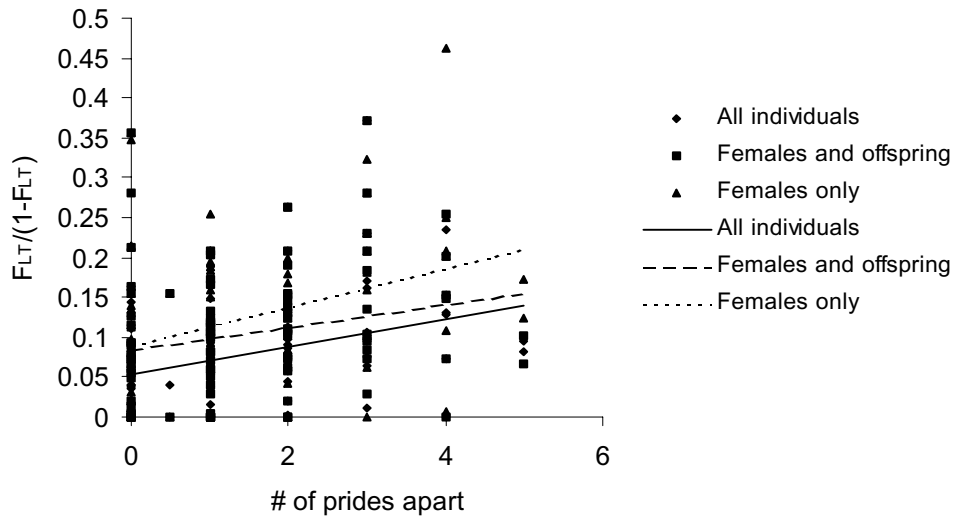


Figure 1. Pairwise $F_{LT}/(1-F_{LT})$ for all defined demographic groups (all pride members, females and cubs, and adult females only) plotted against intervening number of prides. Lines simple linear fit. Regression lines were not significantly different ($F < 1.04$, ns; for all three pairwise comparisons). Slopes of regression lines not significantly different ($t < 0.79$, ns; for all three pairwise comparisons).

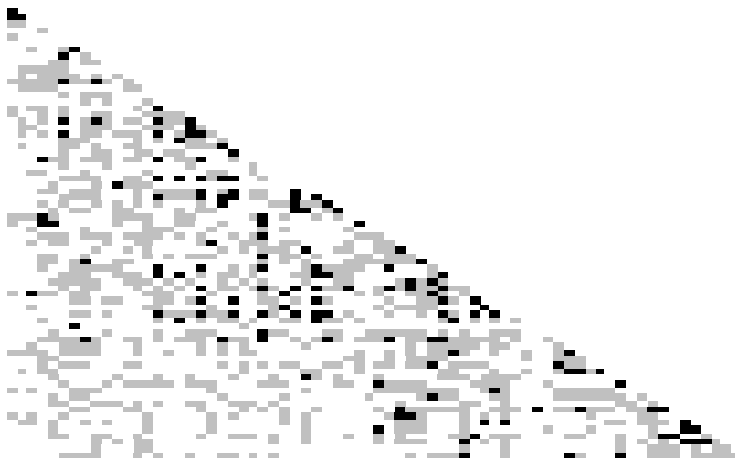


Figure 2. Matrix of pairwise relatedness estimates (obtained with the software DELRIOUS). Proximity of individuals in the matrix correlates with behavioral and geographical proximity (i.e. proximate prides in the matrix are geographically proximate, and individuals within prides are listed as a cohesive unit). Black spaces $r > 0.25$, grey spaces $0 \leq r < 0.25$, and white spaces $r < 0$.

Lion Group Living; Spong

Transient kinship ties between pairs of adjacent prides have earlier been shown using minisatellites (Gilbert *et al.* 1991; Packer *et al.* 1991). However, the clustering of several groups of prides into a significant genetic structure has not been shown before. While the correlation of $F_{LT}/(1-F_{LT})$ to distance is not significant ($p < 0.06$), the correlation of pairwise relatedness estimates (r) between individuals to distance is highly significant (figure 2, Mantel's $p < 0.01$; see also paper II).

