# Investigating the Social Structure of Female Asiatic Lions

**Dissertation submitted to Saurashtra University, Rajkot, Gujarat**
**For the partial fulfilment of Master's Degree in Wildlife Science**


**By**

**Doli Borah**

**XVI MSc, Wildlife Science**
**Wildlife Institute of India**


**Under the supervision of:**

**Dr. Vishnupriya Kolipakam**

**Dr. Yadvendradev V. Jhala**

**Dr. Sutirtha Dutta**

**June, 2019**

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

Dedicated to Maa, Papa

&

The Lionesses of Gir Landscape

# DECLARATION

I, **Doli Borah**, hereby declare that the research work titled "**Investigating the Social Structure of Female Asiatic Lions**" carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of work. These investigations were carried out under the supervision of Dr. Vishnupriya Kolipakam, Dr. Y. V. Jhala and Dr. Sutirtha Dutta at the Wildlife Institute of India from December 2018 to June 2019. I also declare that this work has not been submitted for any other degree of any university.

Date: 30th June, 2019

Place: Dehradun Doli Borah

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

# CERTIFICATE

This is to certify that **Ms. Doli Borah** has carried out an original piece of research from Wildlife Institute of India, titled **"Investigating the Social Structure of Female Asiatic Lions"**, in partial fulfilment of Master's Degree in Wildlife Science from Saurashtra University, Rajkot, India. The study was carried out under our supervision from December 2018 to June 2019. We hereby certify that this work has not been submitted for any degree to any university.

K. Vishnupriya

Vishnupriya Kolipakam, PhD
Supervisor
Scientist - C

Jhala

Y. V. Jhala, PhD
Co-Supervisor
Scientist - G

Dutta

Sutirtha Dutta, PhD
Co-Supervisor
Scientist - D

Date: 30th June, 2019
Place: Dehradun

पत्रपेटी सं० 18, चन्द्रबनी, देहरादून – 248 001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun - 248 001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स : +91-135-2640114, 2640115, 2646100 फैक्स : 0135-2640117
EPABX : +91-135-2640114, 2640115, 2646100 Fax : 0135-2640117
ई–मेल/E-mail : wii@wii.gov.in वेब/Website : www.wii.gov.in

# ACKNOWLEDGEMENTS

This study would not have been possible without the help and support from a long list of people at various stages of my dissertation journey. I feel privileged to take this opportunity to express my sincere gratitude towards all those people who have supported me throughout this whole journey and extended their valuable assistance and contribution imperatively to this thesis in any possible way.

First and foremost, I would like to thank my supervisors, Dr. Vishnupriya Kolipakam, Dr. Y. V. Jhala and Dr. Sutirtha Dutta for their constant support, guidance, inputs and encouragements right from inception of my dissertation idea, till the final defense. I think I got the best faculties of WII to begin my research career with and no matter how much I thank them it would be always less to express my eternal indebt towards them for everything they did for my dissertation. I shall always be indebted to you all for your constant support, for being patient to listen to me, for prioritizing my opinion, for your time, for all your valuable suggestions, inspirations and blessings and for all the sacrifices you did for me. Along with my supervisors my sincere gratitude to Qamar Qureshi sir, to whom I really have no word which can explain my gratitude for your willingness and kindness to guide me and help me logistically throughout the dissertation journey. Thank you so much, I had a great working experience with you all.

My sincere thanks to the forest department of Gujarat, PCCF, CCF D. T. Vasavada, DCF Wildlife, East and West Gir, range officers, beat guards all the trackers for your kind help and support and for all the facilities you provided during my field days.

I convey my sincere thanks to Director, Dean, Research Coordinator, all the faculties and staff members of WII for their support. Special thanks to Prem Sir for helping us with all the academic work.

Thanks to our Course Director Dr. Gopi G. V. and Assistant Course Director Dr. Samrat Mondal for all the help you provided.

My heartful thanks to the people of conservation genetics lab of WII – Bhavna di and Sneha for helping me with Genetic analysis. My sincere thanks to the Researchers of Gir Lion Project for the long-term data that I used for my study.

I owe my deepest gratitude to my field assistants Bhiku bhai, Hanif Bhai, Irfan Bhai, Sameer Bhai and Maharaj bhai without whom this study was impossible. Thank you very much for all your hard work, support and assistance during every step of my field days which I will appreciate throughout my life.

A big thanks to Keshab, for being always there by my side whenever I needed. Starting from field to analysis till presentation in every step you helped me and guided me. Specially during the difficult times, you are the one who supported me and kept me strong to fight back.

The best part of this whole journey was to have 19 best people around you all the time going through the same phases to share the joy and support each other during difficulties. My heartiest thanks to all my batchmates – Aaranya, Abhisekh, Abir, Bhavya, Buffy, Himanshu, Indira, Kush, Laxmi, Mohit, Nisam, Pratik, Suma, Subha, Sakshi, Siva, Sayanti Titto and Varun for being there with me all the time, for all those sweet memories we shared, all the care and mental support you gave, all the laughter we shared and finally for giving me the best two years of my life.

Finally, thanks to Maa and Papa for being the greatest support throughout my life, always supporting and encouraging me to do something good and for giving me everything I wanted, keeping their own desires behind. Thanks to Jun and Poli ba for all the inspiration and moral support and special thanks to Joli ba because of whom I gained all the strength to do something good and prove myself.

Last but not the least, my heartiest thanks to my study species- the majestic lionesses of Gir for giving me an opportunity to be with them and to understand them. Specially the Ambari Pride with whom I made a special bond and by going through all the family/social issues they had during that time. I feel like, you all the seven lionesses with the naughty cubs are my family members, each one of you with a unique personality who accepted me as a part of their pride.

# Contents

# LIST OF TABLES

# LIST OF FIGURES

# Abstract:

Amongst felids, lion is the only social cat who lives in prides formed of related females and related males forming coalitions. The social structure of Asiatic lioness has not been studied in any depth. In this study I studied the social structure of lion prides in the Gir landscape through behavioural observation. The questions I attempt to answer were a) is there a social dominance within lionesses in a pride, b) If there is dominance hierarchy, then how is it related to age and c) kinship between pride members. I spent 2040 hours observing seven prides ranging from two to seven adult females and their offspring. I identified each lioness individually based on their vibrissae and permanent markings, and collected fresh scat for genotyping each lioness. A panel of 15 microsatellites was used for genotyping lions and subsequently computing their kinship. I constructed social networks, indices of dominance and correlated these with group sizes and age-category of lionesses. My results indicate a strict linear order of hierarchy (based on both affiliative and agonistic interactions) in the upper strata of the dominant females while in the lower strata this linearity tapers off into more amorphous dominant-subordinate relationships. Surprisingly I found unrelated lionesses within prides of related individuals. These non-kin lionesses were usually at the lower strata of dominance within a pride. Dominance was found to be age related with older females mostly being dominant over younger ones. My study opens up new questions for an in-depth long-term study on kinship related fitness within social prides.

# 1. Introduction:

**Why do animals have varied social organization?** Social organization in animals basically refers to the spatial relationship, pattern of social interaction among individuals, group composition, relatedness and the overall manner in which these variables interact with each other to characterize a population (Bekoff and Wells 1986). Among carnivores, inter and intra-specific variations in social organization are evident (Cafazzo, et al., 2010). The evolution of such varied social groups of carnivores has been contributed by diverse selective pressures (Macdonald, 1983). The quantity and distribution of resources and the strategy for acquiring those resources is often considered as the primary selective pressure for group living in carnivores (Fournier, 1995). However, there are other ecological pressures which might govern group living in animals such as the need for defense against intra or inter-specific competitors, division of labour, communal cub rearing, reproductive opportunities etc. (Ewer, 1973; Macdonald, 1983). However, all these benefits of group living must operate within a limit determined largely by the dispersion and abundance of available resources (Macdonald, 1983). Survival, growth, development and reproduction oblige resource acquisition (Ricklefs, 1979) and it ultimately compels competition (Darwin, 1859). When a population is structured into groups, the within-group competition for resources influences the form and function of its social organization (Wittemyer and Getz_2006). Hence, despite the clear advantages of living and coordinating with others in a group, the fact that limitation in resources ensures within-group competition, results in social

groups being often stratified by a dominance hierarchy (Hawley 1999, Wittemyer and Getz_2006).

**How does hierarchy work in shaping social structure?** In social animals dominance has an overwhelming importance, governing not only the pattern of their social interactions but also the overall social structure of a species (Rowell 1974, Creel et al, 1997). Generally, hierarchy within a group is defined as the asymmetry amongst the group members in winning competition over each other (De Waal, 1989). Individuals of a social group may differ amongst themselves in many aspects- having asymmetries in physical power, stamina, age, relatedness, personality, weight, weaponry and so on (Smith and Parker 1976). These differences in their personal traits are likely to influence their relationships (Borg et al., 2015). Since the first ever description of dominance hierarchy in the classic work on 'peck order' in groups of domestic fowl (Schjelderup-Ebbe 1922), the existence of dominance hierarchies has been documented in a wide variety of social vertebrates (Wilson 1975). A dominant -subordinate relationship can be defined as long-term dyadic interaction amongst individuals characterized by an asymmetric distribution of certain traits. It is generally measured in terms of the degree of unidirectionality of those behaviours exhibited by the dyad (Van Hooff & Wensing, 1987). According to Drews and Hand, dominance is considered as the outcome of agonistic dyadic interactions resulting in consistent winner having a dominant status and losers with subordinate status (Drews, 1993; Hand, 1986). However, there are some other measures also which can be considered while understanding dominance (De Waal, 1989). Distinguished by primatologist de Waal, formal dominance can be considered which develops via the exchange of status

information through ritualized and/or greeting signals that are independent of context (De Waal, 1989).

**How kinship influences social structure?** Kinship can have a decisive influence on the form and function of social systems (Ren, 2017). It is also found to have a profound effect on within group interactions in many social species (Guo et al., 2015). The kin selection theory (Smith, 1964) postulates that inclusive fitness benefit is received (Hamilton,1964) by an individual which behaves in an altruistic manner towards its relatives (Michod, 1982). In various taxa, it is found that high kinship among individuals facilitates positive social interaction amongst the group (Foster et al. 2006, Mateo 2002). Lion is one such taxa which lives in social groups with huge importance of kinship. (Schaller 1972). In African Lions, a pride generally comprises of 2-9 related females, their dependent cubs, sub-adults and a resident coalition of 2-6 males (Schaller 1972; Bygott et al., 1979). The Prides of related females and their dependent young ones occupy a permanent territory and defend it against intruders along with the male coalition (Packer & Pusey, 1983). Here, the female members of the prides are genetically closely related siblings with varying degree of relatedness (Spong, G., et al., 2002) and the pride males are mostly unrelated partners to the pride females (Pusey & Packer, 1987; Packer et al., 1991). However, in the case of Asiatic Lions, males form separate coalitions, encompasses several female groups within its territory (Jhala et al., 2009), and move and feed independently (Banerjee 2012). Pride size generally varies between 2-9 females, which are believed to be related to each other (as in African system) and their dependant cubs. Among social animals, interaction among group member are believed not to be random (Fraser et al., 2008), but rather an outcome of selective forces influencing individual behaviour (Wu et al., 2018). Kin preference is one such

selective force that is known to bias affiliative behaviours more towards kin than non-kin members in various species (Silk et al., 2006; Berman et al., 2018). Hence, in societies where animals interact in hierarchies, kin preference can have strong influence on their social structure.

**How social system varies geographically?** Among all the felids, Lion is the only member who lives in distinct fission-fusion social groups called prides (Schaller, 1972). Their social system is dynamic, which may vary with respect to habitat, prey availability, competition, dependency on livestock and anthropogenic pressure (Schaller, 1972). There are two distinct subspecies of extant lions recognized to have diverged in recent times, namely- *Panthera leo leo* in Africa and *Panthera leo persica* in India (O' Brien et al. 1987). In India the Gir forest of Gujarat has the last free ranging population of Asiatic Lions (Singh, 2007). The social system of Lions in these two different landscapes has been found to be different (Jhala et al. 2009, Chakrabarti and Jhala 2017). In African system male lions stay along with the females and their cubs in a pride (Schaller 1972, Bertram 1975); while in Asiatic system males do not associate with females in a pride and tends to move and feed independently or by forming coalition of 2-3 males (Jhala et al. 2009). The male Asiatic lion forms weak bonds with females, associating only at the time of mating and occasionally in large kills (Jhala et al. 2009). In African lion there is no dominance hierarchy reported within the pride members (Schaller 1972; Bertram 1975; Bygott et al. 1979; Packer and Pusey 1982) while in Asiatic lions pronounced dominance hierarchies have been observed within coalitions of male Asiatic lions (Chakrabarti and Jhala, 2017).Where they observed a distinct feeding order and higher mating access of the dominant males than the subordinates among the coalition partners, demonstrating the presence of a dominance hierarchical system

among them (Chakrabarti and Jhala, 2017). However, the social structure of female Asiatic lions has not been studied scientifically so far. In this study we investigated the social structure of female Asiatic lions through behavioural observation in Gir Protected Areas of Gujarat. I investigated if there is any social hierarchy among the pride members and if present what type of hierarchy is there and do age and kinship has any influence to their hierarchy.

