

SOCIALITY IN ASIATIC LIONS

THESIS
SUBMITTED TO THE FOREST
RESEARCH INSTITUTE (DEEMED)
UNIVERSITY

FOR THE AWARD OF THE DEGREE OF
DOCTOR OF
PHILOSOPHY

In

FORESTRY

(Discipline: Wildlife Science)



By

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**WILDLIFE INSTITUTE OF INDIA
DEHRADUN, UTTARAKHAND
2018**

DECLARATION

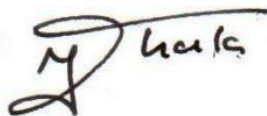
I hereby declare that the dissertation “**Sociality in Asiatic Lions**” constitutes original research conducted by me under the supervision of **Dr. Yadvendradev V. Jhala**, faculty at the Wildlife Institute of India. The thesis has been submitted to the Forest Research Institute (Deemed) University for the award of the degree of Doctor of Philosophy in Forestry (Wildlife Science), and has not formed the basis for the award of any other degree. It embodies my own work and observations; and in that respect, the investigation advances knowledge on the subject.

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This is to certify that the dissertation “**Sociality in Asiatic Lions**” submitted to the Forest Research Institute (Deemed) University embodies original research carried out by **Mr. Stotra Chakrabarti** under my supervision. This work has not been submitted, in part or full, for any other degree. The dissertation fulfils the requirements for the award of the degree of Doctor of Philosophy in Forestry (Wildlife Science), as specified in the ordinance of FRI (Deemed) University.

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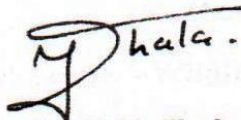
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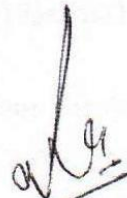
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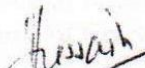
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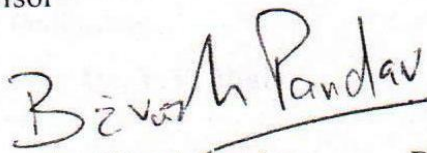
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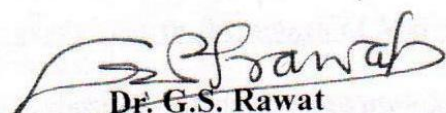

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This research work has been a lovely journey, since the days of its inception to the point where I am penning these words down. This road has only strengthened my faith in what my professor keeps telling me: *a career in wildlife science is an eternal romance.*

Stotra Chakrabarti
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Executive Summary

1. Lions (*Panthera leo*) are the only true social felids that live in functional fission-fusion units called prides. A pride comprises of 2-18 adult females, their dependent cubs and a coalition of adult male(s). Coalition males maintain exclusive rights on the females and sire cubs born to the females during their tenure. Unlike most other animal societies, lion groups are egalitarian: all adult females have equal opportunities to breed and all males in a coalition share food and mates with remarkable equity. Pride females come into estrus synchronously, litter around the same time and communally suckle each other's cubs. Asiatic lions (*P. l. persica*), living as a single relic population in the Gir forests and the adjoining landscape of Gujarat, western India, exhibit a contrasting social structure. Males and females do not stay together, instead form like-sex groups, **male coalitions**: 1-5 males and **female prides**: average of 2 adult females and their dependent cubs. These gender groups have independent survival strategies and interact primarily during matings and feeding events. In the current study, I investigate: **i)** how resources are shared between male partners of Asiatic lion coalitions; **ii)** the costs and benefits for male lions in forming alliances; and **iii)** female mating strategies and mate-selection in lions. The three questions pertaining to socio-biology of Asiatic lions are compared with studies from Africa to explore differences in the two systems and their potential causes.

2. My study area was ~1200 km², comprising of a part of the Gir Protected Area (Gir PA) and the adjoining agro-pastoral landscape lying to the south-western fringes of the PA. The part within the PA was a dry deciduous forest patch dominated by teak *Tectona grandis*, *Zizyphus* spp., *Butea* sp. and *Acacia* spp.; along with certain pastoral 'Maldhari' settlements/nesses. The pastoralists reared livestock with dairy products being their main source of livelihood. The agro-pastoral landscape consisted of private farmlands, industrial, and pastoral lands of private and government ownership. Lions were studied in this area between 2012-2017, and

the study population comprised of 11 male coalitions (ranging in size from 1-4 males) and nine female prides (ranging between 3-8 adult lionesses and their cubs).

3. Unique to Serengeti lion coalitions is equity of resource sharing between partners wherein literature suggests that all males have similar resource securities owing to abundant food and mates. Skewed mating and feeding rights were only reported in very large coalitions where all males were genetically related; kin selection easing the success disparity between partners. However, smaller modal prey size coupled with less simultaneous mating opportunities from small female prides for Asiatic lions necessitate investigation of resource allocation within male partners of coalitions. Observations on mating-events (n=127) and feeding-incidents (n=44) were made on seven male coalitions and nine female prides to assess resource procurement and distribution among male partners in a coalition. Pronounced dominance-hierarchies were seen between coalition partners, with one male getting >70% of all matings appropriated by his respective coalition. Competition between coalition partners at kills increased with decline in prey size, increase in number of male partners at the site and their appetite states (quantified through belly scores). The males dominant in reproduction were found to be dominant in feeding when kills were shared between partners. The dominant partners were found to appropriate 47% more food than his subordinates from shared kills. A linear hierarchical system was found for male Asiatic lion coalitions, where the 1st dominant was overriding over all his partners, the 2nd in rank was dominant over all except the 1st one and dominance progressively declined with respective ranks. However, when more than one lioness in a pride were in estrus simultaneously (n=2), male partners of the mating coalition (both cases were coalitions of 2 males) consorted one lioness each and were found to mate in each other's proximity without any heightened aggression between them. This further corroborates my *resource hypothesis*, wherein a temporary abundance of resources dilutes

competitive dominance between partners, thereby indicating to resource availability being the primary cause behind hierarchy formation in male coalitions.

4. Staying alone or forming coalitions are alternative survival/reproductive strategies for males in social mammals, including lions. However, in African lions, males in coalitions are more successful than single males, producing more number of offspring. For coalitions to evolve as a strategy: a) coalitions should be able to secure more resources compared to singletons, and b) if dominance hierarchies are present within coalitions, then subordinate members should also get higher benefits than males which do not form coalitions. To test this postulate, I compared reproductive fitness of single males (n=4) with those that form coalitions (n=7) through observations on their territory holdings/tenures and mating events (n=134). Reproductive success of males was computed through a synthetic product of: *the annual tenure holding probability*annual mating frequency*. Reproductive fitness of single males were significantly lower than coalition males; with the former having lower tenure holding probabilities and less frequent matings. Annual tenure holding probability for single males was 0.47 ± 0.19 , which was much lower than coalition males having a probability of 0.81 ± 0.07 . Single males had smaller territories (95% MCP= 31.2 ± 3 km²) compared to coalitions with ≥ 2 males (95% MCP= 119.5 ± 18.9 km²). However, males at the bottommost ranks of large coalitions (>2 males) had similar fitness to that of single males. Declining benefits to partners with increasing coalition size, with individuals below the immediate subordinates having fitness comparable to single males, suggest to an optimal coalition size of two lions in the Asiatic system.

5. To maximize fitness, males and females of the same species often adopt strategies that are at loggerheads. Infanticide is a male strategy which is costly for females, as killing of dependent young by males cause considerable loss to maternal investment. Infanticide is prevalent among lions where incoming males kill cubs during a ‘takeover’ after ousting the

resident males, to hasten reproductive receptivity of the lionesses. To investigate the consequences of inter-gender segregation on the social organization and mating strategy of Asiatic lions, range use and matings (n=134) were observed of 21 males belonging to 11 coalitions and 49 females from 9 prides. Adjacent contemporaneous male ranges overlapped considerably with each other, with an average overlap of $32.1 \pm 4.1\%$. Female prides had an average home range of $61.6 \pm 14.5 \text{ km}^2$; with negligible $8.2 \pm 1.1\%$ overlap between adjacent prides. Female pride core areas (70% FK) were almost exclusive from other prides. Female pride home ranges were encompassed by ranges of 2-4 male coalitions, with each pride having one *primary coalition* (overlap of $64.8 \pm 7.2\%$ of pride ranges) and 1-3 *peripheral coalitions* (average overlap of $25.6 \pm 4\%$ of pride ranges). Male ranges overlapped with each other primarily at areas with high female use/pride cores. A social network of the mating events revealed that lionesses are promiscuous, females readily mating with adjacent rival coalitions. Among all the promiscuous matings that were observed (n=28), where females were found to be mating with males of their *peripheral coalitions*, n=25 (89.3%) were performed by *experienced females* who had littered before, while the *maiden breeders* rarely mated with such coalitions (n=3/28 events; 10.7%). Among 69 events involving interactions between adult males and cubs, 53 ($77.1 \pm 1.4\%$) times the cubs were found to be associated with males of their *primary coalitions* and the remaining 16 ($22.9 \pm 1.5\%$) times cumulatively with males of their *peripheral coalitions*. There were no aggressive overtures towards cubs by primary- or peripheral- coalitions. Infanticide was limited to new and unfamiliar males that came into the locality.

6. My study reveals a novel social structure, not reported for lions till date. Unlike African lions, Asiatic male lions form hierarchical coalitions, wherein partners utilize resources asymmetrically, yet coalesce for personal gains. Selective female promiscuity has considerably buffered cub infanticide by confusing paternity amongst males, and also have

enhanced the genetic variability amongst litters. Such a strategy not only helps individual females but might have invigorated an inbred population that was at the brink of extinction. In the case of Asiatic lions, it appears that the females have the upper hand, and have won the arms race of sexual conflict by maximizing their fitness. This social structure and mating strategy might be a behavioural response to spatial segregation between genders; the latter likely been caused by smaller and non-migratory prey base in the Asiatic system.

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Figure 1.1. Degrees of association in social mammals: Living in big groups (a. Wolf, *Canis lupus*; b. Bottlenose dolphins *Tursiops* sp.); Paired-units (c. Golden jackals, *Canis aureus*; d. Maned wolf *Chrysocyon brachyurus*).

Figure 1.2. A) Historical and current geographic distribution of lion, *Panthera leo*. A three-letter code pointing to a white dotted circle represents the geographic location of the 11 lion populations GIR, Gir Forest, India; UGA, Uganda (Queen Elizabeth National Park); KEN, Kenya (Laikipia), SER, Serengeti National Park, Tanzania; NGC, Ngorongoro Crater, Tanzania; KRU, Kruger National Park, South Africa; BOT-I, southern Botswana and Kalahari, South Africa; BOT-II, northern Botswana; and NAM, Namibia. Green squares represent captive individual samples to explore the relationship of lions from more isolated/endangered/depleted areas: ATL, Morocco Atlas lions; ANG, Angola; and ZBW, Zimbabwe (source: Antunes et al. 2008); B) Historical range of *Panthera leo persica* (source: Nowell and Jackson 1996).

Figure 1.3. Current *tehsil* level distributions of Asiatic lion in Gujarat state, India. The map inset shows outline map of India with location of the Gir landscape. The red boundary indicates areas most frequented by lions. (Source: Banerjee 2012).

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Organization of Dissertation

The dissertation is organized into the following chapters:

Chapter 1. Introduction & Review of Literature

Introduces sociality and group living trends in species. Gives a brief overview of sociality in lions. Discusses the status, distribution and history of Asiatic lions and briefs about their ecology and behaviour in the context of their sociality.

Chapter 2. Questions & Objectives

Elucidates the major questions posed in the dissertation and the hypotheses behind each of those ecological queries. Also discusses the primary field objectives of the dissertation.

Chapter 3. Study Area

Informs about the area where the study was conducted, its vegetation and climatic factors, its faunal and floral assemblages and anthropogenic relationships.

Chapter 4. Coalition Males: comrades in arms or a twist in the tale?

The ‘*1st Objective Chapter*’, deals with resource partitioning between partners of male Asiatic lion coalitions.

Chapter 5 A Lion’s Dilemma: to form coalitions or to stay alone?

The ‘*2nd Objective Chapter*’, represents the proximate and ultimate causes why male Asiatic lions form coalitions

Chapter 6 The Great Game of Sexes: mating strategy in Asiatic lions

The ‘*3rd Objective Chapter*’ and deals with the effects of social organization on the mating strategy of Asiatic lions.

Chapter 7. Synthesis

Synthesizes and concludes the key findings of the *Objective Chapters*.

Introduction & Review of Literature



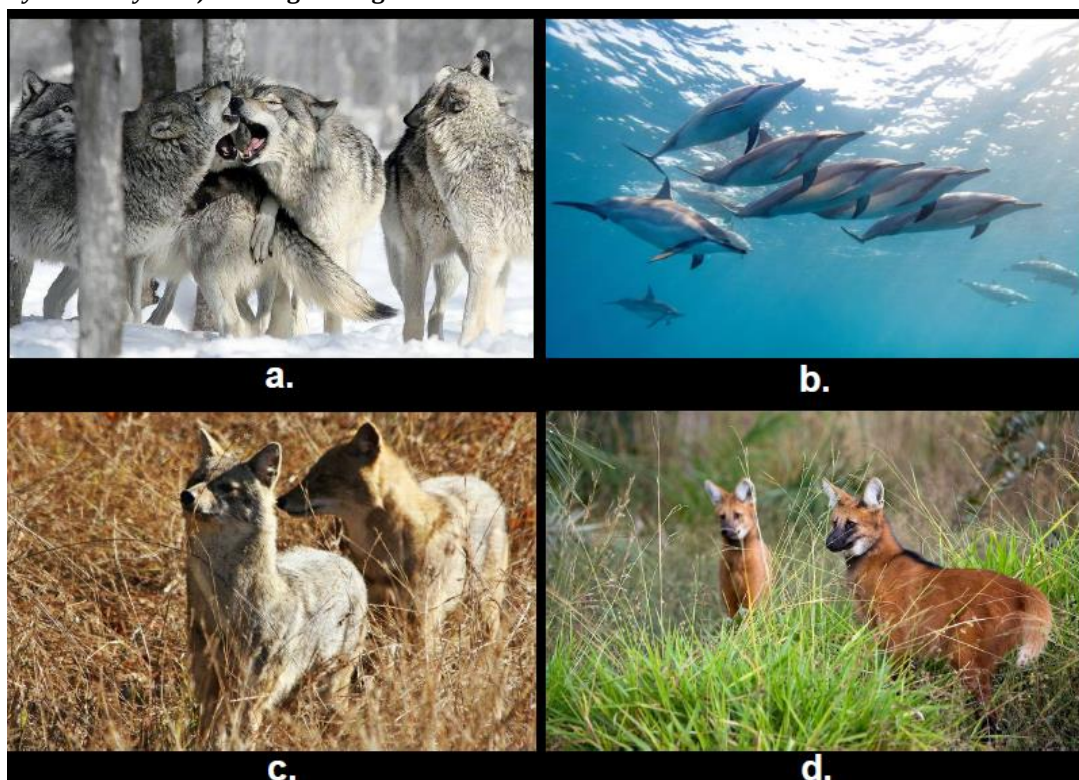
Introduction & Review of Literature

1. Comparative trends in group living

Group living is an evolutionary strategy that exhibits a range of alternatives between and within species (Krebs and Davies 1987). Sociality refers to the degree of association between individuals of a population and their relative spacing patterns (Gittleman 1989). The underlying principle of any society is the tendency to form groups. A 'group' can be defined as a set of individuals of the same species which remain together and interact with each other more than what they do with other conspecifics (Wilson 2000). Since sociality does not exhibit a serial evolutionary trend across taxa, it may have originated independently in different families (Gittleman 1989). This hints towards convergent evolution of adaptive behavioural responses to similar environments (Silk 2007). Sociality evolves when the net benefits of association with conspecifics outweigh the costs (Krause and Ruxton 2002). Living in groups can be beneficial for individuals because it provides greater protection from predators through increased vigilance and 'dilution' of targets (Jarman 1974; Kenward 1978; Bertram 1980), enhances success in locating, appropriating and maintaining access to resources (Caraco and Wolf 1975; Macdonald 1983; Bekoff and Wells 1982; Courchamp *et al.* 2002; Blundell *et al.* 2004), creates mating opportunities (Caro and Collins 1987; Packer *et al.* 1988) increases reproductive success (Packer *et al.* 1988; Mech and Boitani 2003) and/or reduces vulnerability to infanticide (Packer and Pusey 1994). Simultaneously, sociality can be costly for individuals because it increases competition over access to resources and mating opportunities (Isbell and Young 2002; Clutton-Brock 2009), enhances exposure to infection from parasites or contagious diseases (Creel and Creel 2002) and may increase the groups'

conspicuousness to predators (Krebs and Davies 1987). The nature and relative magnitude of the benefits and costs of sociality are expected to vary across species and habitats (Silk 2007). When sociality is favoured, animals form groups that range from small pair-bonded units to spectacular aggregations. The size and composition of social groups have diverse effects on species morphology and behaviour, ranging from the extent of sexual dimorphism (primates: Clutton-Brock and Harvey 1977; Plavcan 2003; ungulates: Clutton-Brock et al. 1980; Perez-Barbería et al. 2002) and reproductive strategies (Clutton-Brock 1989) to relative brain size (primates: Sawaguchi and Kudo 1990; Barton and Dunbar 1997; cetaceans: Connor 2007; carnivores and insectivores: Dunbar and Bever 1998; ungulates: Shultz and Dunbar 2006) and the prevalence of infanticide (Hausfater and Hrdy 1984; van Schaik and Janson 2000). A study of group formation further aids in our understanding of the evolution of parental care (Trivers 1972), combat strategies (Parker 1974), mate choice (Andersson 1994) and cooperation (Dugatkin 1997; Nowak 2006) as all of these behavioural responses are intricately linked to the degrees of association between individuals.

Figure 1.1. Degrees of association in social mammals: Living in big groups (a. Wolf, *Canis lupus*; b. Bottlenose dolphins *Tursiops* sp.); Paired-units (c. Golden jackals, *Canis aureus*; d. Maned wolf *Chrysocyon brachyurus*) © Google Images & Stotra Chakrabarti



1.1. Sociality and lions

Lions (*Panthera leo*) are the only true social felids that live in functional fission-fusion units called prides (Schaller 1972). A pride essentially comprises of 2-9 (range: 2-18) adult females, their dependent cubs and a coalition of adult male(s) that has entered the pride from elsewhere and associate with the pride during their tenure (Schaller 1972; Bertram 1975b; Bygott et al. 1979, Packer and Pusey 1982). Mean pride sizes are variable: 7.1 in the Serengeti (Schaller 1972), 9.2 in Masai Mara (Ogutu and Dublin 2002), 4.2 in the woodlands of Etosha (Stander 1991), 4.2 in Kruger (Smuts 1976), 3.5 in Luangwa Valley (Yamazaki 1996), 4 in Kalahari Transfrontier Park (Funston 2011) and 2 in Gir (Meena 2009; Jhala et al. 2009). Pride sizes appear to be positively correlated with prey abundance and size of the modal prey during the period of least abundance (lean season), as availability of prey is highly erratic and ephemeral in some lion areas whereas stable in others (Van Orsdol et al. 1985; Hanby et al. 1995; Packer et al. 1988). The uniqueness of lion societies is their egalitarianism, with the absence of reported dominance hierarchies between members of a pride (Packer et al. 1988). In a pride, all adult females have equal opportunities to breed and all males in a coalition are reported to share food and mates with equity (Schaller 1972; Bygott et al. 1979; Packer and Pusey 1982). The lack of a distinctive social hierarchy amongst lions is an important facet of their sociality as each and every individual may therefore be affected equally by factors enhancing or reducing the fitness of the group (Packer et al. 1988). However, a featured feeding hierarchy exists between pride males and females for the rights to a kill, where males being much bigger than females, gain the first rights (Schaller 1972; Bertram 1978). Female pride-mates are always related; they either join their mothers' prides or form new ones with members of their natal cohort (Pusey and Packer 1987). Females cooperate to defend hunting grounds, refuge sites and water holes from other prides and also communally suckle and raise their cubs, and protect them from infanticidal

males (Packer and Pusey 1997). Male coalition partners are either closely related or unrelated, but mating partners are usually unrelated (Packer et al. 1990). However single males hold territories too, thus being single or forming an alliance with other males seems to be alternative survival strategies for male lions (Grinnell et al. 1995). Group territoriality, safeguarding of kills and resources from competitors, group hunting and communal cub-rearing form the basis of this cooperation (Grinnell et al. 1995; Coulson 2007).

Units of lion sociality: studies from Africa

Pride females: At the age of around 2-3 years, a sub-adult female is either recruited into the pride or driven out of it depending upon the number of existing adults in the pride and availability of food and resources (Schaller 1972; Bertram 1975b). Females come into estrus when they are 2.5-3 years of age and start breeding, median age of first reproduction being 4 years (Pusey and Packer 1987). After a period of 98-110 days of gestation, a lioness gives birth to a litter of one to six blind cubs, and 98% of litters are one to four (Packer and Pusey 1987). Females often abandon single cubs (Packer and Pusey 1984). Females lactate for a period of 4-7 months (Schaller 1972) and resume sexual activity when cubs are about 15-18 months old (Bertram 1975b; Heinsohn and Packer 1995). Lionesses that lose their cubs resume sexual activity within days or weeks of the loss (Schaller 1972; Packer and Pusey 1983). Average inter-birth interval for lionesses whose previous litter has survived is 24 months (Pusey and Packer 1987). Females generally avoid mating with their fathers and would leave the pride temporarily to mate with unfamiliar males (Pusey and Packer 1987). Average lifespan of a lioness is about 14-15 years.

Male coalitions: At three years of age male lions are either expelled or leave their natal prides voluntarily (Schaller 1972; Bertram 1975b). Such ousting of young males happen either: **a)** during a takeover when new males take control of a pride, or **b)** when they are at an age between 2.5-3 years, adult members of the pride (mothers, aunts and fathers) become

aggressive towards them and stop sharing food (Schaller 1972; Bertram 1975b). Male lions form coalitions of 2–7 individuals during the nomadic phase of their lives with brothers and cousins from the same pride or with non-related males (Packer and Pusey 1987). However, single males who do not get a partner before/during the nomadic phase mostly remain and act alone their entire lives (Schaller 1972; Bertram 1975b). Small coalitions are made of related or unrelated partners, but large coalition are nearly always constituted by closely related kins (Packer et al. 1991). Coalitions compete intensively to gain residence and ownership of a female pride. Successful male coalitions become resident in a pride when they are about four to five years old (Packer and Pusey 1987) and remain resident for about two years (Packer and Pusey 1982; Packer et al. 1988). A successful coalition gains temporary but exclusive access to the pride females, till ousted by another coalition (Bygott et al. 1979). Larger coalitions are likely to remain in residence longer, and gain access to more females than do small coalitions (Bygott et al. 1979). They also are able to hold multiple prides in successive tenures (Packer et al. 1988). Group formation thus results in greater reproductive success (Bygott et al. 1979; Packer et al. 1988). Infanticide in lions is a male reproductive strategy whereby males terminate a female's investment in the offspring of other males in order to hasten female sexual receptivity (Hrady 1974; Bertram 1975b). Incoming males that takeover a pride kills all dependent cubs and ousts sub-adult females below breeding age and resident sub-adult males (Packer and Pusey 1983). The average reproductive lifespan of males is 33 months (range: 5-130 months) (Packer et al. 1988). Aggressive encounters during pride defence and takeovers cause injuries limiting their effective lifespan of males to ~12 years (Packer et al. 1988).

Nomads: Nomadic lions are not necessarily of a different population but are 'surpluses' from the breeding populations (Schaller 1972; Bertram 1975). Most nomads are males looking to gain control over prides from other coalitions (Schaller 1972) and include both sub-adult to

young males, as well as old males who have been expelled from their territories (Schaller 1972). Nomadic females are those ousted from their natal territories. Nomads that do not establish territories, have shorter lifespan, have reduced reproductive success, and have fewer litters that are less likely to survive (Schaller 1972, Bertram 1975b).

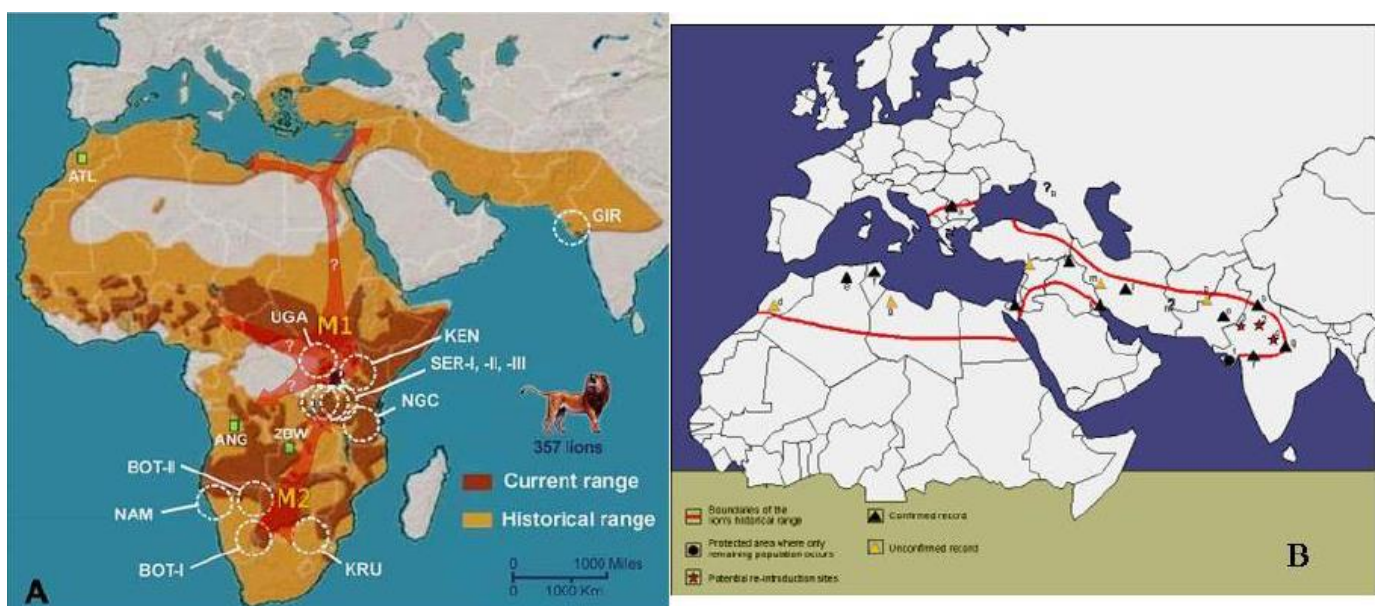
1.2. Asiatic Lions: distribution and status

Asiatic lion (*P.l.persica*) historically had a wide distribution (**Figure 1.2**). The erstwhile range of the Asiatic lion, reconstructed mainly based on paleontological evidence, literature, art-culture-sculpture and old *shikar* (game hunting) documents suggest an extensive area from Syria across the Middle East to Eastern India (Kinnear 1920; Joslin 1973). In India, lions inhabited the entire northern Indo-Gangetic Basin in North and Central India and were abundant in the states of Punjab, Haryana, Rajasthan, Uttar Pradesh, Madhya Pradesh, Gujarat, western Bihar and Orissa (Pocock 1936; Dalvi 1969). By mid 1800s they were exterminated from most of their range due to hunting and development induced natural habitat loss and modifications (Divyabhanusinh 2005). By 1880s they were restricted as a single free-ranging population in and around the Barda hills, Alech hills, Mitiyala, Girnar and Gir forests in the Saurashtra peninsula of Gujarat, western India (Dalvi 1969). Further fragmentation of forested patches and irreversible loss of habitat connectivity due to agricultural expansion and grazing needs in the region finally restricted lions to the 1,883km² of the Gir forests (Divyabhanusinh 2005).

With the consistent shrinkage in the lions' distribution, there has also been a wide fluctuation in population numbers over the years and lion number was believed to be as low as 50 individuals in the early 1900s and very close to extinction (Wynter-Blyth and Dharmakumarsinhji 1950; Divyabhanusinh 2005). Owing to the timely protection measures taken by the erstwhile local rulers (*Nawabs* of Junagadh), the lion population survived (Divyabhanusinh 2005) and reached 287 in 1936 census (Dalvi 1969). From mid 1900s, lions

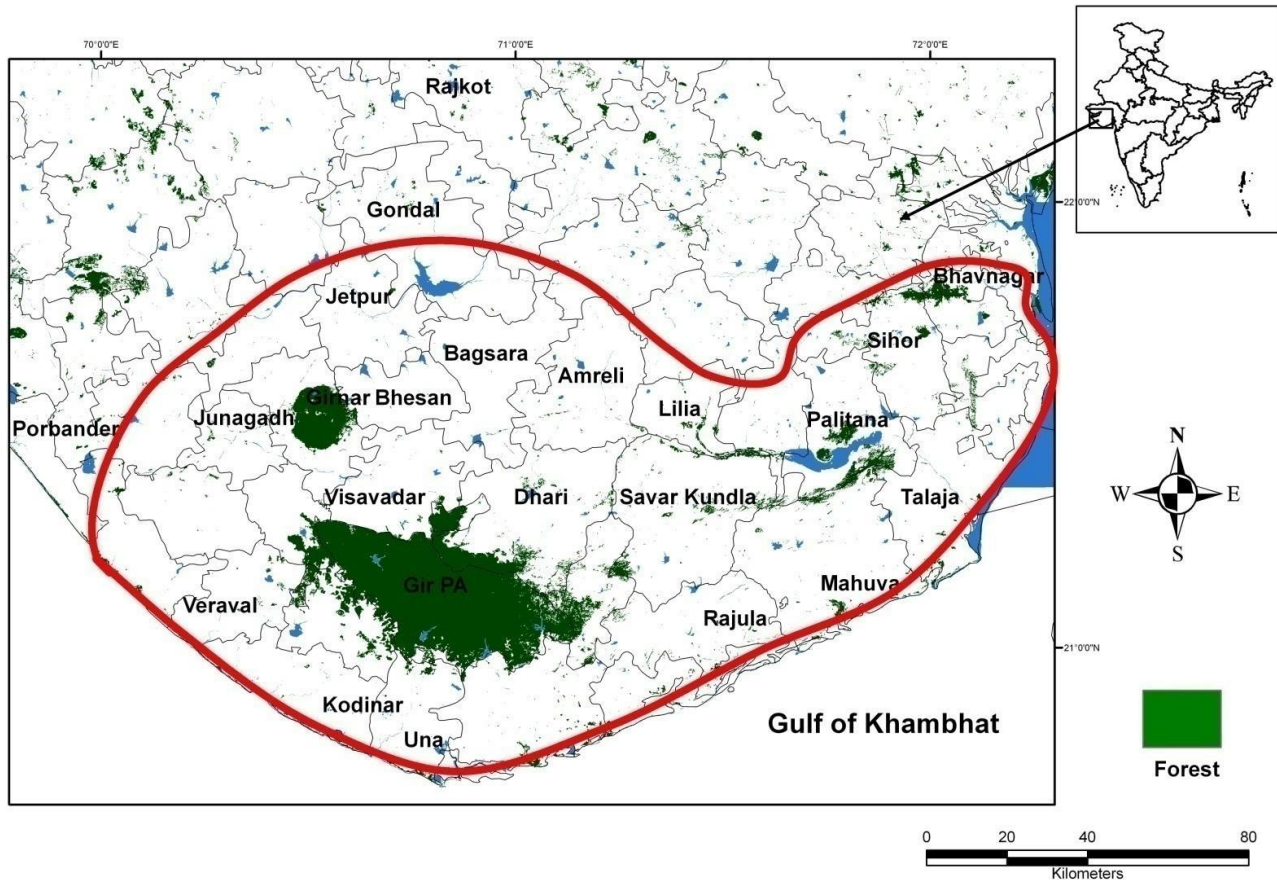
started to move out occasionally in the adjoining forests of Gir and started appearing in Mitiyala hills in the dominion of the erstwhile princely state of Bhavnagar from 1917. Lions were frequently seen in small numbers in Girnar hills adjoining Junagadh (Singh 2007).