Female lions have never been observed to join unfamiliar females, and the finding of prides with unrelated individuals can probably be explained by persistent matriline. Female lines within prides will diverge, unless a single male fathers all offspring. In prides composed of unrelated females, inclusive fitness cannot be an important part of the total fitness. This is not to say that inclusive fitness benefits therefore are unimportant for group formation and maintenance of sociality in lions. If the criterion of a relative is having been born in the same pride, we would expect exactly this pattern. Prides would usually contain close relatives, but a few prides might contain distantly related individuals. Since all females breed in lion prides, direct fitness is clearly an important component of individual fitness, especially in small prides. Furthermore, living with a familiar female, although unrelated, might still be a better option than solitary life. The selection for kin discrimination ability among pride mates is therefore probably weak.

Dispersal patterns (Paper II).

Attempts to measure dispersal distances directly in natural populations are often thought to underestimate true dispersal distances. This is mainly due to the difficulties associated with tracking individuals leaving the study site. If dispersal occurs across more than one or two territories, the number of territories within dispersal distance not included in the study site quickly becomes large. In other words, even for large study sites, there are usually more unknown animals within this distance than the number of known animals on the study site.

To remedy this problem, we present a new method based on genetic data. It allows unbiased estimations of mean dispersal distances and its distribution, although the method only works in species where philopatric individuals can be identified. First, the correlation between genetic differentiation and distance for the philopatric sex must be quantified. Second, dispersed individuals of the other sex have to be identified. Third, genetic similarity among mating partners must be established. Lastly, the average genetic similarity can be used to derive mean dispersal distance in the population.

Lions are especially amenable to this analysis for two reasons. Females show extreme philopatry and males associate for relatively long periods with prides of females, facilitating identification of dispersed individuals. Since males are sampled after the dispersal event, actual dispersal distances do not affect the distribution of dispersal distances in the sample, unlike studies where individuals are monitored prior to and after dispersal. This renders the method truly unbiased.

Lion Group Living; Spong

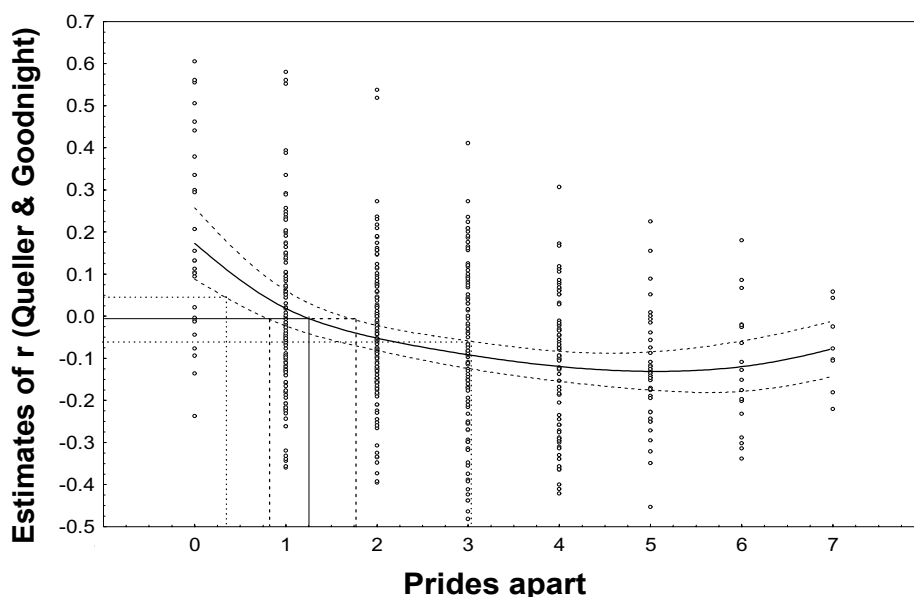


Figure 3. Estimates of r for pairs of females plotted against the number of pride ranges apart (zero = within prides, one = neighboring prides, etc). 95% confidence bands are shown by dashed curves. The vertical dashed lines identify extrapolated 95% confidence intervals for the mean dispersal distance estimate (0.8-1.8) due to the uncertainty of the regression line. The vertical stippled lines identify extrapolated overall 95% confidence intervals for mean dispersal distances (0.4-3.0). The fitted lines are least square regressions based upon means and confidence intervals derived by bootstrapping.