# 3. Literature Review:

Group living has both cost and benefit associated with it (Alexander, 1974). Individuals may cooperate among themselves for gaining access to food and mate, but they may also need to compete among themselves for those same resources (Veherencamp, 1983). This competition can lead to conflicts among the group members that may compromise group stability. It can be resolved by dominance hierarchies built from stable dyadic dominance relationships, allowing regulation of priority of access to highly valuable resources, and thereby preventing ferocious conflicts. (Borg et al.,2015).

## 3.1 Different types of Animal Societies:

According to one predominant view; in many species, predation pressure forces them to live in group and availability of resources determines the strength of within group competition along with their social structure (Archie et al., 2005). Species that are dependent on abundant and widely dispersed resources are expected to live in **egalitarian** societies, where there is no prominent differentiation in social rank among the members (Isbell & Young 2002). It might be because, when food resource is widely distributed and abundant within group competition would be reduced and hence animals do not need to maintain strict social hierarchy to gain access over resources (Wrangham, 1980). In contrast, animals form **despotic** societies where resources are clumped and monopolizable, with strong linear dominance hierarchies among the members (Isbell & Young

2002, Wittig and Boesch, 2003). In such societies high dominance rank confers fitness benefit by easy access to resources (van Schaik, 1989, Wittig and Boesch, 2003). In **Nepotistic** hierarchies dominance rank is determined by relatedness where related individuals rank close together (Archie et al., 2005). They mostly rely on coalitionary support from kin and acquire a rank adjacent to their mother (Frank 1986, Holekamp et al., 1996), gain direct or inclusive fitness benefits from mutual aid with their relatives (Sterck et al. 1997). Study by Archie et al., on female African Elephants tried to understand the dominance rank relationship by testing three possibilities - (a) Egalitarian (b) Linear, nepotistic (c) Linear, age/size ordered. It was found that in female African elephant's dominance hierarchy is transitive and age-ordered such that older and larger females consistently dominate smaller and younger females (Archie et al., 2005). Published studies on Spotted Hyaena (*Crocuta crocuta*) have found close association among females with their adult female kin than with unrelated adult females. Female kin from high ranking matrilines were also found associated more closely than did kin from lower-ranking matrilines (Holekamp et al., 1997). Studies also suggest that maternal rank gets inherited to the offspring and the rank of the females in the pride influences the fitness of their cubs (Frank 1986, Holekamp et al. 1997, Drea and Frank, 2003). In Spotted Hyaena the cubs of higher-ranking female get many advantages over their mother's rank like – feeding access at kills than other cubs of lower-ranking mothers (Frank 1986, Holekamp et al. 1997), and starts feeding on kill at an earlier age than others. Only the male offspring of alpha female becomes dominant over adult females and gets the advantage of remaining in the natal clan significantly longer than other males before dispersing (Frank 1986). Similar findings obtained from the study done by Engh et al. on Mechanism of maternal rank inheritance in spotted Hyena (Engh et

al., 1999). Similar pattern can also be seen in African wild Dog (Lycaon pictus) and Wolves (Canis lupus) (Haber 1977, Creel et al. 1997). Thus, the dominance rank of females positively correlated with their reproductive success by aiding higher infant survivability, faster maturation of offspring and more rapid production of offspring (Wittig and Boesch, 2003, Pusey et al., 1997). For females the most important resource is usually food (Trivers, 1972), as a better fed female can invest more energy in reproduction and thereby produce more offspring or can supply more food to offspring (Wittig and Boesch, 2003).

## 3.2 Types of Dominance hierarchy:

There are basically two forms of dominance hierarchies- Linear and Non-linear or Despotic hierarchies. Simply in a linear hierarchy (pecking order), each member has a relative rank while in a despotic hierarchy, one member is dominant over all other. Within a strictly linear hierarchy, all dyads have a dominant subordinate relation, and dominance relations for every set of three individuals (triads) are transitive i.e. when individual A dominates B and B dominates C, then A also dominates C (Chase 1982; de Vries 1995). In contrast, a triad arranged in a cycle where A dominates B, B dominates C, and C dominates A. These cyclic triangles result in dominance relations that are unresolved and prevents the linear arrangement of ranks (Shizuka and McDonald 2012).

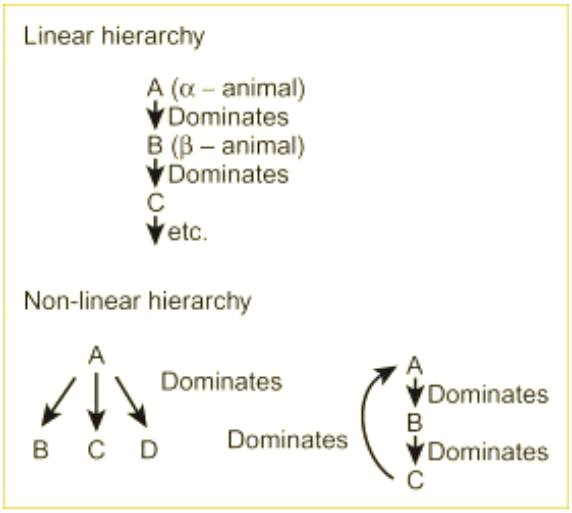



**Figure 1. Showing two forms of dominance hierarchy; Source- ScienceDirect**

### 3.3 Greetings as a measure of Dominance:

According to many authors, dominance can also be described in terms of formal dominance (De Waal, 1989). Formal dominance is characterized by the exchange of ritualized signals or greeting rituals among members of group living animals (De Waal, 1989). These are basically the affiliative interactions among individuals, whose direction does not vary across social contexts (Cafazzo et al.,2010). Various affiliative interaction describing formal dominance could be – greeting, grooming, postural displays, pant-grunt, mouth licking, tail wagging etc. depending upon various taxa. Formal sign of dominance or submission have been described in wild wolves and captive wolves (Schenkel, 1947; Feddersen-Petersen, 2004), where they found postural display as indicator of formal dominance. They

found in the study that the higher the wolves were in rank, the more greetings they received. Also, 60.99% of greetings were received by the breeding pair and at the dyadic level, greeting was directed mainly from subordinates towards dominant individuals (Cafazzo et al.,2016). A distinct and directional greeting pattern has been observed in female Chimpanzees (Pan troglodytes) directed from subordinate to the dominant female (Wittig and Boesch, 2003) where greeting serves the function of formalized submission by providing context free assessment of dominance relationship (Bygott,1979). However, so far signals of formal dominance have been systematically tested only in domestic dogs (Cafazzo et al., 2010). In the study they found that mouth licking associated with tail wagging (greeting behaviour in Dog) served the criteria of a formal signal of subordination in both free-ranging (Cafazzo et al., 2010) and group housed dogs (Van der Borg et al., 2015). Bauer and Smuts (2007) reported that play in adult dogs reflects the existing dominance structure. In fact, dogs may use play to establish stable social relationships and test their place in the existing social structure of a group (Bekoff 1972).

When the agonistic dominance is accepted by the subordinates, dominance relationships becomes stable and formal and agonistic dominance coincide (Fournier & Festa-Bianchet, 1995). In such case, the exchange of hierarchical status information may be conveyed mainly through formalized submissive signals, resulting in a low frequency of overt aggressive conflicts (Cafazzo et al.,2016). In such case the subordinate acknowledges the higher dominance status of the other by showing formalized submissive signals (de Waal 1989).

### 3.4 Sociality in Lion:

The traditional explanation for lion sociality is that Lion live in social groups because cooperative hunting increases food availability by allowing the lions to kill prey that would be too large for an individual to tackle (Coulson, T., 2007). However, the later studies done on African lion, argues that cooperative hunting is not the actual reason for sociality in lion, as living in groups decreases the amount of food intake even if the prey is also gregarious and also lions do not hunt as cooperatively as believed (Coulson, T., 2007). Fryxell et al. showed that there is a 90% reduction in the food-intake rate per lion compared with the rate when lions forage solitarily (Fryxell et al.,2007). Also, mostly they hunt cooperatively only when they need to. If it is a large and dangerous prey, lions certainly do pull together. But if the prey is relatively easy for a singleton to capture, the rest of the pride mostly watches the hunting scene rather than joining the hunt (Packer, 2015). According to the studies the true hallmark of lions' sociality is territory defense due to which it is necessary for lions to hold a high-quality territory for successful reproduction (Packer,2015).

Lions are the only Felidae species known for their high degree of sociality. Observation by Joslin on Asiatic Lions, suggests the possibility of presence of dominance hierarchy. He observed lionesses acting as dominant and subordinate members. He also observed litter mates feeding together and being more tolerant to each other than offspring from another litter. Along with that he observed distinct feeding order on smaller prey (Joslin 1973). Recent study on male Asiatic lions found distinct dominance hierarchy among the male coalition partners based on the observation on their mating events and feeding incidents (Chakrabarti and Jhala, 2017). In this study it was recorded that within male coalitions, having pronounced

dominance hierarchy the dominant individual gets more than 70% of all mating and 47% more food compared to the subordinate individual (Chakrabarti and Jhala, 2017). Literature suggests that there is no dominance hierarchy in African lion prides (Schaller 1972). However, as mentioned earlier, there is distinct dominant hierarchy in male Asiatic lion coalitions. In this context there is little quantitative data concerning the dynamics of social organisation, dominance hierarchy, affiliative relationships, coalition/alliance formation and reconciliation behaviour of female Asiatic Lion. Given the current scenario of their rescue-rehabilitation of expanded population across human dominated landscape and future reintroduction plans, the findings of this study would be extremely helpful to decide on carrying out these exercises without disrupting their social structures.

# 4. Research Questions:

1. Is there any social hierarchy among the pride members of female Asiatic lions?
2. What is the type of social hierarchy operating among the female pride members (if any)?
3. How are the pride members related to each other and what influence age and relatedness has to their dominance hierarchy?

## 4.1 Possibilities:

1. Is there any social hierarchy among the pride members of female Asiatic lions?

**Rationale 1:** The within group competition for critical resource influences the formation of social hierarchy in group living animals (Wittemyer and Getz_2006). Generally, species dependent on monopolizable resources (clumped or patchy) tends to evolve strict, transitive dominance relationship (Wittemyer and Getz_2006). Species like spotted hyena, African elephant, Hanuman Langur shows such dominance hierarchy. A Recent study has observed a pronounced dominance hierarchy within the coalitions of male Asiatic lions with distinct feeding order and mating access among the coalition partners (Chakrabarti and Jhala, 2017).

***Possibility 1:*** There would be an observable strict hierarchy among the pride members of female Asiatic lion during their feeding, grooming and greeting interactions based on age and/or relatedness.

**Rational 2:** Furthermore, the nature of interaction among the members of a group living species may be conditional based on the availability of food resources (Mech,

1999). As in case of Wolves (*Canis lupus*) pack members of all ranks feed simultaneously around a carcass when it is a large prey but when the prey size is smaller the dominant animals feed first and control the subordinates from feeding (Mech 1966; Haber 1977).

***Possibility 2:*** There would be conditional dominance among the pride members.

***Possibility 3:*** There won't be any dominance hierarchy among the pride members.

2. How are the pride members related to each other and what influence age and relatedness has to their dominance hierarchy?

**Rationale 1**: In social animal's dominance hierarchies can be individualistic where ranks are independent of relatedness or nepotistic where kin tend to rank close together. Nepotistic hierarchies are typically observed in kin-based philopatric species, where individuals mostly stay in natal group and receive inclusive fitness benefits from aid to their relatives (e.g. Spotted Hyena).

***Possibility*:** Based on the context of African system, for female Asiatic lions we expect pride formation to be determined by genetic relatedness and age and/or genetic relatedness will have influence in their dominance hierarchy.

We expect that the most dominant animals within a pride would be closely related with each other while the others in lower hierarchical rank would be distantly related and there should be high collinearity between relatedness and dominance.

## 5. Objectives

To explore the above-mentioned questions, my study objectives are as follows-

1. To understand the social structure of female Asiatic lions.
2. To understand the relatedness among the pride members of Female Asiatic Lion
3. To study whether age and relationship of the animals influences the hierarchical system of Asiatic lion (if hierarchical dominance is present).