Figure 1.2. A) Historical and current geographic distribution of lion, *Panthera leo*. A three-letter code pointing to a white dotted circle represents the geographic location of the 11 lion populations GIR, Gir Forest, India; UGA, Uganda (Queen Elizabeth National Park); KEN, Kenya (Laikipia), SER, Serengeti National Park, Tanzania; NGC, Ngorongoro Crater, Tanzania; KRU, Kruger National Park, South Africa; BOT-I, southern Botswana and Kalahari, South Africa; BOT-II, northern Botswana; and NAM, Namibia. Green squares represent captive individual samples to explore the relationship of lions from more isolated/endangered/depleted areas: ATL, Morocco Atlas lions; ANG, Angola; and ZBW, Zimbabwe (source: Antunes et al. 2008); B) Historical range of *Panthera leo persica* (source: Nowell and Jackson 1996)



After the enforcement of complete ban on lion shooting in 1955 by the Government of India, declaration of Gir forests as Gir Wildlife Sanctuary in 1965 and subsequent protection and habitat manipulations by the state run Gujarat Forest Department (GFD); the lion population has shown a steady increase (Singh and Kamboj 1996) with an annual growth rate of 2.2% (Banerjee and Jhala 2012) and have reached a figure of 523 in 2015 lion census conducted by the GFD (Gujarat Forest Department 2015). During the past two decades, lions have dispersed from the Gir Protected Area into agro-pastoral landscape of the surrounding districts of Junagadh, Amreli and Bhavnagar covering about 20,000 km² of human-dominated landscapes (Singh 2007; Banerjee et al. 2010; Singh and Gibson 2011; **Figure 1.3**)

Figure 1.3. Current *tehsil* level distributions of Asiatic lion in Gujarat state, India. The map inset shows outline map of India with location of the Gir landscape. The red boundary indicates areas most frequented by lions. Source: Banerjee 2012

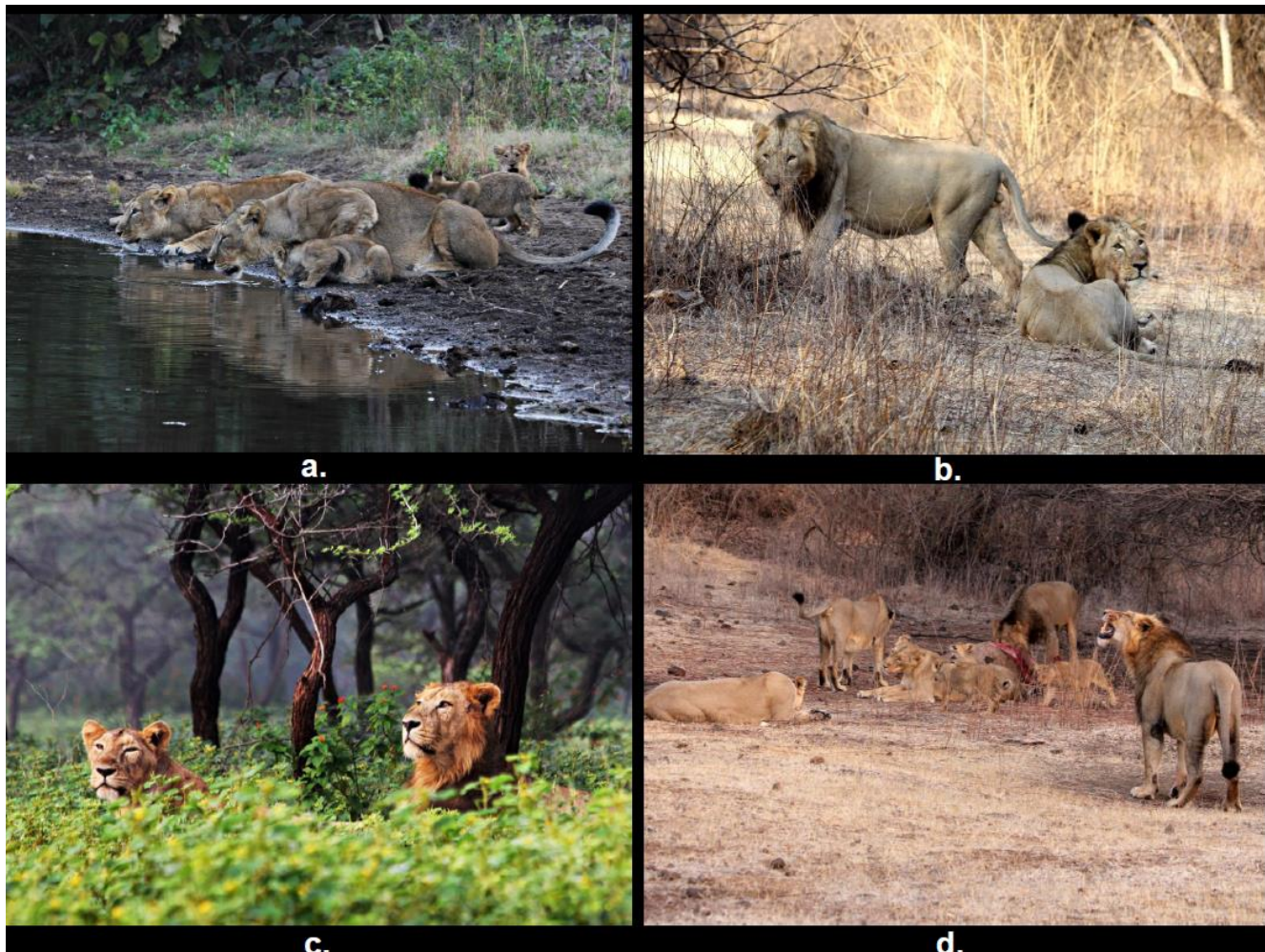


1.3. Asiatic Lions: ecology and behaviour

Asiatic lions considerably differ from their African counterparts in having marked intersexual segregation, with adult males and females staying separately (Chellam 1993; Meena 2008; Banerjee 2012). In the Asiatic system, a pride comprises only of females and their cubs, with an adult female group size of ~ 2 (Jhala et al. 2009). Males live their lives alone or in coalitions of 2-5 (Joslin 1973; Chellam 1993). Male coalitions have larger territories (average: 103 km^2 inside PA and 333 km^2 outside PA) than breeding female groups (40 km^2 inside PA and 132 km^2 outside PA) (Banerjee 2012). Male and female associations are restricted primarily to matings and infrequent congregation on large kills (Chellam 1993; Meena 2009; Chakrabarti and Jhala 2017). Male territories overlap with one to many female prides (Meena 2008; Banerjee 2012). Chital (*Axis axis*) formed the bulk of lion diet inside PA

whereas nilgai (*Boselaphus tragocamelus*) and scavenged livestock were the most consumed prey outside the PA (Meena et al. 2011; Banerjee 2012; Chakrabarti et al. 2016). Lion density ranges from 15/100 km² within Gir to 2/100 km² in the agro-pastoral landscape (Banerjee 2012; Banerjee et al. 2013). Average litter size in Gir was estimated at 2.4 ± 1.4 , with lionesses having an average inter-birth interval of 1.4 ± 0.3 years (Banerjee and Jhala 2012). Demographic parameters of Asiatic lions through long-term monitoring aided with radio-telemetry were found comparable to that of the lion populations in Africa, indicating that inbreeding has not depressed the population parameters of Asiatic lions as of yet (Banerjee and Jhala 2012).

Figure 1.4. Pictorial representation of key life stages in Asiatic lion sociality: a) A typical pride with females and cubs; b) A coalition of 2 adult males, the males are around 4-5 years old and just have taken over a territory by ousting the former coalition; c) A mating pair of lions, male and female associations are restricted mostly to such mating events; d) Infrequent congregations of prides and coalitions on large kills (in this case a male sambar, *Rusa unicolor*) do happen, when both parties share the bounty. © Stotra Chakrabarti



Questions & Objectives



Questions & Objectives

Asiatic lions differ from their east African cousins primarily in the degrees of social bonding between gender groups. Also, typical group sizes in the Asiatic system are smaller compared to that found in Africa. Group size and sociality are reported to vary with respect to habitat and resource availability (Gittleman 1989; Clutton-Brock 2009; de Silva et al. 2016). The Asiatic and African systems considerably contrast in their resources; with the African Serengeti harbouring large bodied yet migratory prey (Schaller 1972), whereas Gir has an array of small-medium bodied non-migratory ungulates (Joslin 1973). Such difference in resources and their availability might be the directive force behind the disparity in group living behaviour between Asiatic and the much studied Serengeti lions. To effectively discern the consequences of such resource differences on the social structure of gender groups and the resultant survival strategies in Asiatic lions; I have attempted to answer the following questions in my dissertation:

2.1. How are resources shared between coalition partners?

Published studies on Serengeti lions suggest that male coalition partners do not show a strict hierarchical system in terms of sharing of resources like food and mates (Schaller 1972; Bertram 1975b; Bygott et al. 1979). However, smaller modal prey (chital) and less mating opportunities (small female group size) for male Asiatic lions as compared to that in Africa might enhance competition between coalition partners.

Hypothesis: Given a heightened competitive setting, male partners in a coalition would exhibit social hierarchy with the presence of dominant and subordinate individuals.

Prediction: Male partners in a coalition would show dissimilar mating and feeding success, and dominant males would appropriate more food and matings.

2.2. Why males form coalitions?

If such a hierarchical system exists for male coalitions in Asiatic lion, in order for coalitions to become a successful strategy, being in a coalition should be more beneficial for a male than to stay alone.

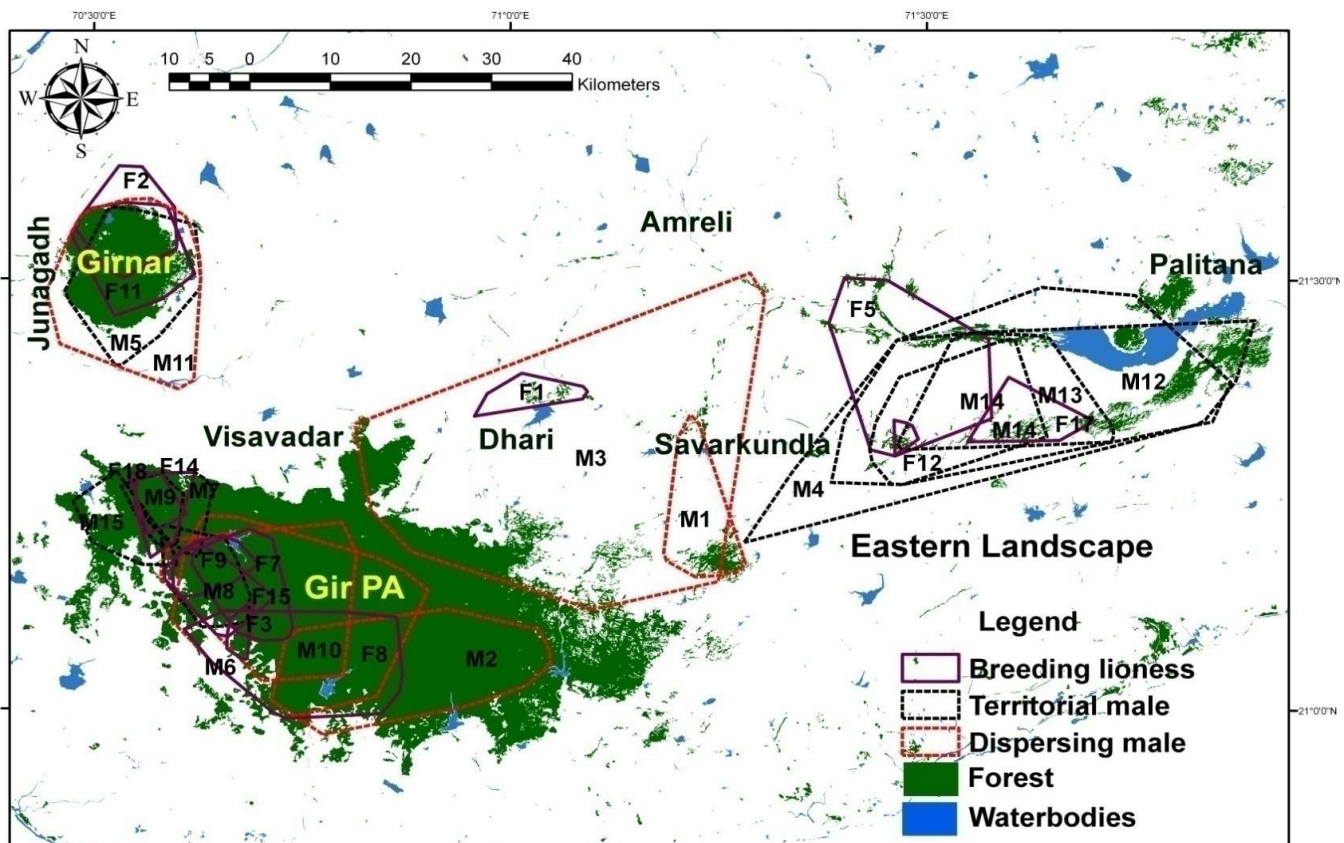
Hypothesis: Male lions team up to safeguard and enhance their lifetime fitness.

Prediction: Males in a coalition would have higher survival probability, gain access to more matings and defend a territory for longer durations than resident singletons.

2.3. What is the extent of inter-gender spatial segregation in Asiatic lions and its effect on their mating strategy?

In African lions, a reigning coalition maintains exclusive rights on the females of a pride and the males sire all cubs born to the pride during their tenures (Schaller 1972; Bertram 1975b, Packer et al. 1988). However, in Asiatic lions, males maximise their reproductive potential by having range overlaps with one to many female prides (**Figure 2.1.**; Banerjee 2012).

Figure 2.1. 95% MCP of radio-telemetered lions (n=28) across the Gir landscape (Source: Banerjee 2012)



Hypothesis: Since more than one coalition has territorial overlaps with a female pride, females of a pride might interact and/or mate with males belonging to adjacent coalitions.

Prediction: If females of a pride mate with more than one coalition, females should have direct benefits from such promiscuity in terms of enhanced reproductive fitness.

To explore the aforementioned questions, my study objectives were as follows:

- I. To estimate individual resource utilization by male partners in a coalition, and subsequently investigate intra-coalition social structure based on resource sharing.
- II. To estimate and compare the reproductive fitness of individuals belonging to male coalitions of different sizes.
- III. To evaluate the prevalent mating system in Asiatic lions through quantification of female reproductive strategy and mate choice.

Figure 2.2. A prime-adult Asiatic male lion of 7-8 years on his regular territorial patrol. A previous study has shown that territorial males spent 63% of their active time vocalizing and patrolling their territories (Meena 2008). © Stotra Chakrabarti



Study Area

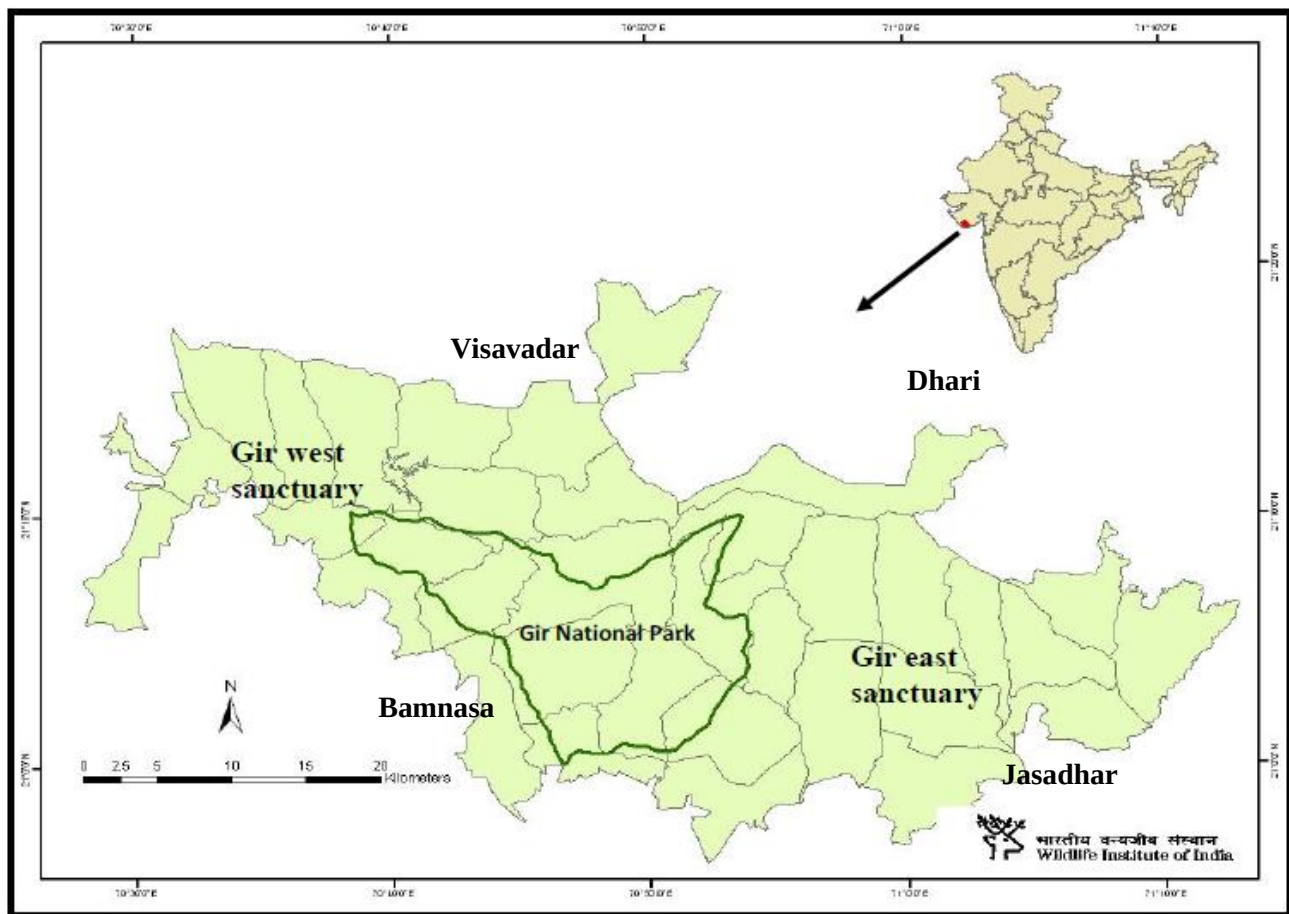


Study Area

The study was carried out in about 1200 km² of the Gir Protected Area (Gir PA) and the adjoining agro-pastoral landscape to the south-western fringes of the PA.

Gir PA (Gir wildlife sanctuary and national park): is located in the southern part of the Kathiawar peninsula, in the state of Gujarat, western India, extending across districts of Amreli, Junagadh and Gir Somnath between 20° 57' and 21° 20' N latitude and 70 ° 27' to 71 ° 13' longitude (**Figure 3.1**). It covers an area of 1412.13 km² of which 258.17 km² comprises of the national park and 1153.42 km² is the wildlife sanctuary. The forest extends about 70 km along the west to east axis and about 20 km on an average along the north to south. Recently the Chachai-Pania wildlife sanctuary (39.64 km²) at the northern boundary of Gir PA has also been included as part of the Gir Conservation Unit (GCU). Additionally, there is a buffer area of reserved forest (245.90 km²), protected forest (107.51 km²) and unclassified forest (77.19 km²) comprising of valuable grassland and forests. The Gir protected area is divided into three managerial zones: *sanctuary west*, *sanctuary east* and *central national park*. Due to a rainfall gradient increasing from east to west, these three zones subtly differ; and that reflects in their vegetation types (Qureshi and Shah 2004) and associated productivity. Gir is located about 50 km south west to Junagadh city. The coast line is 25 to 50 km away from southern park boundary.

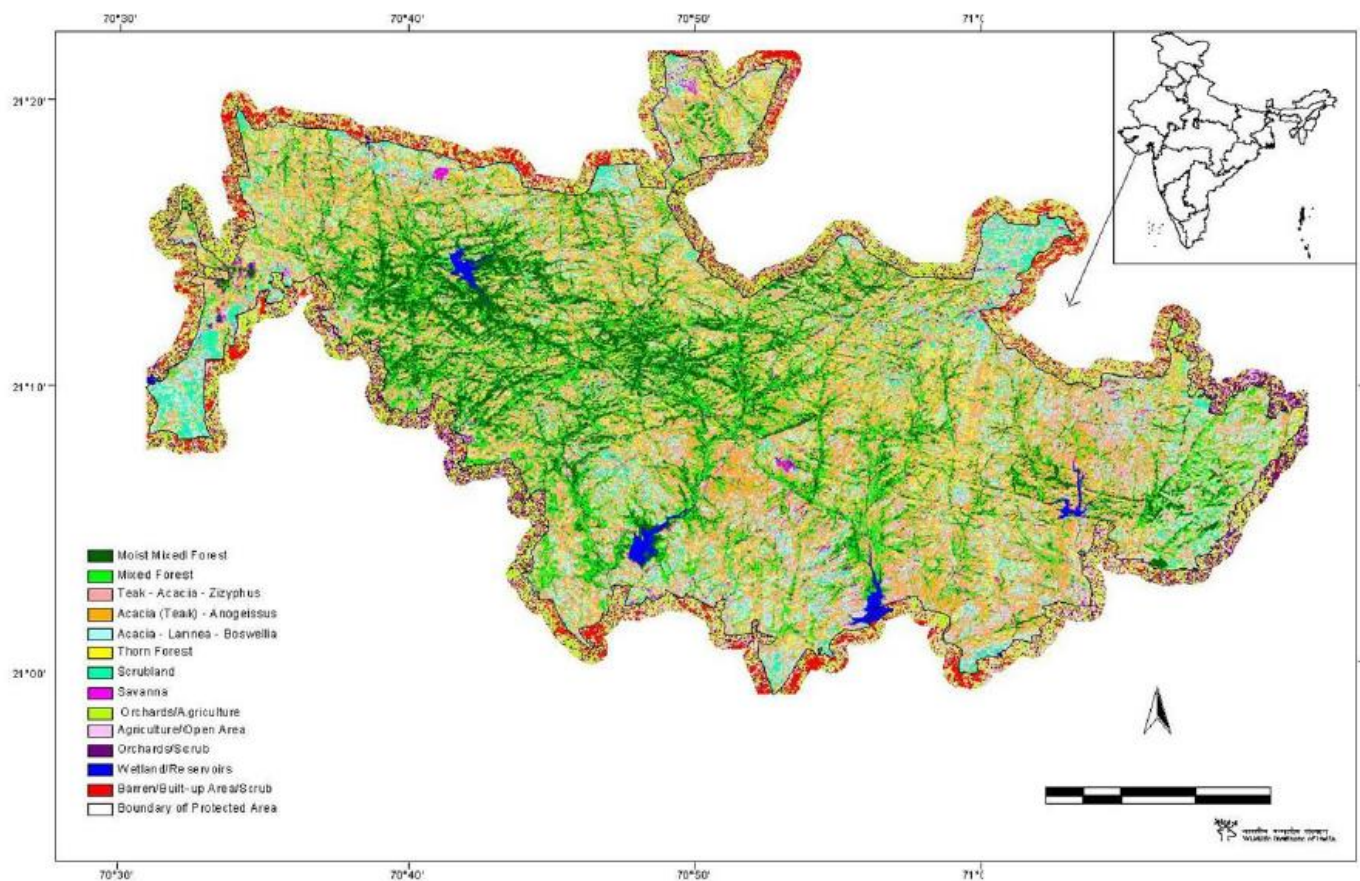
Figure 3.1. Relative Location of Gir PA in Gujarat, India. Source: Meena 2008



According to Koppen's (1931) classification, the area comes under *tropical savanna* climate. According to Rodgers and Panwar's biogeographical classification of India (1988), Gir has been placed in zone 4 (semi-arid). It is a dry, hot semi-arid patch. Rainfall is brought by south-westerly winds from Arabian Sea during the monsoons between June and September. There is a distinct dry spell in winter but heavy dewfall is common. The area experiences three distinct seasons as the other part of the country. There is cool dry winter in Gir from December to March (average minimum temperature 9°C.) followed by a hot dry summer (average maximum temperature 42°C), which lasts until mid-June. The monsoon breaks in June and continues till September and is followed by a dry post monsoon season till mid-December. The average rainfall in the west and eastern part of the PA are approximately 1000 mm and 800 mm, respectively (Khan et al. 1996). The rainfall gradient increases from

east (850 mm at Jasadhar) to west (1000 mm at Sasan). However, the annual variation in rainfall is large. About 94 % of the rainfall is received during monsoon, with July and August receiving the highest downpour. The area is roughly affected by a four year drought cycle. The floral wealth of the Gir forest includes ~500 flowering plant taxa (Singh and Kamboj 1996). Gir lies within the Afro tropical realm (Singh and Kamboj 1996) in the 4B Gujarat Rajputana biotic province of *Biogeographic Classification of India* (Rodgers and Panwar 1988). Gir comprises of one of the largest compact tracts of dry deciduous forest, which comes under the 5A/C1b forest subtype (Champion and Seth 1968). Gir vegetation has been classified into three broad categories namely: *moist mixed vegetation, thorn forests and hill forests*. Major vegetation includes Teak (*Tectona grandis*), *Zizyphus* spp., *Acacia* spp., *Butea monosperma*, *Anogeisus* spp., and *Boswellia serrata*.

Figure 3.2. Vegetation classes of Gir PA with a 1 km buffer around it. Source: Qureshi and Shah 2004

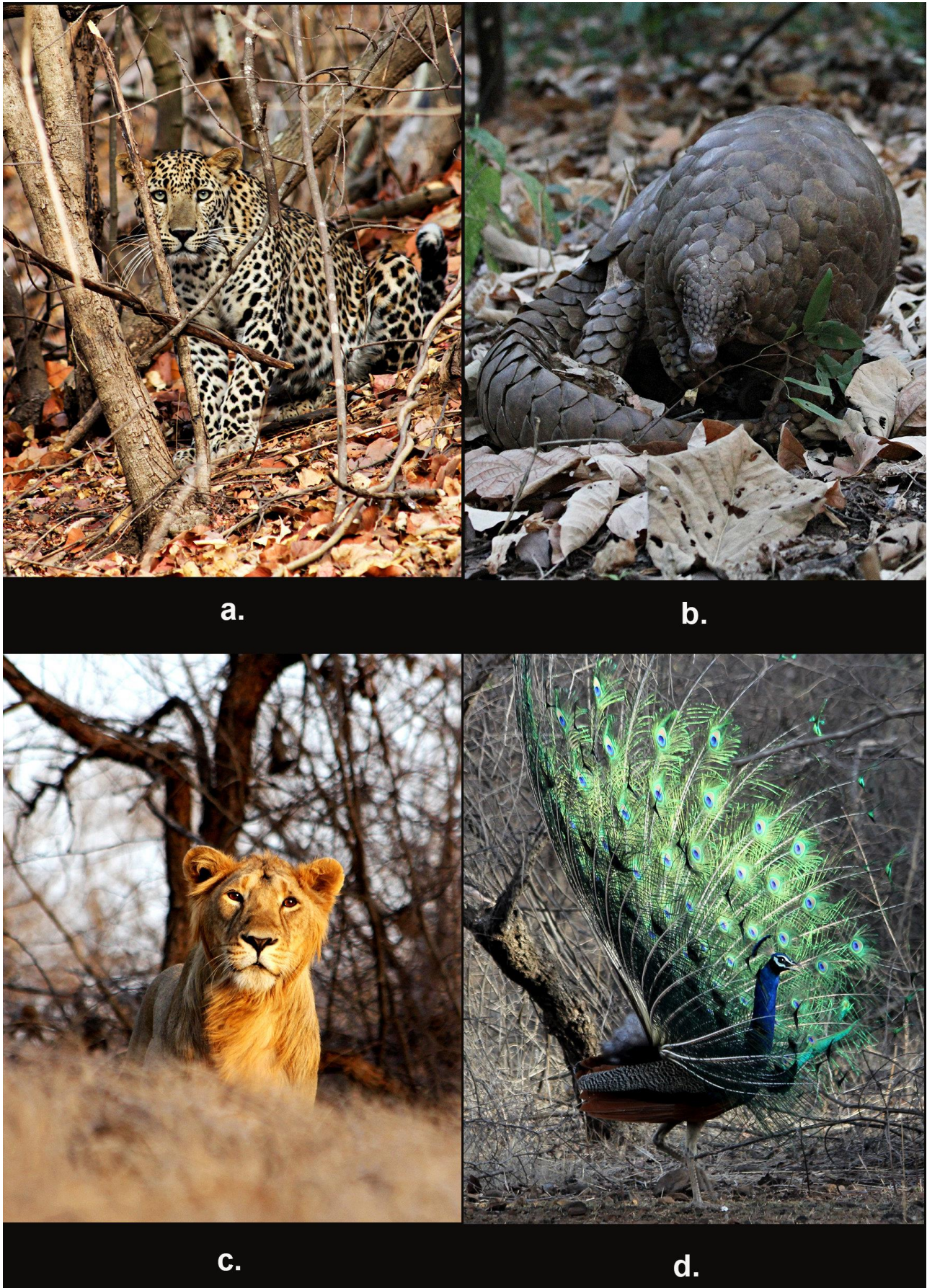


The Gir forest has a diverse assemblage of wild fauna: about 32 species of mammals, 26 species of reptiles and over 300 species of birds (Divyabhanusinh 2005; Mena and Kumar 2012). Apart from the Asiatic lion, some of the other carnivores are leopard (*Panthera pardus*), jungle cat (*Felis chaus*), striped hyena (*Hyaena hyaena*), jackal (*Canis aureus*), Indian fox (*Vulpes benghalensis*), ratel (*Mellivora capensis*), mongoose (*Herpestes edwardsi*), small Indian civet (*Viverricula indica*) and rusty spotted cat (*Prionailurus rubiginosus*). Major ungulates include chital, sambar (*Rusa unicolor*), nilgai, wildpig (*Sus scrofa*), four horned antelope (*Tetracerus quadricornis*), and chinkara (*Gazella gazella*) (Singh and Kamboj 1996). Chital is the most abundant wild ungulate with a density of $56.1 \pm 8.3/\text{km}^2$ (Jhala et al. 2016).

Figure 3.3. Although reptile diversity is scanty in Gir owing to its semi-arid nature, we do come across occasional rarities like the red sand boa (*Eryx johnii*) . ©Stotra Chakrabarti



Figure 3.4. Representative fauna of Gir PA. a. Leopard, b. The rare Indian pangolin (*Manis crassicaudata*), c. A sub-adult male Asiatic lion, and d. Male Indian peafowl (*Pavo cristatus*) displaying at the advent of monsoon. ©Stotra Chakrabarti



The PA has ~97 peripheral villages (human population of approximately 150,000 and a livestock population of 95,000) (Singh and Kamboj 1996). Within the PA, there are 52 *Maldhari* settlements/*nesses* (333 families with a human population of about 2,300 and livestock population of about 12,000) and 14 forest-settlement villages (human population of 4,500, nearly 4,200 livestock) (Singh 2007). The sale of dairy products has always been their traditional source of economy (Varma 2009). Gir forests are inhabited by a trans-nomadic, multi-ethnic pastoral community called *Maldharis* for past one and a half century (Casimir 2001). Their main religion is Hinduism and they have strong religious ethics and sentiments towards nature and natural resources. *Maldhari* is not a traditional tribe but an occupational community comprising different livestock holding castes. A recent study elucidates that *Maldharis* living inside the PA make 76% more profit than their outside-PA counterparts, owing to free grazing rights along with the prompt compensation paid by GFD for livestock depredation (Banerjee et al. 2013).

Outside PA south-western landscape: The stretch outside the PA comes under the administrative districts of Junagadh and Gir-Somnath. The landscape is interspersed with agricultural fields, *Prosopis* sp.- *Acacia* sp. patches and mango-orchards. Major crops grown are cotton (*Gossypium* sp.), ground-nut (*Arachis* spp.), legumes, wheat (*Triticum* spp.), and soybean (*Glycine max*). Land-use is private farms, industrial and pastoral lands with some government owned community grazing lands and grasslands/*vidis*. Public lands are managed for multiple uses including seasonal cattle grazing. Lions inhabit these areas, using small patches as day-time refuges and roam inside the villages at night in search of unguarded livestock (Banerjee 2012). Major natural prey are nilgai and wildpig. Lions in this area are connected with the Gir population through source-sink dynamics, with certain riverine patches acting as movement corridors.

Figure 3.5. Intensive study area of $\sim 1200 \text{ km}^2$, comprising of parts of the Gir PA and the SW agro-pastoral landscape. Centroids of home ranges of observed coalitions and prides between 2012 and 2017 are marked. All coalitions depicted here are not contemporaneous, overlapping male centroids indicate sequential territoriality, with one gaining residence by ousting the former.