Results from this analysis on the genetic data from the focal population (see paper I) show that dispersal distances are surprisingly short in lions (figure 3) and only average slightly above one pride range (mean 1.3, CI= 0.4-3.0). This result concurs with observations of male lions in the Serengeti lion population (Packer and Pusey 1993).

Dispersal is often thought to have evolved to minimize inbreeding. On the other hand, for many species, dispersal is associated with highly elevated mortality risks. Striking a balance between the risk of inbreeding and the mortality risks associated with dispersal predicts that dispersal will have evolved to be a distance just beyond the limit of detrimental inbreeding. Genetic and behavioral data show that mating between close relatives is uncommon in lions. Furthermore, the effects of occasional mild inbreeding is debated and may not be serious (Keane *et al.* 1996). The dispersal distances of male lions found in the present study thus concur well with theory.

Population genetic structure (Paper III)

Species capable of long distance dispersal seldom show strong genetic structuring unless populations far apart are compared. On the other hand, if typical dispersal distances are short, small scale genetic structuring can emerge. Since both females and males have been found to disperse short distances in lions, genetic structuring might occur over relatively small distances in this species.

To investigate if the Selous lion population is genetically structured and to obtain an indirect estimate of dispersal distances based on the genetic neighborhood size (as estimated from the regression of a_r on the logarithm of distance), tissue samples from throughout the reserve were collected (figure 4). Fifteen microsatellite loci were applied to tissue samples from 70 males.

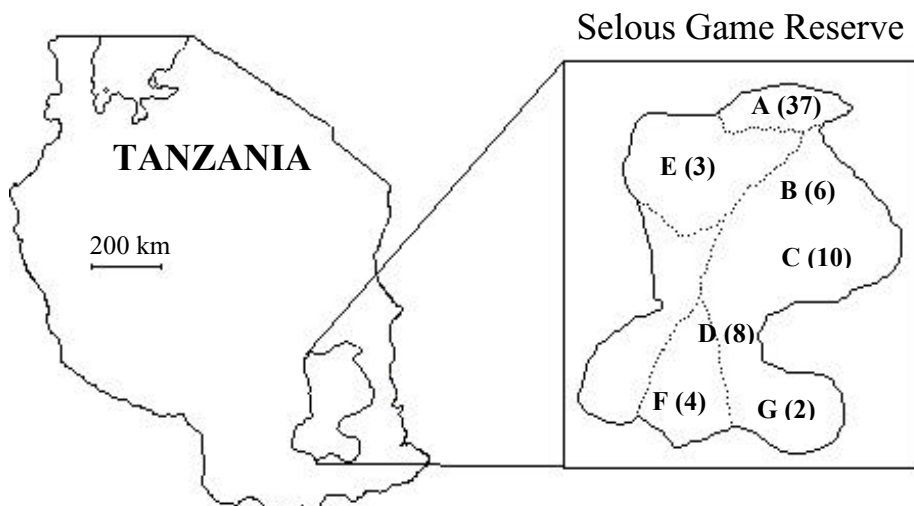


Figure 4. Map of Tanzania showing sample locations. Enlarged section shows the Selous Game Reserve, with dashed lines marking permanent rivers. Numbers within parenthesis indicate number of samples from each general area.

Lion Group Living; Spong

Pairwise F_{ST} values did not significantly correlate to geographic distance, probably due to a lack of data points. However, pairwise a_r estimates between individuals showed a significant correlation to distance (figure 5), albeit weak. The derived mean axial parent-offspring distance, or in this case simply mean male dispersal distance, was about 8.6 km and the neighborhood size was 49 individuals.

In lions, genetic structuring can thus be detected over relatively short distances, even when only sampling dispersed individuals. The mean male dispersal distance, concurs well with previous findings of short male dispersal distances (Spong and Creel in press).