## 6. Study Area:

The study was carried out in and around Gir Protected Area of Gujarat. In India the Gir forest only has the last free ranging population of Asiatic Lions. Gir Protected Area (1,888 km2, 210 20' N to 200 40' N latitude and 700 30' E 710 15' E longitude) falls under the semi-arid biogeographic zone of Gujarat Rajputana Biotic province 4 b. It is a dry deciduous forest (Champion & Seth, 1968) situated in the Saurashtra region of Gujarat state, western India and is made up of a Sanctuary (with human settlements, regulated grazing, wildlife and religious tourisms and other rights) covering 1,153 km2, a 259 km2 National Park (inviolate area devoid of any human habitation or use) and 471 km2 of additional reserve, protected and unclassified forests (Meena & Kumar, 2012). Gir has a semi-arid climate with an average annual temperature ranging from 5º C (winter) to 44 º C (summer) and an average annual rainfall of 980 mm (Meena & Kumar, 2012). Rugged hilly terrain (elevation ranging from 83 m above msl to 648 m above msl) forms the catchment

of seven perennial rivers. Dominant vegetation includes *Tectona grandis*, *Anogeissus spp*, *Acacia spp* and *Ziziphus spp* (Qureshi & Shah, 2004). Along with the last free-ranging population of the Asiatic lion, other carnivores found in Gir PA are leopard (*Panthera pardus*), striped hyena (*Hyaena hyaena*), jackal (*Canis aureus*), ratel (*Mellivora capensis*), jungle cat (*Felis chaus*), rusty spotted cat (Prionailurus rubiginosus), ruddy mongoose (*Herpestes smithi*), common Indian mongoose (*Herpestes edwardsi*) and small Indian civet (*Viverricula indica*). Major wild prey species were chital (*Axis axis*), sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelus*), wild pig (*Sus scrofa*), chinkara (*Gazella bennettii*) and four horned antelope (*Tetracerus quadricor nis*).

Seven groups of Female Asiatic Lion were selected for the study from in and around Gir Protected area. Out of the 7, six groups are from west Gir and only one group from eastern landscape of Gir Protected area. The groups were selected randomly based on availability of preferred group size. However, there was no obvious bias that would influence social organisation of groups based on their selection. Below is the Map showing the location of the groups during the study period (Figure 2).

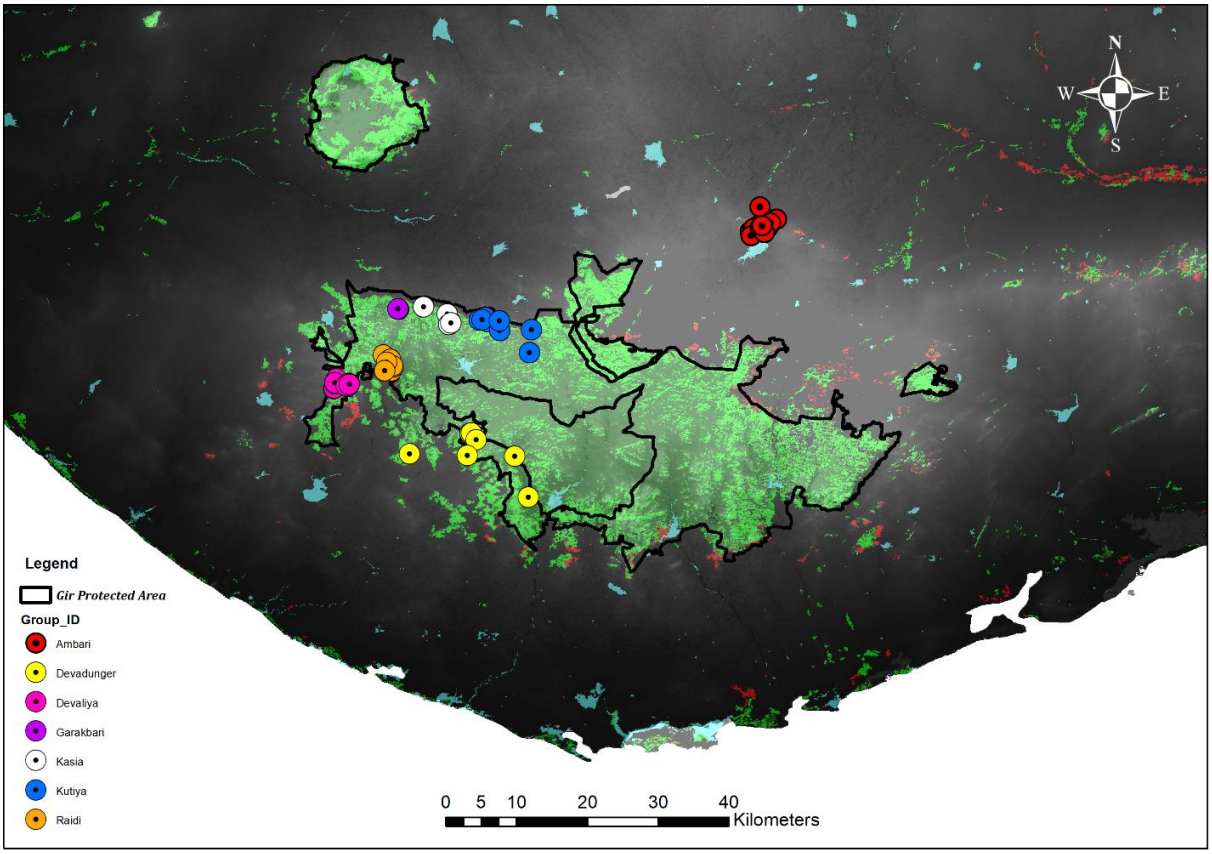



**Figure 2: Study area and locations of Female prides in Gir Landscape, Gujarat**

# 7. Methodology

## 7.1 Study design:

For the study 7 female prides were selected belonged to group sizes- small (2 individuals), medium (3-4 individual) and large (5 and > 5 individuals) (Table 1). Prior to data collection all the individual of the prides were identified based on their whisker pattern, ear-notches, special body mark and approximate age (Jhala et al. 2009), a catalogues has been prepared for each individual of the study prides for easy field identification and data were subsequently entered into the program "Lion" (Figure 3) (Jhala et al., 2005). Groups were followed continuously day and night to gather information on their interactions and detect predation or feeding events. Groups were followed until a minimum of three feeding observation were

made. To reduce the impact of observer's presence on the groups behaviour a required distance is maintained while following the group or while observing.

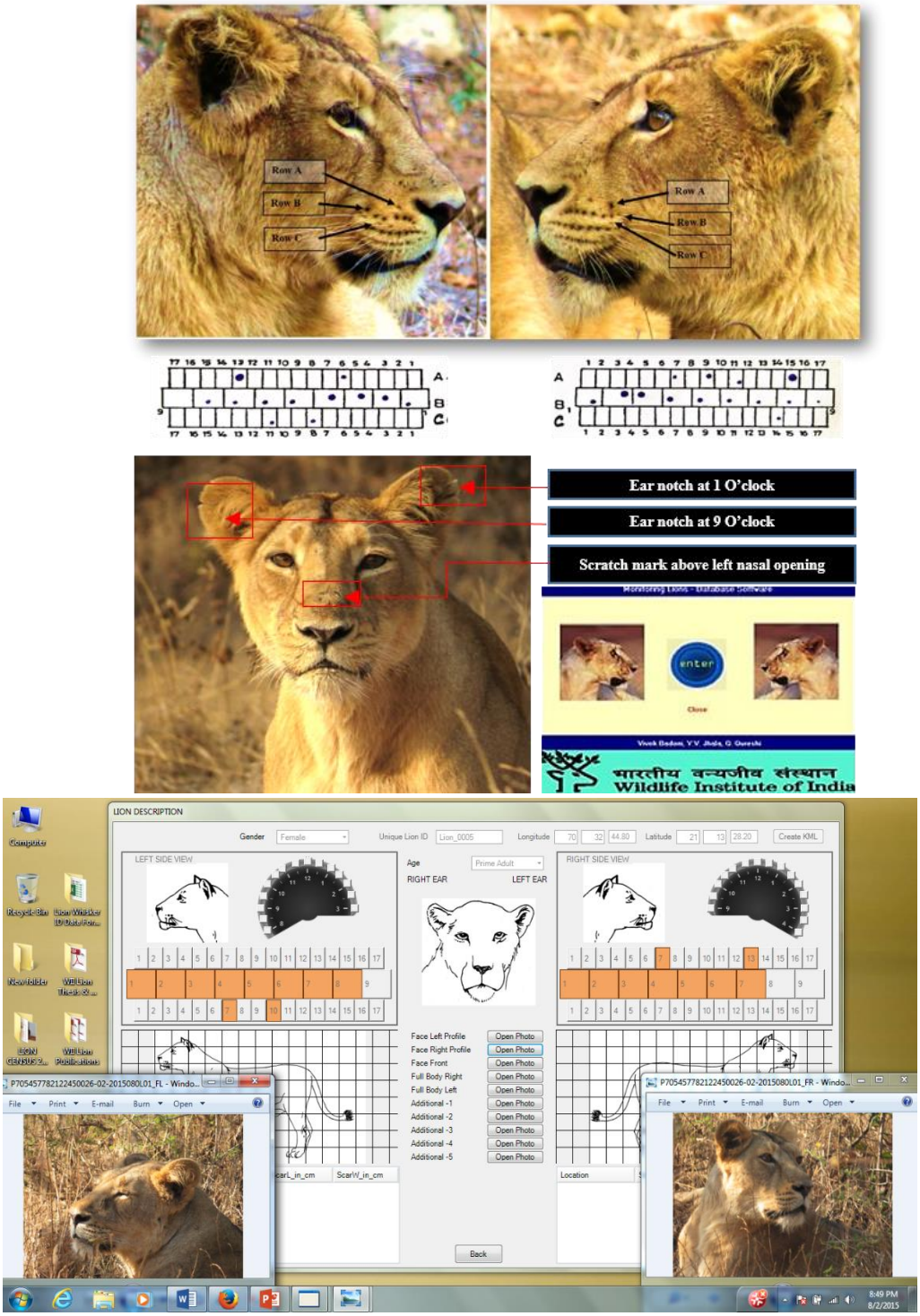



**Figure 3: Catalogue used for identification of Lion. Source: Program "Lion"**

**Table 1: Groups and approximate age of study lionesses in the seven prides in Gir landscape.**

| Group No | Category | Goup ID | Adult Female Group Size | Individual ID | Age | Age categories |
|---|---|---|---|---|---|---|
| 1 | Large | Ambari | 7 | Amb_F1 | 7-8 | Prime adult |
| | | | | Amb_F2 | 9-10 | Old Adult |
| | | | | Amb_F3 | 8-9 | Prime adult |
| | | | | Amb_F4 | 4-5 | Young adult |
| | | | | Amb_F5 | 4-5 | Young adult |
| | | | | Amb_F6 | 7-8 | Prime adult |
| | | | | Amb_F7 | 9-10 | Old Adult |
| 2 | Large | Kutiya | 6 | Kt_F1 | 8-9 | Prime adult |
| | | | | Kt_F2 | 4-5 | Young adult |
| | | | | Kt_F3 | 9-10 | Old Adult |
| | | | | Kt_F4 | 6-7 | Prime adult |
| | | | | Kt_F5 | 11-12 | Old Adult |
| | | | | Kt_F6 | 7-8 | Prime adult |
| 3 | Medium | Devaliya | 3 | Dv_F1 | 8-9 | Prime adult |
| | | | | Dv_F2 | 6-7 | Prime adult |
| | | | | Dv_F3 | 7-8 | Prime adult |
| 4 | Medium | Raidi | 3 | FLG 15 | 11-12 | Old Adult |
| | | | | FLG 22 | 7-8 | Prime adult |
| | | | | FLG 43 | 4-5 | Young adult |
| 5 | Medium | Kaisia | 3 | Ks_F1 | 4-5 | Young adult |
| | | | | Ks_F2 | 4-5 | Young adult |
| | | | | Ks_F3 | 4-5 | Young adult |
| 6 | Small | Gadakbari | 2 | FLG 1 | 9-10 | Old Adult |
| | | | | FLG 25 | 7-8 | Prime adult |
| 7 | Small | Devadunger | 2 | FLG 30 | 10-11 | Old Adult |
| | | | | FLG 31 | 6-7 | Prime adult |

## 7.2 Field Method:

Continuous focal and scan sampling has been used for recording overall behaviour of the group members. The continuous focal sampling method is ideal for recording social interaction between two or more animals in a group, where all the activity that occur is recorded while the animals are being watched (Altmann J,1974). All occurrences sampling was used for recording agonistic and affiliative interactions among the female pride members (Lehner, 1998). Their interactions with respect to varying food resource characteristics were also recorded. Agonistic and affiliative behaviour has been recorded mentioning the donor and receiver of the particular behaviour. Where affiliative behaviour includes greeting and grooming interactions whereas agonistic behaviour includes any kind of aggressive interactions between individuals. will be recorded. Data based on the donor and receiver of the interactions has been recorded along with the duration of the behavioural state and frequency of the events.