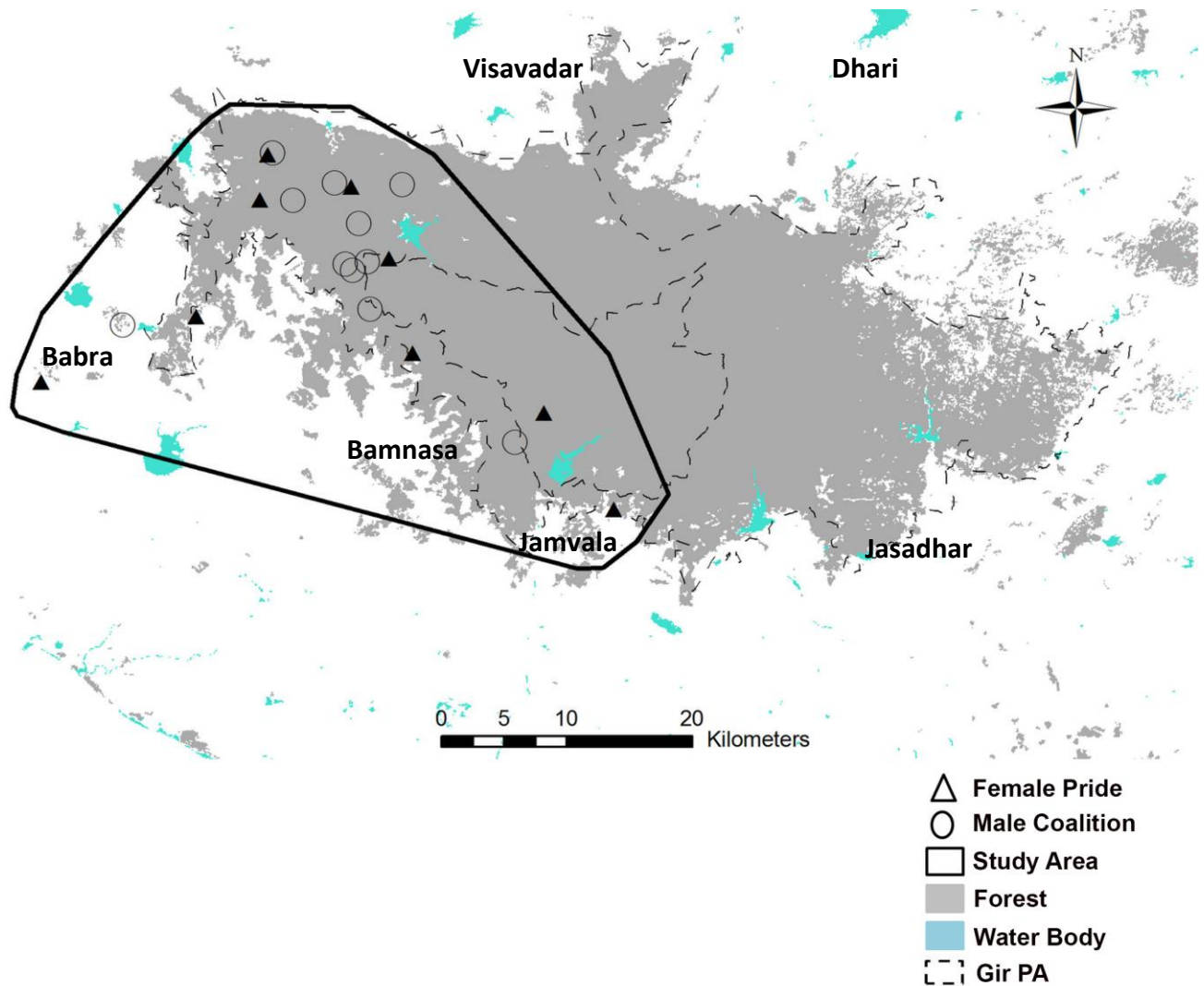


Figure 3.6. Glimpses of the study area inside Gir PA: a.) Mixed thorn forest with *Zizyphus sp.* and *Acacia sp.* in the foreground; b.) A bird's eye-view of western Gir in the dry season with teak (*Tectona grandis*) mixed thorn forest as the major vegetation type; c.) A riparian patch of a non-perennial stream, such patches dominated by *Syzygium sp.* are green and mesic throughout the year and lions use them extensively for resting in the shade; d.) Gir during the monsoon with flush of new green leaves. ©Stotra Chakrabarti

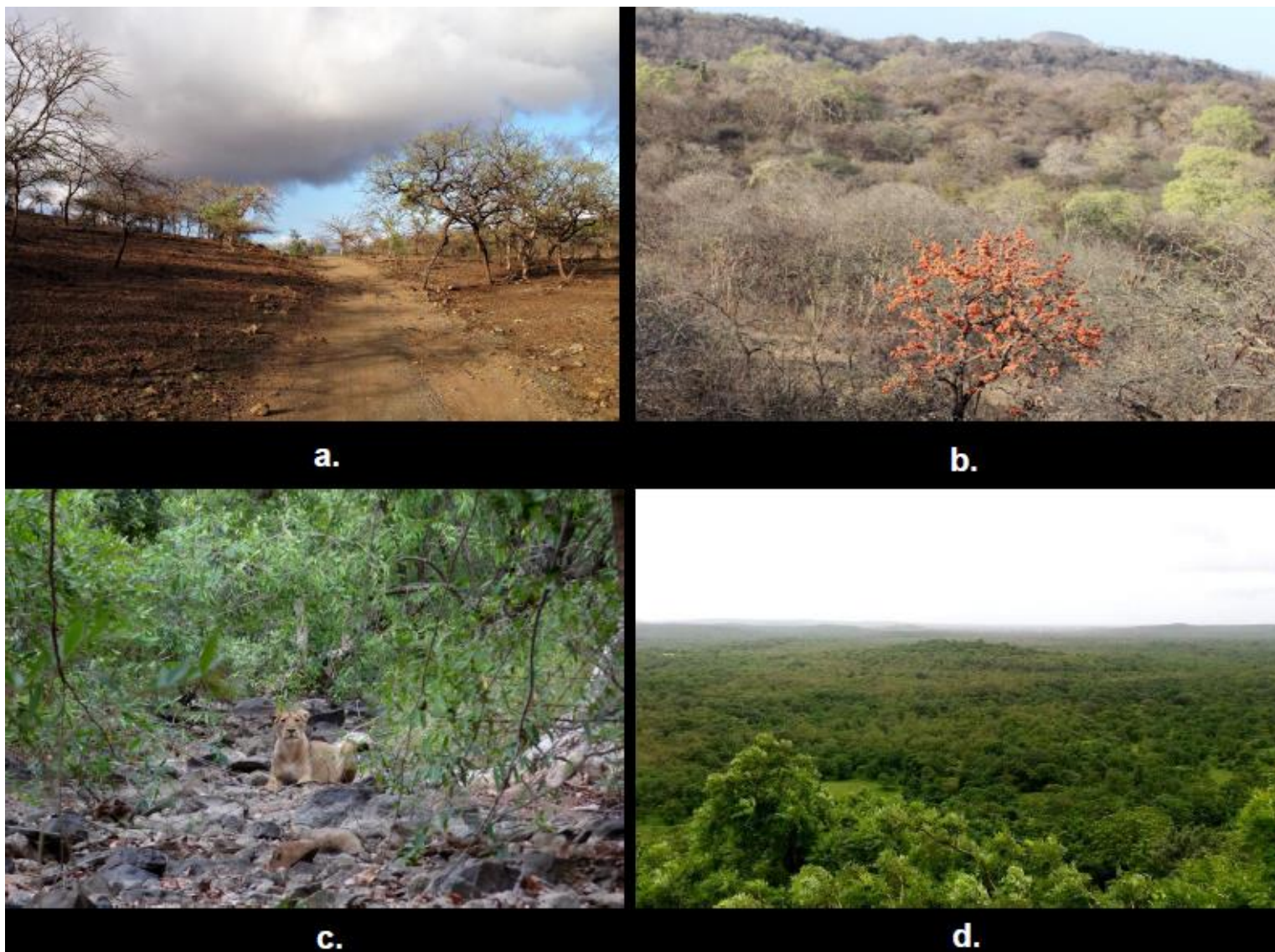
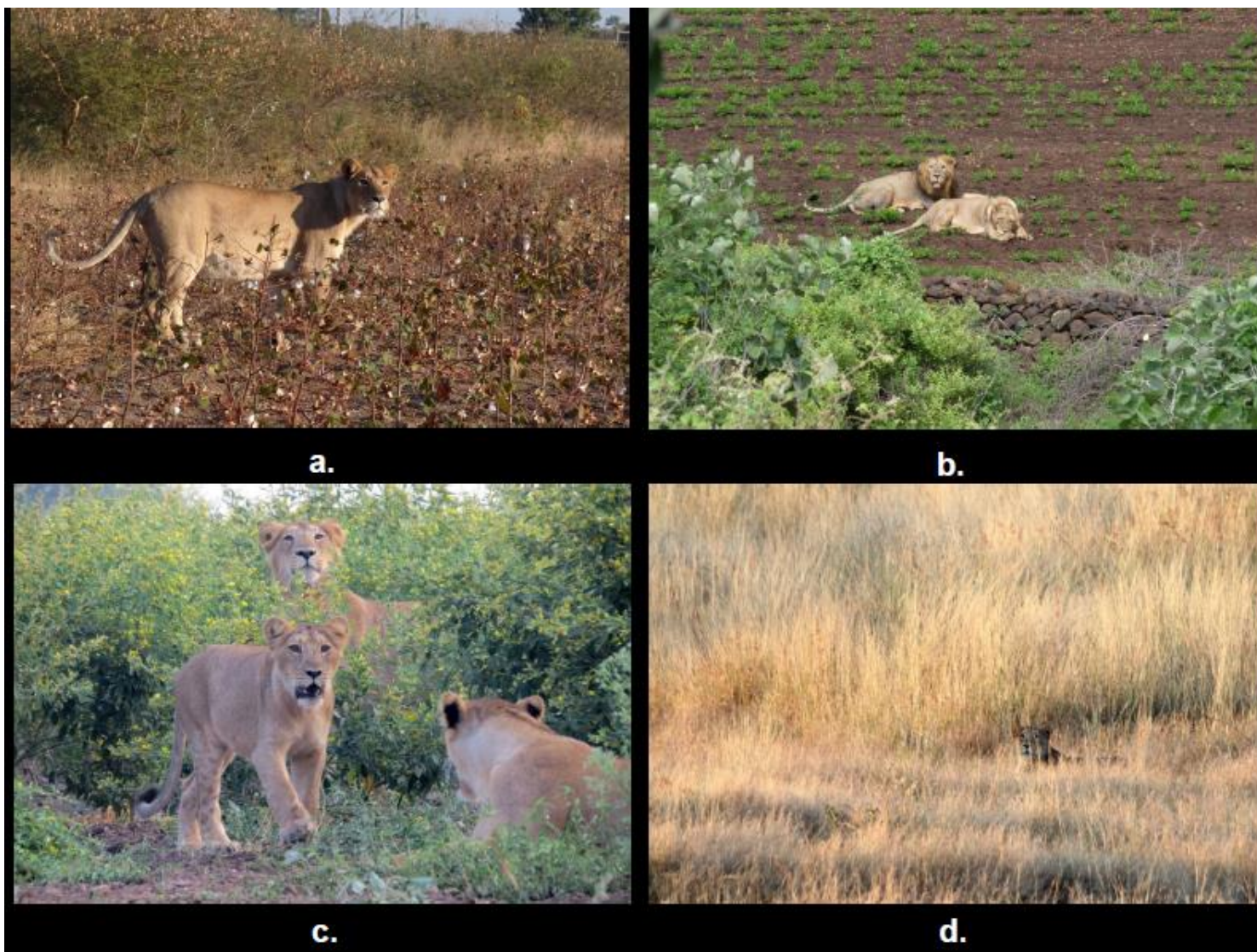


Figure 3.7. Glimpses of the study area outside PA: a.) a young adult lioness of around 4 years in a cotton farm; b.) a pair of lions mating on a ground-nut farm; c.) 2 juvenile females and 1 sub-adult male in a farm of pigeon pea (*Cajanus cajan*); d.) a sub-adult lioness in a forest owned grassland/vidi, such protected vidis act as good refuges for lions in this landscape © Stotra Chakrabarti and YV Jhala



Coalition Males



Comrades in Arms or a Twist in
the Tale?

Coalition Males: comrades in arms or a twist in the tale?

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1. Introduction

Intra-specific cooperation among males in obtaining and defending resources has been reported in many species, namely lions (Schaller 1972; Bertram 1978; Bygott et al. 1979; Packer and Pusey 1987; Grinnell et al. 1995; Meena 2009), cheetahs *Acinonyx jubatus* (Caro and Collins 1987), native hens *Tribonyx mortierii* (Ridpath 1972), howler monkeys *Alouatta seniculus* (Pope 1990), baboons *Papio spp* (Smuts 1985; Bercovitch 1988; Noë 1994), feral horses *Equus caballus* (Feh 1999), striped hyaenas *Hyaena hyaena* (Wagner et al. 2008), meerkats *Suricata suricatta* (Doolan and Macdonald 1996), chimpanzees *Pan troglodytes* (Watts 1998; Nishida 1996; Mitani et al. 2000) and bottlenose dolphins *Tursiops truncatus* (Connor et al. 1992). However, the proximate and ultimate causes of such cooperation can differ between species and are often difficult to discern (Pope 1990). Degrees of cooperation vary dramatically between species, from complex male groups in non-human primates (Harcourt 1992) to loosely-tolerant aggregations in coastal river otters *Lontra canadensis* (Blundell et al. 2004). Male groups may be formed for varied reasons: extra vigilance and predator-protection (Cape ground squirrels *Xerus inaurus*, Waterman 1997), enhancement of hunting success (coastal river otters, Blundell et al. 2004), effective utilization of clumped resources (native hens and golden jackals, Ridpath 1972; Macdonald 1973). These types of cooperation can be explained by the mutualistic benefits of aggregation (Olson and Blumstein 2009), whereas complex ‘coalitions’ in which male partners incur *costs-of-sharing* valuable resources (like food, mates and territory) seem to challenge

Darwin's (1859) theory of natural selection (Smith et al. 2010). Coalitions are known to occur when multiple individuals cooperate against a common opponent or for a common goal (Krebs and Davies 1987). A typical coalition is defined as cooperation between 2 or more individuals against a third-party during a competitive encounter (Harcourt 1992; Olson and Blumstein 2009). Such agonistic aiding in which a third individual intervenes to support one of the two opponents (coalition formation) is hard to understand since selection is not expected to favour individuals who reduce their own fitness to increase the fitness of others (Smith et al. 2010).

Coalition formation in males can be explained through 3 major evolutionary pathways: a) kin-selection, where cooperation is extended to closely related individuals to enhance inclusive fitness of donors and recipients through shared genes (Maynard Smith 1964; Hamilton 1964); b) reciprocal-altruism, where cooperation enhances the chances of future benefits between partners (Trivers 1971; Packer 1977); and c) selfish support, which provides immediate benefits to the donor (Wrangham 1982) (for eg. male chimpanzees act selfishly while helping non-kins against certain opponents to enhance their own dominance status [de Waal and Harcourt 1992]). Complex pathways for coalition formation necessitate species to be long lived, with frequent interactions between individuals and a cognitive ability permitting past interactions to be remembered (Ridley et al. 2005). Coalitions are thus, essentially found in highly social and cognitively developed species (Olson and Blumstein 2009), although cognitive constraints on coalition formation have been debated recently (Bissonnette et al. 2014).

Among non-human primates, the most well studied coalitions are in African lions where males cooperate to maintain exclusive access to groups of females (Schaller 1972; Bertram 1978; Bygott et al. 1979; Packer and Pusey 1982; Grinnell et al. 1995). Competition between coalitions is intense, with only a small proportion of males gaining residence in a pride. Few coalitions are

able to maintain residence and hold territories long enough to sire one cohort of cubs to full independence (Schaller 1972; Bertram 1978; Pusey and Packer 1994b), as infanticide of dependent cubs by new males during pride takeovers is an inherent element of lion sociality (Schaller 1972, Bertram 1978; Packer and Pusey 1983a and b; Banerjee and Jhala 2012). Akin to developed primates in lifespan, cognitive abilities and social bonding, the uniqueness about lions is the absence of dominance hierarchies in their societies (pride/coalition) (Schaller 1972; Bygott, et al. 1979; Packer and Pusey 1982). However, a featured feeding-hierarchy exists between pride males and females for the rights to a kill, where males being much bigger than females, gain the first rights (Schaller 1972; Bertram 1975b). Literature suggests that there occurs a symmetrical utilization of resources between the coalition partners, where each male gets an (approximately) equal share of mating chances and feeding bouts (Bertram 1978; Bygott et al. 1979; Packer and Pusey 1982). Such a state of equal rights among coalition males is attributed to two factors: a) frequent presence of large bodied prey in the African savanna, reducing the costs of sharing a meal, and b) large number of simultaneous mating opportunities for coalition males (average African pride sizes range between 9-15 adult females exhibiting *synchronous estrus*), leading to a competitive release over female ownership (Bertram 1978; Koykka and Wild 2016). Moreover, reproduction in lions is highly *inefficient*, with an average of 1000 copulations required for a litter to be born (Bertram 1978). Thus, it is beneficial for a male lion to consort a single female for the entire estrus duration (2-5 days) to maximize chances of successful fertilization, leaving other coalition partners a chance to mate with other females (also in estrus ‘synchronously’). Reproductive inefficiency is viewed as a *peace-keeping adaptation* to reduce skew in mating opportunities between coalition males (Bertram 1975b; Koykka and Wild 2016). However, within large coalitions (5-7 males), competition for food and mates is more

intense, reduced only by kin-selection (large coalition partners are nearly always closely related, Packer et al. 1991). In such coalitions reproduction is skewed with few partners acting as non-breeding helpers, increasing the overall fitness of the coalition through group protection (Packer et al. 1991).

Male Asiatic lions in the Gir forests of Gujarat, Western India, live under selective pressures likely different from their African cousins; with smaller modal prey size (chital, averaging at around 45 kg) (Meena et al. 2011; Banerjee et al. 2013; Chakrabarti and Jhala et al. 2016) and lesser simultaneous mating opportunities (smaller female group/pride sizes, averaging at 2 adult lionesses that lack estrous synchrony) (Meena 2008; Banerjee 2013; current study). Lower resources and higher stakes should set the stage for enhanced competition between coalition males. Based on this, I hypothesize that coalitions of Asiatic male lions would show dominance hierarchies, with asymmetric resource (food and mates) utilization among the partners, akin to primate societies. In this chapter I test this hypothesis through my observations on mating- and predation events of male coalitions (n=7), ranging in strength from 2-4 males.

Figure 4.1. A coalition of two Asiatic male lions in western Gir PA, Gujarat. The males are in prime condition; note their luxuriant manes covering their heads till their napes. ©Stotra Chakrabarti



2. Materials and Methods

2.1. Study site and population

Between December 2012 and December 2016, I studied 66 adult lions (17 males and 49 females) belonging to 7 coalitions and 9 prides, encompassing an area of about 1,200 km² in the western part of the Gir PA and its adjoining human-dominated landscape (21°17'-20°55'N and 70°20'-70°52'E) in Gujarat, India. The study animals were a subset of the larger lion population in Gir PA (1800 km²) of around 250 individuals, which has been studied continuously since early 1990s (Jhala et al. 1999, 2004, 2006; Meena 2008; Jhala et al. 2009, Banerjee et al. 2010; Banerjee and Jhala 2012; Banerjee 2012; Jhala et al. 2016). The intensive study area comprised of parts of the western Wildlife Sanctuary and the central National Park, and parts of the south-western agricultural landscape which is outside the formal boundaries of the PA. Gir PA is a dry-deciduous forest tract characterized by a semi-arid climate (Champion and Seth 1968) with *Tectona grandis*, *Anogeissus spp.*, *Acacia spp.* and *Ziziphus spp.* as the dominant vegetation (Singh and Kamboj 1996; Jhala et al. 2009, Banerjee et al. 2013). The stretch outside the PA comprised mainly of farmlands, croplands, mango-orchards and *Prosopis sp.-Acacia spp.* thickets (for detailed information regarding study site see **Study Area chapter 3**).

2.2. Selection of coalitions

Males were categorized to be in a coalition when they were frequently seen in each other's company, shared kills, hunted, vocalized and patrolled their territories together (Schaller 1972). Due to long-term research and intensive monitoring system in the study area since early 1990s, many lions were individually identifiable along with information on their ranging patterns and life-histories. Using this prior information, territorial male coalitions: a) of varying sizes, and b) with information since they became residents in the area were selected. I chose coalitions with neighbouring ranges as coalitions dispersed over a very large area were difficult to monitor

simultaneously with intense rigor. A total of seven breeding male coalitions comprising doubletons/2-male coalitions ($n=5$) and >3-male coalitions ($n=2$) and their interacting nine female prides ($n=49$ adult females) were selected for behavioural observations and were monitored for periods ranging between 1.5-4 years.

2.3. Identification and monitoring

Each lion was individually identified using its vibrissae pattern and additional body marks (Pennycuick and Rudnai 1970; Jhala et al. 1999). Subsequently an identity datasheet was made for each individual with its right and left whisker-profile photographs, notes about ear-notches, approximate age, and a code based on the areas where it was frequently seen (**Figure 4.2**). One male from a coalition of 4 (Babara coalition) was radio-collared (GPS collar, Vectronics Aerospace GmbH, Berlin, Germany, weighing <1% of the animal's bodyweight and scheduled to obtain a GPS fix every 1 hour) by anesthetizing it with a combination of ketamine hydrochloride and medetomidine (Kreeger 1996) injected intramuscularly using a gas-powered projectile (Telinject Inc., Agua Dulce, California) dart delivery system. The reversal agent atipamezole resulted in the total recovery from anesthesia within 3–10 min. The radio-collared lion (and its coalition) was tracked on foot or a 4 wheel-drive vehicle, using a 3-element yagi antenna (AF Antronics Inc., Urbana, Illinois) and a handheld receiver (*Wildlife Materials* receiver model TRX-2000S; *Wildlife Materials*, Inc.; and Vectronics GPS Plus Handheld Terminal Unit; Vectronics Aerospace GmbH) (**Figure 4.5**). The non-collared males were monitored through intensive searches using cues such as pugmarks, prey-alarm calls, roars, and information from forest department lion-trackers and tourists. The entire monitoring period of each male was divided into 2-day sampling occasions as mating observations necessitated each male to be visually located at least once in 2 days, so as not to miss recording a mating event (lion mating

events typically range from 2-6 days, Schaller 1972; Bertram 1978; Packer and Pusey 1983). Such intensive monitoring was possible owing to rigorous fieldwork aided with an age-old practice of the forest department to track individual lions every day within the study area (Singh and Kamboj 1996; Divyabhanusinh 2005; Meena and Kumar 2012). Efforts led to the detection of each male in 92 ± 1 % of all the sampling occasions (**Table 4.1**).

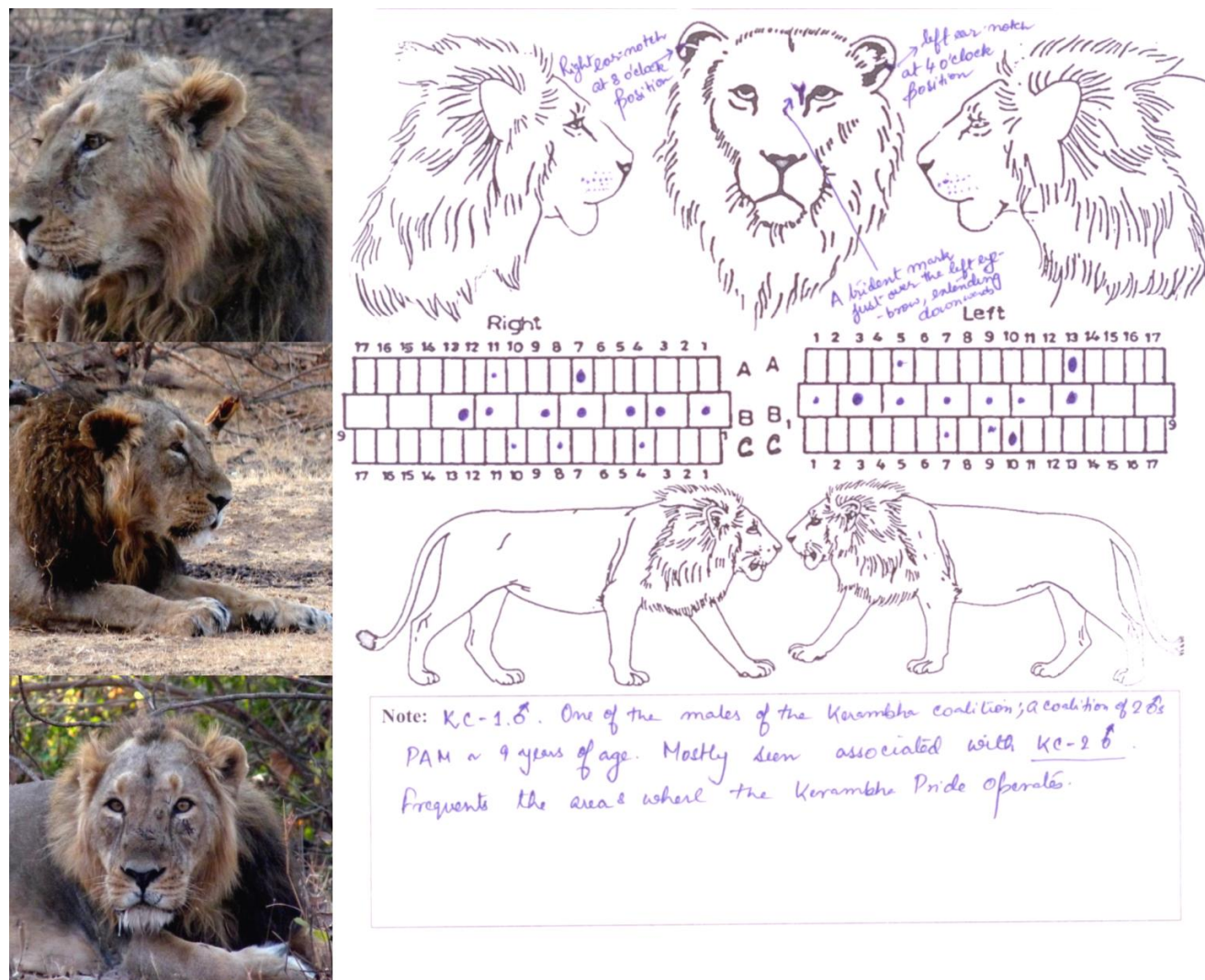
2.4. Familiarization

For observing behaviour of wild animals it is imperative to familiarize them to the observers' presence (van Lawick Goodall 1971; Schaller 1972; Bertram 1978; Mech and Boitani 2003). Lions were acclimatized to our (entire research team) presence by approaching them on foot or on a vehicle, slowly (approach distance reducing by only a few meters in weeks with certain lions), keeping a low profile and a body-language which '*meant no harm to them*' (no sudden startling movements, ceasing approaches as soon as animals became restless and showed mild aggression). At a later stage this familiarization allowed us to observe them from distances of 10-20 m and in my opinion did not hinder their daily behaviour repertoires (**Figure 4.5**).

Table 4.1. Sampling effort for monitoring male coalitions on which behavioural observations were made.

Male id	Coalition size	Monitored Occasions	Detected Occasions	Detection proportion (%)
M22	1	246	231	94
M14	1	196	174	89
M19	1	268	255	95
M4	1	214	184	86
M20	2	415	403	97
M21	2	415	394	95
M6	2	552	530	96
M7	2	552	513	93
M11	2	451	419	93
M12	2	451	428	95
M9	2	288	262	91
M10	2	288	251	87
M24	2	492	438	89
M25	2	492	423	86
M28	4	274	258	94
M29	4	274	249	91
M31	4	274	241	88
M32	4	274	219	80
M13	3	300	276	92
M16	3	300	287	96
M17	3	300	264	88

Figure 4.2. Identity datasheet following Jhala et al. (2004) of an adult male lion belonging to a coalition of 2 males. The right and left vibrissae spot profiles along with information on permanent body marks like scars, ear notches and wound marks make each lion uniquely identifiable. Females were also identified using the same technique as used for males.

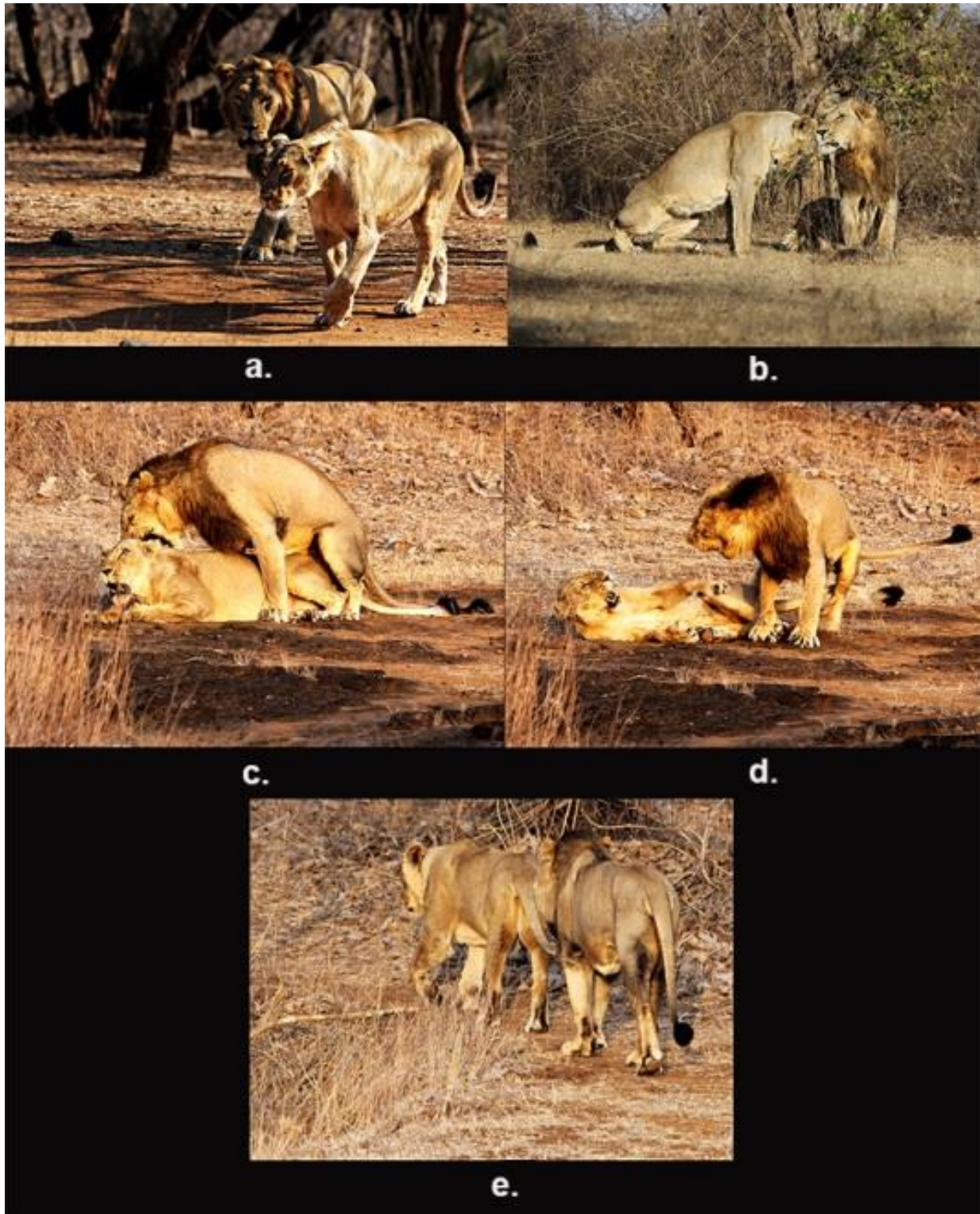


2.5. Behavioural Observations

A. Mating events: Mating events were recorded by locating each study male every day or every alternate day. Upon locating a male, the GPS coordinates, surrounding habitat, state of activity and associated animals were noted. One mating event was considered to be the entire duration when a male consorted a lioness in estrus (included the initial courting phase, actual copulations and intervals between successive copulations, see **Figure 4.3** for details) till the pair parted ways

and returned to their respective groups. Once a mating pair was found, the male and female were identified to their coalition and pride respectively, and a continuous 24-hour focal behaviour-sampling (Altmann 1974) was done for all days the mating event lasted. Pairs were kept in view within 50 m from observers day and night. During dark nights a flash-light was used every 15-30 minutes to ascertain location of the mating pairs and copulations outside visible range were confirmed with the distinctive loud 'yowl' that males make while ejaculating (Schaller 1972; Bertram 1978). Total mating durations and partner-switching instances were recorded. For computing mating durations, I used only those events (n=119) where I could observe pairs from the beginning of the events (courting phase). Since study coalitions differed in their total monitored-durations (depending upon their initiation of residence/being territorial in the area), to remove bias emanating from differential sampling efforts, number of mating events of a male was expressed as a ratio to the number of days the male was actually detected in the field. Also, I attempted to locate study males once in each of the sampling occasions (2 days), but failed to detect them in a few cases (8%). Thus, there were chances that I could have missed mating events and the above mentioned calibration addresses this problem. For each male, calibrated mating frequency was expressed per year and this mating frequency [MF = (no. of mating events/no. of days detected in field)*365] was then compared between partners and tested for differences using a chi-square test at an α -value of 0.05.