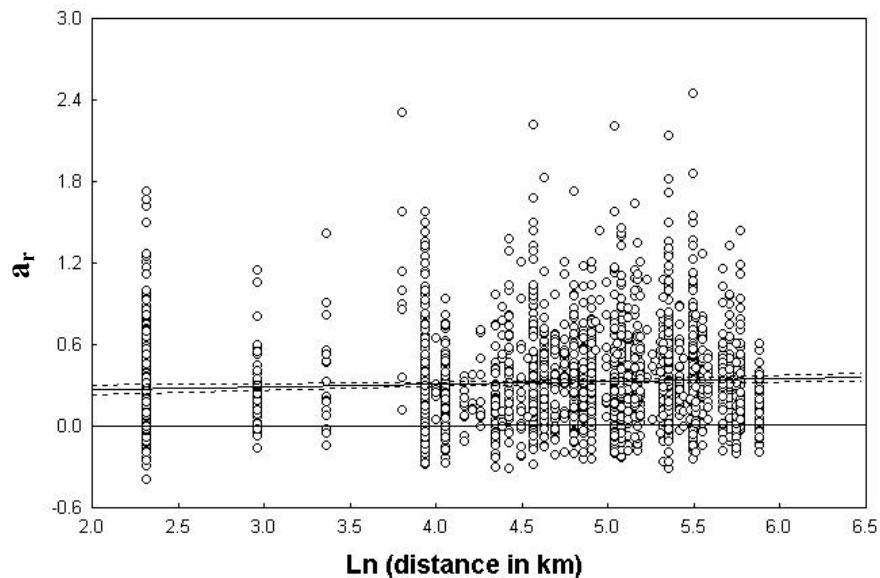


Figure 5. Pairwise estimates of a_r between individuals (see Rousset 2000) plotted against the logarithm of distance in km. Line is linear regression; $a_r = 0.227 + 0.0205 \cdot \ln(\text{distance})$, Mantel's $p < 0.0026$. Dashed lines indicate the 95% confidence interval.

Territory defense (Paper IV)

Studies of kin selection have focused on interactions within social groups. However, due to the process by which new lion prides form, prides sometimes share territorial borders with close relatives, creating the potential for kin selection effects among prides (see paper I).

The importance of kin during territorial contests was tested by playback experiments. In these playbacks, behavioral data of individually known females were collected to determine responses to territorial intrusions. All broadcast roars were recorded from known females in the study population. Genetic analyses allowed estimation of kinship between roarer(s) and listener(s), see paper I.

Analyses of this data set revealed a number of important factors for decision making during such exchanges (table 4 and 5). During approaches, poor odds, presence of cubs, high temperatures, more number of bouts played, more simulated intruders, and exposure to more playback experiments, all resulted in slower approaches (table 5). However, no effect of kin could be detected.

Recent models have highlighted competition among kin as an evolutionary force opposing natal philopatry and kin selection. In lions, our results suggest kin selection has little effect on interactions among prides during territorial intrusions, i.e. indirect fitness benefits are less important than direct fitness benefits.

Table 4. Logistic regression model of the binary variable “response” (1’s n=75) or “no response” (0’s n=44). $\chi^2=33.7$, $df=8$, $p=0.00005$, likelihood= 123.5 (intercept= 156.8).

Model term	Effect	p
Constant	-2.67	0.53
Distance to border	-1.61	0.02
Temperature	0.22	0.08
# of bouts	-0.13	0.79
# of roars	-1.09	0.10
Odds	1.38	0.48
Playback number	-0.23	0.00
Presence of cubs	-0.66	0.20
Mean relatedness (r)	0.66	0.60

Lion Group Living; Spong

Table 5. Generalized linear mixed models with a log-link function of the factors affecting the response times to a) the halfway (100m) and b) the speaker (200m). Individuals within playbacks were fitted as a random term to control for repeated measures within each playback. The best models were chosen based on Akaike's information criteria (AIC). Initial models included the same variables as the minimal model b.

a. Minimal model for the variables affecting response time to halfway:

Model terms	Effect	SE	Wald statistic	df	p
Intercept	-2.36	2.03	1.35	1	0.24
Temperature	0.26	0.06	20.00	1	<0.01
# of bouts	0.92	0.20	20.92	1	<0.01
Odds	-2.89	0.73	15.67	1	<0.01
Playback #	0.04	0.02	3.91	1	<0.05
Mean relatedness (<i>r</i>)	0.78	0.49	2.57	1	0.11

b. Minimal model for the variables affecting response time to the speaker:

Model terms	Effect	SE	Wald statistic	df	p
Intercept	1.05	1.49	0.50	1	0.48
Distance to border	-0.32	0.12	6.46	1	0.01
Temperature	0.14	0.04	9.54	1	<0.01
# of bouts	0.79	0.13	37.71	1	<0.01
# of roars	1.10	0.17	42.73	1	<0.01
Odds	-1.82	0.45	15.97	1	<0.01
Playback #	0.09	0.02	28.83	1	<0.01
Presence of cubs	-0.50	0.14	13.27	1	<0.01
Mean relatedness (<i>r</i>)	0.46	0.33	1.92	1	0.17

Space use (Paper V)

Space use analyses of lions, performed with Geographic Information System (GIS) software are here combined with genetic and behavioral data. I present descriptive data on properties of lion territories and test if territory size is determined by pride size, among pride relatedness, prey availability or habitat type.

The results showed that territory size was not correlated to pride size (table 6, see next page). Analyses of habitat choice showed that lions had a strong preference for riverine and short grass habitat, whereas long grass, thorn woodland and deciduous forests were avoided (table 7). This concurs well with prey availability in these habitats, when accounting for the large number of prey passing through riverine habitats to drink. Proportionally, outer parts of territories overlapped extensively, whereas core areas more seldom overlapped (table 8). The overlap was not correlated to kinship ties among prides. Overlap zones did not differ from overall habitat composition of territories, as would be expected if overlap only occurred in preferred habitats. Conclusively, lion space use seems to be influenced mainly by prey availability.

Table 7. Habitat use, habitat availability, habitat preference and prey availability within 14 lion territories.

Habitat	Use (% of fixes)	Availability (% of area)	Preference (use/avail.)	Prey encounter rates ¹
Riverine	0.47	0.10	4.56	4.6
Short grass	0.19	0.08	2.25	16.4
Palm swamp	0.12	0.11	1.14	n/a ²
Long grass	0.02	0.04	0.49	11.3
Thorn woodland	0.19	0.56	0.34	7.2
Deciduous woodland	0.02	0.11	0.18	3.8

¹⁾ Measured as prey individuals per kilometer; from (Creel and Creel in). ²⁾ Palm swamps are impenetrable in a vehicle, preventing systematic data collection.

Table 8. Overlap between pride neighbors as mean proportion \pm standard deviation.

Focal Range	Adjacent range			
	50%	70%	80%	90%
50%	0.02 \pm 0.06	0.08 \pm 0.22	0.09 \pm 0.25	0.18 \pm 0.33
70%	0.08 \pm 0.22	0.08 \pm 0.20	0.11 \pm 0.25	0.19 \pm 0.33
80%	0.09 \pm 0.25	0.11 \pm 0.25	0.15 \pm 0.27	0.21 \pm 0.33
90%	0.18 \pm 0.33	0.19 \pm 0.33	0.21 \pm 0.33	0.19 \pm 0.31

Table 6. Descriptive statistics of lion territories in Selous Game Reserve, see text for details.