Behavioural observations were recorded with a digital video recorder for future references and verification. Observations during night time was done using flash light and an infrared light with infrared camera was used for recording behavioural observations. Dictaphone is used for voice recording the observations when the animal is moving or in cases when many interactions happens in a single moment.

I collected faecal samples of known individuals, through visual confirmation, of my study prides. Collected faecal samples were labelled with the identity of the animals that defecated, date, geographic coordinates, time, area, name of the

observer and sealed in Ziplock pouch filled with silica gel. Samples were immediately sent to the lab for further analysis.

**Figure 4: A glimpse of field data collection**

### 7.2.1 Age Determination:

Age of individuals lions were determined by looking at teeth wearing, gum line recession, teeth colouration, slack jaws, nose pigmentations and mane formation and colouration in case of males (Jhala et al. 2004). All the lions were further categorised into broad age classes as follows:

**Table 2 : Age classes of Lion**

| | |
|---|---|
| Below 1 year | Cub |
| 1-2 years | Juvenile |
| 2-3 years | Sub-adults |
| 3-5 years | Young adults |
| 5-9 years | Prime adults |
| >9 years | Old adults |

## 7.3 Lab Method:

The Lab work was carried out by experienced laboratory technicians in the Conservation Genetics Lab, Wildlife Institute of India.

DNA were extracted using the technique mentioned by Boom et al., 1990. Extracted DNA was amplified for 15 Microsatellites standardised for Asiatic lions (Kolipakam et al., Pers. comm) - FCA304, FCA126,F85, FCA077, FCA441, (Menotti-Raymond, et al. 1999), PLE57, PLE21, PLE23, PLE86, PLE56, PLE65, PLE51 (Singh et al., 2002) 6HDZ700 (Williamson et al., 2002), E7(Bhagavatula and singh, 2006) through standardised PCR protocols (Maroju et al., 2016). Genotyping was done for the individuals within a pride to arrive at individual genotypes for our samples.

## 7.4 Analytical Method:

For the genetic analysis I used the data from the on-going work on Lion genetics from the Long-term monitoring project at Gir, to compute a population level relatedness of lions which is already optimized through a microsatellite panel (Kolipakam et al., Personal communication). Subsequently, I computed a relationship index for each pair of females within each pride and compared it to the population relatedness index generated from the database of long-term research on Gir lion (Jhala et.al., Personal communication). Based on the genotypes scored, relatedness of individuals was estimated using Genalex 6.5 (Peakall& Smouse, 2012) through Queller & Goodnight's estimator (Queller & Goodnight, 1989).

### 7.4.1 Landau's linearity test

For linearity test Landau's linearity index h' was used. Landau's linearity index is used to measure the degree of linearity in a set of dominance relationship (Landau,1951).

The Landaus linearity index (h) is calculated by the following formula-

$$h = \frac{12}{N^3 - N} \sum_{i=1}^{N} [V_i - (N-1)/2]^2$$

Where,

N= Total number of Individual

Vi= The number of individuals dominated by the individual i

However, there might arise unknown dyadic relationships in interaction matrixes as these are common because in natural situation certain pairs of individuals might fail to interact thereby creating null dyads. Hence, to take care of such null dyads de Vries formulated modified Landau's h value (de Vries 1995).

The modified Landau's h value can be calculated using the following formula

$$h' = h + \frac{6}{N^3 - N} \times u$$

Where,

u = number of unknown relationships

A strict linear hierarchy is the one in which higher ranked individuals dominate all individuals of lower rank. Within a strictly linear hierarchy, all dyads have a dominant-subordinate relation, and dominance relations for every set of triads are transitive when individual A dominates B and B dominates C, then A also dominates C (Chase 1982; de Vries 1995).

The value of Landau's modified linearity index h' varies from 0 to 1. Value of 0 indicates a complete absence of linearity i.e. no hierarchy and values of 1 indicates a perfect linearity where every individual dominates all animals ranked below and none of those ranked above.

An associated p-value based on a sampling process using 10,000 randomizations assesses the statistical significance of the linearity index (Klass, K. and Cords, M., 2011).

### 7.4.2 Triangle transitivity

Triangle transitivity (ttri) is used to measure the transitivity of dominance relations among sets of three individuals that all interact with each other. Triangle transitivity and linearity are essentially equivalent when dominance relations of all dyads are known, but such complete observations are rare in empirical studies (Shizuka and McDonald 2012).

A hierarchy will be called non-transitive when the interaction among three individual (triad) creates a cyclic triangle, i.e. when A dominates B, B dominates C, and C dominates A.


The Triangle transitivity (ttri) value is calculated by the following formula --

$$P_t = \frac{N_{\text{transitive}}}{N_{\text{transitive}} + N_{\text{cycle}}}$$

In random networks, the proportion of transitive triangles ($P_t$) relative to all possible triangles among the individuals is expected to equal 0.75. With an expected value of Pt = 0.75, the transitivity can be scaled so that it runs from 0 for the random expectation to 1 (all triangles are transitive, no cycles).

The proportion of transitive triangles relative to all triangles (Pt) is given by=

$$t_{\text{tri}} = 4(P_t - 0.75)$$

Where,

$N_{transitive}$ = the number of transitive triangles

$N_{cycle}$ is the number of cyclic triangles.

The value of both ttri and Pt ranges from 0 to 1, where ttri, Pt = 1 represents a completely linear hierarchy, as all dyads have a dominant-subordinate relationship, and all dominance relations are transitive and ttri,pt =0 represents a non-transitive, non-linear hierarchy. The value of ttri could be negative if more cyclic triangles occurred than would be expected in a random network.

Study done by Shizuka and McDonald on measurements of dominance hierarchies found that the network size (number of Individuals in a group) affects the Landau's h' value of linearity (Shizuka and McDonald, 2012). The expected value of h decreases with increasing group size (Landau 1951). This issue arises due to the presence of null dyads (dyads without any interaction) in a group, as large group tends to contain more null dyads. However, the Triangle transitivity (ttri) value remains unaffected by the overall group size and it remains high even in large

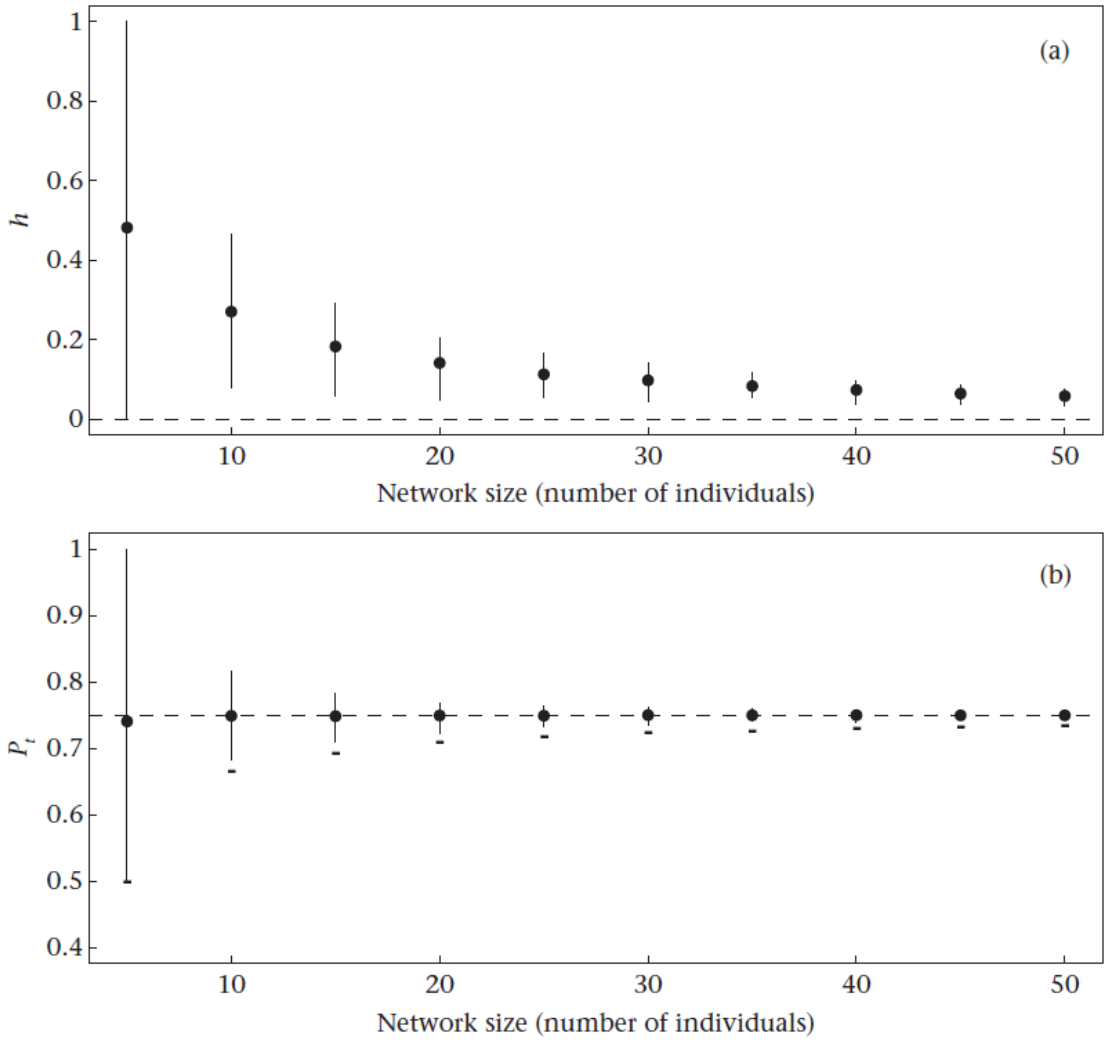



**Figure 5: Change in average value of Landau's h and transitivity pt with network size or group size (Shizuka et al., 2012)**

groups. Also, the ttri value is scaled relative to a constant value (Pt = 0.75), regardless of the group size (Figure 5).

### 7.4.3 Test for Inconsistency:

In a natural scenario, the number of dominance interaction per dyad is not necessarily always a fixed number (Foris et al., 2019). There might be dyads without any dominance interaction between them or there might be dyads with equal number of interactions. Here, the first case would be considered as having an **unknown relationship** and the later with a **tied relationship** (Foris et al., 2019). The I and SI method considers the presence of such dyadic interactions and gives them a proper ranking (de Vries,1997). In this method they construct a dominance rank order for the individuals with minimum inconsistency among them by switching their positions (Schmid and de Vries 2013).

The term inconsistency for a hierarchical ranking system arises when an individual A dominates another individual B in spite of being in a lower rank to A (de Vries, 1997). Here, **I** stand for number of inconsistency and **SI** stands for strength of inconsistency (Cafazzo et al., 2016). The I and SI value for a ranking system is calculated by counting the number of inconsistencies among the dyads and by counting the number of ranks above which the inconsistency appears (Schmid and de Vries 2013).

The I and SI values for the dyads of the 7 groups were calculated to check if there is any inconsistency present based on the best matrix given by the method using R package “compete” (Curley, 2016).

### 7.4.5. Test for directionality:

The directional consistency index (DCI) is used to quantify the directionality of the interactions among the individuals (DC; van Hooff & Wensing, 1987). It is obtained by the following formula-

$$DC = \frac{(H-L)}{(H+L)} = \frac{\sum_{i=1}^{n}\sum_{j=i+1}^{n}\left|x_{ij}-x_{ji}\right|}{N};$$

Where,

H= number of the total interactions in the most frequent direction

L= number of interactions in the less frequent direction

H+L = total of interactions performed by all individuals in the group.

The value of directionality ranges from 0 to 1. Where a DC index value close to 0 indicates that social reciprocity is near its maximum. On the other hand, a DC value close to 1 implies that most dyadic interactions are unidirectional and social reciprocity is near its minimum value (Leiva et al., 2008).

The Directional consistency Index is calculated for the groups in R using package “compete” (Curley, 2016).

### 7.4.6. David's Score, to assign hierarchical rank

When significant linearity was detected, dominance ranks were determined using David's Score. David's Score calculates dominance ranks for individuals based on the outcomes of agonistic encounters with other group members, while taking the relative strength of their opponents into account (David, 1988). David's Score uses the proportion of wins by each individual within each dyad or the proportion of the interactions of each individual that result in wins or losses. David's score is calculated by the following formula-

$$DS = w+w_2 -l-l_2$$

Where,

$w$ = sum of proportion of wins by the subject

$w_2$ = sum of weighted proportion of wins of the individuals against whom the subject has won

$l$ = sum of proportion of losses by the subject

$l_2$ = sum of weighted proportion of losses of the individuals against whom the subject has lost.