Figure 4.3. Different behavioural stages in a mating sequence of Asiatic lions: a) A male walks in tandem with a lioness in estrus, never leaving her unguarded or out of sight, b) Solicitation of copulation by the lioness, c) Mounting and copulation, with nape and ear biting movements by the male who yowls loudly at ejaculation, d) The lioness snarls semi-aggressively at this stage, and turns and swats at the male, e) The male follows the lioness persistently throughout her entire estrus period, often just steps behind, his nose almost touching her rear. ©Stotra Chakrabarti



B. Feeding events: Feeding behaviour of coalition partners was recorded from the beginning of a feeding event (when the males started feeding on a kill) to the full utilization of the carcass (when the males permanently left it). Data was used from only those events ($n=44$) where initiation of feeding was known with certainty and $\geq$ two males were present at the site, within 50-100 m of the carcass. I postulated that competition at kills and hence dominance-hierarchies, if any, would depend upon: i) prey size, ii) appetite state/hunger of the males, and iii) number of individuals sharing a kill. Prey weights were visually estimated. Before collecting data in the field, I practiced and compared my prey-weight estimating skills by accurately weighing different sized whole carcasses used for feeding-trials on lions in a zoo facility (Chakrabarti et al. 2016). I could accurately estimate weights of small carcasses up to 15 kg (with an error of ± 1 kg) and medium carcasses up to 100 kg (with an error of ± 5 kg). Visual-estimates of very large carcasses (>200 kg) differed slightly among observers and hence a consensus-weight between 2-3 observers was taken for such prey in the field. The appetite state of every male lion was recorded for each event by scoring their belly-sizes following Bertram's (1975a) technique for African lions. Each lion was given a belly score between 1 (fully gorged) - 5 (starved) (detailed in **Figure 4.4**). Information regarding the feeding sequence (males taking turns or feeding simultaneously) and aggression at kills was documented. Total time spent by each male feeding on a carcass was recorded through continuous 24-hour monitoring of the feeding events for all days a carcass was being fed upon. Akin to mating observations, each carcass was kept in sight and night monitoring was done using flashlights. Feeding durations were taken as surrogates of biomass consumption. However, lions (like other carnivores) tend to selectively feed first on the choicest body parts of prey (visceral organs and flesh, which need very low handling time), and then the less digestible body parts like skin, bones and hide, which require considerably higher

handling durations (Chakrabarti et al. 2016). Consequently, a male eating first would consume more of higher quality food in relatively less time feeding on viscera and flesh than the next ones having to negotiate skin, bones and hide. Thus, using absolute feeding duration alone would not account for quality and amount of consumption. To circumvent this problem, I used data (from feeding trials on wild-caught lions which mimicked free-ranging conditions, Chakrabarti et al. 2016) on consumption rates (kg eaten/hour) of lions for successive days feeding on the same carcass. Whenever male partners fed sequentially from small-medium carcasses (<100 kg) in the wild, a correction factor of **0.53** (=consumption-rate ratio of 2nd to the 1st day in the captive trials, Chakrabarti et al. 2016) was multiplied to the feeding time recorded for males eating second, third and so on. For larger carcasses (>100 kg), the correction factor was used for males eating after 12 hours from the initiation of feeding. The disparity in consumption between partners was then calculated as the difference in *corrected feeding time* on a kill. Also, aggressive behaviour between the partners on a kill (a measure of competition) was categorized into 2 classes: **i) aggressive exclusion** – when the feeding male(s) thwarted the advance of at least one of his (their) partners through heightened aggression and didn't allow him (them) to feed, and **ii) meal sharing** – mild aggression between partners (squabbles and occasional swats), but all partners shared a kill simultaneously.

I examined whether difference in consumption between partners was significantly different from zero using a one-tailed t-test, expecting a significant positive difference in consumption between male partners. The difference (if significant) was then modelled with estimated prey size, number of males at the site/coalition size and the appetite state of the males. I expected pronounced competition (hence dominance) at smaller kills with greater number of 'hungry' partners at the kill site. I tested 4 models bearing additive as well as interactive effects of prey

size, appetite state of males (belly scores) and coalition size against the null model. I ranked models using Akaike Information Criterion corrected for sample size (AICc) (Akaike 1974) and significance levels, and assessed their goodness-of-fit using R^2 statistic and residual diagnostics.

Errors represent SEs if not mentioned otherwise

Figure 4.4. Belly scores to determine the state of appetite or hunger of lions. a. Fully gorged with a bloated belly, belly-fold taut and almost invisible, scored as 1; b. Well-fed individual with a distended belly and a hint of the belly-fold seen underneath, scored as 2; c. Belly-line almost parallel to the ground with a prominent belly-fold, animal not too fed, neither too starved, scored as 3; d. Semi-starved individual with a very prominent fold and hints of lateral pelvic-depressions, scored as 4; e. Fully starved individual, with a very loose belly-fold and prominent lateral depressions, scored as 5. ©Stotra Chakrabarti

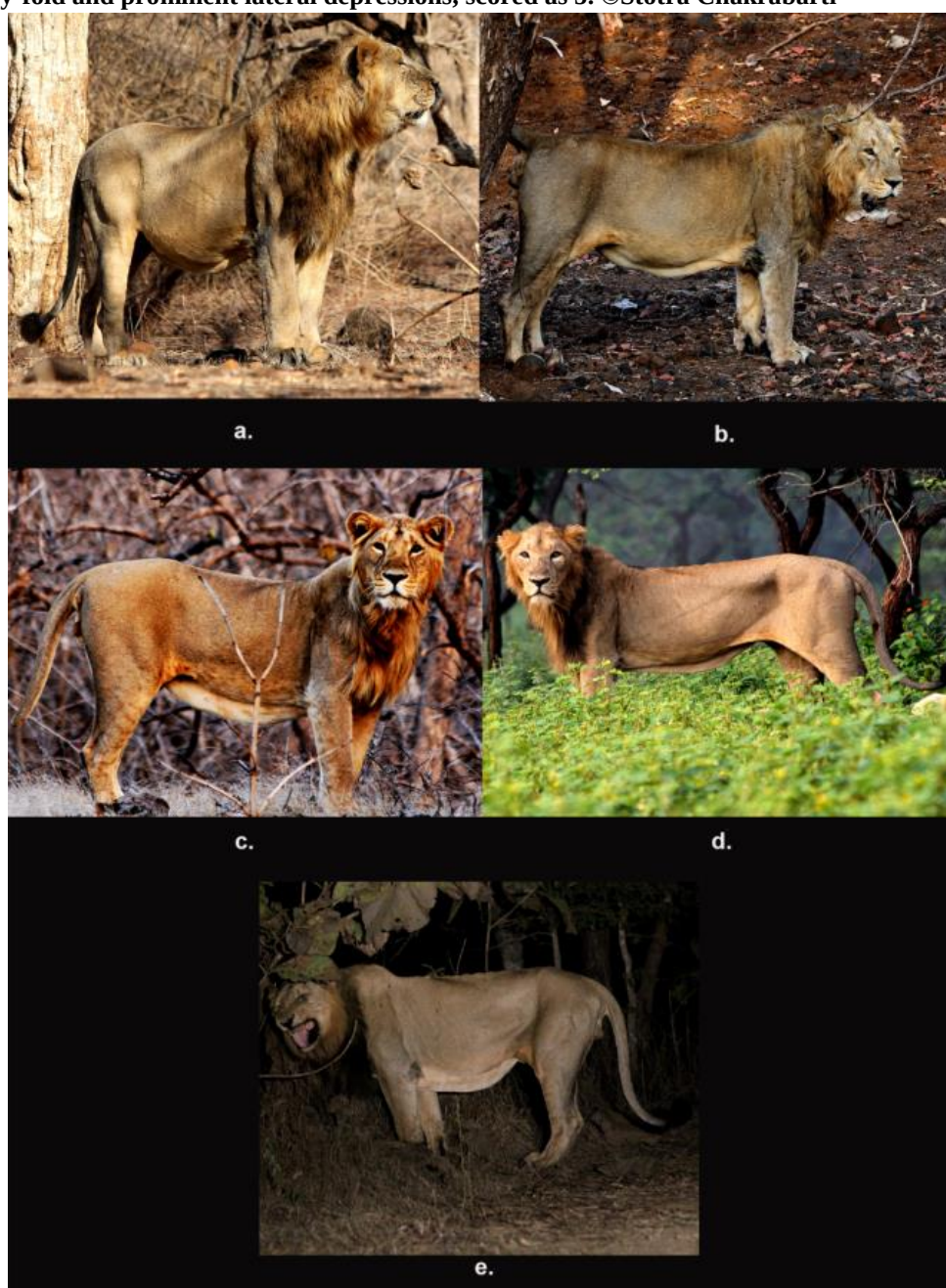
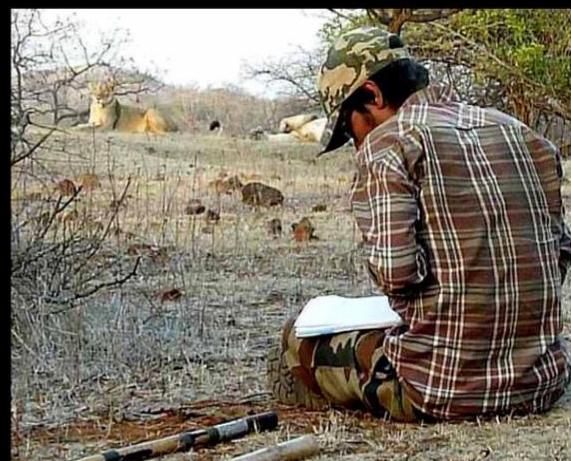


Figure 4.5. Field activities for monitoring coalitions. a. Radio-collaring a male lion belonging to a coalition of 4 males, such coalitions are rare to find; b. Radio-collared male in its habitat with a GPS collar; c. Radio-tracking collared individuals from a vehicle; d. Observations on mating events with the pair familiar to our presence; e. 2 males from Cln.K feeding on an adult chital kill. The 2 males eating together owing to a medium-sized carcass and a satiated state of the dominant male. ©Stotra Chakrabarti

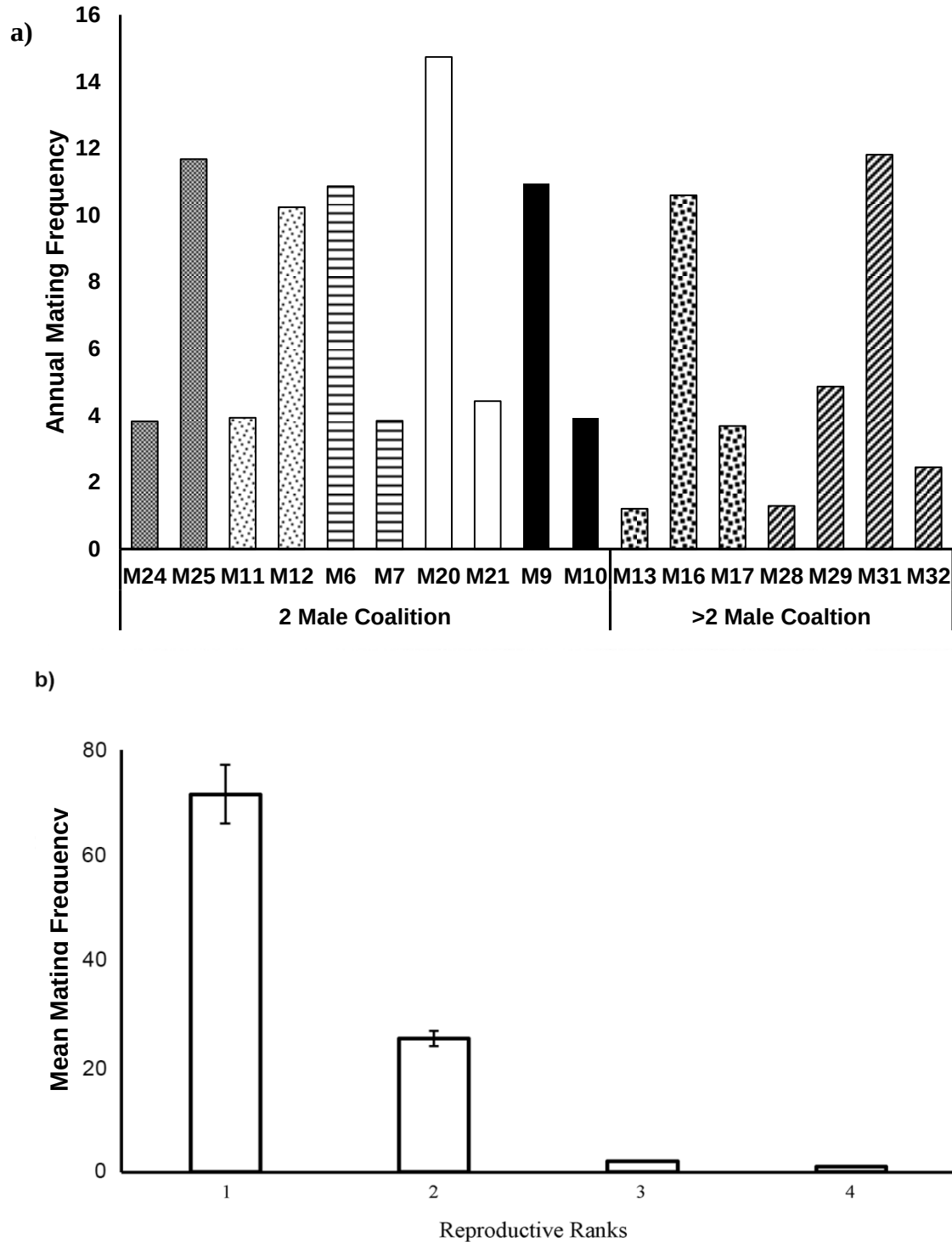
**a.****b.****c.****d.****e.**

3. Results

3.2. Mating Observations

Mating events: A total of 9305 hours of focal sampling were invested in recording behavioural observations from 134 mating events (this includes 7 events monitored for territorial single males described in Chapter 5 of current dissertation). Male-female mating association lasted for an average of 72.9 ± 2.8 hours. Also, in only 1% (2 out of 127 events) of all the recorded mating events I found another female of the same pride in estrus contemporaneously. When compared between partners within a coalition, mating frequencies differed significantly ($\chi^2=41.22$, $df=16$, $p=0.0005$), with one male being consistently involved in more matings than his partner(s) (**Figure 4.6a**). Skew in the distribution of mating events between partners was highly conserved among different coalitions. The partners with most matings appropriated $71.6 \pm 3\%$, the partners with next-highest matings had $25.3 \pm 1\%$ and the partners with least matings had 1-2% of the total events of their respective coalitions (**Figure 4.6b**)

Figure 4.6. Distribution of observed mating events within and between coalition males. Plots showing: a) Mating frequency of monitored lions (annual mating frequency calibrated by the total number of days each male was detected in the field), adjacent bars with similar patterns represent lions from the same coalition; and b) Lions were ranked in a descending order of mating index within each coalition. The figure shows percent matings procured by lions within a coalition averaged for each rank across coalitions. Error bars represent 95% CIs.



B. Feeding events: Data from feeding events of free-ranging lion coalitions revealed a similar trend as found from mating observations. Biomass consumption was highly skewed (difference in consumption between partners >0 , one-tailed $t=6.06$, $df=43$, $p<0.001$) and the reproductively dominant males consumed 0.47 ± 0.07 times more from kills than their partner(s). This difference in consumption was best explained by a 3 parameter linear model (GLM of the Gaussian family) having the additive effects of prey size, appetite state of the male with highest matings (reproductively dominant) in the coalition and the number of males at the kill site/coalition size ($R^2=0.48$, $df=5$, $p<0.001$, **Table 4.2, Figure 4.7, Supplementary Information S1**). The model was given by:

$$\begin{aligned} \text{Difference in biomass consumption} = & -1.045(\pm0.331) - 0.002(\pm0.0005)*\text{prey size} + \\ & 0.313(\pm0.091)*\text{coalition size} + 0.312(\pm0.083)*\text{belly score} \end{aligned}$$

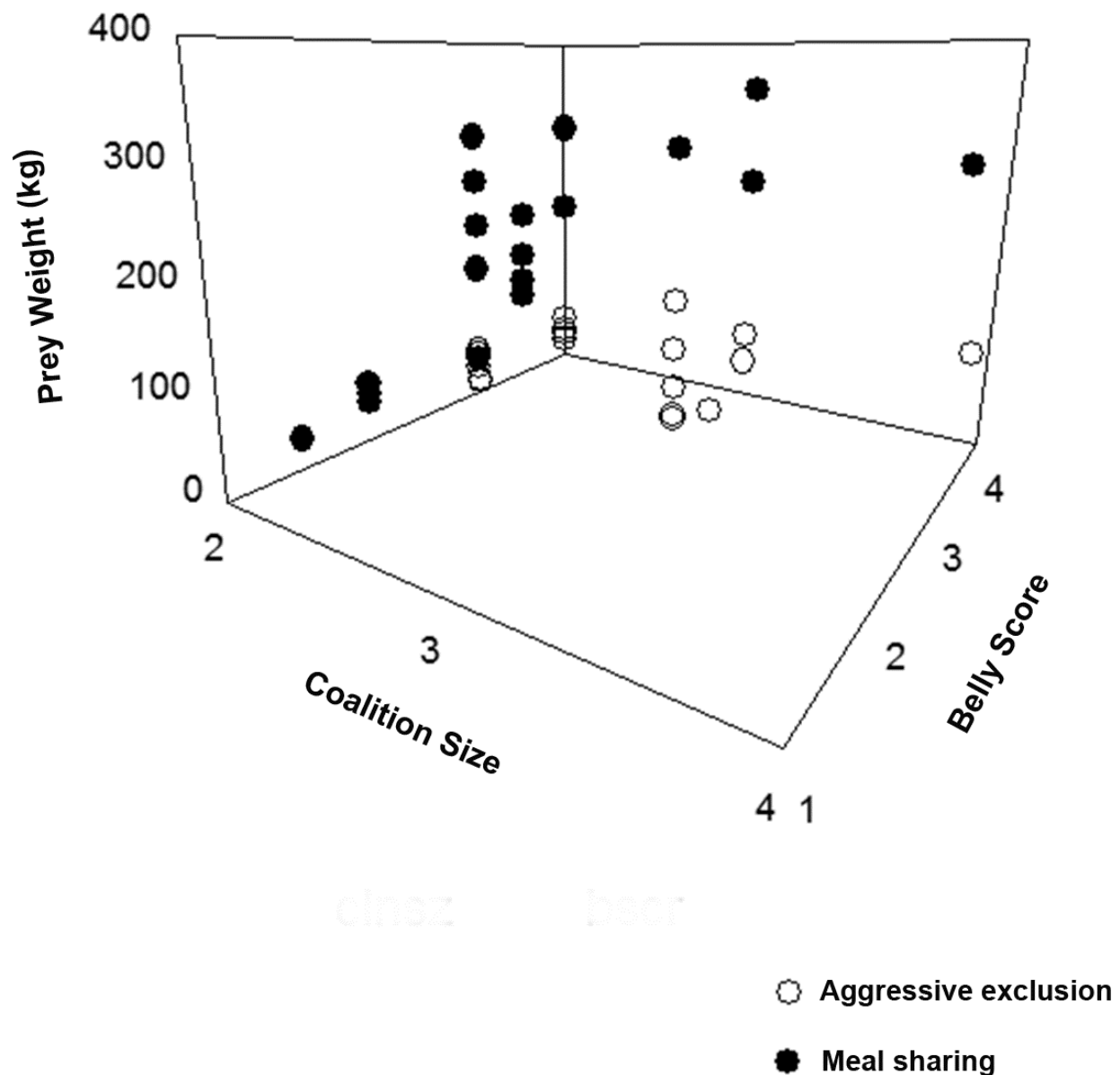
I recorded high levels of aggression between partners which increased with decline in prey size, increase in number of partners at the kill site and the appetite states of dominant males (**Figure 4.8**). Dominant males aggressively excluded other partners and consumed 47% more from kills. This further indicated that above mentioned variables were important in parameterizing feeding hierarchies. However, none of the interaction terms were significant and hence were not included in the best model which differed from the next best model by a $\Delta AICc > 9$ (**Table 4.2**).

Table 4.2. Model selection statistics and parameter estimates of the best model relating difference in biomass consumed by coalition partners to prey size, coalition size and appetite state of the reproductively dominant male (quantified through belly scores) in the coalition.

Model	n	$\Delta AICc$	AICc	R^2	Int.(SE)	Pr.Size(SE)	Cln. Size(SE)	Appt.(SE)	Pr.Size*Appetite (SE)	Pr.Size*Cln.Size(SE)
Pr.Size+Cln.Size+Appt.	44	0	34.12	0.48	-1.045(0.331)	-0.002 (0.0005)	0.313(0.091)	0.312(0.083)		
Pr.Size+Appetite	44	9.41	43.53	0.32	-0.382(0.302)	-0.002(0.0005)		0.323(0.093)		
Pr.Size*Cln.Size	44	11.33	45.15	0.32	-0.588(0.412)	0.002(0.002)	0.534(0.176)			-0.001(0.001)
Pr.Size *Appt.	44	11.39	45.51	0.31	-0.421(0.421)	-0.001(0.003)		0.334(0.126)	-0.0001(0.001)	
Null	44	21.85	55.97		0.462(0.066)					

Feeding events [n], Akaike Information Criterion corrected for sample size [AICc], Prey Size [Pr.Size], Coalition Size [Cln.Size], Appetite of reproductively-dominant male [Appt.], parameters: mean $\pm$ SE

Figure 4.7. Scatter plot showing how aggression between male coalition partners on a kill change with prey size, appetite of the reproductively dominant partner (quantified through belly scores) and number of male partners at the kill (coalition size). Aggression between males increased with lower prey size, greater number of partners and higher appetite of the reproductively dominant males. Empty circles: aggressive exclusion, when feeding male(s) thwarted the advance of at least one of his (their) partners through heightened aggression and didn't allow him (them) to feed; and Filled circles: meal sharing, mild aggression between partners (squabbles and occasional swats), but all partners fed on a kill simultaneously.



4. Discussion

Functional responses of behaviour to different drivers of selection are crucial for species survival. Evolutionary strategies exhibit plasticity to aid species cope with varying environmental conditions. Male-cooperation to form coalitions is one such strategy which exhibits a wide array of variation in mammals. Coalition formation can vary within species depending upon habitat and resource heterogeneity (Connor et al. 2017). Being charismatic and social, lions have attracted the human psyche since centuries (Bertram 1978; Rangarajan 2001; Divyabhanusinh 2005). Owing to the relevance as a flagship-umbrella species in their extant habitats, lions have evoked extensive scientific research (99,000 published studies since 1970), and have become the most studied carnivore after the wolf (<https://scholar.google.co.in>). However, most/all of our ideas regarding lion behaviour, sociality, population dynamics, prey selection and conflict with humans arise from the African system where they have been studied for around half a century in the savanna and adjoining east African forests (for eg. Schaller 1972; Bertram 1975b,1978; Bygott, Bertram and Hanby 1979, Packer and Pusey 1982,1985; Grinnell et al. 1995, Packer et al. 1991, Packer et al. 2011).

My results indicate a markedly different social structure among male Asiatic lions than reported for their east African counterparts. Mate and food sharing between male-partners were highly skewed, suggesting a pronounced dominance hierarchy within coalitions. One of the males in every coalition was consistently involved in more matings and the same individual got the *lion's share* from kills compared to his partner(s). I also recorded 3 instances of intra-coalition mate switching where the female switched from one male to its coalition partner within the same estrus duration, and in all of the three cases the switch happened in favour of the dominant male. As postulated, competition at kills was high amongst partners, very prominent at small carcasses,

with high appetite-state of the dominant males and more partners in a coalition. A distinct feeding order was observed among the partners, where they took turns to eat from relatively smaller carcasses. The reproductively dominant males invariably had the first rights to carcasses, even if they were not the killers or first possessors. However, dominant partners were observed to share small kills amicably with their partners when the former had their bellies full (**Figure 4.7**). Also, when more than one lioness in a pride were in estrus simultaneously ($n=2$), male partners of the mating coalition (both cases were coalitions of 2 males) consorted a lioness each and were found to mate in each other's proximity without any heightened aggression between them. This further corroborates my *resource hypothesis*, wherein a temporary abundance of resources dilutes competitive dominance between partners, thereby strengthening resource availability to be the primary cause behind hierarchy formation in male coalitions. Reproductive dominance across different ranked individuals within coalitions was found to be highly preserved among coalitions, with males at the bottommost ranks hardly getting any matings (**Figure 4.6b**).

Observations on predation and mating events of male lion coalitions indicated that male partners exhibit pronounced dominance hierarchies in the Asiatic system, with one of the males getting more food and mating resources than his partner(s). As postulated, competition was high among partners, very prominent at smaller kills and with more partners in a coalition (**Table 4.1**). A prominent feeding order was recorded among the partners, where they took turns to eat from a carcass. High levels of aggression were recorded at kills which increased with decline in prey size and increase in appetite of the dominant male (**Figure 4.7**). Field observations also showed that male Asiatic lions express a linear hierarchical system wherein, in a coalition of more than two males, the highest ranked individual is dominant over all, the next in rank is dominant over all except the 1st ranked individual and, number of individuals dominated declines progressively

with decrease in rank. The results further corroborate the findings of de Silva et al. (2016) where African and Asian elephant groups (*Loxodonta africana* and *Elephas maximus*) show different hierarchical systems shaped by resource competition, and Connor et al. (2017) where male alliances of bottlenose dolphins exhibit considerable variation in habitats differing in resources and threats.

Reproductive dominance across different ranked individuals in a coalition was found to be highly preserved among coalitions, with males at the bottom-most ranks hardly getting any matings (**Figure 4.6b**). Thus, in an Asiatic system, individuals in large coalitions (3-4 males) have very asymmetrical resource securities, which might be a plausible explanation of such coalitions being rare. However, the question still looms over the evolutionary significance behind the tendency to coalesce among males, despite reduced resource securities for subordinates, which I will try to objectify in my next chapter.

Figure 4.8. A male lion continues to feed on a sambar kill even after his coalition partner (the dominant in the coalition) has had his full and retired. A large carcass like one in this case allows coalitions males to feed simultaneously without one getting excluded ©Stotra Chakrabarti



A Lion's Dilemma



To Form Coalitions or to Stay Alone?

A Lion's Dilemma: to form coalitions or to stay alone?

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1. Introduction

Male-male cooperation is an evolutionary strategy exhibiting a wide array of alternatives between and within species (Olson and Blumstein 2009). However, the relative contributions of direct and indirect selection to the evolution of such cooperation have been debated since long (Ridley et al. 2004). Formation of male coalitions to gain reproductive benefits is difficult to explain because the main resource of interest: successful fertilization is mostly non-divisible (van Hooff and van Schaik 1992). Apparently it would be most beneficial for a single male to attempt to monopolize as many females as possible and to be intolerant to the presence of competing conspecifics (Pope 1990). The reproductive trade-offs for each participant in a coalition thus would depend upon: **(i)** the extent to which matings are shared among coalition partners, and **(ii)** the advantage that each individual in the coalition gains over competing alone (Pope 1990). In many, perhaps most species exhibiting male-cooperation like in Asiatic lions, males compete as both single individuals and as coalitions (Smuts 1987). Thus, the decision to join a coalition is one of several alternative reproductive strategies.

As elucidated in the previous chapter, Asiatic male lions form hierarchical coalitions much unlike their egalitarian African counterparts. Our results indicate strong dominance hierarchies between coalition partners, with pronounced asymmetry in resource utilization between them. Such coalitions in which male partners incur *costs-of-sharing* valuable resources (like food, mate and territory) seem to challenge Darwin's (1859) theory of natural selection (Clutton-Brock

2009), wherein all individuals are supposed to compete for survival and reproduction, and not aid each other at their own costs. Given such unequal sharing within coalitions, with subordinate males having inferior resource securities, in this chapter I investigate the probable ultimate-causes of coalition formation in Asiatic lions. I postulate that although subordinate males get lesser resources, yet they would benefit directly from coalescing and should have higher reproductive success compared to single males.

Figure 5.1. Asiatic male lions exhibit alternative cooperative strategies with a. single male and b. coalitions ranging from 2 to 5 males (in this case a coalition of 3). ©Stotra Chakrabarti



2. Materials and Methods

2.1. Study Site

This aspect of the study was conducted in Western Gir PA encompassing the same study area as for the previous objective (see **chapter 3 and chapter 4 section 2 for details**).

2.2. Overall Success of Males

To understand the underlying principles of coalition formation in male Asiatic lions it is imperative to compare and contrast the fitness of singletons with that of coalition males. I used the following parameters to quantify overall fitness of males:

a. Territory Size: Asiatic male lions differ in their land-tenure system from their African cousins in holding territories rather than female-prides (Joslin 1973; Chellam 1993; Meena 2009). Male lions hold territories primarily on which female pride territories overlap (Banerjee 2012). Thus, the size of male territories directly influences chances of encounter with receptive females and hence, mating success. For computing territory sizes of males, in addition to male-coalitions (n=7, detailed in **Chapter 4 of current dissertation**), territorial single males (n=4) were observed between December 2012 to December 2016. Identification and monitoring techniques have been described in Chapter 4, section 2.3 of current dissertation. I attempted to locate each study male once in every two days. Therefore, individuals had a good opportunity of being sampled anywhere, even outside their ‘normal’ ranges and movement forays. Upon locating a male/coalition, GPS coordinates were noted and subsequently used to compute home ranges. The radio-collared individual provided a GPS fix every hour. I used 95% Minimum Convex Polygons (MCP) for computing home ranges for allowing comparisons with earlier estimates (Jhala et al. 2009; Banerjee 2012).

b. Reproductive fitness: Staying alone or forming coalitions are alternative survival/reproductive strategies for males in social mammals, including lions (Smuts 1987; Pope 1990; Bygott et al. 1979; Feh 1999). However, in African lions, males in coalitions are more successful than single males in producing more number of offspring (Bygott et al. 1979). For coalitions to evolve as a strategy: a) coalitions should be able to secure more resources compared to single males, and b) if dominance hierarchies are present within coalitions, then subordinate members should also get higher benefits than males which do not form coalitions. To test this postulate, I compared reproductive fitness of single males with those that form coalitions. Since it was difficult to enumerate the number of actual surviving offspring of individual males in the wild with certainty, I used two variables to index reproductive fitness of males: **i) tenure holding ability:** tenure length is an important facet of lifetime success as reproductive fitness of male lions depends upon their ability to acquire and defend territories (Packer et al. 1988), **ii) annual mating frequency:** a surrogate for the number of offspring produced, assuming higher chances of successful fertilization with more matings. The 4 single males were monitored to document their mating observations exactly the same way as done for the coalitions, elucidated in Chapter 4 of current dissertation (computation of annual mating frequency has been described in **Chapter 4 section 2.5A**). For recording mating events, along with the males their interacting 9 female prides comprising of 49 adult females were monitored intensively (**see Chapter 4 section 2.1**). Reproductive success of a male was given by:

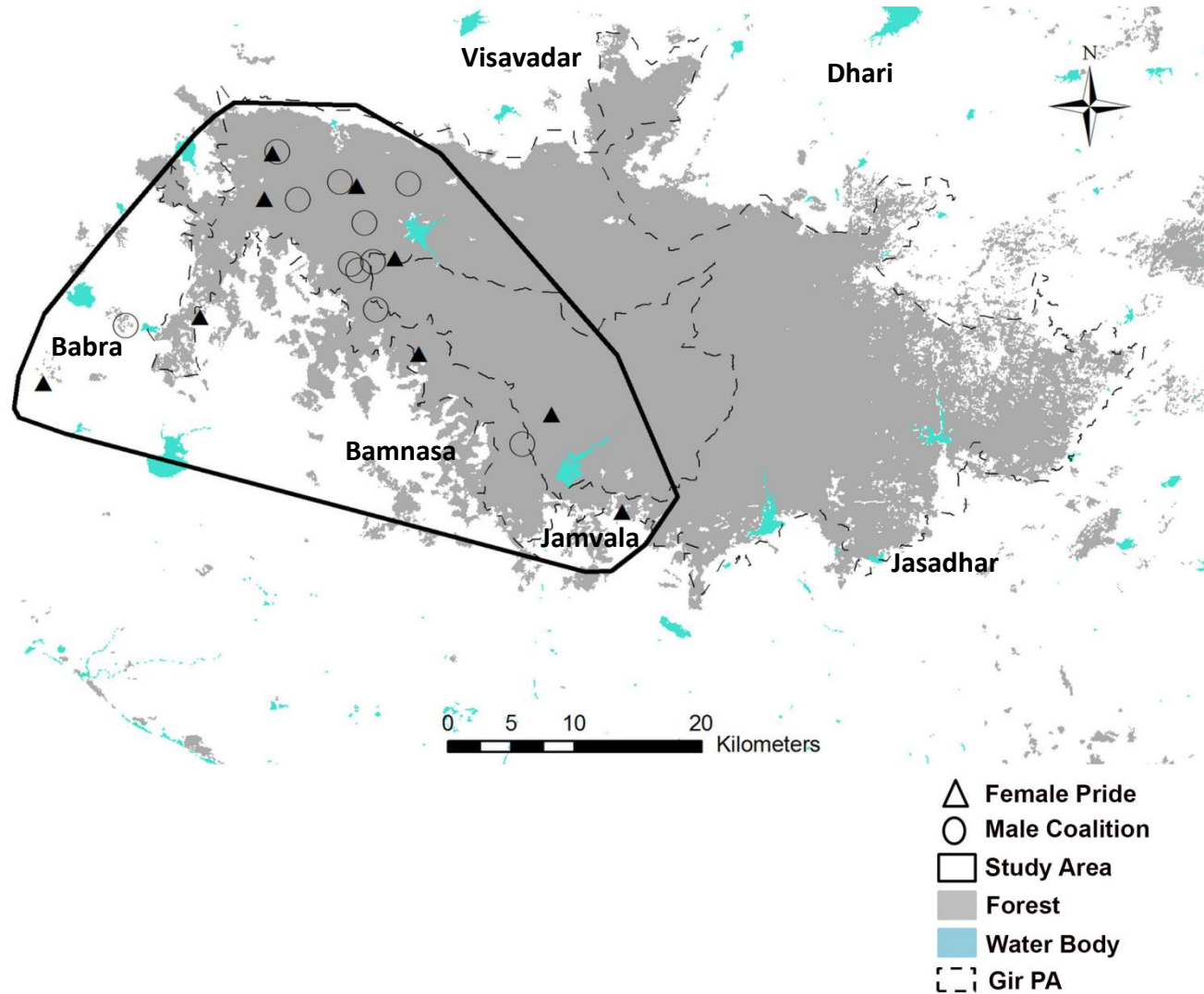
Fitness quotient of a male = annual tenure holding probability*annual mating frequency

Annual and span tenure holding probabilities of adult single males and males belonging to different coalition sizes (2 and >2) were computed using a known-fate model as the fate of the males were known with certitude (similar to computing survival probability using Kaplan-Meier

estimator, Williams et al. 2002; Skalski et al. 2005) in program MARK (White and Burnham 1999). Since the date of tenure acquirement was known with certainty to the month for each of the males used in this analysis, I considered them to have commenced their tenureships contemporaneously. Information on tenure-holdings was gathered on a monthly basis for the males and subsequently the encounter histories were entered in a matrix where ‘10’ signified the survival of the coalition for that month and whenever a male or a coalition was ousted/died, it was coded as ‘11’. Some coalitions continued to hold tenures at the end of this study and they were right censored and coded as ‘00’. Subsequent analysis provided monthly survival probabilities from which annual probabilities were derived for different sized coalitions. For this analysis, in addition to the 21 males (7 coalitions and 4 single males) monitored for behavioural observations (**see section 2.2**), we also used information from males (n=18 in 10 coalitions) monitored between 2004-2011 (Jhala et al. 2006 and 2011). Data from a total of 8 single males, 9 doubletons and 4 coalitions with >2 males were analyzed. Fitness quotients were then compared between coalitions.