Pride	Fs	Fixes	Area (km ²)			Prop. exclusive			Compactness ratio			Prop. of 95% contour		
			50%	70%	80%	90%	50%	90%	50%	90%	50%	70%	80%	
SR	5	8	0.1	0.6	1.2	2.5	1	0.98	0.21	0.44	0.04	0.22	0.49	
TA	2	11	0.0	0.2	0.4	1.7	1	0.97	0.33	0.75	0.88	0.88	0.94	
SG	7	61	22.5	31.9	36.5	53.6	0.94	0.93	0.73	0.85	0.42	0.60	0.68	
BB	3	6	0.2	0.7	1.1	2.5	0	0	0.26	0.61	0.10	0.31	0.43	
BN	1	12	0.4	2.4	3.1	3.8	1	1	0.40	0.89	0.09	0.61	0.82	
SH	5	75	4.7	9.3	12.3	17.9	0.94	0.7	0.86	0.96	0.26	0.52	0.69	
MA	4	69	5.7	9.5	14.7	19.8	0.83	0.8	0.53	0.75	0.29	0.48	0.74	
NZ	5	162	15.5	35.3	48.2	62.7	0.39	0.49	0.82	0.81	0.25	0.56	0.77	
MB	3	11	0.5	2.8	4.8	9.6	0	0	0.33	0.50	0.05	0.29	0.49	
SW2	2	71	10.3	17.4	24.7	53.5	0	0.43	0.60	0.85	0.19	0.33	0.46	
SW	3	22	1.0	6.5	7.0	7.5	1	1	0.33	0.73	0.13	0.87	0.93	
Totals	40	508												
Mean±SD			11.7±7.4	20.7±11.3	27.3±15.1	41.5±20.0	0.63	0.68	0.49	0.75	0.27	0.53	0.69	

Pride names: SR-Sand River, TA-Tagalala, SG-Selous Grave, BB-Behobeho, BN-Behobeho Ndogo, SH-Shortcut, MA-Manze, NZ-Nzerakera, MB-Mbuyuni, SW2-Siwando2, SW-Siwando. Prides with more than 60 fixes in bold. Territory size means only use prides with >60 fixes. Fs= # of adult females, Fixes= # of GPS fixes.

CONCLUSIONS

Both males and females disperse short distances in lions. This creates genetic ties among some prides and local kin structure. Despite the potential inclusive benefit gains arising from positive interpride interactions, this work has found no evidence in support of this theory. Among pride relatedness does not affect the response of females to territory intrusions or their utilization of space. Furthermore, in some prides female relatedness is practically zero. The importance of inclusive fitness gains for the cohesion of lion prides can thus be questioned, and the relative importance of indirect versus direct fitness benefits for the maintenance of lion group living and natal philopatry is at present unclear.

POPULÄRVETENSKAPLIG SAMMANFATTNING

Studieart

Få djur är så väl igenkända som lejonet, vars latinska namn är *Panthera leo*. De lever i flockar av besläktade honor och eventuell avkomma. Hannarna i flocken är oftast obesläktade med honorna och försvarar flocken mot andra hannar. Hannarna stannar bara i flocken under ett fåtal år och förlorar vanligen kontrollen över flocken i strid med andra hannar. Den stabila enheten i lejonens samhälle är därför honorna. De samarbetar under jakt, försvarar reviret mot honor från andra flockar, samt skyddar ungarna från att dödas av främmande hannar. En del av dessa beteenden är mycket riskfyllda och om vissa individer inte samarbetar lika mycket som andra kan det få allvarliga konsekvenser för övriga flockmedlemmar. Honor värvas oftast in i flocken när dom nått vuxen ålder, medan hannar alltid lämnar flocken och söker en egen flock att ta kommandot över. Nya flockar etableras ibland av honor som bryter sig ur sin moderflock. Dessa nyetableringar sker alltid i ett område som angränsar till ursprungsflockens.

Föga förvånande finner forskare lejonet intressant, kanske främst på grund av att det är det enda sociala kattdjuret. Men varför är lejon sociala när alla andra katter är ensamlevande, och vad upprätthåller detta beteende? Detta är frågor som jag sökt svaret på under mitt arbete i Selous viltreservat i södra Tanzania.

Frågeställningar

Varför samarbetar vissa individer? Det enkla svaret är att det maximerar antalet gener som lyckas föra vidare till nästa generation. Gener sprids bäst genom att individen får många framgångsrika avkommor (direkta fördelar/direkt fitness), men gener kan också spridas genom släktingars avkomma (indirekta fördelar/indirekt fitness). Vissa individer hjälper därför besläktade individer att föda fram ungar. I sociala grupper bestående av släktingar kan således individer sprida sina gener på två sätt. Men betydelsen av respektive sätt är svår att fastställa. Under mitt arbete har jag därför undersökt den genetiska strukturen både inom och mellan flockar. Hur långt individer som lämnar sin födelseplats sprider sig påverkar den genetiska strukturen. Nya genetiska metoder möjliggjorde indirekta studier av detta, något som inte varit möjligt tidigare. När den genetiska strukturen kartlagts fokuserades arbetet på att observera olika beteenden för att se hur dessa påverkades av släktskap och genetisk struktur inom och mellan flockarna.

Metoder

Drygt hundra individuellt ingenkända lejon i 14 flockar följdes under tre års tid. Studieområdet var ungefär 1000 km² stort och därför bara en liten del av det 43 000 km² stora Selous. Alla observationer utfördes från ett fordon som utrustats med hjälpmedel såsom kompass, satellitnavigator, infraröda strålkastare, radiomottagare för radiomärkta lejon, kommunikationsradio, säng och campingkök. Kameror, videokamera, nattglasögon, kikare, bandspelare etc användes för att dokumentera lejonens beteende.

Resultat

Manuskript I.

Det stora flertalet flockar är sammansatta av besläktade honor, men inte alla. Att obesläktade honor håller ihop kan tolkas på två sätt: **a)** antingen är de direkta fördelarna av att leva i grupp så stora att den extra fördelen att samarbeta med släktingar inte är så viktig, **b)** eller så är kriteriet för en släkting att hon finns i samma flock. Denna metod skulle i de flesta fall fungera, men inte alltid. Om man tänker sig två linjer av honor som alltid parat sig med olika hannar, så minskar snabbt släktskapet mellan deras avkomma.

En del flockar bildade grupper av flockar som var mer besläktade än genomsnittet. Dessa flockar kan ha uppstått genom delning av flockar eller genom att hannar som fötts i en flock etablerat sig i angränsande flock. Huruvida släktskap mellan flockar har någon betydelse för honornas beteende när dom möts redovisas i manuskript IV och V.

Manuskript II och III.

Två olika genetiska metoder visar att hannar inte sprider sig långt när dom lämnar sin födelseflock utan ofta bara rör sig till direkt angränsande flock. Eftersom detta innebär en viss risk för inavel är detta resultat intressant. Spridning verkar hos ett flertal arter vara långt kortare än vad som allmänt antagits och riskerna för inavel verkar ha överdrivits i förhållande till de risker som själva spridningen innebär.

Manuskript IV.

Eftersom angränsande flockar kan innehålla nära släktingar kanske aggresivitet mellan individer när flockar träffas varierar beroende på släktskap. För att testa detta utförde jag experiment där rytande från honor i populationen spelades upp för andra honor. Eftersom lejon reagerar på simulerade intrång genom att gå mot ljudet kan deras beteende mätas. Snabbt svar visar på aggresivitet och ett långsamt svar kan visa på försiktighet eller lägre aggresivitet. Släktskap visade sig inte ha någon betydelse för hur honor reagerade. I stället var t. ex. antal honor som röt jämfört med hur många som fanns tillgängliga för försvar viktigt. Detta har också visats tidigare av amerikanska forskare i en annan lejonpopulation i norra Tanzania.

Manuskript V.

Analyser av hur lejonen rörde sig inom reviren visade att tillgången på bytesdjur styrde var lejonen befann sig, och att reviröverlapp mellan flockar inte var beroende av vare sig habitat eller släktskap.

Sammanfattning

Socialt beteende och samarbete är ett av de mest fascinerande resultaten av naturlig evolution. Trots att vår kunskap om vad som orsakar och upprätthåller samarbete i naturen ökat de senaste årtiondena, är mycket ännu oklart.

Hos lejon sprider sig både honor och hannar korta avstånd. Detta gör att lejon ofta har nära släktingar i angränsande flockar. Trots dessa släktband verkar detta inte påverka deras beteende vid möten med honor från andra flockar. Upptäckten att vissa flockar består av obesläktade individer och att hannar sprider sig mycket korta avstånd kan betyda att direkta fördelar med flockliv är viktigare än vad som tidigare antagits och att betydelsen av indirekta fördelar är liten.

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