To calculate $w_2$ and $l_2$, weight is given by multiplying an opponent's proportion of wins or losses by its respective $w$ or $l$ value.

David's score (DS) is a cardinal ranking method in which rank differences express the magnitude of power differentials between individuals. David's scores form the basis of a measure of hierarchy steepness (de Vries et al., 2006), where steepness is the slope of the line derived from graphing DS, ranked from highest to lowest, against individual identity (de Vries et al., 2006). If there are large

differences in the DS assigned to individuals, the hierarchy is steep; if many individuals have similar scores, the hierarchy is shallow. To obtain a steepness measure that varies between 0 and 1, it is necessary to convert DS into a normalized-DS. The normalized David score is calculated by the following formula-

$$\text{NormDS} = \{\text{DS} + N(N-1)/2\}/N,$$

Based on normalized DS, which account for the variation in numbers of interactions between individuals throughout the matrix, steepness can vary between 0 and 1, and the steepness index is independent of group size (de Vries et al., 2006).

Linearity, Triangle transitivity and David's Score was calculated in R using the packages-"aniDom" (Farine and Tojar, 2019) and compete (Curley, 2016).

### 7.4.7. Pearson Correlation test between David score for affiliative and agonistic interactions

Among the seven selected groups in three groups- Kutiya (N=6), Devaliya (N=3) and Devadunger (N=2) no agonistic interaction have been recorded during the study period. I tried to find out if affiliative interactions can be used to measure dominance rank in a similar manner as agonistic interactions. The outcome of affiliative interaction has been recorded as a win and lose situation considering- an affiliative interaction received but not reciprocated as **win**, whereas an affiliative interaction given but not reciprocated as **lose**. After attaining win and lose information for affiliative interactions for all the groups, David score has been

calculated for each individual in a group in a similar manner it has been done for aggressive interaction. A **Pearson correlation test** has been performed between the normalized David's Score values of both aggressive and affiliative interaction for each group. The correlation coefficient (r) obtained from the test will give the numerical measure of the degree of association between two variables. The coefficient value always lies between -1 and 1 and it measures both the strength and direction of the linear relationship between the variables.

### 7.4.8 Social Network Analysis

To characterize and examine the interactions between individuals and thereby understanding the social organisation of female Asiatic Lion, social network analysis was done using UCINET software (Borgatti et al.,2002). Separate social networks are created for both affiliative and agonistic interactions. To understand the strength of the interactions, scores assigned for different types of agonistic and affiliative interaction was used as a weight for the edges.

### 7.4.9 Linear mixed effect models to evaluate effect of age on hierarchical rank

To determine whether age has any influence on the hierarchical ranks of female Asiatic Lion linear mixed-effect was used in program R3.4 (R core Team 2018) by using package "lme4" (Douglas et al., 2014). I run three models where dominance score was modelled as a response to various combination of fixed and random effect of Age category of lionesses. Best model was selected based on AIC (Akaike, 1974) and model output was plotted using ggplot by using package "ggplot2" (Wickham, 2015) in R3.4 (R core Team 2018).

# 8. Results

Continuous behavioural observations were carried out both day and night on the above mentioned 7 female groups with their dependent cubs over a period of 3 months (February 2019 to April 2019). Total of 380 behavioural events were collected with an expense of 740-man days. A total of 22 feeding observations were made out of which Ambari group was observed in 5 events, Kutia group was observed in 3 events, Gadakbari group was observed in 2 events, Raidi group was observed in 4 Events, Devadunger group was observed in 2 events, Kasia group was observed in 2 events, and Devaliya group was observed in 4 events.

## 8.1 Social Network Analysis:

Below are the separate social networks created for each group, where size of the nodes represents the degree of aggression given in Fig (a) and degree of affiliation received in Fig (b), whereas size of the edges is representing the intensity of the interactions with the arrows pointing towards the receivers. Where - node represents Individuals, edges represent interactions, width of edges represents intensity of the interactions, size of node represents the degree of aggression given for aggressive network and affiliation received for affiliative network.

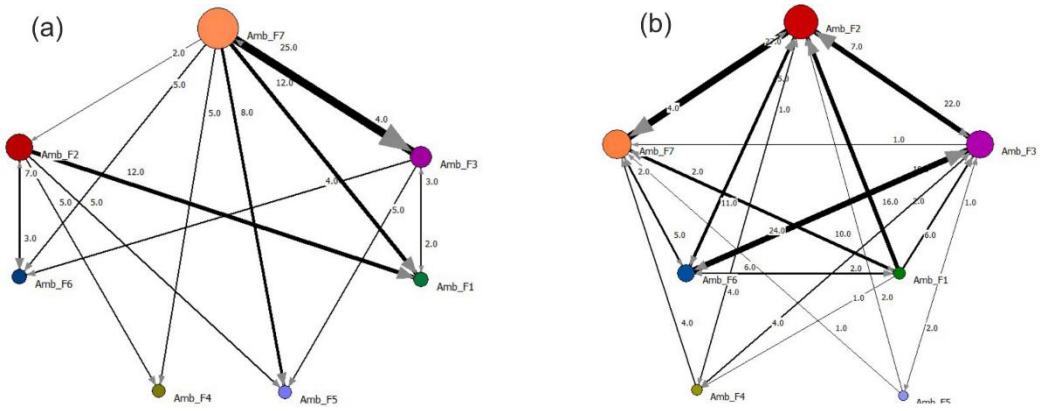



**Figure 6: Social networks for Ambari Group (a) Agonistic Network (b) Affiliative Network**

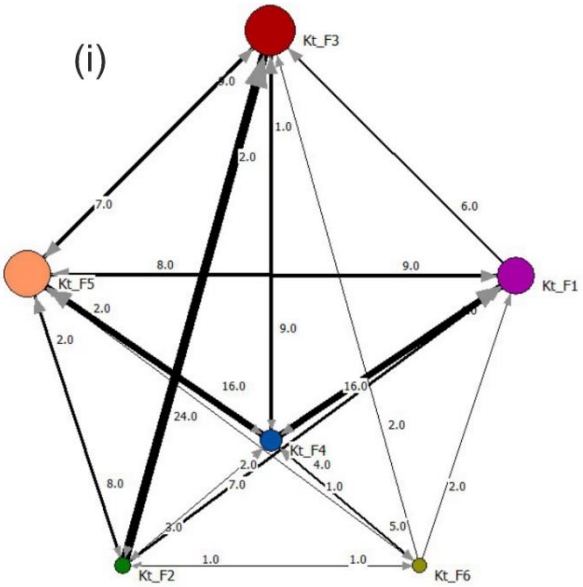



**Figure 8: Social networks for Kutiya Group -Affiliative Network, no agonistic interaction observed**

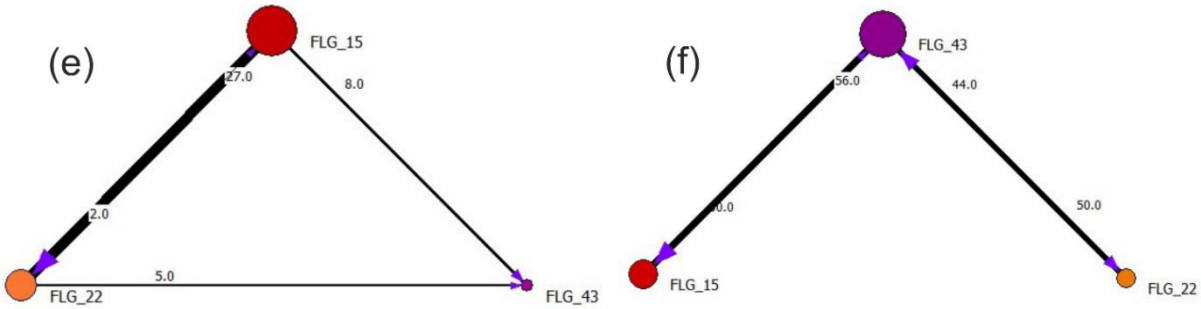



**Figure 7: Social networks for Raidi Group (e) Agonistic Network (f) Affiliative Network**

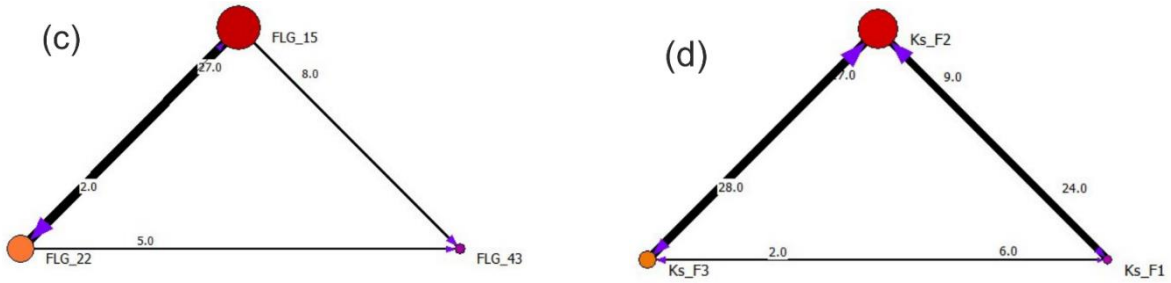



**Figure 9: Social networks for Kasia Group (c) Agonistic Network (d) Affiliative Network**

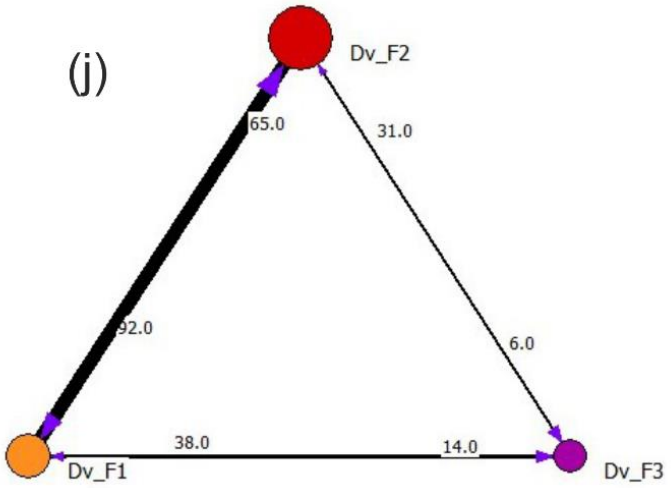



**Figure 10: Social networks for Devaliya Group - Affiliative Network, no aggressive interaction was observed**

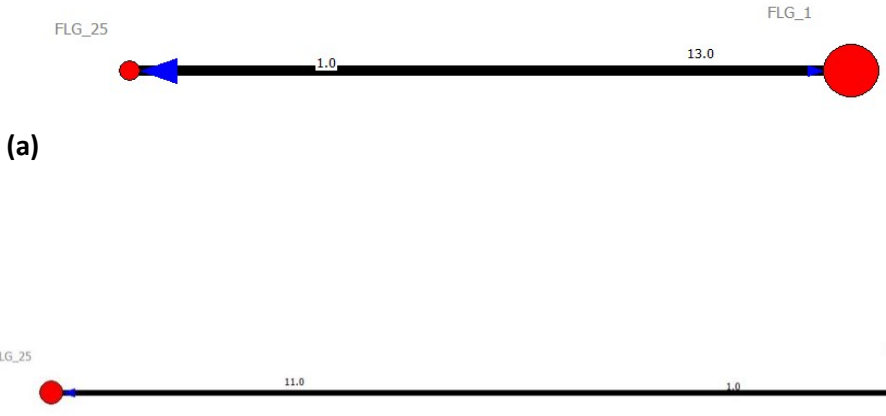



**Figure 11: Social networks for Gadakbari Group - (a) Agonistic Network (b) Affiliative Network**


**Figure 12: Social networks for Devadunger Group - Affiliative Network**

In Ambari group**, Amb_F7** was giving maximum aggressive interaction to all other female. Whereas she was the receiver of minimum aggressive interaction from the other group members**.** (Fig 6(a)). However, there is a high intensity

aggressive interaction from **Amb_F7** to **Amb_F3** as well represented by a heavily weighted edge with strength value 25. After **Amb_F7** the next individual is **Amb_F2** giving 2nd highest out-degree of aggressive interactions. She is the recipient of two low intensity aggression from Amb_F6 and Amb_F7.