All data processing was done using MS Excel and analyses using program R v15 (R Core Team 2013) and MARK (White and Burnham 1999). I used Hawth’s Tools (Beyer, H. L. 2004) in ARCGIS 9.3 (ESRI, Redlands, CA: Environmental Systems Research Institute, USA) and Biotas Alpha 2.0 (Ecological Software Solutions LLC) for computing home ranges (MCPs). Errors represent SEs if not mentioned otherwise.

Figure 5.2. Study area map home range centroids of males (4 single males and 7 coalitions) and their interacting female prides (n=9). Male centroids which are overlapping or in close proximity indicate sequential ownership of the same area, one evicting the other. The study males didn't hold tenures contemporaneously, rather in a total span of 4 years.



3. Results

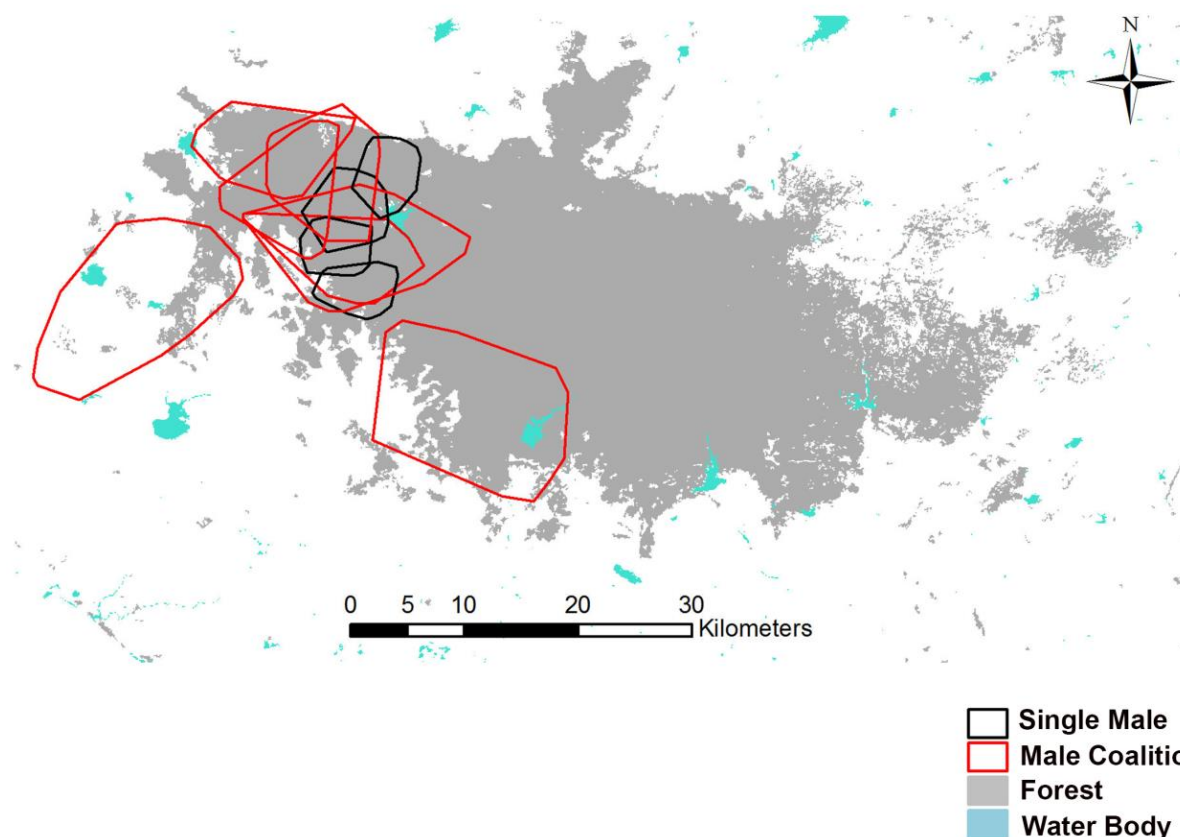
3.1. Territory Size: An average of 294 ± 21 locations from 21 males (range = 148-418) were used for computing home-range sizes (**Table 5.1**). The plots of 100% MCP ranges versus sample sizes stabilized for all lions. Each study individual had locations more than the average locations required for meeting sampling adequacy for home range estimation in case of Asiatic lions (117 locations, Banerjee et al. 2012). Average home range of coalition males was $119.5 \pm 18.9 \text{ km}^2$ while that of singletons was $31.2 \pm 3 \text{ km}^2$ (**Figure 5.3, Table 5.1**).

Table 5.1. Identity and home ranges (95% MCP) of 21 males (7 coalitions and 4 single males) studied in Gir PA between 2012-2016

Identity Code	Coalition Size	Number of locations	95% MCP (km^2)
Sngl.Alv	1	162	30
Sngl.Kpu	1	148	27
Sngl.Ks	1	197	40
Sngl.Ppt	1	210	27
Cln.Kg	2	355	79
Cln.Ke	2	328	81
Cln.Ks	2	376	91
Cln.J	2	322	193
Cln.Kw	2	199	138
Cln.Rtn	3	199	77
Cln.Bbr	4	418	178

Abbreviations: Single male [Sngl]; Coalition [Cln.]

Figure 5.3. 95% MCP home ranges (km²) of Asiatic lions (n = 4 singletons and 7 coalitions) in and around Gir PA. The study males did not hold tenures contemporaneously, rather in a total span of 5 years.



3.2. Reproductive Success: Single males held territories for shorter durations (annual tenure holding probability = 0.47 ± 0.19) than males in coalitions. Coalitions of 2 males and >2 males had similar annual tenure holding probabilities (0.85 ± 0.05 and 0.81 ± 0.07 respectively). Single males appropriated fewer matings than coalition males (**Figure 5.4**). Annual mating frequency of single males (2.61 ± 0.29) was much lower than that of coalitions (6.72 ± 1.06). Single males had far lower fitness quotients than even subordinate males in a coalition of 2 (**Figure 5.5**). However, in coalitions with >2 males, the males at the bottommost ranks (rank 3 and below) had fitness comparable to that of singletons, indicating that they would fare equally good (*or poorly*) if they remained alone.

Figure 5.4. Distribution of observed mating events within and between coalition males. Plot showing annual mating frequency calibrated by the total number of days each male was detected in the field, adjacent bars with similar patterns represent lions belonging to the same coalition.

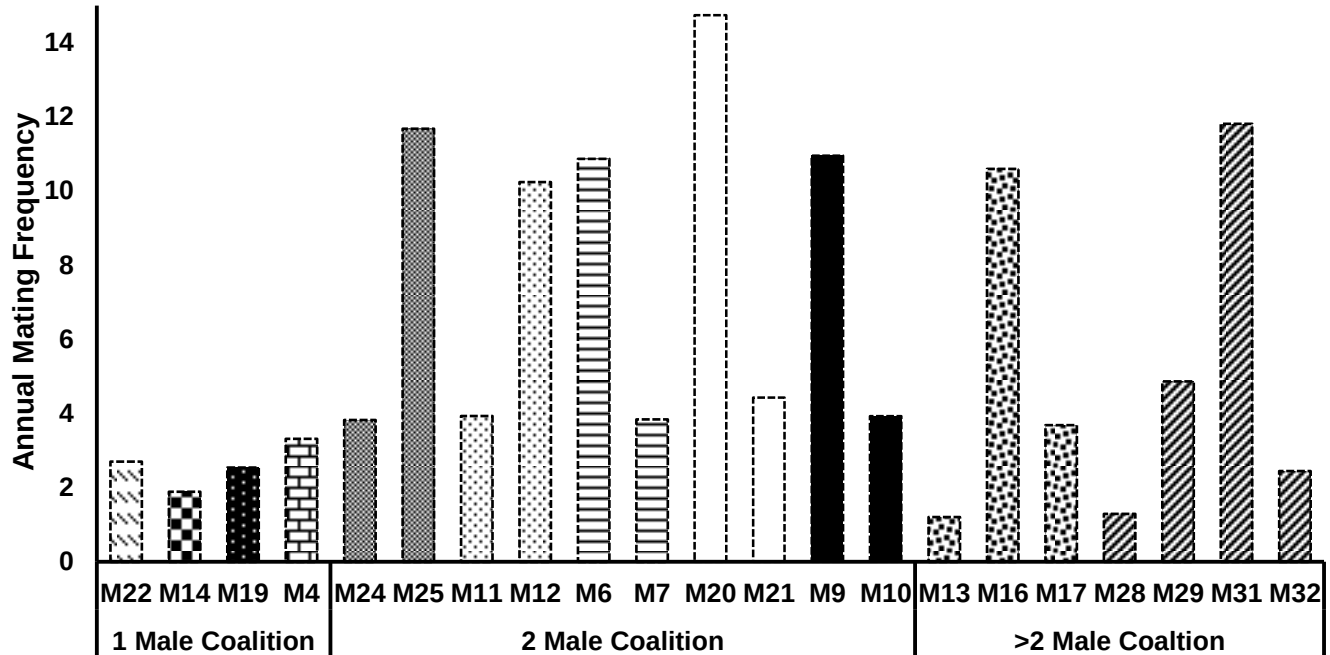
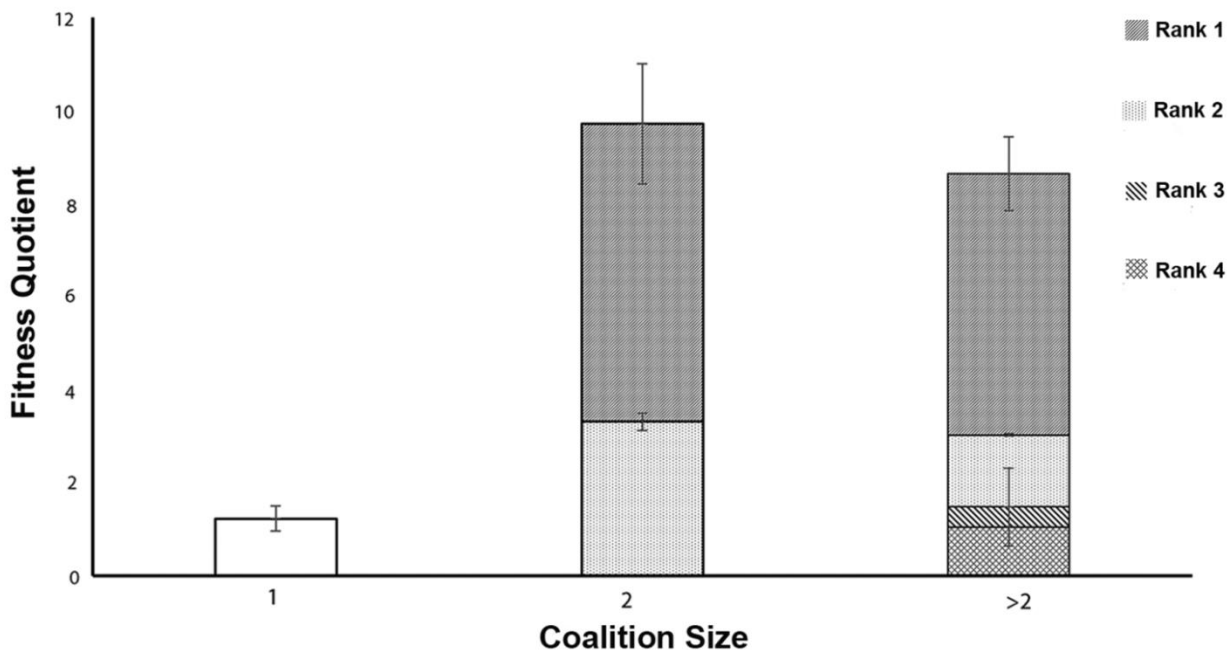


Figure 5.5. Reproductive-fitness quotients of male lions in different sized coalitions. Error Bars represent 95% CIs.



4. Discussion

Coalition formation among males is an evolutionary strategy to better safeguard rights and access to resources (Krebs and Davies 1987). However, teaming-up necessitates resource sharing which is apparently costly for team members. The decision to join with another conspecific who is simultaneously a helper as well as a competitor is an optimal selection decision where the benefits of staying together should outweigh the costs of sharing valuable resources. In most social mammals exhibiting male-cooperation, singletons and coalitions exist as alternative reproductive strategies. Asiatic male lions also exhibit dual strategies where they compete either alone or in coalitions. Living in a higher competitive scenario with smaller modal prey and less simultaneous mating opportunities, coalitions of Asiatic male lions exhibit pronounced dominance-hierarchies within partners (**Chapter 4**). Degrees of sociality and land-tenure system are different among Asiatic lions with males defending territories rather than female prides (Joslin 1973; Meena 2009; Jhala et al. 2009).

Our results primarily indicate that although male-coalitions exhibited pronounced hierarchies, coalitions fared better in overall success than single-males. Coalitions held larger territories and defended them for longer durations, having access to more receptive females than singletons. However, in large coalitions (>2 males) the partners at the bottom-most ranks had success equivalent to that of singletons. Declining benefits to partners with increasing coalition size, with individuals below the immediate subordinates having fitness comparable to single males, suggest to an optimal coalition-size of two lions (**Figure 5.5**). Thus, I predict an optimum coalition size of 2 for male Asiatic lions, below and beyond which reproductive success of single-males and

low-ranking subordinates respectively are low. This is in accord with the ground reality of an average adult male group size of 2.1 ± 0.3 in Gir (Gogoi 2015).

However, apparent reproductive fitness alone cannot explain coalition strength since in large coalitions (>2 males) lowermost ranked individuals had very low reproductive fitness, yet such coalitions exist. Other than mate and territory acquisitions, a coalition may also provide other direct benefits through group protection and food procurement. These may be vital for subordinate lions for survival, gaining vigor and subsequently attempt to either go up on the dominance ladder in the same coalition or join/form other coalitions, as reported in feral horses (Feh 1999). Moreover, the decision for a male to join with other partner(s) also depends upon the availability of other loners or coalitions which are open to member-recruitment (Packer et al. 1991). Thus, the size of a coalition at a particular time is a function of the average male-group size of the non-territorial male population in that area. We have observed lions that have lost their coalition partners join other males to form new coalitions, sometimes differing widely in their ages. In African lions different aged coalition-partners were mostly found in small coalitions and large coalitions were typically composed of similar aged closely related kins (Packer et al. 1991). Kin-selection is one of the major forces driving large coalition sustenance in the African system, where such coalitions are almost always constituted of closely related individuals (Packer et al. 1991). Thus, genetic analysis of relatedness within different male Asiatic lion coalitions would shed more light on the underlying mechanisms of the observed patterns.

**Figure 5.6. A coalition of males differing greatly in their ages, the one in the front is of ~10-11years, while the other in the background is 4-5 years old.
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The Great Game of Sexes



Mating Strategies in Asiatic Lions

The Great Game of Sexes: mating strategies in Asiatic lions

1. Introduction

Mating strategies exhibit plasticity among and within species in accordance to territoriality, spacing patterns and social organization (Emlen and Oring 1977; Clutton-Brock and Harvey 1978; Sandell 1989). Such strategies, being an outcome of sexual selection, primarily stems from reproductive asymmetries between genders (Darwin 1871), with the two sexes being at conflict under differential selective pressures (Krebs and Davies 1987; Bellemain et al. 2006). Male reproductive success has been known to be governed by the number of acquired mates, whereas female success is determined largely by access to resources (Sandell 1989; Bellemain et al. 2006; Gottelli et al. 2007). Such competing interests have led to a whole array of reproductive strategies in species (Parker 1984; Gross 1991; Zamudio and Sinervo 2000) governed by eco-geographical factors affecting resource- abundance and distribution (Macdonald 1983; Johnson et al. 2003).

Large carnivores are territorial, with individuals/groups guarding resources fiercely from competing conspecifics (Gittleman 1989). Such exclusivity of access to resources between individuals and sexes make carnivores a group of interest to lend evidence to the effects of resource availability in shaping social organization and mating strategies. Although carnivores have dominated wildlife research for the past few decades (Macdonald 2010) with annual publication rates increasing by 16% (<https://scholar.google.co.in>), investigation of their sociality and mating strategies has been unusually less with disproportionate focus given to certain species and systems (Clutton-Brock 1988). Till date, carnivores are primarily known to exhibit two major forms of mating strategies in relation to their social organization:

1) solitary carnivores, where male-female interactions are limited only to matings, display

resource defense polygyny with males actively defending female territories (Emlen and Oring 1977; Krebs & Davies 1987). Herein, male ranges overlap with one-to-many females and each male has access to a number of females (e.g., in tigers *Panthera tigris* Sunquist 1981; Goodrich et al. 2010; Chundawat et al. 2016 and pumas *Puma concolor* Logan and Sweeney 2001); **2) social carnivores**, living in multi- male-female groups, typically show *reproductive suppression* of subordinate individuals, and matings are performed mostly by a dominant pair (e.g., in wolves *Canis lupus* Mech and Boitani 2003 and African wild dogs *Lycaon pictus* Creel and Creel 2002). Lions are the only true social felids which live in functional units or groups called ‘prides’ (Schaller 1972; Bertram 1975b; Packer and Pusey 1982). Unique to African lion societies is their egalitarianism, with all lionesses having equal reproductive opportunities and they rear cubs communally (Schaller 1972; Bertram 1975b; Bygott et al. 1979; Packer and Pusey 1982; Packer et al. 1988; Packer et al. 2001). Each pride comprises of 2-18 adult females, their dependent cubs and a pride-owning male coalition of 1-7 males (Schaller 1972; Bygott et al. 1979; Packer and Pusey 1983a; Packer et al. 1988). A pride-centric mating system has been described for lions with lionesses mating only with their resident coalition (Packer et al. 1988; Packer et al. 1991). Coalition males share resources in equity and form an integral part of an African lion pride, living alongwith the lionesses and siring all cubs born to the pride during their tenures (Schaller 1972; Bertram 1975b; Bygott et al. 1978; Packer et al. 1988; Packer et al. 1991). Resident males aggressively defend females and cubs from intruding males because the latter kill all dependent cubs to hasten reproductive receptivity of females after a pride/territory takeover (Schaller 1972; Bertram 1975b; Packer & Pusey 1983 a,b).

Asiatic lions, living as a single relic population in the Gir forests of Gujarat, western India, exhibit a contrasting social organisation wherein: prides essentially comprise only of females and their dependent cubs, while adult males live their lives separately in hierarchical

coalitions (Joslin 1973; Chellam 1993; Jhala et al. 2009; Meena 2009; Chakrabarti & Jhala 2017). Male ranges encompass territories of one-to-many female groups (Chellam 1993; Jhala et al. 2009; Banerjee 2012; present study), but interactions between the two sexes are limited only to matings and infrequent congregations on large kills (Meena 2009; Banerjee 2012). Thus, although Asiatic lions show intra-gender grouping, each gender group behaves like a solitary carnivore having resource segregation between sexes. This behavioural divergence from the east African lions can be attributed to a plasticity of social behaviour in response to differences in resource availability between the two systems: Asiatic lions subsist on prey much smaller (Meena et al. 2011; Chakrabarti et al. 2016) than their African counterparts (Hayward and Kerley 2005). This has likely caused males and females to segregate their hunting times (females hunt when males are inactive) possibly to reduce kleptoparasitism of female kills by males. Furthermore, in the Asiatic system prey species are non-migratory and evenly distributed at reasonably high densities; resulting in smaller female pride territories (average: 34.7 km²; Jhala et al. 2009) that allows males to maximize their reproductive potential by encompassing many female prides within their home ranges. In the Serengeti however, owing to the seasonal out-migration of major lion-prey like zebras *Equus quagga*, wildebeest *Connochaetes taurinus* and cape buffaloes *Syncerus caffer*, lion territories are large (200 km²; Hanby et al. 1995) that reflect their resource needs during the *lean period* (Schaller 1972). The latter reduces the chances of male Serengeti lions to encompass >1 female pride territories because of energetic constraints of having extra-large ranges. Since mating strategies are governed by inter-sex spacing patterns and sociality (Emlen and Oring 1977; Clutton-Brock and Harvey 1978; Sandell 1989), I hypothesize that given such a land-tenure system in Asiatic lions where males overlap with multiple female groups, lionesses could potentially have interactions with many contemporaneous adjacent coalitions. This should set the stage for female promiscuity in Asiatic lions. I investigate this

postulate through observations on matings and cub-tolerance by adult males from concurrent adjacent coalitions. My results show that Asiatic lionesses are promiscuous and confuse neighbouring coalitions regarding paternity of litters. Since female promiscuity is most likely an evolutionary strategy to reduce infanticide (Hardy 1979; Wolff & Macdonald 2004) and/or increase genetic diversity in litters (Jennions and Petrie 2000), the two benefits might singularly or synergistically (if present together) affect female mate-choice. While the former would reduce selection of certain males over others as such selection might enhance the chances of infanticide from non-selected suitors, the latter would increase selection of certain unfamiliar/new males to increase genetic diversity. I check for the drivers of such alternative benefits in Asiatic lions by testing for male selection by females belonging to different age-classes and provide empirical evidence of age based mate-choice in a social carnivore.

2. Methods

2.1. Study site and population

I observed seventy adult lions (21 males and 49 females) from December 2012 to April 2017. The individuals belonged to 11 male coalitions (ranging in size from 1-4 males) and 9 female prides inhabiting an area of about 1,200 km² in the western part of the Gir PA and the adjoining human-dominated landscape (21°17'-20°55'N and 70°20' - 70°52'E) in Gujarat, India. Males were assigned to be in a coalition if they were frequently seen vocalising, hunting and patrolling territories together (Schaller 1972; Chakrabarti & Jhala 2017). Females which were often found in each other's presence; hunted, vocalised and reared cubs communally were categorised to be pride-mates (Schaller 1972; Bertram 1975b). We selected only those coalitions and prides which held adjacent territories contemporaneously, so as to effectively understand ranging patterns and interactions between individuals and sexes. Details of the intensive study area and selection of prides and coalitions can be found in Chapters 4 and 5 of current dissertation.

Figure 6.1. Female pride-mates from western Gir, Gujarat. Females of a pride are highly social, much more than male partners in a coalition. They hunt together, socialize more often, suckle and raise cubs together ©Stotra Chakrabarti



2.2. Monitoring of lions

I identified study individuals using a combination of vibrissae patterns (Pennycuick and Rudnai 1970) and body marks like permanent scars and wounds (Jhala et al. 1999). Radio-telemetry and cues such as pugmarks, prey-alarm calls, roars, kills, and information from tourists and forest department personnel were used to track and monitor the individuals (Chakrabarti and Jhala 2017). Two adults (1 male and 1 female) were fitted with GPS collars (Vectronics Aerospace GmbH, Berlin, Germany, weighing <1% of the animal's bodyweight). I intensively searched and located study lions at regular intervals to avoid having long enough durations between successive encounters that might lead to non-detections of matings and pregnancy/cub-birth events (see Chapters 4 and 5 for details).

2.3. Spacing patterns

I visually located lions at different times of the day and night, and recorded their positions using a handheld GPS unit (make: Garmin 30, Garmin International, Kansas, USA). The radio-collars were pre-set to provide hourly fixes and the locations were downloaded using an UHF handheld downloader (make: Vectronics Aerospace GmbH). I aged each individual to the nearest age-class based on teeth wear and colour, mane growth, nose pigmentation, jaw scowl and gum-line recession (Smuts et al. 1978; Jhala et al 2004; Whitman et al. 2004). I additionally categorised adult females into two broad groups based on the presence of cubs and/or teat colour: *experienced females* (lionesses with cubs or had littered before, typically with brown to black keratinised teats) and *maiden breeders* (have never given birth, typically with pinkish-white non-keratinised teats) (Sadhu et al. 2017). Tracking and monitoring of lions were either done on foot or a four-wheel drive vehicle. I merged location data for all females of the same pride and male partners of a coalition to calculate pride and coalition ranges respectively. 95% MCPs were used to compute home ranges (Jhala et al. 2009; Banerjee 2012). Overlap between adjacent home ranges was computed as the average proportion of overlap between two home ranges (Kernohan et al. 2001; Mizutani and Jewell 1998). I also calculated core areas of female prides using 70% Fixed Kernel (Millspaugh and Marzluff 2001). During my study period I witnessed five territory takeover events with resident coalitions being ousted by new males. I checked whether female pride ranges changed over time concurrent to such takeovers by computing the average shift in their home range centroids before and after such events. Also, during and following takeovers I intensively monitored prides with cubs and juveniles to record infanticide events.

2.4. Mating interactions

To understand male-female interactions, I recorded mating events by locating each study male every day or every alternate day (see Chapter 5 for details). A mating event was

considered to be the entire duration when a male consorted a lioness in estrus (included the initial courting phase, actual copulations and intervals between successive copulations) till the pair parted ways and returned to their respective groups (Chakrabarti & Jhala 2017). Individuals of a mating pair were always identified to their respective coalition and pride and a continuous 24-hour focal behaviour-sampling (Altmann 1974) was done for all days of the mating event. Pairs were kept in view within 50 m from observers. During dark nights a flash-light was used every 15-30 minutes to ascertain location of the mating pairs (Chakrabarti & Jhala 2017). I built a social network of observed matings (links) between individuals (nodes) belonging to study prides and coalitions to understand the kind of mating system present in lions. In this network (hereafter individual mating network) the strength of the links between the nodes (individuals) represented the number of matings observed between a female and a male expressed as a proportion to the total matings observed of that particular female. Since any form of selection in social species, be it natural or sexual; occur at two levels- **i)** individual, and **ii)** group (Krebs and Davies 1987); to check for group level mating strategies I developed another social network with coalitions and prides as entities. For this, we merged all matings acquired by males from a single coalition. Similarly matings by all pride females were combined together. In this group level network (hereafter group mating network), each link between a pride and a coalition (nodes) represented the number of cumulative matings observed between females of a pride and males of a coalition expressed as a proportion to the total matings observed of females of that pride. For developing the individual- and group- mating networks, I used a subset of the mating dataset as reported in Chapter 4 of current dissertation (n=76/127 mating events between 5 prides and 5 coalitions). This is because owing to intensive monitoring, I was reasonably certain of recording all interactions between females of these prides and males of the coalitions. However, possibility

of missing out on matings did exist for the remaining four prides and hence were omitted from this analysis.

Figure 6.2. A mating pair of lions in central Gir, Gujarat. ©Stotra Chakrabarti



2.5. Cub tolerance by males

Male lions usually kill cubs of a pride which are not sired by them (Schaller 1972; Bertram 1975b; Packer and Pusey 1983 a,b). Assuming female promiscuity to be a possible strategy to reduce infanticide by confusing males regarding cub parentage (Hardy 1979; Wolff and Macdonald 2004; Bellemain et al. 2006), I hypothesize that if females of a pride have mating interactions with multiple coalitions, then all these males would tolerate and be non-hostile to cubs of that pride. To test this, I observed adult male-and-cub interactions (n=69 events, 15 litters with a total of 26 cubs from 5 prides) wherein adult males were within 30-50 m of the cubs. This distance was sufficiently short for males to show intent of infanticide if they considered the cubs not to be their own. I categorized interactions into: **a) hostile** - males chasing cubs with the possible intent of infanticide and/or mauling/killing cubs, and **b) non-hostile** - males sharing kills with cubs, grooming them or being neutral to their presence

(**Figure 6.3**). For every such interaction, I identified males to their respective coalitions and cubs to their mothers and prides.

Figure 6.3. Adult male and cub interactions. Non-hostile interactions (a. Neutral; b. Sharing of kills) ©Stotra Chakrabarti, and Hostile interactions: c. Infanticide of a month old cub and partly eaten by the incoming males. Photo courtesy: Rahim Bloch.



2.6. Space-use and mating strategies

In Asiatic lions the two sexes remain largely unassociated but have spatial overlaps (Chellam 1993; Meena 2009; Banerjee 2012). Thus, the interactions between male coalitions and female prides are likely governed by one sex encountering the other, which in turn is a function of the spatial overlap between the sexes. The chances of a male lion discovering a female in estrus would thereby be governed by their mutual encounter rates. Consequently, mating events being outcomes of associations between coalitions and prides, should be determined by the degrees of spatial/range overlap between them. I investigated mate-choice by lionesses hypothesising that matings between females of a pride and males of a coalition would happen in accordance to the frequency of their mutual encounters (indexed by their range overlaps) if there was no active mate choice by females. I tested the frequency of matings between a pride and a coalition (expressed as a percentage of total matings of the pride) against their percentage home range overlap using a chi-square test at an α -value of 0.05. In this test the *observed values* were that of the mating frequencies and the *expected* were the home range overlaps. To further understand female choice for mating, I compared observed mating frequencies versus availability of males (home range overlaps) using Ivlev's selectivity index (Ivlev 1961). Mate choice of *experienced females* and *maiden breeders* were analysed separately.

2.7. Reproductive parameters of Asiatic lionesses

I calculated the mating success of lionesses, given by: $(\text{number of pregnancies} / \text{number of mating events}) * 100$ cumulatively for all lionesses. This would give an idea of mating success, as female conception remains a key for understanding physiological factors affecting multi-male mating strategy in females (Wolff and Macdonald 2004). Mating success was only calculated for females (n=27 from 5 prides) where all male coalitions in their vicinity were monitored simultaneously and mated at least once during the study period. By pregnancies I

refer only to visible pregnancies, where females have very conspicuously swollen bellies and udders (Schaller 1972; Packer and Pusey 1983b). Such a stage happens only during the last two weeks of pregnancies (Sadhu et al. 2017) and fetal losses in the interim period might have gone unnoticed. Also, I report maximum mating success of females as we have tried and monitored all the matings done by the resident coalitions of the study area (see Chakrabarti and Jhala 2017). However, I do not rule out the possibility of non-detections of sneaking, nomadic males mating with the study females. The latter would be extremely rare due to high intensity of territory patrolling by resident coalitions coupled with mating events in lions being a long, noisy and conspicuous affair (average mating duration in Asiatic lions ~72 hours, Chakrabarti and Jhala 2017). I also computed average litter-size and sex-ratio of cubs from data across all monitored females in the study area who littered at least once and cubs survived long enough to get detected (n=24 litters). I report these parameters only after about a month of littering, as lionesses keep their cubs hidden for the first one month and thus, inspection of cubs to ascertain litter size and sex-ratio at birth was not possible.

All data processing was done using MS Excel, analyses using program R v15 (R Core Team 2013) and UCINET 6 (Borgatti et al. 2002), and mapping of home ranges using ARCGIS v9.3 (ESRI, Redlands, CA: Environmental Systems Research Institute, USA). Errors represent SEs if not specified otherwise.

Figure 6.4. A monitored prime adult lioness and her two (~2 month old) cubs. ©Stotra Chakrabarti



2. Results

2.1. Spacing patterns

An average of 294 ± 21 from 11 coalitions that included single males (**Chapter 5, Table 5.1**) and 246 ± 82 locations from and 9 prides were used to compute home ranges (**Figure 6.5, Table 6.1**). Adjacent male ranges overlapped considerably with each other, with an average overlap of $32.1 \pm 4.1\%$ (**Figures 6.5 a and b**). Male coalitions overlapped at places of intense female use/female pride cores (**Figure 6.6**) Female prides had an average home range of $61.6 \pm 14.5 \text{ km}^2$; with negligible $8.2 \pm 1.1\%$ overlap between adjacent prides (**Figure 6.5c, Table 6.1b**). Female pride home ranges were encompassed by ranges of 2-4 male-coalitions with each pride having one *primary coalition* (overlap of $64.8 \pm 7.2\%$ of pride ranges) and 1-3

peripheral coalitions (cumulative overlap of $25.6 \pm 3.9\%$ of pride ranges) (see **Figures 6.5 a and b, Table 6.2**). Space use by males was dynamic with new males coming in and ousting resident coalitions. Such male turnovers caused the incoming males to carve out new territorial boundaries in the vacant spaces so produced (**Figures 6.5 a and b**). However, female pride ranges remained more or less the same across years with minor shifts (average home-range centroid displacement of 0.69 ± 0.15 km) during the period of takeovers, indicating prides to be constant spatial entities (**Table 6.3**).