## 8.2 Test for Linearity:

The values of modified Landau's linearity index for the small and medium category groups (Kasia, Raidi, Devaliya, Gadakbari and Devadunder) was found to be 1. While for the larger groups, Ambari (N=7) and Kutiya (N=6) it is 0.79 and 0.8 respectively (Table-3). However, the Landau's p value is found to be significant for only Ambari group (p=0.03) and not for the others (P > 0.05) (Table-3). However, in Shizuka and McDonald's study (Shizuka and McDonald, 2012), they found that the expected value of *h* decreases with network size but *pt* (proportion of transitive triads) remains constant over various network. Hence, we did triangle transitivity (*ttri*) test for the large groups and the test results in a value of 1 validating the presence of strict transitive linear hierarchy in them. However, the p value of *ttri* is not significant due to low sample size. For inconsistency test, both the large groups scored an I and SI value of 0, depicting the absence of any inconsistency in the best hierarchical matrix given by the method. Using Directional Consistency Index (DCI), the directionality of the social interactions was measured for each group. The DCI value is found to be varying across groups– Kasia (N=3), Raidi (N=3), Gadakbari (N=2) and Devadunger (N=2) scoring highest DCI value of 1, while the other three groups – Ambari(N=7), Kutiya (N=6) and Devaliya (N=3) scoring 0.72, 0.64 and 0.4 respectively (Table 3)

**Table 3: Value of Landau's linearity index (Landau h'), Triangle transitivity (Pt and ttri) with their statistical significance (Landau p and ttp), I and SI value and Directional consistency Index (DCI) for all the 7 selected groups summarized below.**

| Sl. No | Group ID | Landau_h' | Landau_p | Pt | ttri | ttp | I | SI | Directionality (DCI) |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Ambari | 0.78 | 0.03 | 1 | 1 | 0.24 | 0 | 0 | 0.72 |
| 2 | Kutiya | - | - | | | | | | |
| 3 | Kaisia | 0.5 | 0.75 | | | | | | |
| 4 | Raidi | 1 | 0.75 | 1 | 1 | 0.74 | 0 | 0 | 1 |
| 5 | Devaliya | | | | | | | | |

## 8.3. Hierarchical ranking of group members using David's Score

There are many methods for hierarchical ranking of individual in a group. Various dominance hierarchy indices have been formulated which has their own pros and cons (De Vries, 1995) In order to choose the most appropriate index relevant to my study I calculated the dominance rank of individuals using- David's score (David,1988), Frequency-based index of dominance (Premnath et al.,1990), Zumpe and Michale's Index of Dominance (Zumpe andMichael, 1986), I & SI method (de Vries, 1995) and finally Balance Index (Foris et al.,2019). The rank of individuals is calculated using these five indices and David score is found to be the most relevant index for my study considering the inputs used for calculation of rank. The ranking given by David score is correlated with the ranking given by all other

indices and found that it shows high correlation with the ranking given by Frequency-based index of dominance, I & SI method and Balance Index.

After obtaining the presence of a linear hierarchy among the pride members in the selected groups, David score (DS) and normalized David Score (nDS) is calculated for each individuals of the groups. The DS, nDS and the Dominance Rank obtained for each group is summarized below in the table (Table 4). The rank given by David Score validates the presence of a linear hierarchy in them (Figure 13). The ranking found for the groups are-

Ambari group –Amb_F7 > Amb_F2 > Amb_F3 > Amb_F4 > Amb_F41 > Amb_F6 > Amb_F5
Kutiya Group- Kt_F3 > Kt_F5 > Kt_F1 > Kt_F6 > Kt_F4 > Kt_F2
Raidi Group- FLG_15 > FLG_22 > FLG_43
Kasia Group- Ks_F2 > Ks_F3 > Ks_F1
Devaliya Group- Dv_F3 > Dv_F1 > Dv_F2
Garakbari Group – FLG_1 > FLG 25
Devadunger Group – FLG 31 > FLG 30

The hierarchical ranking of the individuals of each group has been plotted against their David score values which shows the steepness of the ranks (Figure 13 and 14). Figure 13 shows the steepness based on agonistic interactions and Figure 14 shows the steepness based on affiliative interactions.

**Table 4: The hierarchical ranking based on David's score along with age of the individuals. DS- David's score, nDS- normalized David's score**

| Group_id | Hierarchical_Rank | Animals | DS | David_Score | Age | Age_cat |
|---|---|---|---|---|---|---|
| Ambari | 7 | Amb_F2 | 6.89 | 3.98 | 9 | Old Adult |
| Ambari | 6 | Amb_F7 | 5.79 | 3.83 | 9 | Old Adult |
| Ambari | 5 | Amb_F4 | 1.04 | 3.15 | 6 | Young adult |
| Ambari | 4 | Amb_F5 | -0.56 | 2.92 | 6 | Young adult |
| Ambari | 3 | Amb_F3 | -2.42 | 2.65 | 8 | Prime adult |
| Ambari | 2 | Amb_F6 | -4.55 | 2.35 | 7 | Prime adult |
| Ambari | 1 | Amb_F1 | -6.19 | 2.12 | 7 | Prime adult |
| Kutia | 6 | Kt_F3 | 6.4 | 3.57 | 9 | Old Adult |
| Kutia | 5 | Kt_F5 | 4.5 | 3.25 | 11 | Old Adult |
| Kutia | 4 | Kt_F1 | 2.5 | 2.92 | 8 | Prime adult |
| Kutia | 3 | Kt_F6 | -2.06 | 2.16 | 7 | Prime adult |
| Kutia | 2 | Kt_F2 | -4.88 | 1.69 | 4 | Young adult |
| Kutia | 1 | Kt_F4 | -6.46 | 1.42 | 6 | Prime adult |
| Raidi | 3 | FLG_15 | 0.81 | 1.27 | 12 | Old Adult |
| Raidi | 2 | FLG_22 | 0.15 | 1.05 | 8 | Prime adult |
| Raidi | 1 | FLG_43 | -0.96 | 0.68 | 5 | Young adult |
| Kasia | 3 | Ks_F2 | 1.59 | 1.53 | 5 | Young adult |
| Kasia | 2 | Ks_F3 | -0.16 | 0.95 | 5 | Young adult |
| Kasia | 1 | Ks_F1 | -1.43 | 0.53 | 5 | Young adult |
| Devaliya | 3 | Dv_F3 | 2.04 | 1.68 | 7 | Prime adult |
| Devaliya | 2 | Dv_F2 | -0.94 | 0.69 | 6 | Prime adult |
| Devaliya | 1 | Dv_F1 | -1.1 | 0.63 | 8 | Prime adult |
| Garakbari | 2 | FLG_1 | 0.75 | 0.88 | 9 | Old Adult |
| Garakbari | 1 | FLG_25 | -0.75 | 0.13 | 7 | Prime adult |
| Devadunger | 2 | FLG_31 | 0.83 | 0.92 | 10 | Old Adult |
| Devadunger | 1 | FLG_30 | -0.83 | 0.08 | 6 | Prime adult |

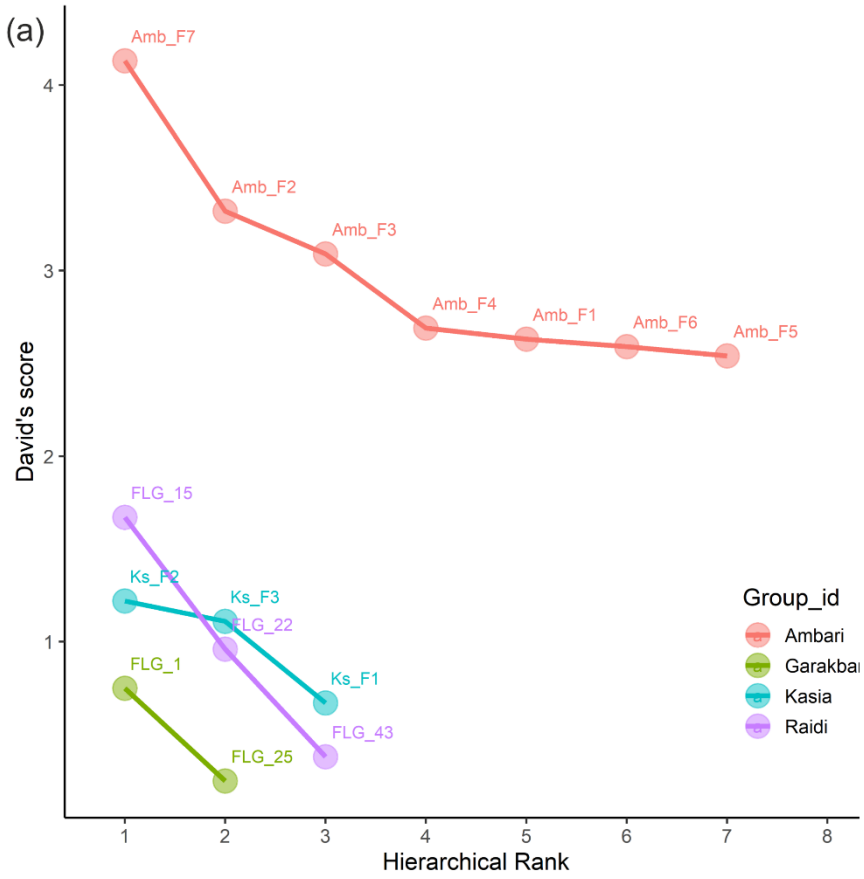



**Figure 13: Graph showing the steepness of hierarchical order among pride members based on Agonistic Interactions**

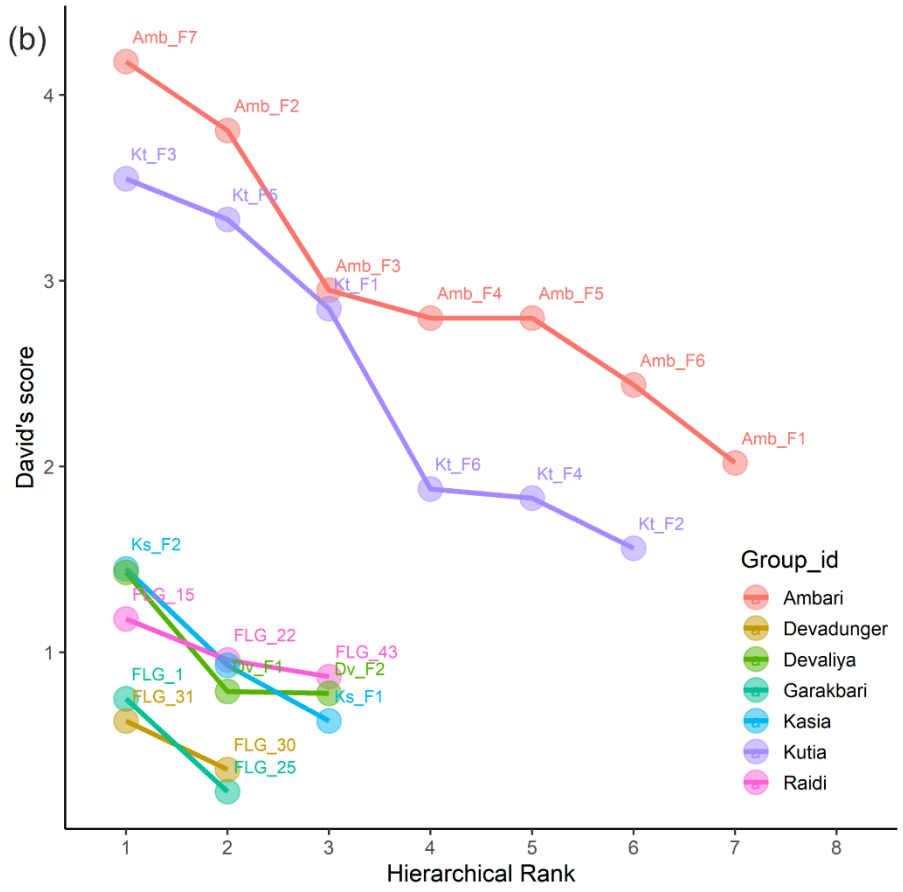



**Figure 14: Graph showing the steepness of hierarchical order among pride members based on Affiliative Interactions**

## 8.4 Affiliative interactions as Formal Dominance

To test whether affiliative interactions can be considered as a measure of formal dominance I ran a correlation test between the Normalized David score obtained for both affiliative and agonistic interactions. Out of the seven groups, in four groups Ambari (N=7), Kasia (N=3), Raidi (N=3) and Garakbari (N=2), we recorded both affiliative and agonistic interaction among the individuals. The correlation coefficient values ranged from 0.92 (Ambari Pride with 7 members and Raidi pride with 3 members) to 1 (Kasia pride with 3 members and Garakbadi pride with 2 members).

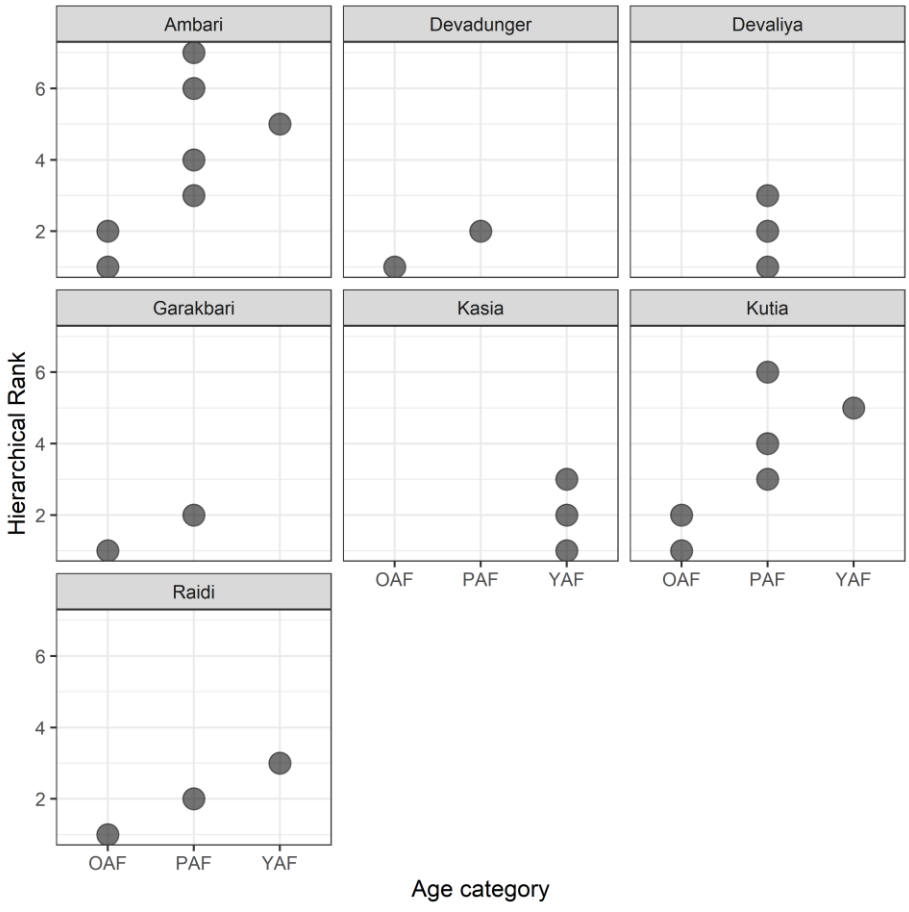
## 8.5 Influence of Age on Dominance Rank

To test whether dominance rank of an individual in a group is influenced by its age or not, a linear mixed effect models were used. Coefficients of the best model is presented below (Table 5) and model predictions are plotted (Figure 15). The best model explains the significance of age categories of individuals within a group as a function of fixed effect on the hierarchical ranks they hold. The Ambari group (N=7) shows a positive linear relationship between dominance rank and Age, the Kutiya group (N=6) is also showing a similar pattern, Raidi group (N=3) showed a strong linear pattern. However, in Devaliya group (N=3) it did not show linearity, since all the individuals were of same age category, similarly in Kasia group (N=3) I did not see any pattern. Although comprises of two individuals each, the Garakbari (N=2) and Devadunger (N=2) group is showing linearity of hierarchical order with respect to the age categories (Figure 15).

**Table 5: Coefficients of the best model in linear mixed modelling**

| **Model** | **Random Effect** | **Variance** | **Std. Dev.** | |
|---|---|---|---|---|
| Feeding Rank ~ Dominance rank + (1\|Group) | Group Id (Intercept) | 0.01 | 0.07 | |
| | Residual | 0.14 | 0.37 | |
| | | | | |
| | **Fixed effect** | **Estimate** | **Std. Error** | **P value** |
| | (Intercept) | 0.16 | 0.14 | 0.00 |
| | Dominance rank | 0.91 | 0.04 | |

**Figure 15: Output of the best model in linear mixed modeling analysis. The dots represent the predicted values of ranking across different age classes of the individuals.**



## 8.6 Influence of Relatedness on dominance

The results obtained from genetic analysis are plotted in Table 7 for Ambari, Devaliya, Raidi and Devadunger group. It shows the pairwise relatedness of each female in the group with the dominant female of the group. The population relatedness index generated from 69 random lion pairs from the Gir population had an average relatedness index of 0.56 with a 95%confidence interval range from **0.52 to 0.61**. By computing the relatedness index for each female with the dominant female in a pride, the relatedness value is compared with the 95% population relatedness index. If the females were related then the relatedness index score would be in the right tail of the distribution and if unrelated the value would be in the left tail of the CI.

**Table 6: Groups with dominant female with their relatedness with the other individual**

| Dominance Rank | Age category | Pride members | Amb_F7 | Amb_F2 | Amb_F3 | Amb_F1 | Amb_F6 |
|---|---|---|---|---|---|---|---|
| 1 | OAF | Amb_F7 | 1.00 | 0.84 | 0.47 | 0.42 | 0.27 |
| 2 | OAF | Amb_F2 | 0.84 | 1.00 | 0.45 | 0.28 | 0.47 |
| 3 | PAF | Amb_F3 | 0.47 | 0.45 | 1.00 | 0.58 | 0.50 |
| 5 | PAF | Amb_F1 | 0.42 | 0.28 | 0.58 | 1.00 | 0.27 |
| 6 | PAF | Amb_F6 | 0.27 | 0.47 | 0.50 | 0.27 | 1.00 |

# 9. Discussion

Understanding animal societies is a key aspect of behavioural ecology wherein hierarchical arrangement of individuals plays an important role influencing the life history of group-living animals (Drews, 1993; Whitehead, 2008). This study gives an in depth understanding about the social structure of female Asiatic Lion.

## 9.1 Social Hierarchy

In this study I examined the existence of social hierarchy in prides of Female Asiatic Lions. The possibilities are that there would be an observable strict hierarchy among pride members or there would be conditional dominance or, there won't be any dominance hierarchy at all. To answer this question, I did a social network analysis to understand the within group interactions among pride members. From the separate networks made for both agonistic and affiliative interactions, I found that for all groups, there is a distinct pattern in terms of being donor or recipient of agonistic and affiliative interactions. In my largest study group, Ambari (n=7), based on their agonistic and affiliative social networks, it can be clearly seen that there is a hierarchical relationship present among the pride members which is driving the way they interact with each. The variation in node (refer to social network figure here) size based out-degree and in-degree of interactions depicts the presence of a rank for the individuals. In large groups (n=7), there is a significant large proportion of aggressive interactions by some female members and at the same time these females receive disproportionately large

affiliative interactions. The lopsided is also true, where some females are the donor of minimum aggressive interaction and donor of maximum affiliative interactions. Similarly, for the medium and small sized groups (n=3 and n=2), the social networks clearly depict the presence of a skew in their directionality of interactions indicating a dominant - subordinate relationship amongst them. These findings of social network analysis with an asymmetry in their interactions refers to a hierarchical system in Female Asiatic Lion.

## 9.2 Dominance Ranking

As I found evidence for the presence of a social hierarchical system in Female Asiatic lion prides, moving to my second research question, I aimed to examine the type of social hierarchy operating amongst them. The prediction was that the hierarchy might be linear or non-linear. Using Linearity test (De Vries,1995), Triangle transitivity (Shizuka & McDonald,2014), Directional Consistency (DC; van Hooff & Wensing, 1987) and Test for inconsistency (De Vries,1997), I found the existence of a linear, transitive hierarchy in female Asiatic Lion. The value obtained from Landau's linearity index explains that the hierarchical relationship between pride members is not randomly distributed, but rather it showed the presence of a distinct linear social hierarchy among the pride members. All the 5 groups scored a high value for Landau's h', which says that all the groups follow a similar pattern of linear dominance hierarchy. I did not consider the two small groups (N=2) for the above-mentioned test as it is inappropriate to do any statistical analysis for a sample size of two. But the social network analysis done for those small groups also shows strong linearity in their relationship being one individual dominant over the other in terms of their agonistic and affiliative interactions (Figure 6). In the larger groups

the hierarchy is found to be near linear while in the smaller and medium group they follow a strict linear hierarchy. Also, for the larger groups the hierarchy is steep in the upper strata but it becomes shallow in the lower strata of dominance rank. These finding explains that when group size increases the dominance hierarchy becomes amorphous for the individuals in the lower rank but for small group sizes, those few individuals maintains a strong hierarchical difference among them in terms of social interactions. The members of a female Asiatic lion pride maintain directionality in their interactions also with minimum social reciprocity. All the groups showed unidirectionality in social dyadic interactions with an exception of the Devaliya group. However, for Devaliya group the bidirectionality is in terms of Affiliative interactions which might be due to the effect of group cohesion or can be explained as a consequence of maintaining alliance with the pride members.

## 9.3 Formal Dominance

There are various studies which suggest that dominance can be measured in terms of formal dominance also (De Waal,1989). Study done on free ranging Dogs by Cafazzo et al., in 2010 observed that submissive-affiliative behaviour shown by free ranging dogs in a group fulfils the criteria of formal signal of dominance (Cafazzo et al.,2010). They found that this behaviour is unidirectional and it is independent of the social context (Cafazzo et al.,2010). Similar study done on arctic wolves found that the higher the rank of the individual the more greetings they received and at the dyadic level it was directed mainly from subordinates towards the dominant individual (Cafazzo et al.,2016). However, in my study I found a strong positive correlation between the ranking given by affiliative and aggressive interaction for Ambari, Kasia, Raidi and Garakbari group. Both type of interaction

provided similar ranking of individuals in a group in terms of dominance. This finding validates the relevance of using affiliative interaction as a measure of formal dominance.

## 9.4 Age and Dominance

Dominance rank of an individual in a hierarchy could be influenced by many factors based on the asymmetries present among the group members (Smith, J.M. and Parker, G.A., 1976). Studies done on African elephants found that the dominance hierarchy in them is age ordered and older and larger females consistently dominates the smaller and younger females (Archie et al., 2005). As older age also depicts an experienced female, I examined the influence of age on dominance rank of an individual in a group and found that in most of the groups the higher ranks were occupied by older females. This finding explains the influence of age on hierarchical system of female Asiatic Lion by assigning the top ranks to the older and experienced females.

## 9.5 Kinship and Dominance

In social animals where females stay in their natal pride and breed, the general assumption is that most female group members are closely related to each other (Lukas et al.,2005). However, the average kinship between resident females may also be low in such cases, if group includes multiple breeding female, including individuals from successive generations with a polygynous or polyandrous mating system (Seyfarth & Cheney 2012). The various social traits like well-defined dominance hierarchies, competitive alliance, reciprocal cooperation and other behavioural traits to maintain social status are expected to be highly developed in

societies where all the group members are not closely related to each other and kinship plays a role in their social ranking (Silk, 2006). The pride formation in African lions have been so far found to be among related females, their dependent cubs, sub adults and a resident male coalition (Packer and Pusey 1993). The females in a pride are mostly closely related to each other being siblings, cousins, daughters or granddaughters (Schaller 1972). With same assumption a similar pattern has been expected for Asiatic lions that Asiatic lion prides are also formed of related females and their dependent cub.

However, regarding African lion, a study in Selous game reserve, Africa; found that in two prides females had comparatively low relatedness with each other (Spong et al. 2002). This was previously undocumented in African lion system. Similar pattern is observed from the genetic relatedness analysis on Asiatic lions, which may change our entire view on evolution of sociality in Lions. For the first time, with reasonable scientific authenticity, my data suggest that unrelated female Asiatic Lions can come together to form a pride. My data suggest that prides of Asiatic lioness are composed of closely related females while also having adult females that are unrelated. In the largest study pride 'Ambari' I found that out of five females, two females were unrelated with the other pride members which suggests the formation of groups by relatively unrelated female also. However, for the other groups Raidi, Devaliya and Devadunger, the pride members were found to be closely related. In consonance with the findings by Spong et al., (2002), I found evidence for pride formation by unrelated females, and agree with the hypothesis that familiarity can have significant amicable behavioural consequences.

According to inclusive fitness theory, the cost of being tolerant to kins or relatives is lower than non-relatives (Hamilton,1964) and there arises conflict of interest between group members (Abbott et al., 2003), which supports my finding on hierarchical ranking of related females in Asiatic Lion prides. I found that there is a clear kin-relationship between high ranked individuals in a pride. The low ranked females were the least related to the dominant individuals in large prides. This is similar to the findings on spotted Hyenas (*Crocuta crocuta*), where there is evidence for the existence of 'Kin discrimination' (Wahaj, S.A., et al.,2004). In hyaenas it was found that they can recognise kin and discriminate among various types of siblings by associating more closely with their close relatives than to distant relatives or show more affiliation or less fight with the close kins (Holekamp et al.,1997, Wahaj et al.,2004).