Table 6.1. Home range details of nine female prides monitored between 2012-2017

Pride Code	Adult Group Size	Maiden Breeders	Experienced Females	Number of Locations	95% MCP (km ²)
Prd.R	5	2	3	201	16.6
Prd.K	8	4	4	171	25.8
Prd.J	8	2	6	136	82.1
Prd.Kw	3	1	2	174	72.8
Prd.Rs	6	2	4	139	80.9
Prd.B	4	1	3	157	24.7
Prd.D	6	2	4	112	42.1
Prd.M	4	1	3	882	156.9
Prd.S	5	1	4	107	137.8

Table 6.2. Percentage home range overlap between coalitions and prides (*designates primary coalitions) Abbreviations: Coalition [Cln.]; Pride [Prd.]

	Cln.J	Cln.Kw	Cln.Kg	Cln.K	Cln.Ke
Prd.J	0.00	27.45	48.20	81.60*	29.87
Prd.Kw	0.00	75.88*	10.75	15.49	0.00
Prd.K	0.00	0.00	32.04	29.97	65.98*
Prd.R	0.00	9.20	60.46*	22.36	45.43
Prd.Rs	39.96*	11.10	0.00	0.00	0.00

Table 6.3. Home range shift of prides after takeover. Abbreviations: Home Range [HR]

Pride Code	HR Centroid shift (km)
Prd.R	0.18
Prd.K	0.77
Prd.J	0.62
Prd.Kw	0.81
Prd.Rs	1.1

Figure 6.5. Relative position of home ranges (95% MCP) of study male coalitions and female prides in the years: a) 2012-2014, b) 2014-2017 and c) Overall monitored female prides. This figure shows the dynamism of space use by males with new coalitions coming in 2014 and ousting resident coalitions to carve new territorial boundaries. Female prides territories remained more or less constant between years.

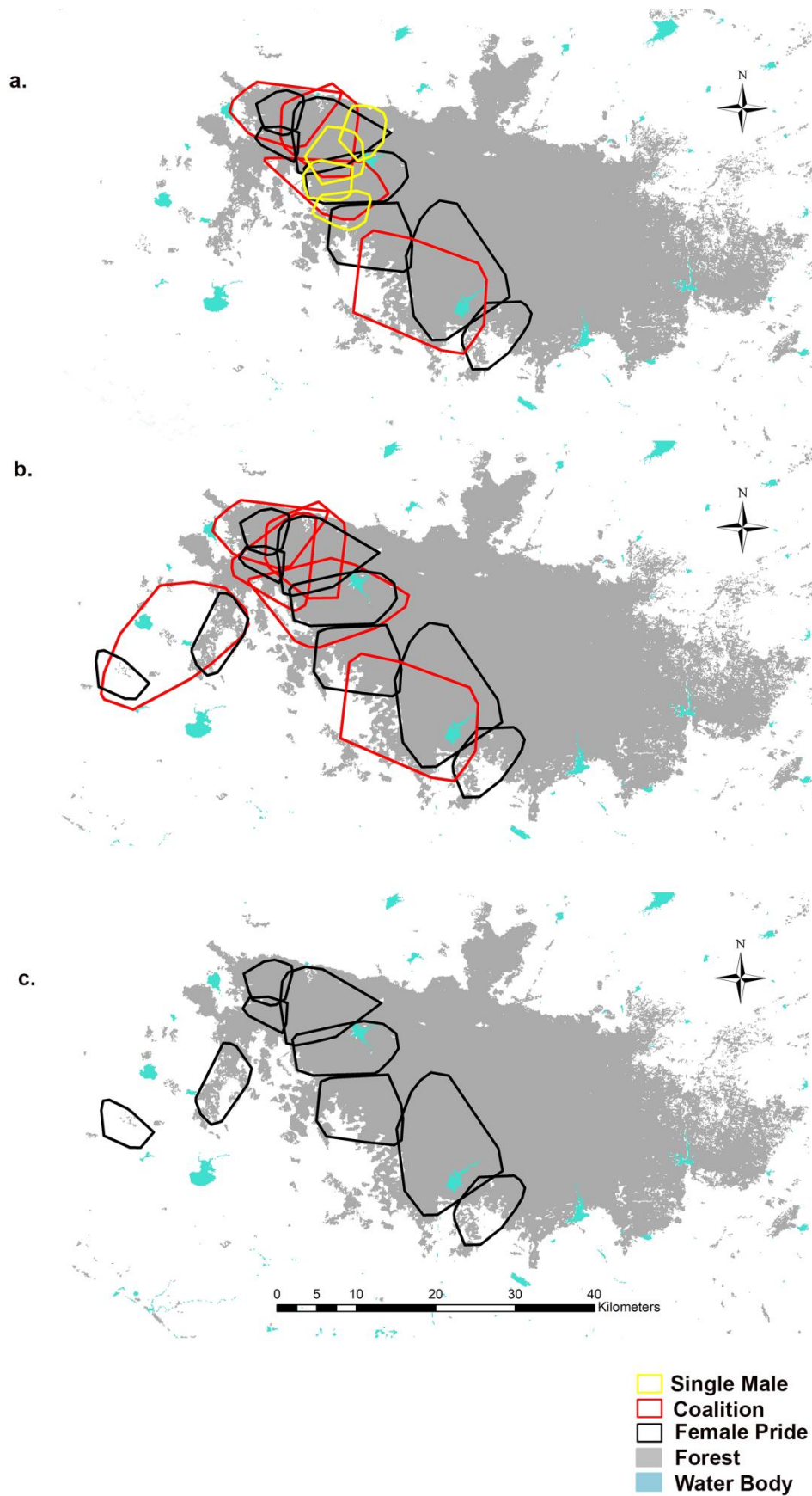
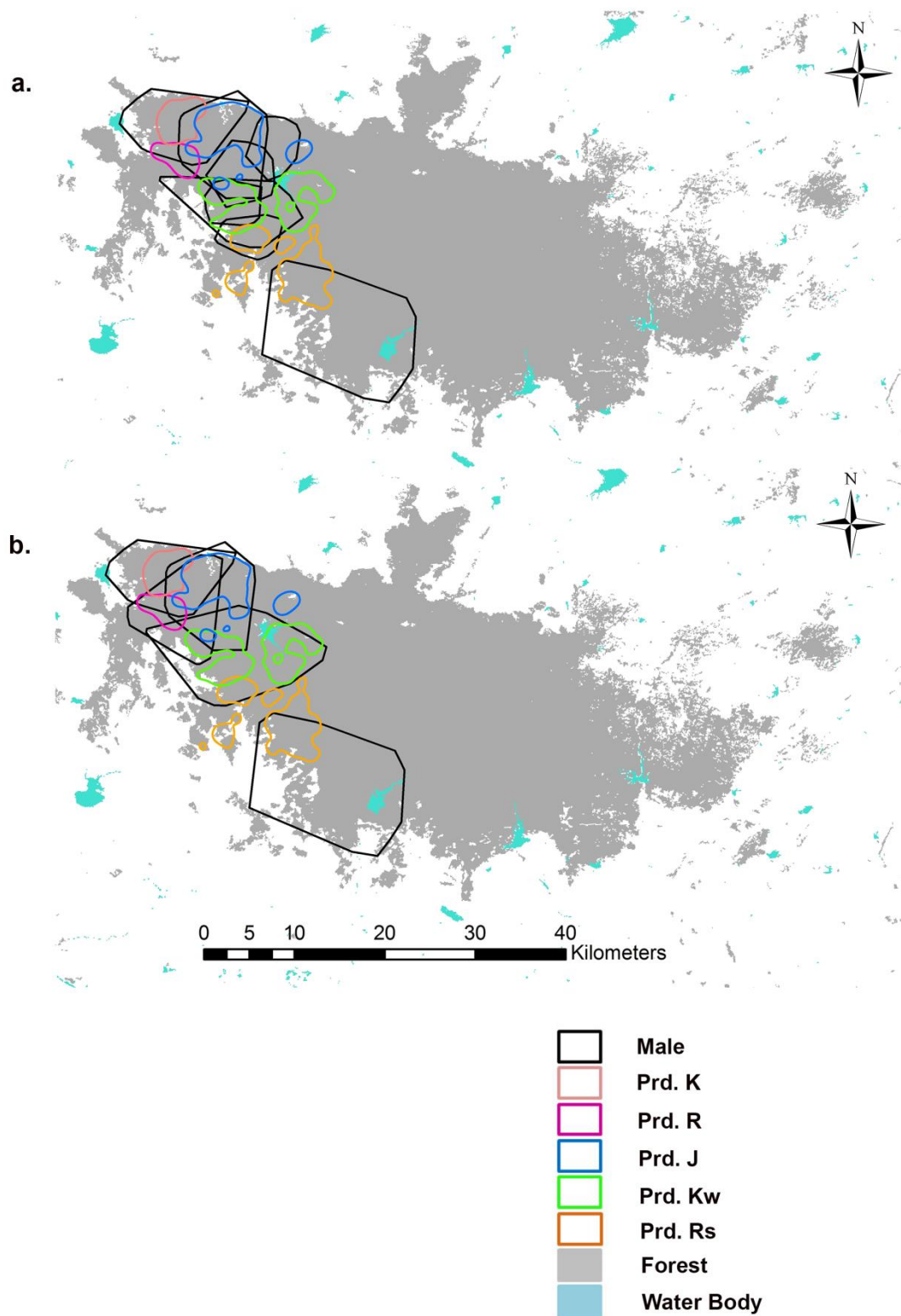


Figure 6.6. Relative position of home ranges (95% MCP) of study male coalitions and female prides cores (70% FK) in the years: a) 2012-2014, and b) 2014-2017. Male ranges overlapped at places of female cores, but adjacent female core areas were almost exclusive. Female pride codes are as per Table 6.1



2.2. Mating interactions

Observations on mating events between contemporaneous female prides and male coalitions revealed that among all matings appropriated by females of a pride, $61.7 \pm 5.1\%$ were with males of their *primary coalition*, while $38.3 \pm 5\%$ were cumulatively with males of the *peripheral coalitions*. Both the individual- and group- mating networks of these mating interactions showed a high degree of mate-sharing between adjacent male coalitions, indicated by a complex connected network (**Figure 6.7 a and b**). However, the intensity of promiscuity differed between experienced females and maiden breeders (contingency $\chi^2=11.9$, $df=1$, $p<0.001$). Among all the promiscuous matings that I observed ($n=28$) where females were found to be mating with males of their *peripheral coalitions*, majority of them were performed by *experienced females* ($n=25/28$; 89.3%) while the *maiden breeders* rarely mated with such coalitions ($n=3/27$ events; 10.7%) (**Table 6.4 a and b**).

Table 6.4. a) Frequency of mating interactions (expressed as percentages) between coalitions and experienced females of prides, b) frequency of mating interactions (expressed as percentages) between coalitions and maiden breeders of prides (*designates primary coalition)

a.

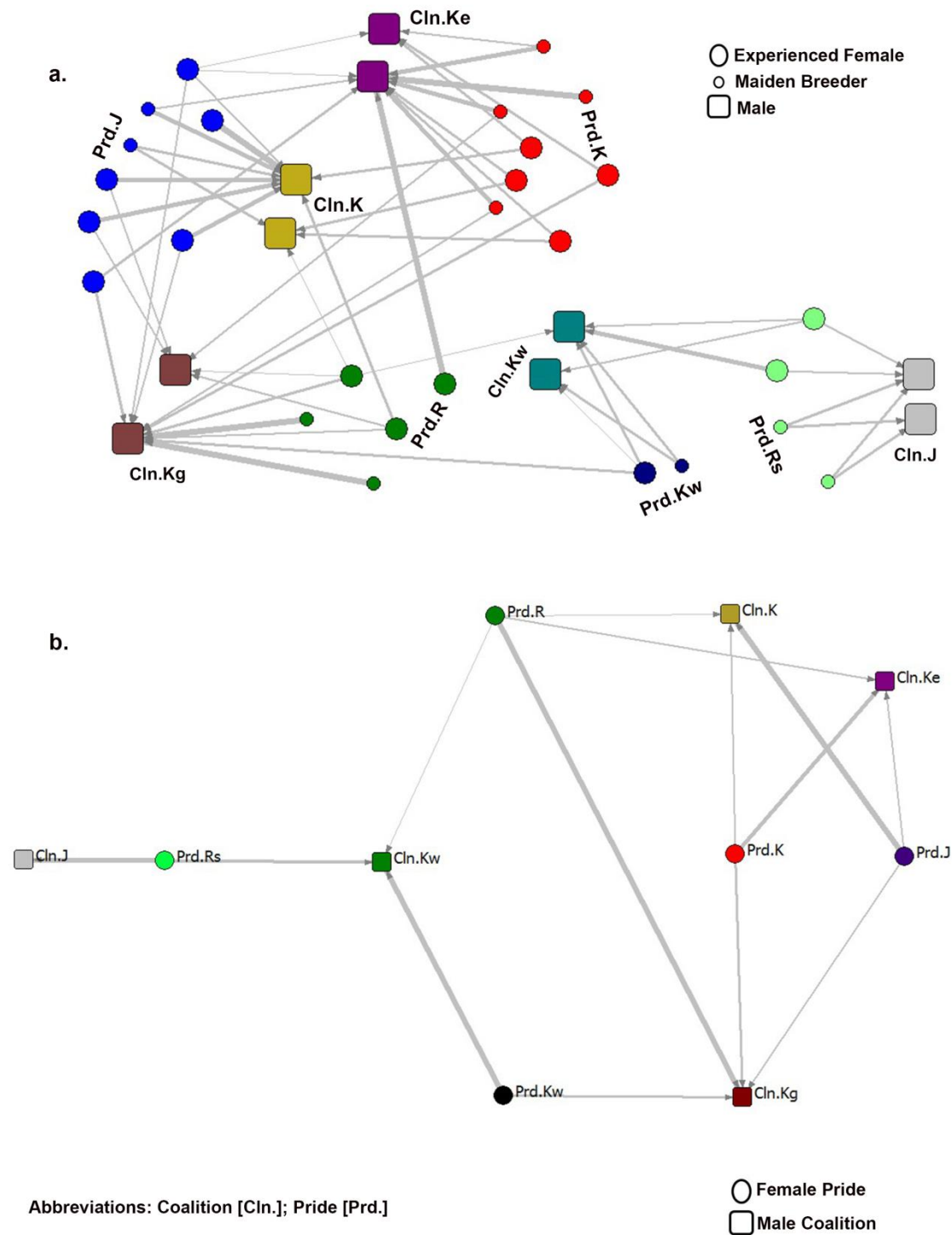
	Cln.J	Cln.Kw	Cln.Kg	Cln.K	Cln.Ke
Prd.J	0.00	27.45	48.20	81.60*	29.87
Prd.Kw	0.00	75.88*	10.75	15.49	0.00
Prd.K	0.00	0.00	32.04	29.97	65.98*
Prd.R	0.00	9.20	60.46*	22.36	45.43
Prd.Rs	39.96*	11.10	0.00	0.00	0.00

b.

	Cln.J	Cln.Kw	Cln.Kg	Cln.K	Cln.Ke
Prd.J	0.00	0.00	18.18	81.82*	0.00
Prd.Kw	0.00	100.00*	0.00	0.00	0.00
Prd.K	0.00	0.00	0.00	20.00	80.00*
Prd.R	0.00	0.00	100.00	0.00	0.00
Prd.Rs	100.00*	0.00	0.00	0.00	0.00

Abbreviations: Coalition [Cln.]; Pride [Prd.]

Figure 6.7. Individual- and group- mating networks. Social networks with: a) nodes as individual males and females, the links/arrows between the nodes are the number of matings observed between a female and a male expressed as a proportion to the total matings observed for that female. Shapes of same colour represent individual belonging to the same group with *filled squares* as males, *large filled circles* as experienced females and *smaller filled circles* as maiden breeders, b) nodes as coalitions and prides with the links/arrows representing the matings of females of a pride and the coalition males expressed as a proportion to the total matings observed of females of that pride. *Filled squares* represent male coalitions and *filled circles* represent female prides. The width of the arrows depicts the strength of the links.



2.3. Cub tolerance by males

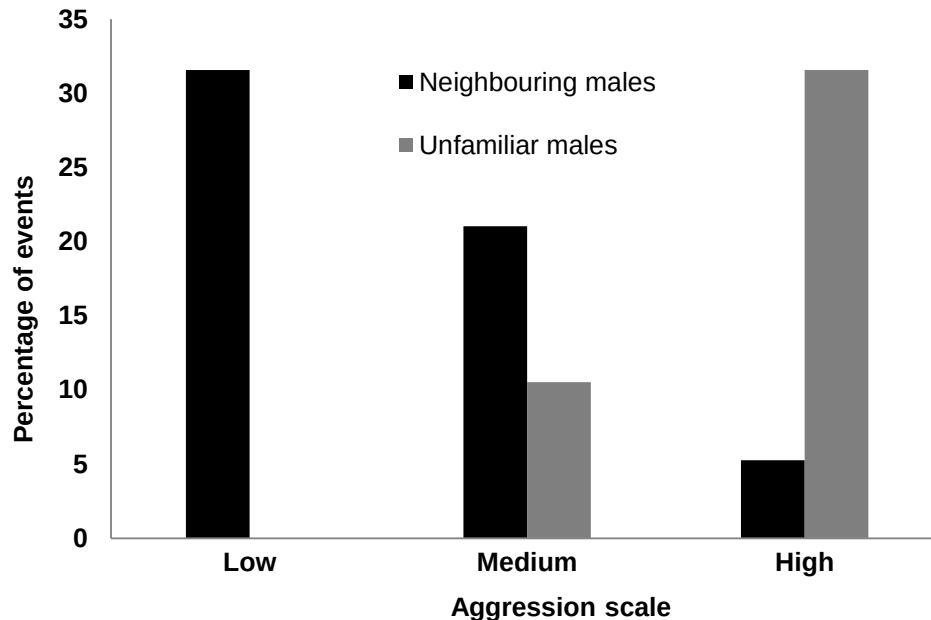
Among 69 events involving adult male and cub interactions, 53 ($77.1 \pm 1.4\%$) times the cubs were found to be associated with males of their *primary coalitions* and the remaining 16 ($22.9 \pm 1.5\%$) times cumulatively with males of their *peripheral coalitions* (**Table 6.5**). Both *primary* and *peripheral coalitions* were found to be tolerant towards the cubs. However, coalitions showed low-medium aggression when they encountered their neighbouring coalitions (**Figure 6.8**). Pronounced aggressive encounters were recorded only for events when territorial coalitions encountered new unfamiliar males (**Figure 6.8**). Although I did not record any non-hostile interactions between adult males and cubs among these 69 events, during territory takeovers ($n=5$) I witnessed infanticide of cubs ($n=11$ cubs) and ousting of dependent juveniles and sub-adults ($n=6$), all of the latter subsequently died within 1 year of getting expelled from their respective prides.

Table 6.5. Tolerance events between cubs of a pride and males of a coalition, expressed as a percentage to the total number of events observed of cubs of that pride. * designates primary coalitions.

	Cln.J	Cln.Kw	Cln.Kg	Cln.K	Cln.Ke
Prd.J	0.00	0.00	12.50	75.00*	12.50
Prd.Kw	0.00	81.82*	18.18	0.00	0.00
Prd.K	0.00	0.00	13.33	13.33	73.33*
Prd.R	0.00	5.56	77.78*	11.11	5.56
Prd.Rs	77.78*	22.22	0.00	0.00	0.00

Abbreviations: Coalition [Cln.]; Pride [Prd.]

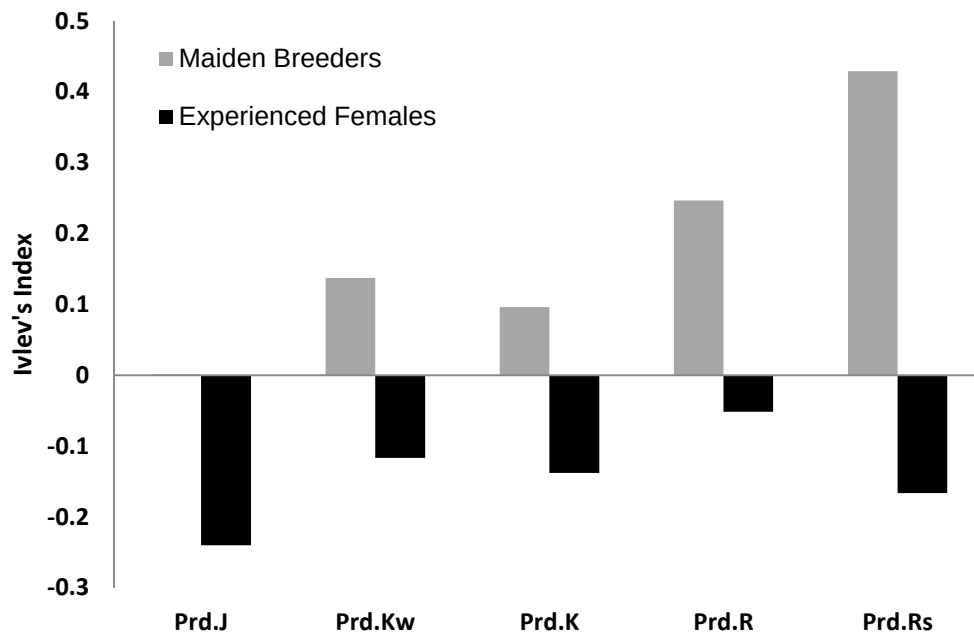
Figure 6.8. Aggression levels between male coalitions. Levels of aggression when male coalitions encountered each other were scaled into 3 classes: *Low*- roaring and body-posturing at each other, spraying and ground-scraping at visible distances, *Medium*- mock charges, back-and-forth chases, growls and roars, and *High*- charges and contact, mauling, injuring and/or killing each other. Percentage of each aggression class from observed encounters (n=19) are represented differently for neighbouring coalitions and between unfamiliar strangers



2.4. Space-use and mating strategies

Observed mating frequencies were significantly different from what expected from range overlaps between females of a pride and male coalitions. *Experienced females* had fewer matings with *primary coalitions* than expected ($\chi^2=23.3$, $df=4$, $p<0.001$), while *maiden breeders* mated with *primary coalitions* in frequencies higher than expected ($\chi^2=126.7$, $df=4$, $p<0.001$). Selectivity indices revealed a similar trend with negative values of selection for *experienced females* for primary coalition males and positive values for *maiden breeders* (Figure 6.9). Also, experienced females were found to mate with certain neighbouring coalitions significantly more than what expected from their range overlaps (Appendix S2)

Figure 6.9. Ivlev's Selectivity Index ($U-A/U+A$) for male choice by females belonging to different age classes. In this, observed mating frequencies between females of an age-class (*experienced females or maiden breeders*) with a coalition represent use (U) and home-range overlap between them represent availability (A).



2.5. Reproductive parameters of Asiatic lionesses

Mating success of lionesses ($n=27$) was 19.7% (**Appendix S3**), indicating to an average of 5 mating events required for a successful detectable conception/littering. Average litter size was found to be 2.3 ± 0.1 , with a sex-ratio (M/F) of 1.5 ± 0.3 ($n=52$ cubs; 31 M/21 F). However, the litter sex-ratio was not significantly different from 1:1.

3. Discussion

Plasticity in behaviour is an adaptive response; aiding individuals survive under differential selection mechanisms. Social organization and mating strategies are a set of inter-linked behavioural traits, one reinforcing the other in a steadily increasing helix (Krebs and Davies 1987; Creel & Creel 1991). Such traits exhibit a diverse array of combinations among and within taxa in accordance to the extant selective pressures (e.g., resource availability) and the level of conflict between the sexes (Parker 1984; Gross 1991; Zamudio & Sinervo 2000). In

lions, akin to other mammals exhibiting infanticide, sexual conflict has caused male- and female- interests to be at odds with unrelated males killing dependent cubs to enhance reproductive fitness by quickening estruses in females (Packer & Pusey 1983 a,b). Such acts are detrimental for lionesses that lose considerable investment in cubs. Females therefore should try and minimize infanticide as is often documented by them resisting takeovers when having dependent cubs (Schaller 1972; Packer & Pusey 1983 a,b). However, a flip side to such ‘harmful’ infanticide also provides opportunities for females to have diverse lineage in their progeny, with new ‘better’ males siring subsequent litters. Using Asiatic lions as a study model I corroborate female promiscuity as a likely strategy to reduce infanticide by confusing paternities and also to enhance variability amongst litters. These two alternative benefits have resulted in disparate mate-selection by females of different age classes. My results lend evidence to the ‘paternity uncertainty’ and ‘offspring quality’ hypotheses (Wolff and Macdonald 2004), both operating synergistically in lions.

The results reveal that in Asiatic lions, adult groups are formed only between like-sexes and such groups live separately, but have spatial overlaps between them. Every female pride is encompassed by the ranges of 2-4 male coalitions and these adjacent coalitions share considerable range overlaps with each other, exhibiting low-to-medium aggressive rivalry between themselves. Lower levels of aggression between neighbouring coalitions in contrast to what shown to new unfamiliar males supports the ‘dear enemy’ hypothesis where territorial animals are less hostile towards familiar neighbours than strangers (Ydenberg et al 1988; Temeles 1994; Muller and Manser 2007). Lionesses readily mated with multiple rival coalitions, questioning the theory of ‘social monogamy’ known for lions till date (Schaller 1972; Bertram 1975b; Packer et al. 1988; Packer et al. 1991).

The propensity of female promiscuity was however found to be significantly different between females belonging to different age classes, with *maiden breeders* primarily mating

with males of their primary coalitions whereas *experienced females* selecting neighbouring males more frequently (**Figures 6.7a; 6.9**). Such disparity in mate-selection can arguably be an outcome of the separate benefits of promiscuity, with *maiden breeders* maximizing habituations with primary coalitions to reduce infanticide as they are the males most encountered by these females (sharing highest range overlaps). On the other hand, experienced females, that already have established such familiarity because of former matings with primary males, choose neighbouring males to likely have diverse lineages in litters in addition to reducing infanticide. This two-pronged mate-choice seems to be an evolutionary *win-win* situation for lionesses, as multiple rival males were found to be non-hostile to the same litters. No infanticide from neighbours *versus* heightened infanticide by new unfamiliar males leads me to revisit the ‘kin-recognition’ hypothesis, wherein it has been proven in most mammals that males do not recognise their own offspring (stand-alone) but rely on secondary cues to ascertain paternity probability (Widdig 2007). In this case, it is very likely that familiarity with mothers is the primary factor for adult male lions to ascertain cub parentage, since infanticide never occurred when cubs were associated with females that were familiar to the males. This directs me to conclude that lionesses likely use matings to familiarize with multiple males and convince them regarding cub parentage, a system reported in social primates (van Schaik 2000), brown bears *Ursus arctos* (Bellemain et al. 2006) and cheetahs *Acinonyx jubatus* (Gotteli et al. 2007). Rare instances (n=3) where lionesses with small cubs exhibited behavioural estruses with unfamiliar new males, and were seen to draw these males away from their hidden cubs on the pretext of mating, also indicate to an adaptive significance of such interactions in reducing infanticide.

I also found that mating success of Asiatic lionesses were poor, much lower than Serengeti lions (~36-38%, Schaller 1972; Packer et al. 1988). This might be owing to reported deformities in sperm -structure and -motility of a highly inbred Asiatic lion population

(Driscoll et al. 2002; O'Brien 2003), resulting in failure of effective insemination. Alternatively, such poor success rates might also be a female physiological adaption to let them indulge into multi-male matings before conceiving. Felids are known to be induced ovulators (Brown 2006) and such ineffective insemination/infertility in Asiatic lionesses can be an outcome of post-copulatory mate choice in females (Wolff and Macdonald 2004), similar to that found in cheetahs where females maximize the number of mating partners (Gotteli et al. 2007). Studies reveal that this strategy of female cheetahs might have evolved to enhance chances of multiple-paternities thereby improving genetic variability in the litters (Gotteli et al. 2007), given cheetahs being a highly homozygous species (O'brien et al. 1986). Furthermore, study lionesses mating with multiple rival males in the same estrus (n=6) prompt to the likely occurrence of sperm competition and cryptic sexual selection in females (Møller and Birkhead 1989; Baker and Bellis 1994).

From the results I highlight the proximate behavioural consequences of female promiscuity and hint towards its possible causal mechanisms, however, a genetic study on paternity of Asiatic lion litters might reveal more on these patterns. By being selectively promiscuous, Gir lionesses seem to have won the gender arms race and facilitated a strategy which might be beneficial for the entire species as a whole.

I also show that inter-gender space use, that is directed by resources (prey -size and -availability), remains a major selective mechanism driving social organization and mating strategies in lions. Tigers and leopards (*P. pardus fusca*) in the Indian subcontinent harness similar resources in terms of prey species to that of Asiatic lions (Chakrabarti et al. 2016) and are also known to exhibit alike inter-gender space use patterns (Sunquist 1981; Chundawat et al. 2016). Such similarity warrants the need for a comparative behavioural study of different species experiencing similar selective mechanisms from comparable eco-geographical

settings to reveal dissimilarities and/or commonalities in mating strategies and thus, underpin the evolution of such behaviour in carnivores.

Figure 6.10. A mating pair of lions in a bed of *Senna uniflora*. The male grimaces and yowls loudly upon ejaculation. ©Stotra Chakrabarti



Synthesis



Synthesis

In this research dissertation I document and investigate sociology and factors governing it in Asiatic lions. Males and females of this subspecies live in like-sex groups that exhibit independent socio-biology. These groups interact primarily for procreation and at kill sites. Male lions in Gir formed linearly hierarchical coalitions, with partners in small coalitions reaping higher benefits of association than males that stayed alone. Reproductive fitness of males in coalitions were significantly higher than single males. However, owing to pronounced linearism in their hierarchies, males at the bottom ranks of large coalitions (of >2 males) missed out significantly on feeding and mating opportunities. Field data on group sizes of Asiatic lions mirrored the optimal coalition size (2 males) as per my predictions of optimal benefits. Female groups almost had exclusive territories, while male ranges overlapped with that of one to many female groups and neighbouring males. Each female pride shared their territories with 2-4 coalitions. Lionesses of a pride mated with multiple males from adjacent coalitions; however, promiscuity was shown primarily by experienced females who have had litters before. Primary and peripheral coalitions were tolerant towards cubs of a female pride, thereby considerably reducing cub infanticide probably owing to confused paternities in the males. Promiscuity thus benefits females by increasing the survival and genetic diversity of their progeny.

I reveal that although a pride of lions represents a quintessential example of between-gender cooperation in animal societies, it might not be as ubiquitous as it seems. My results indicate that Asiatic lions, living in a more forested ecosystem with small and non-migratory prey differ greatly in their social organization from their much studied east African counterparts. Through my results I highlight the plasticity of social behaviour in mammals and lend more

evidence to comparative studies done on other group living species like **i)** African and Asian elephants; and **ii)** bottlenose dolphins, inhabiting areas with differential selective pressures from dissimilar resources and threats (de Silva et al. 2016; Connor et al. 2017).

Figure 7.1. A male and female lion walks in tandem, characteristic of consorting behaviour before mating
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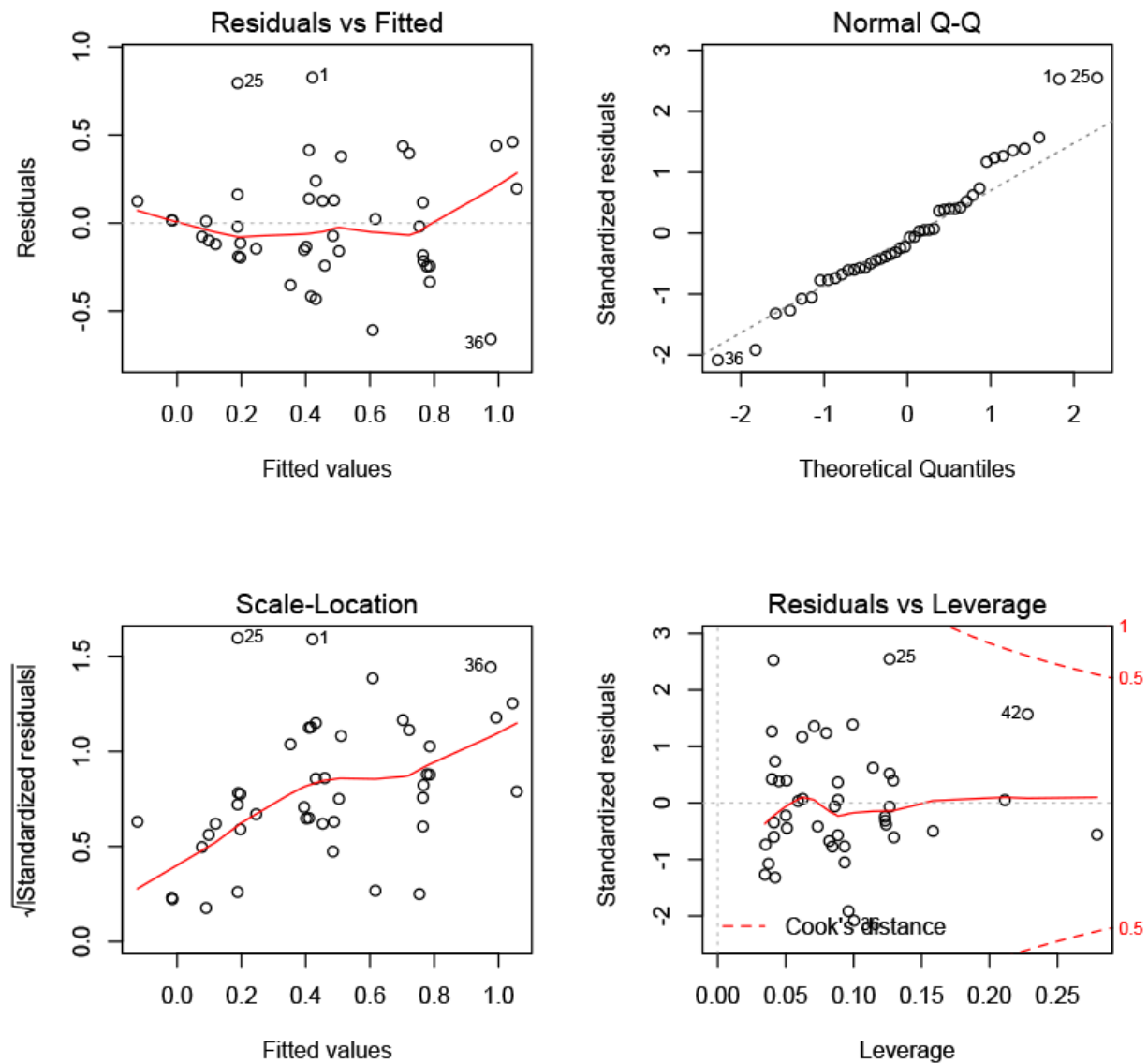
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Supplementary Information

S1. Residual-diagnostic plots of best model relating difference in biomass consumption between coalition partners to prey size, coalition size and the appetite of the reproductively-dominant male.



S2. Mating frequencies and extent of home-range overlap between *experienced females* of a pride and males of their respective neighbouring coalitions. Values in bold represent matings significantly more than home-range overlaps.

	Mnbr1	HRnbr1	Mnbr2	HRnbr2	Mnbr3	HRnbr3
Prd.J	0.00	27.45	12.50	48.20	37.50	29.87
Prd.Kw	40.00	10.75	0.00	15.49		
Prd.K	33.33	32.04	16.67	29.97		
Prd.R	9.09	9.20	9.09	22.36	27.27	45.43
Prd.Rs	71.43	11.10				

S3. Details of mating events, breeding class (1-*maiden breeders* and 2-*experienced females*), litters and consequent mating success of monitored females in a subset of the study area where all male and female groups were monitored simultaneously. Rows with litter numbers but with no information for cub genders indicate events where either: i) cubs could not be sexed, or ii) they did not survive long enough to get detected, although mothers were observed to be pregnant.

Female id	F breeding class	Pride	Mating events	Litters	Mating success (%)	Cubs (#)	M	F
F10	1	Prd.K	3	0	0.0	-	-	-
F12	1	Prd.K	2	1	50.0	2	1	1
F17	1	Prd.J	4	0	0.0	-	-	-
F20	1	Prd.J	3	1	33.3	-	-	-
F21	1	Prd.J	1	0	0.0	-	-	-
F26	1	Prd.J	3	0	0.0	-	-	-
F29	1	Prd.Kw	2	0	0.0	-	-	-
F3	1	Prd.R	3	1	33.3	-	-	-
F4	1	Prd.R	2	0	0.0	-	-	-
F48	1	Prd.Rs	2	0	0.0	-	-	-
F48	1	Prd.Rs	2	0	0.0	-	-	-
F1	2	Prd.R	4	1	25.0	2	0	2
F13	2	Prd.K	1	0	0.0	-	-	-
F15	2	Prd.K	2	1	50.0	3	2	1
F19	2	Prd.J	2	1	50.0	2	2	0
F2	2	Prd.R	6	1	16.7	3	2	1
F23	2	Prd.J	2	0	0.0	-	-	-
F24	2	Prd.J	2	1	50.0	2	0	2
F25	2	Prd.J	2	1	50.0	1	1	0
F27	2	Prd.Kw	5	1	20.0	2	1	1
F5	2	Prd.R	1	0	0.0	-	-	-
F6	2	Prd.K	6	1	16.7	2	2	0
F7	2	Prd.K	3	1	33.3	3	2	1
F8	2	Prd.K	3	1	33.3	2	0	2
F9	2	Prd.K	3	0	0.0	-	-	-
F46	2	Prd.Rs	3	1	33.3	2	1	1
F47	2	Prd.Rs	4	1	25.0	-	-	-

Abbreviations: id [identity]; Pride [Prd.]; Male [M]; Female [F]; Frequency of matings between females and their neighbouring coalitions [Mnbr]; Extent of range overlap between a pride and the respective neighbouring coalitions [HRnbr]

Appendix

1. Glimpses of fieldwork pertaining to observations on mating events, radio-collaring, documentation of feeding incidents and monitoring of female prides of Asiatic lions in Gir



2. The habitual resting posture of lionesses (on their sides, displaying the white of their underbelly) allowed me to check for the colour of their teats to ascertain their breeding stage (elucidated in Chapter 6); our team of research trackers and forest department staff are well familiar to the study lions and venture close to them without disturbing their daily behavioural repertoire. ©Stotra Chakrabarti



3. Long term monitoring and acclimatization allowed us to monitor individuals up close and personal
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List of Publications from Dissertation

Peer-reviewed Articles (attached overleaf):

Chakrabarti S, Jhala YV. 2017. Selfish Partners: resource partitioning in male coalitions of Asiatic lions. **Behavioral Ecology** arx118, <https://doi.org/10.1093/beheco/arx118>

Conference Papers:

1. **Chakrabarti S**, Jhala YV. 2018. Proximity, Infidelity & Confusion: social organization and spacing patterns dictate promiscuity in female Asiatic lions. Oral Presentation at the Behavior Congress, ISBE 2018, Minneapolis.
2. **Chakrabarti S**, Jhala YV. 2017. Dominance & Promiscuity: social organization of the last lions of Asia. Oral Presentation at Ecology Across Borders: British Ecological Society Annual Meet, Ghent, Belgium.
3. **Chakrabarti S**, Jhala YV. 2017. Joining the dots: lessons learnt from a long-term research on Gir lions. Oral Presentation at XXXI Annual Research Seminar. Wildlife Institute of India.
4. **Chakrabarti S**, Banerjee K, Basu P, Gayen S, Jhala YV. 2017. The Last Stand: will lions find a new home? Oral Presentation at Students Conference on Conservation Science, Cambridge, UK.
5. **Chakrabarti S**, Jhala YV. 2016. Dominance & Promiscuity: social organization of Gir lions. Oral Presentation at XXX Annual Research Seminar. Wildlife Institute of India.

Popular Articles (attached overleaf):

1. **Chakrabarti S**. 2018. Tailing the last lions of Asia. *Science Outside, American Blog of Science*
2. **Chakrabarti S**. 2018. Of Men & Manes. *SAEVUS, Vol 7 Issue 1, March-May 2018*
3. **Chakrabarti S**. 2017. Belling the cat: using telemetry to study lions in people's backyards. *Sanctuary Asia, Vol. XXXVII No.12 December Issue*



Original Article

Selfish partners: resource partitioning in male coalitions of Asiatic lions

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Behavioral plasticity within species is adaptive which directs survival traits to take multiple pathways under varying conditions. Male–male cooperation is an evolutionary strategy often exhibiting an array of alternatives between and within species. African male lions coalesce to safeguard territories and mate acquisition. Unique to these coalitions is lack of strict hierarchies between partners, who have similar resource securities possibly because of many mating opportunities within large female groups. Skewed mating and feeding rights have only been documented in large coalitions where males were related. However, smaller modal prey coupled with less simultaneous mating opportunities for male Asiatic lions in Gir forests, India would likely result in a different coalition structure. Observations on mating events ($n = 127$) and feeding incidents ($n = 44$) were made on 11 male coalitions and 9 female prides in Gir, to assess resource distribution within and among different sized male coalitions. Information from 39 males was used to estimate annual tenure-holding probabilities. Single males had smaller tenures and appropriated fewer matings than coalition males. Pronounced dominance hierarchies were observed within coalitions, with one partner getting more than 70% of all matings and 47% more food. Competition between coalition partners at kills increased with decline in prey size, increase in coalition size and the appetite states of the males. However, immediate subordinates in coalitions had higher reproductive fitness than single males. Declining benefits to partners with increasing coalition size, with individuals below the immediate subordinates having fitness comparable to single males, suggest to an optimal coalition size of 2 lions. Lions under different competitive selection in Gir show behavioral plasticity to form hierarchical coalitions, wherein partners utilize resources asymmetrically, yet coalesce for personal gains.

Key words: behavioral plasticity, carnivore behavior, coalition, dominance hierarchy, mating skew, sociality.

BACKGROUND

Cooperation among males is an evolutionary strategy to enhance fitness of partners through a better defense of resources and reproductive opportunities (Krebs and Davies 1987). Such a strategy has been reported in diverse mammalian species like lions *Panthera leo* (Schaller 1972; Bertram 1975b; Packer and Pusey 1987; Meena 2009), cheetahs *Acinonyx jubatus* (Caro and Collins 1987), striped hyenas *Hyaena hyaena* (Wagner et al. 2008), chimpanzees *Pan troglodytes* (Nishida 1994; Watts 1998; Mitani et al. 2000), howler monkeys *Alouatta seniculus* (Pope 1990), baboons *Papio spp.* (Smuts 1985; Bercovitch 1988; Noë 1994), feral horses *Equus caballus* (Feh 1999), meerkats *Suricata suricatta* (Doolan and Macdonald 1996), coastal river otters *Lutra canadensis* (Blundell et al. 2004), and bottlenose dolphins *Tursiops truncatus* (Connor et al. 1992). Yet, the degrees of cooperation among male partners vary dramatically between species, from simple alliances in feral horses (Feh 1999) and coastal river otters (Blundell et al. 2004) to complex coalitions

in nonhuman primates (Harcourt 1992). Loose alliances may be formed to gain “mutualistic benefits from simple aggregations” (Olson and Blumstein 2009) such as: extravigilance and predator protection in Cape ground squirrels *Xerus inaurus* (Waterman 1997), enhancement of hunting success in coastal river otters (Blundell et al. 2004) and effective defense of clumped resources in golden jackals *Canis aureus* (Macdonald 1979). But complex coalitions in which male partners incur costs-of-sharing valuable resources (like food, mates, and territory) seem to challenge Darwin’s (1859) theory of natural selection (Clutton-Brock 2009), wherein all individuals are supposed to compete for survival and reproduction, and not aid each other at their own costs. A typical coalition is defined as cooperation between 2 or more individuals against a third party during a competitive encounter (Harcourt 1992; Olson and Blumstein 2009; Koykka and Wild 2016). Such cooperation is potentially costly for the donors and tends to decrease their apparent fitness (Smith et al. 2010). Coalition formation in males can be explained through three major evolutionary pathways: 1) kin selection, where cooperation is extended to closely related individuals to enhance inclusive fitness of donors and recipients through shared genes (Smith 1964; Hamilton 1964); 2) reciprocal altruism, where cooperation

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improves the chances of future benefits between partners (Trivers 1971; Packer 1977); and 3) selfish support, which provides immediate benefits to the donor (Wrangham 1982) (for e.g., male chimpanzees act selfishly while helping nonkins against certain opponents to enhance their own dominance status, de Waal and Harcourt 1992). Such complex pathways for formation of coalitions necessitate species to be long lived, with frequent interactions between individuals and an ability to recollect past interactions (Ridley et al. 2005). Coalitions are thus, essentially found in highly social and cognitively developed species (Olson and Blumstein 2009), although cognitive restrictions on coalition formation have been debated recently (Bissonnette et al. 2014). Coalitions also show considerable variation within species, with recent literature suggesting competition and resource heterogeneity to be the major drivers of such differences (de Silva et al. 2016; Connor et al. 2017).

Other than nonhuman primates, the most well studied male coalitions are in African lions where groups of males aggressively compete to gain and preserve control over female prides (Schaller 1972; Bertram 1975b; Bygott et al. 1979; Packer and Pusey 1982; Grinnell et al. 1995). Only a few coalitions are able to take over territories and safeguard them for durations sufficiently long to sire one to several cohorts of cubs to full independence (Schaller 1972; Bertram 1975b; Pusey and Packer 1994). A high percentage of cubs fall victim to infanticide by new males during pride takeovers (Schaller 1972; Bertram 1975b; Packer and Pusey 1983a, 1983b; Packer et al. 1988; Banerjee and Jhala 2012). Akin to developed primates in lifespan, cognitive abilities and social bonding, the uniqueness about lions is the absence of dominance hierarchies between like sexes in their societies (Schaller 1972; Bertram 1975b; Bygott et al. 1979; Packer and Pusey 1982; Packer and Pusey 1985; Packer et al. 1988). Literature suggests that all adult pride females have equal opportunities to reproduce unlike in other carnivore societies like canids and hyaenids (Schaller 1972; Bertram 1975b; Packer and Pusey 1983b), and resource utilization is symmetrical between male coalition partners, with each male appropriating approximately equal feeding and mating opportunities (Bertram 1975b; Bertram 1978; Bygott et al. 1979; Packer and Pusey 1982, 1983b). The possible mechanisms giving rise to such a state of equal rights among male partners have been attributed to 2 factors: 1) frequent presence of large bodied prey in the African system, reducing the costs of sharing a meal (Funston et al. 1998), and 2) large number of simultaneous mating opportunities because prides in the African Serengeti comprise of an average of 6 (range: 2–18) adult females which are reported to exhibit synchronous estruses (Schaller 1972; Bygott et al. 1979; Packer and Pusey 1983a; Packer et al. 1988). The latter has been reported to release competition between males over ownership of receptive females (Bertram 1975b; Bygott et al. 1979; Koykka and Wild 2016). Additionally, reproduction in lions is highly inefficient, with an average requirement of about 1000 copulations which span across many mating events for a litter to be born (Bertram 1978). Thus, it is beneficial for a male lion to consort a single female for the entire estrous duration (2–6 days, Schaller 1972) to maximize chances of successful fertilization, leaving his other partners a chance to mate with other females, also most likely in estrus synchronously (Bertram 1975b). This has led to a scenario where coalition partners share their mating rights with remarkable equity, with no male being involved in more than 22% or less than 9% of all mating events (Bygott et al. 1979). However, competition for food and mates is more intense within very large coalitions and reduced only by kin selection, as males in such coalitions are usually closely related (Packer et al. 1991). In such coalitions mating is

skewed with few partners being restrained from reproduction and thus, effectively acting as nonbreeding helpers (Packer et al. 1991). However, these males increase the overall fitness of the coalition through group protection (Packer et al. 1991).

Lions inhabit varied ecosystems which differ widely in resource availability (Van Orsdol et al. 1985). Asiatic lions (*Panthera leo persica*), now found only in the Gir forests of Gujarat, Western India, exhibit a social system wherein: prides essentially comprise only of females and their dependent cubs, while adult males live their lives separately, alone or in coalitions (Joslin 1973; Chellam 1993; Jhala et al. 2009; Meena 2009). Males encompass one-to-many female prides but are not an integral part of any particular pride. Interactions between males and female groups are limited mostly to matings with receptive lionesses and infrequent congregations on large kills (Meena 2009; Banerjee 2012). Male lions being subject to resource and sexual selection are expected to show behavioral plasticity in response to variations in the availability of prey and females (Krebs and Davies 1987). Male Asiatic lions likely undergo selective mechanisms different from their African Serengeti counterparts since their modal prey size (chital *Axis axis*, averaging at around 45 kg) is much smaller (Meena et al. 2011; Chakrabarti et al. 2016) compared to African systems (Hayward and Kerley 2005). Also, female prides of Asiatic lions are smaller, averaging at 2 adult females (Meena 2009; Banerjee 2012) which often lack estrous synchrony (present study), leading to less simultaneous mating opportunities for males. Since functional hierarchies within groups are shaped by competition (de Silva et al. 2016), we hypothesize that these limited resources should set the stage for enhanced competition between coalition males. Thus, if male partners in a coalition had differential abilities then it would result in a definitive hierarchy in terms of resource appropriation between them. We examine this possibility through continuous monitoring and observations on predation and mating events of free-ranging Asiatic lion coalitions of varying size (coalitions of 1–4 males). Our results indicate strong dominance-hierarchies between coalition partners, with pronounced asymmetry in resource utilization between them, indicating functional responses of behavior to changing resource availability. Such a hierarchical system was found both in small and large coalitions. Given such unequal sharing within coalitions, with subordinate males having inferior resource securities, we investigate the probable ultimate-causes of coalition formation in Asiatic lions. We postulate that although subordinate males get lesser resources, yet they would benefit directly from coalescing and should have higher reproductive success compared to single males.

MATERIALS AND METHODS

Ethics statement

All permissions to carry out field work were obtained from the Office of the Chief Wildlife Warden (CWLW), Gujarat under the provisions of the Wildlife Protection Act, 1972 (permit number: WLP/28/C/97–99/2011–16). Radio-collaring of lions was approved by the Ministry of Environment, Forests and Climate Change (MoEFCC), India (permit number: 22–7/2002 WL-I) and CWLW, Gujarat (permit number: WLP/26/B/356–61), and carried out under the supervision of field veterinary officers. Gir lions are quite accustomed to people on foot and in close proximity (Divyabhanusinh 2005; Banerjee et al. 2013) and behavioral observations on the individuals were done only after prolonged acclimatizing to our presence. Such habituations allowed us to observe them from as close as 20 m without hindering their daily behavioral repertoires.

Study site and population

Between December 2012 and December 2016, 70 adult lions (21 males and 49 females) belonging to 11 coalitions and 9 prides were studied, encompassing an area of about 1200 km² in the western part of the Gir Protected Area (Gir PA hereafter) and its adjoining human-dominated landscape (21°17'–20°55'N and 70°20'–70°52'E) in Gujarat, India. The study animals were a subset of the larger lion population in Gir PA (1800 km²) of around 250 individuals, which have been studied continuously since 1995 (Jhala et al. 1999, 2004, 2006; Meena 2008; Jhala et al. 2009, Banerjee and Jhala 2012; Banerjee 2012; Jhala et al. 2016). The intensive study area comprised of parts of the western Wildlife Sanctuary and the central National Park, and parts of the south-western agricultural landscape which is outside the formal boundaries of the PA. Gir PA is a dry-deciduous forest tract characterized by a semiarid climate (Champion and Seth 1968) with *Tectona grandis*, *Anogeissus spp.*, *Acacia spp.* and *Žiziphus spp.* as the dominant vegetation (Singh and Kamboj 1996; Jhala et al. 2009, Banerjee et al. 2013). The stretch outside the PA comprised mainly of farmlands, croplands, mango-orchards and *Prosopis spp.-Acacia spp.* thickets.

Selection of coalitions

Males were categorized to be in a coalition when they were frequently seen in each other's company, shared kills, hunted, vocalized and patrolled their territories together (Schaller 1972). Due to long-term research and intensive monitoring system in the study area since early 1990s (Chellam 1993; Jhala et al. 1999, 2004, 2006; Meena 2008; Jhala et al. 2009, Mena 2009; Banerjee and Jhala 2012; Banerjee 2012; Banerjee et al. 2013; Jhala et al. 2016), many lions were individually identifiable along with information on their ranging patterns and life histories. Using this prior information, territorial male coalitions: 1) of varying sizes, and 2) with information since they became residents in the area were selected. We chose coalitions with neighbouring ranges as coalitions dispersed over a very large area were difficult to monitor simultaneously with intense rigor. A total of 11 coalitions comprising of singletons/single male ($n = 4$), doubletons/2-male coalitions ($n = 5$), more than 3 male coalitions ($n = 2$) and their interacting 9 female prides ($n = 49$ adult females) were selected for behavioral observations and were monitored for periods ranging between 1.5 and 4 years.

Identification and monitoring

Study individuals were uniquely identified using their vibrissae patterns and additional body marks (Pennycuik and Rudnai 1970; Jhala et al. 1999). A combination of radio-telemetry and intensive search using cues such as pugmarks, prey-alarm calls, roars, kills, and information from tourists were used to track and monitor the individuals. Two adult individuals (1 male belonging to a coalition of 4 males and 1 female belonging to a pride of 3 adult females) were radio-collared (GPS collars, Vectronics Aerospace GmbH, Berlin, Germany, weighing less than 1% of the animal's body-weight). The entire monitoring period of each male was divided into 2-day sampling occasions as mating observations necessitated each male to be visually located at least once in 2 days, so as not to miss recording a mating event (lion mating events typically range from 2 to 6 days, Schaller 1972; Bertram 1978; Packer and Pusey 1983a). Such intensive monitoring was possible owing to rigorous fieldwork aided with an age-old practice of the forest department to track individual lions every day (Singh and Kamboj

1996; Divyabhanusinh 2005; Meena and Kumar 2012). Our efforts led to the detection of each male in $92 \pm 1\%$ of all the sampling occasions (Supplementary Table S1). All the study individuals were familiar to our presence, and were followed on foot or a 4-wheel drive vehicle.

Behavioral observations

Mating events

Mating events were recorded by locating each study male every day or every alternate day. Upon locating a male, the GPS coordinates, surrounding habitat, state of activity and associated animals were noted. One mating event was considered to be the entire duration when a male consorted a lioness in estrus (included the initial courting phase, actual copulations and intervals between successive copulations, see Supplementary Figure S1 for details) till the pair parted ways and returned to their respective groups. Once a mating pair was found, the male and female were identified to their coalition and pride respectively, and a continuous 24-h focal behavior sampling (Altmann 1974) was done for all days the mating event lasted. Pairs were kept in view within 50 m from observers day and night. During dark nights a flash light was used every 15–30 min to ascertain location of the mating pairs and copulations outside visible range were confirmed with the distinctive loud “yowl” that males make while ejaculating (Schaller 1972; Bertram 1978). Total mating durations and partner-switching instances were recorded. For computing mating durations, we used only those events ($n = 119/127$) where we could observe pairs from the beginning of the events (courting phase). Since study coalitions differed in their total monitored durations (depending upon their initiation of residence/being territorial in the area), to remove bias emanating from differential sampling efforts, number of mating events of a male was expressed as a ratio to the number of days the male was actually detected in the field. Also, we attempted to locate study males once in each of the sampling occasions (2 days), but we failed to detect them in a few cases (8%). Thus, there were chances that we could have missed mating events and the above mentioned calibration addresses this problem. For each male, calibrated mating frequency was expressed per year and this mating index ($MI = [\text{number of mating events} / \text{number of days detected in field}] \times 365$) was then compared between partners and tested for differences using a chi-square test at an α value of 0.05.

Feeding events

Feeding behavior of coalition partners was recorded from the beginning of a feeding event (when the males started feeding on a kill) to the full utilization of the carcass (when the males permanently left it). Data were used from only those events ($n = 44$) where initiation of feeding was known with certainty and ≥ 2 males were present at the site, within 100 m of the carcass. We postulated that competition at kills and hence dominance-hierarchies, if any, would depend upon: 1) prey size, 2) appetite state/hunger of the males, and 3) number of individuals sharing a kill. Prey weights were visually estimated. Before collecting data in the field, we practiced and compared our prey weight estimating skills by accurately weighing different sized whole carcasses used for feeding trials on lions in a zoo facility (Chakrabarti et al. 2016). We could accurately estimate weights of small carcasses up to 15 kg (with an error of ± 1 kg) and medium carcasses up to 100 kg (with an error of ± 5 kg). Visual estimates of very large carcasses (>200 kg) differed slightly among observers and hence a consensus weight between 2 to 3 observers was taken for such prey in the field. The appetite state of every male lion was recorded for each

event by scoring their belly sizes following Bertram's (1975a) technique for African lions. Each lion was given a belly score between 1 (fully gorged) and 5 (starved) (detailed in Figure 1). Information regarding the feeding sequence (males taking turns or feeding simultaneously) and aggression at kills was documented. Total time spent by each male feeding on a carcass was recorded through continuous 24-h monitoring of the feeding events for all days a carcass was being fed upon. Akin to mating observations, each carcass was kept in sight and night monitoring was done using flashlights. Feeding durations were taken as surrogates of biomass consumption. However, lions (like other carnivores) tend to selectively feed first on the choicest body parts of prey (visceral organs and flesh, which need very low handling time), and then the less digestible body parts like skin, bones, and hide, which require considerably higher handling durations (Chakrabarti et al. 2016). Consequently, a male eating first would consume more of higher quality food in relatively less time feeding on viscera and flesh than the next ones having to negotiate skin, bones, and hide. Thus, using absolute feeding duration alone would not account for quality

and amount of consumption. To circumvent this problem, we used data (from feeding trials on wild-caught lions which mimicked free-ranging conditions, Chakrabarti et al. 2016) on consumption rates (kg eaten/h) of lions for successive days feeding on the same carcass. Whenever male partners fed sequentially from small-medium carcasses (<100 kg) in the wild, a correction factor of 0.53 (=consumption-rate ratio of 2nd to the 1st day in the captive trials, Chakrabarti et al. 2016) was multiplied to the feeding time recorded for males eating second, third and so on. For larger carcasses (>100 kg), the correction factor was used for males eating after 12 h from the initiation of feeding. The disparity in consumption between partners was then calculated as the difference in *corrected feeding time* on a kill. Also, aggressive behavior between the partners on a kill (a measure of competition) was categorized into 2 classes: 1) aggressive exclusion—when the feeding male(s) thwarted the advance of at least one of his (their) partners through heightened aggression and did not allow him (them) to feed, and 2) meal sharing—mild aggression between partners (squabbles and occasional swats), but all partners shared a kill simultaneously.



Figure 1

Belly scores to determine the state of hunger/appetite of individual male lions following Bertram (1975a): (a) Fully gorged with a bloated belly, belly fold taut and almost invisible, scored as 1; (b) Well-fed individual with a distended belly and a hint of the belly fold seen underneath, scored as 2; (c) Belly line almost parallel to the ground with a prominent belly fold, animal not too fed, neither too starved, scored as 3; (d) Semistarved individual with a very prominent fold and hints of lateral pelvic depressions, scored as 4; (e) Fully starved individual, with a very loose belly fold and prominent lateral depressions, scored as 5. Photographs were taken by first author.

We examined whether difference in consumption between partners was significantly different from zero using a one-tailed t test, expecting a significant positive difference in consumption between male partners. The difference (if significant) was then modelled with estimated prey size, number of males at the site/coalition size and the appetite state of the males. We expected pronounced competition (hence dominance) at smaller kills with greater number of “hungry” partners at the kill site. We tested 4 models bearing additive as well as interactive effects of prey size, appetite state of males (belly scores) and coalition size against the null model. We ranked models using Akaike Information Criterion corrected for sample size (AICc) (Akaike 1974) and significance levels, and assessed their goodness-of-fit using R^2 statistic and residual diagnostics.

Fitness quotient

Staying alone or forming coalitions are alternative survival/reproductive strategies for males in social mammals, including lions (Smuts 1985; Pope 1990; Bygott et al. 1979; Feh 1999). However, in African lions, males in coalitions are more successful than singletons, producing more number of offspring (Bygott et al. 1979). For coalitions to evolve as a strategy: 1) coalitions should be able to secure more resources compared to singletons, and 2) if dominance-hierarchies are present within coalitions, then subordinate members should also get higher benefits than males which do not form coalitions, especially if coalition partners are unrelated. To test this postulate, we compared reproductive fitness of singletons with those that form coalitions. Since it was difficult to enumerate the number of actual surviving offspring of individual males in the wild with certainty, we used 2 parameters to index reproductive fitness of males: 1) tenure holding ability: tenure length is an important facet of lifetime-success as reproductive fitness of male lions depends upon their ability to acquire and defend territories (Packer et al. 1988), and 2) mating index of each male: as a surrogate for the number of offspring produced, assuming higher chances of successful fertilization with more matings.

Fitness quotient of a male = Annual tenure holding probability $\times$ Mating index

Annual and span tenure-holding probabilities of adult males belonging to different coalition sizes (1, 2, and >2) were computed using a known-fate model as the fate of the males were known with certitude (similar to computing survival probability using Kaplan-Meier estimator; Williams et al. 2002; Skalski et al. 2005) in program MARK (White and Burnham 1999). Since the date of tenure-acquirement was known with certainty to the month for each of the coalitions used in this analysis, and owing to limited sample sizes and similar conditions spanning our study period, we did not test for the effect of different time periods on coalition tenures. Instead, for computing tenure-holding probabilities we considered all of the study coalitions to have commenced their tenureships contemporaneously. The weekly observations on coalition survival were pooled for a month which was used as the minimum unit for this analysis. Some coalitions continued to hold tenures at the end of this study and they were right censored. Subsequent analysis provided monthly survival probabilities from which annual probabilities were derived for different sized coalitions. For this analysis, in addition to the 21 males (in 11 coalitions) monitored for behavioral observations (see the section “Selection of coalitions” for details), we also used information from males ($n = 18$ in 10 coalitions) monitored between 2004 and 2011 (Jhala et al. 2006 and Jhala et al. 2011). Data from a total of 8 singletons, 9 doubletons, and 4 coalitions with >2 males were analyzed. Fitness quotients were then compared between coalitions.

All data processing was done using MS Excel and analyses using program R v15 (R Core Team 2013) and MARK (White and Burnham 1999).

RESULTS

Behavioral observations

Mating events

We recorded 127 mating events and invested 9305 h of focal sampling for collecting observational data. Male–female mating association lasted for an average of 72.9 ± 2.8 h. Also, in only 1% (2 out of 127 events) of all the recorded mating events we found another female of the same pride in estrus synchronously. When compared between partners within a coalition, mating indices differed significantly ($\chi^2 = 41.22$, $df = 16$, $P = 0.0005$), with one male being consistently involved in more matings than his partner(s) (Figure 2a). Skew in the distribution of mating events between partners was highly conserved among different coalitions. The partners with most matings appropriated $71.6 \pm 3\%$, the partners with next-high-est matings had $25.3 \pm 1\%$ and the partners with least matings had 1–2% of the total events of their respective coalitions (Figure 2b).

Feeding events

Data from feeding events of free-ranging lion coalitions revealed a similar trend as found from mating observations. Biomass consumption was highly skewed (difference in consumption between partners > 0 , one-tailed $t = 6.06$, $df = 43$, $P < 0.001$) and the reproductively dominant males consumed 0.47 ± 0.07 times more from kills than their partner(s). This difference in consumption was best explained by a 3 parameter linear model (GLM of the Gaussian family) having the additive effects of prey size, appetite state of the male with highest matings (reproductively dominant) in the coalition and the number of males at the kill site/coalition size ($R^2 = 0.48$, $df = 5$, $P < 0.001$, Supplementary Table S2, Supplementary Figure S2). The model was given by:

Difference in biomass consumption = $-1.045(\pm 0.331) - 0.002(\pm 0.0005) \times \text{prey size} + 0.313(\pm 0.091) \times \text{coalition size} + 0.312(\pm 0.083) \times \text{belly score}$ [figures in parentheses represent SEs]

We recorded high levels of aggression between partners which increased with decline in prey size, increase in number of partners at the kill site and their appetite states (Supplementary Figure S3). Dominant males aggressively excluded other partners and consumed 47% more from shared kills. This further indicated that above-mentioned variables were important in parameterizing feeding hierarchies. However, none of the interaction terms were significant and hence were not included in the best model which differed from the next best model by a $\Delta\text{AICc} > 9$ (Supplementary Table S2).

Fitness quotient

Singletons held territories for shorter durations (annual tenure holding probability = 0.47 ± 0.19) than males in coalitions. Coalitions of 2 males and more than 2 males had similar annual tenure-holding probabilities (0.85 ± 0.05 and 0.81 ± 0.07 , respectively). Singletons had far lower fitness quotients than subordinate males in a coalition of 2 (Figure 3). However, in coalitions with more than 2 males, the males at the bottommost ranks (rank 3 and below) had fitness comparable to that of singletons, indicating that they would do equally good (or poorly) if they remained alone.

DISCUSSION

Functional responses of behavior to different drivers of selection are crucial for individual fitness. Plasticity in strategies aid individuals in coping

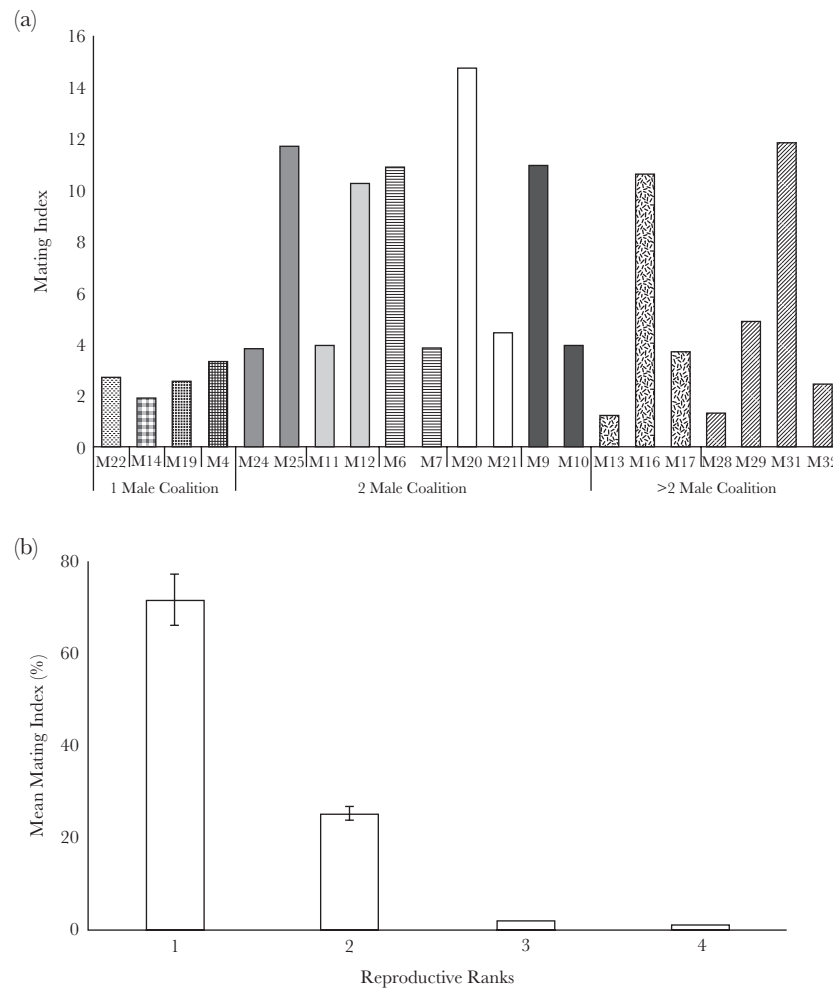


Figure 2

Distribution of observed mating events within and between coalition males. Plots showing: (a) Mating index of monitored lions (annual mating frequency calibrated by the total number of days each male was detected in the field), adjacent bars with similar patterns represent lions from the same coalition; and (b) Lions were ranked in a descending order of mating index within each coalition. The figure shows percent matings procured by lions within a coalition averaged for each rank across coalitions. Error bars represent 95% CIs.

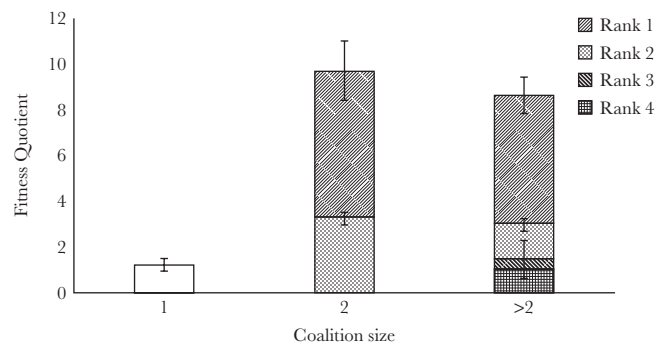


Figure 3

Reproductive-fitness quotients of male lions in different sized coalitions. Error Bars represent 95% CIs.

with varying environmental conditions (Krebs and Davies 1987). Male cooperation to form coalitions is one such strategy which exhibits a wide array of inter- and intraspecific variation in mammals. Coalition formation can vary within species depending upon habitat and resource heterogeneity (Connor et al. 2017). Using lions as model species, we

demonstrate behavioral plasticity to be a possible function of resource availability. Male African lions in the Serengeti system have been found to cooperate amongst themselves to gain access to food and mates, but are not reported to form strict dominance hierarchies (Schaller 1972; Bertram 1975; Bertram 1978; Bygott et al. 1979; Packer et al. 1988). Asiatic lions, living in more forested habitats with smaller modal prey and less simultaneous mating opportunities, likely face selective pressures that results in pronounced dominance hierarchies within male coalitions.

Our results indicate that in male Asiatic lions mate and food sharing between coalition partners were highly skewed. One of the males in every coalition was consistently involved in more matings and the same individual got the *lion's share* from kills compared to his partner(s). As postulated, competition at kills was high amongst partners, very prominent at small carcasses, with high appetite state of the dominant males and more partners in a coalition. A distinct feeding order was observed among the partners, where they took turns to eat from relatively smaller carcasses. The reproductively dominant males invariably had the first rights to carcasses, even if they were not the killers or first possessors. However, dominant partners were observed to share small kills amicably with their partners when the former had their bellies full (Supplementary Figure S3). We also recorded 3 instances of intra-coalition mate switching where

the female switched from one male to its coalition partner within the same estrous duration. In all of the 3 cases the switch happened in favor of the male who also appropriated the maximum mating opportunities and food at kills within that coalition. Reproductive dominance across different ranked individuals within coalitions was found to be highly preserved among coalitions, with males at the bottommost ranks hardly getting any matings (Figure 2b). Thus, in an Asiatic system, individuals in large coalitions (3–4 males) have very asymmetrical resource securities, which might be a plausible explanation of such coalitions being rare. Our results primarily indicate that although male coalitions exhibit pronounced hierarchies, immediate subordinates are better off (higher fitness) than single-males. We predict an optimum coalition size of 2 in male Asiatic lions, below and beyond which reproductive success of single males and low-ranking subordinates respectively are low. This is in accord with the ground reality of an average adult male group size of 2.1 ± 0.3 in Gir (Gogoi 2015). Our results further corroborate the findings of de Silva et al. (2016) where African and Asian elephant groups (*Loxodonta africana* and *Elephas maximus*) show different hierarchical systems shaped by resource competition, and Connor et al. (2017) where male alliances of bottlenose dolphins exhibit considerable variation in habitats differing in resources and threats.

However, apparent reproductive fitness alone cannot explain coalition strength since in large coalitions (>2 males) lowermost ranked individuals had very low reproductive fitness, yet such coalitions exist. Other than mate and territory acquisitions, a coalition may also provide other direct benefits through group protection and food procurement. These may be vital for subordinate lions for survival, gaining vigor and subsequently attempt to either go up on the dominance ladder in the same coalition or join/form other coalitions, as reported in feral horses (Feh 1999). We have observed lions that have lost their coalition partners join other males to form new coalitions, sometimes differing widely in their ages. In African lions different aged coalition partners were mostly found in small coalitions and large coalitions were typically composed of similar aged closely related kins (Packer et al. 1991). Thus, genetic analysis of relatedness within different male Asiatic lion coalitions would shed more light on the underlying mechanisms of the observed patterns. Uniqueness of the observed social structure make Asiatic lions stand out as a distinct behavioral ecotype, highlighting plasticity of social behavior within species facing different selective pressures. Funston et al. (1998) record land tenure system of lions in Kruger to be similar to that found in the Asiatic system wherein males primarily safeguard territories which encompass one-to-many female prides. It would be interesting to see if a social structure similar to what we report for male Asiatic lions exists in Kruger and other lion systems of Africa where forested settings make males interact less with females with the latter living in smaller groups compared to that found in the East African plains.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Chakrabarti and Jhala (2017).

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May 7th, 2018

Mr. Stotra Chakrabarti
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Dear Mr. Chakabarti

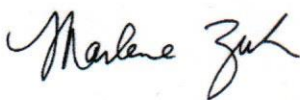
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We have received and processed your registration for the meeting. We are pleased to invite you to make a presentation at the ISBE 2018 entitled **"Proximity, Infidelity and Confusion: social organization and spacing patterns dictate promiscuity in Asiatic lionesses."** You can check the details of your registration at our conference website z.umn.edu/isbe2018.

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Sincerely



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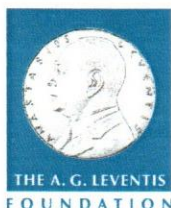


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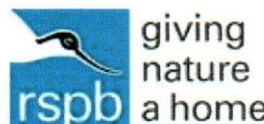
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BELLING THE CAT

Using telemetry to study lions in people's backyards

By Stotra Chakrabarti

Krrrrrr... krrr... krrrr... krrssshh... About half past 12, the sun merciless upon our backs, temperature just a degree short of a half-century and not a single upright shade of respite, as we stood on a rugged barren hillock in search of a slightly-less noisy but more rhythmic beep from the radio-receiver. However, all we could hear was the lifeless static of the radio! It had been 14 days since we had released this lioness after fitting her with a radio-transmitter, and she had miraculously disappeared from the face of the earth! We had been trying to locate her, day-in and day-out, with an antenna attached to a radio-receiver as our main weapon, but there was not a single blip on the radar. We were tired, confused and at a dead-end. About a

fortnight ago, we had captured four adult lionesses living outside the Gir forests in Gujarat, the last-remaining stronghold of the Asiatic lion, and fitted them with GPS radio-collars to study their way of life in a landscape dotted with humans and lion-unfriendly development. The collars provided us with the cats' location through a 'here I am' very high frequency (VHF) beep emitted every second. This signal could be tuned into through a radio-receiver and captured from even two to three kilometres away. The beeps helped us home-in to these regal cats and follow them, as they prolifically (yet perilously) survived in close proximity to humans. With our earlier experience in tracking lions within the Protected Area (PA), we had thought this task would be

fairly easy even outside the PA, but, we were mistaken! All the technological nitty-gritties had failed us and exhaustion and fatigue were taking over man and machine.

NOT AN EASY QUEST

I sat down in the shade of our four-wheel drive and looked at my assistants, a team of determined and experienced lion-trackers who have bled-and-sweated alongside my professor (scientist at the Wildlife Institute of India), Dr. Y. V. Jhala (see page 72), in his lion studies that spanned over 20 years. Over the last two weeks we had tried our luck against the June-sun in Gujarat and clambered-up every thorny vantage point on our path to catch the faintest of VHF signals. This was my first stint

with lions outside their normal refuge, the protected forests, and my ideas of their possible hideouts were nothing but inappropriate. I had been taught the ways of searching and observing animals in forests devoid of people, but finding an elusive carnivore among the hustle-and-bustle of people and roads, took a lot more than bush-craft, grit and patience. Presently about one-third of the total lion population live outside the formal boundaries of protected forests. I relied on my assistants who were familiar with the area since the days the first lions moved out of Gir to colonise this densely-human-populated eastern landscape of Saurashtra in southern Gujarat. However, this lioness had them puzzled too. We had planned to start our day-night monitoring sessions, where we literally lived with lions while we followed them 24 hours a day to document behavioural observations round the clock. For that, the lioness needed much prior habituation to our presence and our knowledge of their frequented places. But for this, I first needed to find the lioness.

FACING PAGE Two lion cubs stare at a truck speeding towards them on a state highway in Amreli district of Gujarat, while their mother disappears into the nearby bushes.

BELOW A collared lioness and her male cub offer their morning prayers at a village temple, which would soon be bustling with humans.





Not a single soul was out in the heat while we drove back to our temporary base about 45 km. away. Even the herders were taking a nap lying close to their prized cattle and buffaloes. Back at our camp, perplexed, empty handed and out of options, I dropped the idea of a cooling shower as water from the over-head tank was steaming hot. Instead, I had a brief lunch with my assistants, who tried to lift my spirits with their lion-stories and how they had lost collared individuals for days. The stories had little effect on me; afterall it was my maiden brush with futile attempts of radio-tracking! July would soon be upon us with her fair share of drenching rains, making fieldwork all the more difficult in the slush and profuse vegetation. It was important that we locate the lioness soon, as an individual with a collar in a human-dominated landscape begets more responsibility on the research team. As I sat contemplating on our future course of action, our lead

ABOVE The vehicle is used by the author as a vantage point to maximise elevation in an attempt to capture VHF signals.

BELOW A collared lioness drags her kill out of the thickets after the team gained her confidence by following and observing her quietly for several weeks.



A lioness stutters to her feet after radio-collaring, still disoriented under the effect of the dissociative anaesthetic, while other pride members inspect her new necklace.

assistant Bhiku, a man in his mid-40s with enviable composure and skill in the jungle, walked up to me and said, "Aaj rewa deo Saheb, kal havar thi naowe-kas thi chalu kariye, mali jahe." He wanted me to drop the evening-night search, and start afresh next morning. Given that both muscle and diesel needed a break from the continuous search, I agreed.

TRACKING A LIONESS

Early next morning, at 5:30 a.m., with renewed spirits pumped up by steaming cups of tea, we set out before the last remnants of the pleasant night-breeze were transformed into a blazing wave. We decided to begin our quest again from where we had collared her: Jabal village in Amreli district. We stopped three times on our way, looking for signals. I stood up on our vehicle-roof extending the telemetry antenna, trying to maximise elevational advantage in an otherwise flat agricultural expanse. My assistants kept a wary eye for any pugmarks on the fields before

the bullocks began their morning ploughing routine (farmers had begun to sow their crops anticipating early showers). The radio-receiver sprang to life incessantly, only to emit crackling statics, but no beeps! We stopped a few farmers heading back from their night shift, guarding standing crops from nilgai and wild pigs to ask if they had seen a lioness with two cubs. The farmers in the landscape are quite welcoming of lions and keep a regular look out for them as the latters' mere presence helps to keep nilgai and wild pigs at bay. With no affirmative answers, we moved on towards the highway, under which flew the main water-channel of the area. The channel was dry barring a few puddles and my assistants went down to explore for tracks on the sand while I tuned into the radio. Tick, tick and it was gone, back to the gurgling noises again! I turned rapidly towards Ismail, another of my assistants in eagerness that he might have heard it too, and from his expression it was clear that he did. In the ensuing minutes, we tried repeatedly but our attempts were not

answered. Could this be it or was it just a figment of our imagination?

Finally, with some tangible hope we climbed an adjacent rocky outcrop and tried once again. Yes! The beeps were faint but very much real. We fathomed that she was over a few kilometres away, towards a series of rugged hillocks infested with scraggly mesquite, locally called as 'bid'. With an antenna in one hand, a stick in the other and the receiver pendulous on my neck, we briskly followed the signals along a livestock trail. Covering the distance as fast as we could, we suddenly stumbled upon a strong stench of a kill as we neared the hillocks. She had possibly dragged one of the unguarded village livestock into the thickets. As we inched forward, we could hear the beeps even without the antenna being attached to the receiver. Our lady was possibly within 50 m.! Pinpointing in the direction of the signal-emitter, I slowly let-go of the antenna and grabbed the stick tightly in my hands. A lioness out of sight is dangerous but a lioness out of sight with cubs is doubly so! Our next





Long familiarisation with the study-area lions and their groups helped the author and his assistants to observe them up-close and personal.

steps were met with a series of angry growls from just behind the closest bush and we knew she would charge if pressed further. We stood there, adrenaline rushing in our veins, while Bhiku muttered from between his teeth pointing towards a small gap in the otherwise dense thicket. A tuft of black-hair twitched as if pulled by invisible strings and I recognised it to be the tail-tuft of a lioness. The growls stopped and the tuft vanished, followed by the soft crackle of twigs when suddenly a golden head popped out of the bush, ears tensed, lips curled and eyes cutting through us! She was barely 10 m. away and she meant business! With no time to lose we thrashed our sticks and shouted loud, the only tried-and-tested deterrent of a lion charge, and after a few minutes of growls and hisses, which felt like an eternity, she obliged. She stopped, turned and vanished into the thickets as fast as she had appeared. One lesson that I have learnt from my

supervisor and assistants was “never show your back to a charging lion, or chances of survival would go down from slim to none!”

Over the next several hours, we slowly gained her confidence as we could see her two cubs peeping behind their mother’s body, who lay sprawled on her back just beside a half-eaten cattle carcass. I was happy and satisfied. It was in these moments when one felt dejected and lost, that the true meaning of perseverance and patience could be found. I never had felt more alive than while listening to an angry lioness growling at close quarters. I guess it is for such moments of indescribable exultation that we, all my fellow wildlife researchers and biologists, painstakingly work in harsh conditions

LEARNING FROM LIONS

That was June 2014. For the next three years, we followed her persistently (even changed her collar once in between) and discovered so

much about this fierce mother, who defended her cubs from intruding males, walked past villages and people sleeping outside their huts, hunted down nilgai and wild pigs, let go of her independent cubs to solicit a younger male and raise another litter. With a lot of patience, uncountable nervous moments and scares, numerous thorns in our boots and a few in our feet, bruised forearms and tattered caps, we gained the confidence of all our study lions, although sporadic charges and their occasional mood-swings kept us on our toes. Such familiarisation helped us gain acceptance in their families to an extent that we could sip hurriedly made tea while they snored peacefully a few metres away in the day and follow them through the long nights when they roamed the countryside as whitish ghosts in the dimly-lit darkness, in search of prey.

I gathered a lot more than just data from these beautiful cats who taught me the power of patience, compassion and bonding as we witnessed in awe the many secrets of a carnivore sharing space with its biped hetero-specifics. Information from these four lionesses (and their groups) and previously-collared individuals from the landscape helped us slowly join the bits of the puzzle about how a large carnivore co-exists with humans. We could infer that lionesses inhabiting outside the PA used areas of about 110 sq. km., twice as large as their cousins living within PAs. Male lions ranged over areas three times larger than their PA counterparts. This was primarily because of the patchiness of available resources (food and refuge) in the human-dominated landscape, which required them to have large territories to encompass their minimum requirements. Non-cultivated and relatively less disturbed green patches of more than three to four square kilometres were ideal for breeding lionesses to hide and raise their cubs, crucial for sustaining a viable lion population in the landscape. The lions used thorny thickets, as small as one hectare, as day-time refuges to conceal themselves from people and roamed around human-settlements and crop-fields at night in search of nilgai, wild pigs and unguarded livestock. These day-time refuges

After four years of studying lions up-close and personal in people’s backyards, I cannot stop but marvel at the adaptability and character of these magnificent predators: tolerant, flexible and so very patient. The story of the Asiatic lions stands as a conservation success because of these traits, and the commendable efforts of the Forest Department and the local people.

were crucial in maintaining human-lion interface to a bare minimum although both lived in very close quarters of each other, and thus, were powerful ingredients of an exemplary coexistence. Though we frequently found lions close to humans, only infinitesimal of those (<0.05 per cent) resulted in aggressive encounters between the two. The lions sustained themselves mostly by scavenging on dead livestock and actively predated on unproductive un-owned live ones and nilgai. Consequently, depredation on productive livestock was low and very promptly compensated (monetarily) by the Forest Department. The losses thus, have not yet made a dent on

the human-coffers, and lions still thrive outside the PA within socially acceptable limits.

After four years of studying lions up-close and personal in people’s backyards, I cannot stop but marvel at the adaptability and character of these magnificent predators: tolerant, flexible and so very patient. The story of the Asiatic lions stands as a conservation success because of these traits, and the commendable efforts of the Forest Department and the local people. The people of Gujarat have shown incredible respect and reverence for these tawny cats, unrivalled in any corner of the world for any other carnivore. Owing to this, the lions have bounced back from

the abyss to a handsome 500 plus individuals while extending their range from just within Gir to an additional 20,000 sq. km. of the agro-pastoral Saurashtra landscape. Lions presently occupy areas, which were out of bounds for them for the last two centuries! However, every time I see a pride of lions cross a highway or move into human settlements, kill livestock and or get into uncomfortable encounters with humans or a *Prosopis* thicket being mowed down to give way to a high-fenced resort; I feel a shudder in my spine thinking about the daunting task that lies ahead of us to reconcile booming development of a progressive state with conservation of the last lions of Asia. 🦁

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Bhiku, Ismail, Hamal and Sameer share a smile over a newly- radio collared lioness as she sleeps peacefully under the potent sedatives administered to her by Dr. Jhala

Of Men and Manes

The league of extraordinary gentlemen behind two decades of Asiatic lion research in the scrublands of western India.

TEXT AND IMAGES: STOTRA CHAKRABARTI

December 2012, my younger self stood in front of five Asiatic lions licking and savouring their freshly bagged trophy – a male sambar. I looked in awe as it was my first on-foot encounter with these fascinating cats but was quickly snapped out of the spell by a hushed tone reminding me that I had to start taking photographs of their face and body profile. These photographs helped us identify each lion from another as their ‘moustache’ patterns are like human fingerprints, unique to their owners. The images would directly be fed into a pattern-recognition software developed by my Professor, Dr. YV Jhala, Senior Scientist at the Wildlife Institute of India, in his quest to understand the last lions of Asia – a task that has spanned over two decades. Next to me stood Dr. Jhala’s most trusted fieldman, Osman (who goes by the name of Bhiku and currently in his mid-40s), who pointed out another adult lioness resting in the thickets. He whispered to follow him.

The effortless ease with which Bhiku negotiated the thickets and reached as close as 10 metres to the

resting lioness was surprising even for the lioness, not just me. I squatted and took photographs while Bhiku watched over my back with a strong bamboo cane in his hand. I think I stood up suddenly from my crouched position, which startled the lioness and she charged! With a 140 kg carnivore charging at me with curled-up lips and unsheathed fangs, I was about to turn on my heels and flee the scene in pure instinct. A firm hand on my elbow stopped me and a voice rang calmly, “*Bhago mat saheb*”. Bhiku was telling me not to run. I stood behind him, flustered and perplexed, as I saw him shout at the top of his voice, thrash his stick and deter what seemed to me an imminent fatal experience. The growls, hisses and shouts were over in a flash (although time had stopped for me as I appreciated Einstein’s theory of relativity in much deeper dimensions). The lioness walked past and joined her companions at the dinner table. That day, Bhiku smiled and taught me the most important lesson that kept me unscathed in the next six years of my association with lions. Showing one’s back to a charging lion is an invitation to an impending death.



Two lionesses feed on a sambar kill while me and Bhiku went to photograph face profiles of one of their group-mates

I’m glad to share many such experiences, where I was fortunate to share the trail with the likes of Dr. Jhala and his league of extraordinary gentlemen in pursuit of lions.

RADIOTAGGING

On the far-eastern side of Saurashtra, the unforgiving summer of May 2014 was taking a toll on our bodies and spirit as we searched incessantly for lions so that we could fix transmitters on them. Dr. Jhala was coordinating the entire operation, discussing with Bhiku, Ismail, Hamal and Taj about the best places to search for lions. After all, locating lions occurring at low densities in an area half the size of Switzerland was nothing less than finding a needle in a haystack! Finally, we got lucky as Bhiku and Ismail managed to track a pride of lions adjacent to a village in Amreli.

Dr. Jhala prepped his equipment and weaponry – a



Radio-collars on lions help us delve into their secret lives as we get to know about their life-histories, what they eat and where they live, their hunting techniques, how they rear their young and interact with other lions



Dr. Jhala and Bhiku with a newly radio-collared lioness

Telinject pneumatic dart-gun – poured a combination of potent sedatives in a plastic-dart, and looked at Bhiku. Every Crusoe needs a Friday. Dr. Jhala had Bhiku. Both shared an unimaginable understanding and temperament in tense situations with aggressive lions under dense brush. As I helped him ready the sedatives, Dr. Jhala gently whispered “*Bhiku, haalin lei leshu na?*” – he was suggesting to dart the lioness on foot. Bhiku nodded in affirmation. The accompanying staff from the forest department raised their brows and murmured their concern regarding this ‘on-foot exposure’ with aggressive lions, only to be silenced by the confidence emanating from Dr. Jhala’s smiles and Bhiku’s determined face.

I was an absolute novice to this process and stayed in the background, watching them from afar as they slowly inched towards the lioness, crouching and moving in tandem. After what seemed like hours, I could see Dr. Jhala take aim and... swoosh... followed by a growl. The dart had hit its quarry. The lioness jumped up from the needle’s prick and disappeared behind the undergrowth. Dr. Jhala looked at his watch and signalled 5-10 minutes while Hamal muttered, “He never misses”. Later, I found this estimate to be precise like clockwork, as every animal darted by him went down within 5-7 minutes of being injected. Soon, we got down to the mammoth task of carrying a snoring lioness out from her thorny refuge, weighing her, taking measurements and putting a transmitter



Dr. Jhala checks the heart-rate of a sedated lioness during a radio-collaring process, just before giving her the antidote

around her neck. As a fresher I stood there bewildered, filling up the collaring datasheet, while the entire team worked with superb coordination and pace to get the lioness back on her feet within 40 minutes of being darted. Unsurprisingly, this team had performed with the same efficiency more than 50 times over the last 20 years! I saw, I learnt and later on was happy to integrate myself into the team in a much more proactive role, as we caught more lions in the years to follow.

TEAM WORK

There were countless moments when Bhiku, Hamal and Ismail narrated their experiences of working with lions in this project since the days they had just sprouted a moustache! One particular story that I am really fond of (as narrated by Bhiku) took place sometime in early 2000.

It was just before the monsoon; sporadic showers had created the first green flush, while Dr. Jhala and his team searched for lions to radio-collar in the western part of the Gir Sanctuary. One fine morning Dr. Jhala and Bhiku set off in the project's 4WD gypsy and stumbled upon chital alarm calls around a place named Sukhnath. Both Bhiku and Dr. Jhala felt the

need to inspect, as such calls at these hours mostly lead to resting lions. After a long walk along a dry stream, they spotted a lioness resting under a Jamun tree. Dr. Jhala's eyes glinted as he told Bhiku that the lioness was perfect to be tagged and must be kept in sight. Bhiku, a young lad back then, assured that he would stay with the lioness since Dr. Jhala had to drive back to the base camp to ready his dart gun and also beckon forest officials to the site, which is necessary for such activities. Bhiku told Dr. Jhala to follow the dry stream-bed to reach back to the vehicle, while he stayed put. It was around 11 am when Dr. Jhala started walking back to the vehicle and Bhiku fondly recalls that "*Shaheb ardhi-kalak ma pacha aiwa, saathe be parikha biscuit ane pani*". After reaching the vehicle, Dr. Jhala had walked back the entire stretch to give a couple of biscuit packets and a bottle of water to Bhiku, since he knew that coordinating such collaring activities could take a lot of time. From the way Bhiku narrated this story, it was clear that he was touched by this act, which lifted his spirits and the day finally culminated in the lioness getting collared. It is this understanding, bonding and mutual respect between Dr. Jhala and his team of lion trackers which has comprehensively pinned down the riddle of lion ecology across its range in Asia.

While completing my Master's degree, I worked at the Junagadh zoo and conducted feeding experiments on lions, leopards and jungle cats in captivity. Curiously, all the leopards and lions in my study were captured as they were reported to have mauled or killed humans. For these experiments I had to visit their enclosures daily and collect their poop, a smelly business but one that gave us crucial insights into their feeding behaviour. Taj shadowed and helped me during those days. One winter morning as I stepped inside the enclosure of a huge male leopard and crouched down, Taj suddenly caught me by scruff of my jacket, dragged me out of the enclosure and started shouting at the keeper. Startled by the incident, I later understood that the keeper had forgotten to lock the bars of the retiring chamber which separated the leopard from where I was operating! A hair's breadth away from turning into the sad subject of a feeding experiment, Taj's quick response saved the day and my life. A father figure, Taj built my skills to live in the bush – right from starting a fire in the strongest of winds to recognising humane qualities in lions. Unfortunately, he passed away in 2014 after a long career of tracking and observing lions, and helping researchers gather information on these beautiful cats.

Time and again, in the last 6 years, I have fathomed that understanding bushcraft and animal behaviour is an acquired art, which is for the most keen and observant field participants. The sheer brilliance

with which Bhiku predicted lion movement from their tracks, Ismail located individuals from prey alarm calls and Hamal spotted the faintest of movements on a ridge line could only be practiced but never preached in textbooks. In one such act, a darted male lion disappeared inside dense mesquite while a dozen-member team searched frantically for the immobilised animal. Bhiku and Ismail stood quietly and listened as they knew that a fully-fed individual under the effect of sedatives would start retching noisily, which an experienced ear could pick up from far. Countless moments spent observing lions from close quarters with Dr. Jhala enriched the way we understood animals. In a lucid manner, he explained the finest intricacies of their ecology, amalgamating his experience and wisdom in the woods. I loved the moments where Dr. Jhala would discuss lion biology, age them based on teeth colour while discussing such details with Bhiku, Ismail and Hamal; learning and teaching conjunctly. I fondly reminisce the way Dr. Jhala asks Bhiku every time just before darting a lion whether to shoot or not to, welcomes opinions and suggestions from the entire team while designing any particular research objective and proudly (and truly) claims that his Gir research trackers are any day better than his researchers. This long association between the captain of a ship and its determined crew has made the Asiatic lion project a unique research experience, unparalleled in duration and conservation outcomes in the Asian research fraternity.

One summer evening, I sat on a lonely hillock in Gir overlooking a grassland where two male lions roared resoundingly to proclaim their presence. The roars echoed through the forest and through all of us, when a revelation dawned. I was on the verge of completing my PhD fieldwork, just like my four predecessors in the last 20 years had done. Doctoral and masters researchers like me come and go, but one perpetual string was our supervisor in the form of a resolute and compassionate scientist and his team of efficient and humble lion trackers. It is essential that we conserve biodiversity and species from going extinct. However, it is equally critical to safeguard the dying breed of Bhikus, Hamals and Ismails who know the dusty trails inside out and work tirelessly for the sheer joy of the natural world. In tandem with the reverberating roar of the lions, I echo that I and my fellow colleagues in this project could see far across the horizon of lion ecology as we stood on the shoulders of giants. ◉



Researchers could comfortably observe lions up close and personal only because of being shadowed by people like Bhiku, Hamal, Ismail and Taj. Here I observe a lioness and take notes while Bhiku watches over me

Science Outside

Tailing the last lions of Asia



A coalition of male Asiatic lions, MLG 11 & 12; they showed the author the meaning of ‘aggression’ while he and his team monitored them between 2012-2016. Photo by Stotra Chakrabarti.

Studying lions was purely coincidental for me. Back in 2012, I did my Master’s dissertation conducting feeding experiments on wild cats in a zoo to delve into their optimal diet-choice. The zoo had the Gir forests, the last home of Asiatic lions, in its backyard. During my dissertation, I occasionally accompanied the Wildlife Institute of India’s research team, who has been studying lions in Gir for the past two decades. As I saw more of these tawny cats and heard field experiences from our research trackers, I realized something was amiss with these lions. Their social behaviour did not match with that of their African cousins. Males and female Asiatic lions live separately and that is strikingly different from what I had read and watched about pride-living African lions. This difference in sociality amongst lions of the two continents intrigued me to such an extent that I dedicated the next five years of my life to tailing the last lions of Asia.

As I started my position in this long-term project as a doctoral fellow, I had the benefit of an extended history of individual information on these lions. With individuals identified, I started my

data collection, often observing lions for long durations. Such monitoring frequently brought us in close contact with lions, and we experienced countless nervous moments. In one such incident I found myself in the middle of a battlefield! I was observing a coalition of two male lions (males form partnerships of 2-5 individuals) feeding peacefully on a sambar (deer) kill, until the relaxed scene turned into a whirl of roars and growls!

Two new males had invaded their territory and the resident males were quick to respond. The very next moment me and my assistants found ourselves bewildered and sandwiched between four angry and hostile lions. Our most experienced field assistant, Bhiku, hissed “*climb a tree, fast!*” and before I could react, both my assistants were up on the canopy (if at all there was one in a semi-arid forest). I clambered up on the first tree I could find, surprised at my own agility! We looked on in awe as the males fought underneath, and then just as suddenly as they had materialized they were gone. Only then did I realise that in this entire rush I had selected a tree studded with thorns! I was bruised everywhere – from my hands to places very implicit – but that was surely better than the angry claws and fangs of a 200 kg predator. My observations on lion feeding-behaviour revealed that Asiatic male lions formed hierarchical coalitions with one male being dominant over his other partners, unlike their egalitarian African cousins.



All eyes on her! A male lion at the heels of his mate while looking diffidently towards the author.
Photo by Stotra Chakrabarti.

Food is the not the only thing that individuals respond to. ‘*Sex in the jungle*’ is another crucial element which decides who’s the boss! Along with food-appropriation, I started observing lions at their most intimate moments: when, where and with whom they mated. 9,300 hours of lion intimacy observations made me realize that testosterone in a male’s head is deadlier than an arrowhead laden

with poison.

Of all the 134 mating events we observed, only a couple were when we were not charged. A male lion consorting with his female considers even a moving bush as a potential rival, and poor us, we got swamped in their emotional frenzy. Once, we were observing a mating pair and my curiosity led us to venture very close to them. The inevitable happened and the male charged. We stood our ground and thrashed our bamboo-canes furiously, and fortunately he stopped. *‘Show your back to a charging lion and your chances of survival would go down from slim to none’* – a lesson learnt from my advisor and our research assistants has kept me alive for the last five years of working with these lions!



A mating pair of lions, the male climaxing with a bite on her nape. Photo by Stotra Chakrabarti.

All the mating data told us that in every coalition, the male who was dominant in feeding was the boss when it came to mating rights with a receptive lioness – again very different from African lions where male coalition partners share such rights with remarkable equity. Such a contrasting social structure between Asiatic and African lions could possibly have evolved because of a smaller “dining-dish” (Asiatic lions’ main prey is chital, a deer around 45 kg) and less mating opportunities (Asiatic lion females live in groups of 2-4) compared to that of African lions. It could be this resource crunch that might have pushed the two sexes to stay separately in the Asian subspecies, as heightened between-sex competition is detrimental to individual wellbeing.

It was not just tangible scientific information that I gathered from these lions. I learnt a lot of patience and adaptability, watching them snore peacefully for hours on end, and then suddenly a miraculous hunt! As I delved more into lion societies and drew parallels to other social mammals like dolphins and chimpanzees, I understood more about how young and naïve human society is. We lack the intricacies in our social system, which natural- and sexual- selection have polished to perfection in these animals.





A male aggressively looks at the author as he observes him and his lady love. Photo courtesy of Stotra Chakrabarti.

Stotra Chakrabarti (https://www.researchgate.net/profile/Stotra_Chakrabarti) is a Senior Research Fellow at the Wildlife Institute of India in Dehra Dun.

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