# 10. Conclusion

Based on my results I conclude that lionesses within Asiatic lion prides exhibit dominance and subordinate behaviour. The pride was found to be composed of related individuals but surprisingly also had unrelated adult lionesses. High ranking individuals in a pride had higher kinship while lower rank lionesses were often unrelated to the dominant individuals. There is linearity in the hierarchy in upper strata of dominant individuals and this linearity was reflected in both aggressive and affiliative interaction. However, my study opens up more questions for research than it answers. Does dominance and relatedness interact to give advantage in terms of food, survival and reproduction? Do related females have higher fitness i.e. do they produce and recruit more cubs in a pride? An in-depth long-term study on lion sociality with genetics and demography is required to understand and answer these interesting questions my study has raised.

# 11. References:


Akaike, H., 1974. A new look at the statistical model identification. In Selected Papers of Hirotugu Akaike (pp. 215-222). Springer, New York, NY.

Alexander, R.D., 1974. The evolution of social behavior. Annual review of ecology and systematics, 5(1), pp.325-383.

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour, 49(3), pp.227-266.

Archie, E.A., Morrison, T.A., Foley, C.A., Moss, C.J. and Alberts, S.C., 2006. Dominance rank relationships among wild female African elephants, Loxodonta africana. Animal Behaviour, 71(1), pp.117-127.

Banerjee, K. and Jhala, Y.V., 2012. Demographic parameters of endangered Asiatic lions (Panthera leo persica) in Gir Forests, India. Journal of mammalogy, 93(6), pp.1420-1430.

Bates, D., Mächler, M., Bolker, B. and Walker, S., 2014. Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.

Bertram, B.C., 1975. The social system of lions. Scientific American, 232(5), pp.54-65.

Bonanni, R., Cafazzo, S., Fantini, C., Pontier, D. and Natoli, E., 2007. Feeding-order in an urban feral domestic cat colony: relationship to dominance rank, sex and age. Animal Behaviour, 74(5), pp.1369-1379.

Boom, R.C.J.A., Sol, C.J., Salimans, M.M., Jansen, C.L., Wertheim-van Dillen, P.M. and Van der Noordaa, J.P.M.E., 1990. Rapid and simple method for purification of nucleic acids. Journal of clinical microbiology, 28(3), pp.495-503.

Bygott, J.D., Bertram, B.C. and Hanby, J.P., 1979. Male lions in large coalitions gain reproductive advantages. Nature, 282(5741), p.839.

Cafazzo, S., Lazzaroni, M. and Marshall-Pescini, S., 2016. Dominance relationships in a family pack of captive arctic wolves (Canis lupus arctos): The influence of competition for food, age and sex. PeerJ, 4, p.e2707.

Cafazzo, S., Valsecchi, P., Bonanni, R. and Natoli, E., 2010. Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. Behavioral Ecology, 21(3), pp.443-455.

Chakrabarti, S., & Jhala, Y. V. (2017). Selfish partners: resource partitioning in male coalitions of Asiatic lions. Behavioral Ecology, 28(6), 1532-1539.

Champion, S.H. and Seth, S.K., 1968. A revised survey of the forest types of India. A revised survey of the forest types of India.

Coulson, T., 2007. Population ecology: Group living and hungry lions. Nature, 449(7165), p.996.

Creel, S., Creel, N.M., Mills, M.G. and Monfort, S.L., 1997. Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. Behavioral Ecology, 8(3), pp.298-306.

Curley, J.P., 2016. Compete: Organizing and analyzing social dominance hierarchy data. R package version 0.1. CRAN.

Darwin, C., 1859. On the origins of species by means of natural selection. London: Murray, 247, p.1859.

De Vries, H., 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Animal Behaviour, 50(5), pp.1375-1389.

de Waal, F.B., 1989. Dominance 'style' and primate social organisation. Comparative socioecology.

Drea, C.M. and Frank, L.G., 2003. The social complexity of spotted hyenas.

Drews, C., 1993. The concept and definition of dominance in animal behaviour. Behaviour, 125(3-4), pp.283-313.

Ewer, R.F., 1973. The Carnivora. Cornell Univ. PreSS, New York, 494pp.

Foster KR, Wenseleers T, Ratnieks FLW, 2006. Kin selection is the key to altruism. Trends Ecol. Evol. 21: 57–60.

Fournier, F. and Festa-Bianchet, M., 1995. Social dominance in adult female mountain goats. Animal Behaviour, 49(6), pp.1449-1459.

Frank, L.G., 1986. Social organization of the spotted hyaena Crocuta crocuta. II. Dominance and reproduction. Animal Behaviour, 34(5), pp.1510-1527.

Fryxell, J.M., Mosser, A., Sinclair, A.R. and Packer, C., 2007. Group formation stabilizes predator–prey dynamics. Nature, 449(7165), p.1041.

Guo, S., Huang, K., Ji, W., Garber, P.A. and Li, B., 2015. The role of kinship in the formation of a primate multilevel society. American journal of physical anthropology, 156(4), pp.606-613.

Haber, G.C., 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem (Doctoral dissertation, University of British Columbia).

Hamilton, W.D., 1964. The genetical evolution of social behaviour. II. Journal of theoretical biology, 7(1), pp.17-52.

Hand, J.L., 1986. Resolution of social conflicts: dominance, egalitarianism, spheres of dominance, and game theory. The Quarterly Review of Biology, 61(2), pp.201-220.

Hawley, P.H., 1999. The ontogenesis of social dominance: A strategy-based evolutionary perspective. Developmental Review, 19(1), pp.97-132.

Holekamp, K.E., Cooper, S.M., Katona, C.I., Berry, N.A., Frank, L.G. and Smale, L., 1997. Patterns of association among female spotted hyenas (Crocuta crocuta). Journal of Mammalogy, 78(1), pp.55-64.

Isbell, L.A. and Young, T.P., 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. Behaviour, 139(2), pp.177-202.

Jhala, Y.V., Chellam, R., Pathak, B., Meena, V., Banerjee, K. and Basu, P., 2011. Social organization and dispersal of Asiatic lions (Vol. 1). Technical Report.

Jhala, Y.V., Mukherjee, S., Shah, N., Chauhan, K.S., Dave, C.V., Meena, V. and Banerjee, K., 2009. Home range and habitat preference of female lions (Panthera leo persica) in Gir forests, India. Biodiversity and conservation, 18(13), pp.3383-3394.

Jhala, Y.V., Qureshi, Q., & Dey, P. (2005) "Lion" a software to identify individual lion and database management, Wildlife Institute of India, http://wii.gov.in/lion_id.

Joslin, P., 1973. The Asiatic lion: a study of ecology and behaviour.

Kalinowski, S.T., Wagner, A.P. and Taper, M.L., 2006. ML-Relate: a computer program for maximum likelihood estimation of relatedness and relationship. Molecular Ecology Notes, 6(2), pp.576-579.

Lehner, P.N., 1998. Handbook of ethological methods. Cambridge University Press.

Leiva, D., Solanas, A. and Salafranca, L., 2008. Testing reciprocity in social interactions: A comparison between the directional consistency and skew-symmetry statistics. Behavior Research Methods, 40(2), pp.626-634

Lukas, D., Reynolds, V., Boesch, C. and Vigilant, L., 2005. To what extent does living in a group mean living with kin?. Molecular Ecology, 14(7), pp.2181-2196.

Macdonald, D.W., 1983. The ecology of carnivore social behaviour. Nature, 301(5899), p.379.

Mateo JM, 2002. Kin-recognition abilities and nepotism as a function of sociality. Proc. R. Soc. Lond. B Biol. Sci. 269: 323–325.

Mech, L.D., 1999. Alpha status, dominance, and division of labor in wolf packs. Canadian Journal of Zoology, 77(8), pp.1196-1203.

Meena, R.L. and Kumar, S., 2012. Management Plan for Gir Protected Areas. Gujarat Forest Department, Gujarat, India.

Meena, V., 2008. Reproductive strategy and behaviour of male Asiatic lions. PhD disserta tion, Forest Research Institute, Dehra Dun.

Meena, V., 2009. Variation in social organisation of lions with particular reference to the Asiatic Lions Panthera leo persica (Carnivora: Felidae) of the Gir forest, India. Journal of Threatened Taxa, 1(3), pp.158-165.

Michod, R.E., 1982. The theory of kin selection. Annual Review of Ecology and Systematics, 13(1), pp.23-55.

Ostner, J., Heistermann, M. and Kappeler, P.M., 2003. Intersexual dominance, masculinized genitals and prenatal steroids: comparative data from lemurid primates. Naturwissenschaften, 90(3), pp.141-144.

Packer, C. 2015. (2015, 20 February). *Evolution of group living*. https://cbs.umn.edu/research/labs/packer/research/evolution-group-living

Packer, C. and Pusey, A.E., 1982. Cooperation and competition within coalitions of male lions: Kin selection or game theory?. Nature, 296(5859), p.740.

Packer, C., Scheel, D. and Pusey, A.E., 1990. Why lions form groups: food is not enough. The American Naturalist, 136(1), pp.1-19.

Packer, C. and Pusey, A.E., 1993. Should a lion change its spots?. Nature, 362(6421), p.595.

Pusey, A.E. and Packer, C., 1987. The evolution of sex-biased dispersal in lions. Behaviour, 101(4), pp.275-310.

Qureshi, Q. and Shah, N., 2004. Vegetation and habitat monitoring. Monitoring of Gir. A technical report submitted to the Gujarat forest department under GEF-India ecodevelopment program. Wildlife Institute of India, Dehra Dun, pp.8-14.

Ren, Y., Huang, K., Guo, S., Pan, R., Derek, D.W., Qi, X., Wang, X., Wang, C., Zhao, H., Yang, B. and Li, F., 2017. Kinship promotes affiliative behaviors in a monkey. Current zoology, 64(4), pp.441-447.

Rowell, T.E., 1974. The concept of social dominance. Behavioral biology, 11(2), pp.131-154.

Schaller, G.B., 1972. The Serengetti lion. Chicago: University.

Schmid, V.S. and de Vries, H., 2013. Finding a dominance order most consistent with a linear hierarchy: an improved algorithm for the I&SI method. Animal Behaviour, 86(5), pp.1097-1105.

Seyfarth, R.M. and Cheney, D.L., 2012. The evolutionary origins of friendship. Annual review of psychology, 63, pp.153-177.

Shizuka, D. and McDonald, D.B., 2012. A social network perspective on measurements of dominance hierarchies. Animal Behaviour, 83(4), pp.925-934.

Silk, J.B., Altmann, J. and Alberts, S.C., 2006. Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. Behavioral Ecology and Sociobiology, 61(2), pp.183-195.

Singh, H.S., 2007. Gir lion. Pugamark Qmulus Consortium.

Smith, J.M. and Parker, G.A., 1976. The logic of asymmetric contests. Animal behaviour, 24(1), pp.159-175.

Smith, J.M. and Parker, G.A., 1976. The logic of asymmetric contests. Animal behaviour, 24(1), pp.159-175.

Spong, G., Stone, J., Creel, S. and Björklund, M., 2002. Genetic structure of lions (Panthera leo L.) in the Selous Game Reserve: implications for the evolution of sociality. Journal of Evolutionary Biology, 15(6), pp.945-953.

Sterck, E.H., Watts, D.P. and van Schaik, C.P., 1997. The evolution of female social relationships in nonhuman primates. Behavioral ecology and sociobiology, 41(5), pp.291-309.

Trivers, R., 1972. Parental investment and sexual selection (Vol. 136, p. 179). Cambridge: Biological Laboratories, Harvard University.

van der Borg, J.A., Schilder, M.B., Vinke, C.M. and De Vries, H., 2015. Dominance in domestic dogs: A quantitative analysis of its behavioural measures. PLoS One, 10(8), p.e0133978.

Vehrencamp, S.L., 1983. A model for the evolution of despotic versus egalitarian societies. Animal Behaviour, 31(3), pp.667-682.

Wahaj, S.A., Van Horn, R.C., Van Horn, T.L., Dreyer, R., Hilgris, R., Schwarz, J. and Holekamp, K.E., 2004. Kin discrimination in the spotted hyena (Crocuta crocuta): nepotism among siblings. Behavioral Ecology and Sociobiology, 56(3), pp.237-247.

Wickham, H., 2016. ggplot2: elegant graphics for data analysis. Springer.

Wittemyer, G. and Getz, W.M., 2007. Hierarchical dominance structure and social organization in African elephants, Loxodonta africana. Animal Behaviour, 73(4), pp.671-681.

Wittig, R.M. and Boesch, C., 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. International Journal of Primatology, 24(4), pp.847-867.

Wrangham, R.W., 1980. An ecological model of female-bonded primate groups. Behaviour, 75(3), pp.262-300.

## 12. Field Gallery: