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ACADEMY *of* HIGHER EDUCATION
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BURROW USE PATTERNS BY TERRESTRIAL VERTEBRATES IN KEOLADEO NATIONAL PARK, BHARATPUR, INDIA

THESIS SUBMITTED TO
MANIPAL ACADEMY OF HIGHER EDUCATION

FOR FULFILLMENT OF THE REQUIREMENT FOR THE
AWARD OF THE DEGREE
OF

DOCTOR OF PHILOSOPHY
BY

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UNDER THE GUIDANCE OF

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SÁLIM ALI CENTRE FOR ORNITHOLOGY AND NATURAL HISTORY (SACON)

April 2018

Dedicated to my parents
for encouraging me to fly towards my dreams

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DECLARATION BY THE CANDIDATE

I declare that this thesis, submitted for the degree of Doctor of Philosophy to Manipal Academy of Higher Education, is my original work, conducted under the supervision of my guide **Dr. H. N. Kumara**. I also wish to inform that no part of the research has been submitted for a degree or examination at any university. References, help and material obtained from other sources have been duly acknowledged

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CERTIFICATE

This is to certify that the work incorporated in this thesis "**Burrow use patterns by terrestrial vertebrates in Keoladeo National Park, Bharatpur, India**" submitted by **Ms. Aditi Mukherjee** was carried out under my supervision. No part of this thesis has been submitted for a degree or examination at any university. References, help and material obtained from other sources have been duly acknowledged.

Research Guide

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Acknowledgements

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~ Aditi Mukherjee

CHAPTER 1

Introduction: Burrows and Their Inhabitants

1.1. General Overview

Most animals use some refuge either daily or seasonally. Burrow in terrestrial habitats is one of the oldest forms of engineered shelters (Voorhies, 1974) reported as early as carboniferous period (Olsen and Bolles, 1975). Burrows appear to be crucial refuge especially in arid and semi-arid regions providing protection against temperature extremes, fire and predation (Campbell and Clark, 1981; Reichman and Smith, 1990). Three major categories of burrowing vertebrates have been identified by Kinlaw (1999). These include ‘primary excavators’ for whom digging burrows is an inevitable part of their survival; ‘secondary modifiers’ that occupy and further transform the burrows of primary excavators and the third category of ‘simple dwellers’ that take advantage of the mere existence of the burrows and occupy them. Burrow inhabitants are even reported to be either in obligate and/or non-obligate commensal associations (Kiviat, 1978; Kinlaw, 1999). Burrowing vertebrates are the potential ecosystem engineers. These organisms have the capability of modifying habitats and directly or indirectly regulate resource availability for other species (Hansell, 1993; Jones et al., 1994; Lynn and Detling, 2008). They are known to have positive and negative effects on the ecosystem, species richness and abundance at small scales, but an overall positive effect at larger scales in ecological and evolutionary time and space (Jones et al., 1997). In Negev desert, Israel, the digging behavior of porcupine *Hystrix indica* has been studied as a model of disturbance and recovery of plant species (Gutterman et al., 1990). The burrows are important for new-born porcupines for their survival (decrease in vulnerability), energy conservation and thermoregulation (Haim et al., 1992).

Underground burrows are home for an array of animals dwelling in the semi-arid and arid environment as they provide optimum climate (temperature and humidity) compared to extreme ambient conditions, hence, the underground burrows have high conservation importance. Burrowing animals have been looked at as problem species for dams and reservoirs as their burrows weaken the embankments and other structures reducing longevity (Witmer et al., 2006; Bayoumi and Meguid, 2011). However, the body of literature (Chapter 2) reveals that the burrowing animals are ecologically significant in wilderness, in terms of providing habitats for other burrow dependent animals. A comprehensive assessment and further detailed understanding of the burrowing behaviors, the activity patterns of the burrowers, time allocation for each activity, variations in burrowing activities with environmental alterations and inter or intra specific interactions between the burrowing species is essential in further understanding the biology of those species (Pianka, 1988). The burrow dwelling animals in different regions have distinct burrow use patterns, along with the evidence of animal assemblages in burrow system of a single species. It is, therefore, an imperative to understand the governing factors influencing the burrowing behaviours in numerous subterranean vertebrates, including their assemblage, specific activity at spatio-temporal scales, their interactions, and their activity. Given this, the present study was undertaken to understand the spatio-temporal burrow use patterns by terrestrial vertebrates and their assemblage in Keoladeo National Park (hereafter KNP), India.

1.2. Objectives

1) Assess the habitat of porcupine burrow locations in KNP.

    i. Do habitat characteristics such as density of woody plants, the proximity of burrows to water body play any role in the selection of burrowing sites by the burrowers?

2) Study the ground burrow characteristics in relation to cohabiting vertebrate species and their assemblages.

    i. Do ground burrow characteristics (orientation of openings and the area of openings) determine animal assemblage in terms of number of species and their abundance?

3) Quantify activity of burrow dwelling animals with respect to their emergence from and retreat into the burrows and factors influencing the same.

    i. Do different environmental parameters such as variation in ambient and burrow temperature, maximum and minimum temperature and relative humidity influence the activity of the burrow dwelling animals?

    ii. Are there any inter or intra-specific interactions between the burrow dwelling animals?

1.3. Study Site

The study was conducted in KNP (27°7.6′to 27°12.2′N and 77°29.5′to 77°33.2′E, Fig. 1.1) Bharatpur, Rajasthan which falls under the semi-arid zone (Province 4A) of India (Rodgers et al., 2002) and is covered by Dry Mixed Deciduous Babul forest (Champion and Seth, 1968). The park is named after Keoladeo (Shiva) temple located in the center of the park and covers an area of 29 km^2 (Ali and Vijayan, 1986; Vijayan, 1991). It is situated on the extreme western edge of the Gangetic basin, 2 km south-east of Bharatpur town, 40 km South-east of Mathura and 50 km west of Agra and 180 km from Delhi and lies in the Golden triangle of tourism (Mathur et al., 2009). It is a flat area with a gentle slope towards the center forming a depression thus creating a wetland, the total area of which is about 8.5 km^2. The average elevation of the park is about 174 m amsl (Vijayan, 1991). The park is divided into 25 management blocks and a masonry wall around the border of the park separates it from the surrounding 14 villages around the park (Mathur et al., 2009).

The climate of KNP is sub-tropical, with distinct summer, monsoon and winter seasons. Bharatpur experiences extreme climatic conditions from a scorching dry summer (March to June) to a chilling winter (November to February). Monsoon is short (July to September) followed by post-monsoon (September to October) season (Vijayan, 1991). The temperature of the area varies from a minimum temperature of 0 ˚C to 2 ˚C and maximum of 48 ˚C to 50 ˚C and the humidity in the area range from 50 to 90%. The average annual rainfall recorded is 655 mm (Mathur et al., 2009). KNP is a monsoonal wetland, which receives water from the monsoon rains. Apart from rainfall, the park gets its water through the Ghana canal, from Ajan Bund reservoir, located about 1 km south-west of the park. Banganga, Chambal, and Gambhir are the sources of water for Ajan Bund. The park’s flora consists of 375 species of angiosperms. The vegetation of the area is a mixture of xerophytic and semi- xerophytic species composed mainly of *Prosopis juliflora, Acacia nilotica*, *Prosopis cineraria, Salvadora persica, Salvadora oleoides, Capparis sepiaria and Capparis decidua*, *Mitragyna parvifolia*, *Syzygium cumini* and *Zizyphus mauritiana* (Vijayan, 1991). The most widespread grasses in the area are *Vetiveria zizanoides, Cynodon dactylon*, and *Desmostachya bipinnata.* Wetland plants include *Paspalum distichum, Ipomoea aquatica* and *Eichhornia crassipes*. Submerged plants like *Hydrilla, Najas, Vallisneria, Potamogeton* and *Ceratophyllum* are found here (Mathur et al., 2009). The fauna of KNP include 34 species of mammals (Singh et al., 2017), 375 birds (Vijayan, 1991), 30 reptiles which include 15 species of snakes (Mukherjee, 2015), 8 lizards, 7 turtles (Bhupathy, 1999), 7 amphibians and 58 species of fishes (Prusty et al., 2007). As the park lies on the Central Asian Flyway of the Asia Pacific Global Migratory Flyway, it is a staging / wintering ground for a huge number of migratory waterfowl that breed in the Palearctic region. KNP is the only place of wildlife importance with all the four statuses in the country, namely, Wildlife Sanctuary, National Park, Ramsar Site and World Heritage Site.

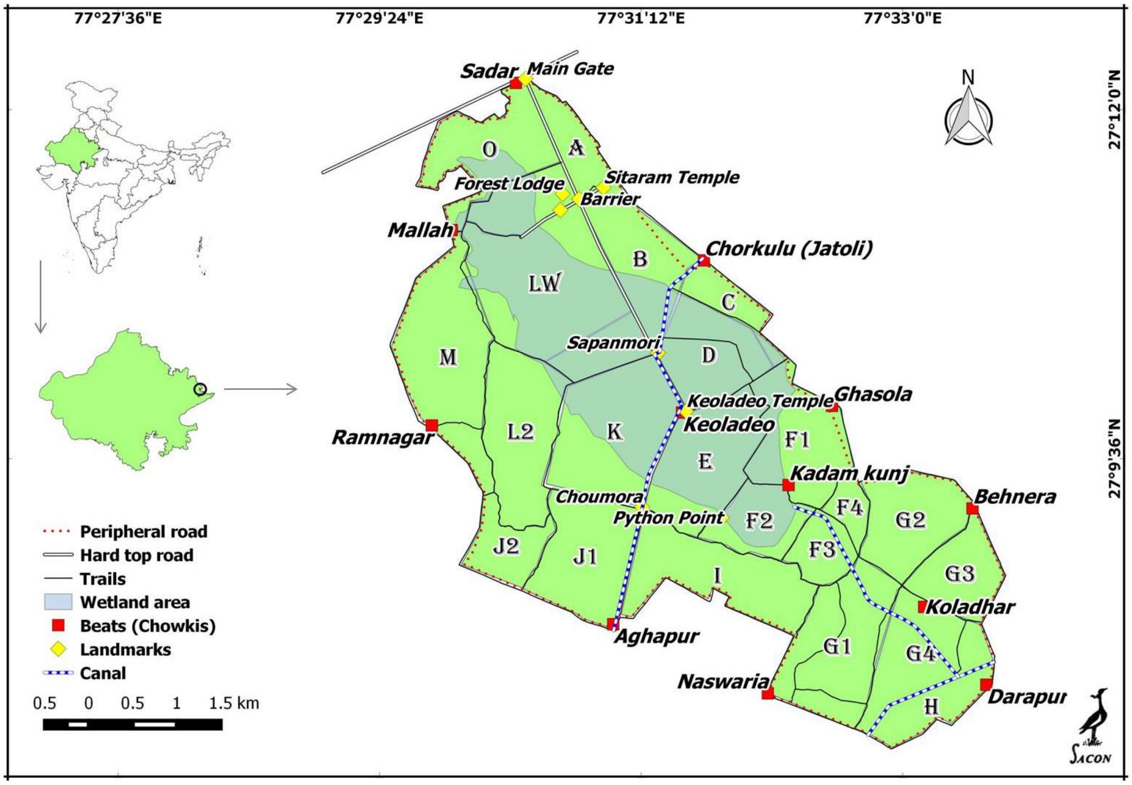

Figure 1.1. Map of Keoladeo National Park

The area of the park is divided into units called sections and blocks, which makes it easy for the management as well as for monitoring purpose. KNP had faced several droughts in its history of existence especially in the first decade of millennia, whereby spreading of invasive exotics like *Prosopis juliflora* and *Lantana camara* also had a destructive effect on the native vegetation of the park. *P. juliflora* had spread not only in the wooded quarters but also to the grasslands, taking advantage of the changes in the ecosystem in the wake of periodic droughts. Though, *Prosopis* still being a menace due to its high rate of propagation, it is continuously checked by the management authority that periodically carries out weeding operations with the action of Eco-Development Committee EDCs.

KNP is one of the most visited parks in the country because of its location at the golden triangle of tourism, Delhi- Agra- Jaipur. The park is a birder's paradise and attracts photographers, bird enthusiasts, researchers, and picnickers. The tourist influx continues throughout the year but it reaches its peak in the months of December- February, the bird watching season when huge flocks of migratory birds visit the park.

1.4. Material and Methods

The proposed study was restricted to animals dwelling in Indian crested porcupine *Hystrix indica* burrows of KNP, Bharatpur, Rajasthan. At the beginning of the study, systematic sampling was carried out by gridding the study area (25 ha) to locate the burrows using GPS (Garmin GPS 60 Map Navigator) and GIS platform. Upon locating the burrows, information on external and internal burrow characteristics, habitat variables including proximity of burrows to water source and boundary, vegetation parameters, soil-type and elevation was collected. Non-invasive methods of camera trapping and burrow video camera were used to assess the animal assemblage and activity pattern. Photographs provided information on date and time of the picture taken, which was used to record the daily activity pattern. The methodology and efforts invested for each objective have been described in detail in the corresponding chapters.

1.5. Study Animals

1.5.1. Indian Crested Porcupine *Hystrix indica*

The Indian crested porcupine (hereafter, ICP) *Hystrix indica*, Kerr 1792 belong to the group of old world porcupine from Hystricidae family. It is the largest (11– 15 kg) burrowing rodent (Prater, 1965; Snyder and Linhart, 1997) and has a wide geographical range from Turkey and the eastern Mediterranean through southwest and central Asia (including Afghanistan and Turkmenistan) to Pakistan, India, Nepal, China and Sri Lanka (Amori et al., 2016). In India, they breed during February-March (Prater, 1965; Prakash, 1997), with a gestation period of 90–

112 days (Khaliq et al., 1991; Kadhim, 1997), followed by giving birth to 1 – 3 litters (Sharma, 2015). The litters are weaned between 13 and 19 weeks, and attain sexual maturity at 2 years (Khaliq et al., 1991; Kadhim, 1997). Although in captivity, they have lived till 27 years, however in wild they have a lifespan of about 6.5 years (Khaliq et al., 1991; Kadhim, 1997). The porcupine is highly elusive and an ecologically-generalist species (Prater, 1965; Snyder and Linhart, 1997) occupying self-constructed and complexly engineered burrow networks (Agrawal and Chakraborty, 1992; Gurung and Singh, 1996; Mendelssohn and Yom-Tov 1999). These porcupines have permanent burrows within their territory along with several others which may be used in times of danger (Chakravarthy and Girish, 2007; Horwitz et al., 2012).

1.5.2. Golden Jackal *Canis aureus*

The golden jackal *Canis aureus*, Linnaeus 1758, is one of the most common canids in its ranges of Asia and Europe (Macdonald and Sillero-Zubiri, 2004; Giannatos et al., 2005; Jhala and Moehlman, 2008). Golden jackals are monogamous (Kleiman, 1977; Moehlman, 1987; 1989; Asa and Valdespino, 1998; Admasu et al., 2004) with rare observations of mate change (Moehlman, 2014). Golden jackals demonstrate elaborate precopulatory sequences (Golani and Mendelssohn, 1971), followed by making or occupying burrows at the onset of the breeding season (Sharma, 1998). During the breeding season, golden jackals use burrows for rearing the pups; therefore, selection of suitable burrowing habitat is essential for the successful persistence of their population (Golani and Keller, 1975). After a gestation of about 63 days (Sheldon, 1992), 1 – 9 pups are born and the lactation usually lasts for about 8 – 10 weeks (Jhala and Moehlman, 2013). They attain sexual maturity at about 11 months, but remain with adults as ‘helpers’ up to two years (Jhala and Moehlman, 2013). In the wilderness, they have a lifespan of eight years, however, there are records of them surviving up to 16 years in the captivity. In India, golden jackal’s search for suitable natal sites commences from February to March (Golani and Keller, 1975) often preceded by scent marking through urination and defecation around burrows (Jhala and

Moehlman, 2008) from November through January. The golden jackal as typical 'secondary modifiers' has been observed to modify and use the existing burrows of Indian fox (*Vulpes bengalensis*), Asiatic gray wolf (*Canis lupus*), and Indian crested porcupines (*Hystrix indica*) (Jhala and Moehlman, 2008).

1.5.3. Indian rock python *Python molurus*

The Indian rock python of Pythonidae family is found in many tropic and sub-tropic areas of southern and southeast Asia ranging from Pakistan, India, southern Nepal, Sri Lanka, Bhutan, Bangladesh and probably in the north of Myanmar (Whitaker and Captain, 2004). It is listed as 'Schedule I' species in Wildlife Protection Act of India, 1972. The Indian rock python is one of the large bodied charismatic non-venomous species. They grow up to six to eight meters in length (Bhupathy, 1995). Pythons are oviparous laying up to 100 eggs and even show maternal care (Shine, 1988), wherein the female coil around and incubate the eggs through a process of metabolic thermogenesis (Ramesh and Bhupathy, 2010). Due to their large and hefty body, they execute 'rectilinear' locomotion, wherein, they move in a relatively straight line with muscular contraction (Kotpal, 1992). They have 'prehensile' tail which facilitates them to twin their bodies while climbing trees and thus can also exhibit arboreal existence. They are efficient swimmers and often use underground burrows in the winters as a refuge site (Bhupathy and Haque, 1986). However, they often come out of the burrows and bask to regulate their body temperature (Bhupathy and Haque, 1986).

1.6. Organization of the Thesis

The thesis represents a step towards the further understanding of the burrowing animals, their habitat and cohabitation in the semi-arid region of India. The *first chapter* provides a general overview of the study; the objectives and specific questions and arguments; details of the study site and the study species. The *second chapter* includes the extensive review of literature, including substantive findings, as well as theoretical and methodological contributions to the field of burrow ecology and the burrowing vertebrates. The chapters three to seven are technical chapters which have been published in peer reviewed journals.

The *third chapter* primarily covers the first objective in detail and discusses the factors responsible for the spatial-occupancy and burrow site-selection by the primary burrower i.e. Indian crested porcupine in KNP. The *fourth chapter* addresses the questions of the second objective and pragmatically identifies the internal and external burrow characteristics and its importance in occupancy of burrow dwelling vertebrates in KNP. The third objective of the study has been discussed in detail in the subsequent three chapters. The *fifth chapter* describes the population structure and abundance of the porcupine in KNP. It also discusses the pattern of the burrow-specific activities by a porcupine and determines whether any factors such as micro-habitat conditions, environmental variations, and seasonal variations influence porcupine's burrow use pattern. The *sixth chapter* examines the burrow use pattern by the secondary burrow user i.e., the golden jackal; and explains the detailed account of their activities around the burrows, specifically during the reproductive season. The *seventh chapter* provides a comprehensive insight into the burrow use regime and thermoregulatory behavior, particularly basking pattern of Indian rock python identified as a simpler dweller of the existing porcupine burrows. The impact of tourist disturbance on the activity pattern of python has also been discussed in detail. The *eighth chapter* culminates into the Synthesis chapter which summarizes the findings of the earlier chapters, highlights the assemblage of the species along with their interspecific interactions, and revisits the contributions of the findings to better informed management of the burrowing species.

Review of Literature

“Look closely at nature. Every species is a masterpiece, exquisitely adapted to the particular environment in which it has survived.”

‡ *E. O. Wilson* ‡

2.1. Burrows as ecological significant microhabitat

All organisms adjust to a diverse set of ecological conditions levied on them by the environment and the conformity between them constitutes an organism's 'adaptation' (Pianka, 2000). Although animals can adapt and occupy nearly every possible habitat, but inhabit only a limited set of ecological conditions (Wiens, 2004), eventually shaping species occupancy in a habitat. A species not only occupy a habitat but also select an appropriate site as a refuge either daily or seasonally, which is an essential prerequisite for the persistence of any population. Several physical, biological and ecological factors significantly influence the refuge site-selection by populations at various spatial scales (Endres and Smith, 1993). Suitable burrowing sites for fossorial animals play a crucial role in the successful rate of reproduction and rearing of offspring's (Haim et al., 1992; Wilson, 1998; Madsen and Shine, 1999; Ciarniello et al., 2005).

The burrow systems represent a fundamental ecological resource for an array of animals (Burns et al., 1989; Hansell, 1993; Kinlaw, 1999). They are a vital refuge, especially in arid and semiarid regions providing protection against extreme weather conditions, fires, and predation (Campbell and Clark, 1981; Alkon and Saltz, 1988a; Reichman and Smith, 1990; Roper et al., 2001; Cudworth and Koprowski, 2011). Globally, there have been few holistic attempts to study the underground earthen burrows, burrow use patterns by terrestrial vertebrates, their assemblage, and associations/ interactions among them. Burrowing vertebrates are the potential ecosystem engineers (Voorhies, 1974) having the capability of modifying habitats, thus directly or indirectly regulating the resource availability for other species (Hansell, 1993; Jones et al., 1994, 1997; Lynn and Detling, 2008). They are known to have varied effects on the ecosystem (positive and/or negative), species richness, and abundance at small scales, but a general positive consequence at larger scales in ecological time and space (Gutterman and Herr, 1981; Jones et al., 1997). Burrowing animals have been looked at as problematic species as they dug out their burrows near dams and reservoirs thereby weakening the embankments which further reduce the longevity of several structures (Witmer et al., 2006; Bayoumi and Meguid, 2011). However, the ecological role of burrowing animals as 'ecosystem engineer' in their natural habitat is important (Kinlaw, 1999) and thus has high conservation implication.

2.2. Associations of burrowing co-occupants

Burrow inhabitants are either in obligatory and/or non-obligatory commensal associations with other co-occupants (Kiviat, 1978; Kinlaw, 1999). The importance of burrows with respect to vertebrate species was recognized several decades ago (Kinlaw, 1999). In burrows of pocket gopher *Thomomys bottae* in Colorado, an assemblage of as many as 22 vertebrate species including amphibians, turtles, lizards, snakes and moles were observed (Vaughan, 1961). Similarly, the burrows of muskrat *Ondatra zibethicus* were used by more than 60 vertebrate species (Kiviat, 1978). An assemblage of 64 vertebrate species including mammals, birds, amphibians and reptiles have been reported cohabiting with white-tailed prairie dog *Cynomys leucurus* and black-tailed prairie dog *Cynomys ludovicianus* in 46 colonies in Wyoming (Campbell and Clark, 1981). The burrows of gopher tortoise *Gopherus Polyphemus* in Florida were reported to be used by 16 vertebrate species (Lips, 1991). Mutualistic association has been observed between cape ground squirrel *Xerus inauris* and suricate *Suricata suricatta* as the former could benefit from the predation detection capability of the latter; and also between yellow mongoose *Cynictis penicillata* and cape ground squirrel *Xerus inauris* with no interactions being pragmatic between the two (Waterman and Roth, 2007). Aboveground counts of black-tailed prairie dogs *Cynomys ludovicianus* showed higher densities of burrow entrances and hence reflected higher prairie dog densities in South Kansas (Powell et al., 1994). In Georgia, USA, patterns of movement and burrows use for gopher tortoise *Gopherus polyphemus*, exhibited that the mean distance per move, number of burrows used, and annual home range size were greater in males than in females (Eubanks et al., 2003).

2.3. The significance of burrows in population growth functions

Burrows are a conversant and safe place for reproduction, thus significant in reproductive success (Hoogland, 1995) and population growth for certain species (Kinlaw, 1999). Burrows also have a strong biological influence on their occupants by reinforcing socialization chiefly during mating and rearing the young (Hansell, 1993). For example, breeding colonies and cooperative pup rearing is observed in burrowers including the Attwater's pocket gopher *Geomys attwateri* Merriam, 1895 (Cameron et al., 1988), the wood mouse *Apodemus sylvaticus* Linnaeus, 1758 (Bujalska and Saitho, 2000), the

Wagner's gerbil, *Dipodillus dasyurus* Wagner, 1842 (Gromov et al., 2000), the Mongolian gerbil *Meriones unguiculatus* Milne-Edwards, 1867 (Gromov, 2009), the bank vole *Clethrionomys glareolus* Schreber, 1780 (Gromov and Osadchuk, 2013), the meerkat *Suricata suricatta* Schreber, 1776 (Brock and Manser, 2016); the black-tailed prairie dog *Cynomys ludovicianus* Ord, 1815 (Grassel et al., 2016); wherein yearling and subadults participate in rearing the litters along with the parents.

2.4. Rodents – The primary burrowers

Among the burrowing mammals, rodents are largely sedentary, possessing a home range for foraging, burrowing or constructing shelters to reproduce and avoid interactions with predators or other conspecifics (Gromov, 2017). In arid and semi-arid regions, rodents form the major group of burrowing mammals with elaborate multi-tier burrow systems (Prakash, 1997), which facilitates them to unload excessive heat due to high mean temperature during summer. The burrow structure of Indian gerbil *Tatera indica* and Indian desert gerbil *Meriones hurrianae* have been excavated and seasonally examined in the Thar Desert, wherein the burrow systems of *Tatera indica* was of simple 'Y' shaped type with one or two surface openings and with the maximum depth of 35 cm in winters to 45-50 cm in summers. However, burrow systems of *Meriones hurrianae* were complicated and extensive with numerous opening and with no significant seasonal change in burrow depth (Goyal and Ghosh, 1993). The burrows structure through excavation and the home range of Indian desert gerbil *Meriones hurrianae* has also been studied in Jaisalmer, Bikaner and Palsana districts of Rajasthan (Fitzwater and Prakash, 2009), wherein, the gerbil burrows were of three types: superficial burrows up to 3 m long and 5-10 cm deep, shallow burrows up to 25 cm deep which usually led to deep burrows with maximum depth reported in Bikaner (110 cm), followed by Palsana (108 cm) and Jaisalmer (65 cm).

2.5. Canids as Secondary burrow inhabitants

Amongst mammals, canids are 'secondary excavators' and take advantage of the work done by 'primary excavators' (Moore, 1949; Sullivan, 1956; Morrell, 1972; Jiménez-Guzmán and López-Soto, 1992; Thomson, 1992; Yamamoto, 1994; Corbett, 1995; Macdonald and Courtenay, 1996; List, 1997; Kowalczyk et al., 2004; Sillero-Zubiri et al., 2004). The canids can dig their own burrows, but adapt to energetically-efficient behavior by being secondary excavators (Murdoch et al., 2009) and scrupulously use the underground burrows of other species as natal or rearing sites where the pups are born and reared until dispersal (Pruss, 1999). For example, the swift foxes (*Vulpes velox*) often use badger burrows and particularly select natal den sites on the top of hills with a gradual slope (Pruss, 1999) and unoccupied burrows with multiple entrances (Hillman and Sharps, 1978). Similarly, kit foxes select natal burrows with more entrances with small entrance diameters (Arjo ,2003). However, in arid landscapes, swift foxes and kit foxes select natal sites in positions with little vegetation that maximize visibility from their burrows (Egoscue, 1962; Kilgore, 1969), thus reflecting the importance of suitable natal sites selection which is often based on burrow location and their physical characteristics (Hillman and Sharps, 1978).

2.6. Indian crested porcupine - The largest and ecologically significant burrow architect

The burrows under observation are primarily engineered by the primary burrower, Indian crested porcupine (hereafter ICP) *Hystrix indica*, Kerr, 1792. The ICP is a nocturnal, highly elusive, ecologically-generalist, large (11-15 kg) burrowing rodent (Prater, 1965; Snyder and Linhart, 1997) that uses complexly engineered burrow-networks (Gurung and Singh, 1996). The porcupine is herbivorous, feeding both hypogeal and epigeal parts of plants including roots, bulbs, succulent tubers, ripe fallen fruits and bark of certain tree species (Arshad et al., 1990; Sharma and Prasad, 1992; Roberts, 1997). Usually, the porcupines occupy self-constructed burrows consisting of long entrance tunnel, multiple exits and large inner chamber (Agrawal and Chakraborty, 1992; Gurung and Singh, 1996; Mendelssohn and Yom-Tov, 1999). Porcupines have permanent burrows within their territory and site fidelity has also been observed for years if not disturbed (Monetti, 2005). The ICP has a broad habitat tolerance (Alkon and Saltz, 1988b; Amori et al., 2016) and is common enough to be considered as a serious pest in parts of its range (Alkon and Saltz, 1985; Khan et al., 2000; Hafeez et al., 2011), thus accorded the status of ‘least concern’ by IUCN Redlist (Amori et al., 2016). Despite its pest status they significantly contribute to ecosystem functions by dispersing vegetative propagules of plants (geophytes) (Gutterman, 1982; Gutterman and Herr, 1981). Their diggings capture water, organic matter and seeds (Dean and Milton, 1991), they provide appropriate refuge sites for other species (Taber et al., 1967) and are also potential prey species (Kadhim, 1997; Bhupathy and Ramesh, 2010; Mori et al., 2013). Thus, the ICP is capable of altering the environment through physical state changes in biotic or abiotic materials and consequently has been classified as an 'allogenic engineer' (Jones et al., 1994; Wilby et al., 2001). The burrows of ICP, in particular, are a crucial refuge for many species (Taber et al., 1967; Bhupathy and Haque, 1986; Bhupathy and Ramesh, 2010) at least in a certain stage of their life cycle, especially during their breeding season.

2.7. The porcupine burrows in Keoladeo National Park- Home for many!

ICP burrows are an important ecological niche as they are also co-occupied by golden jackal, striped hyaena, Indian rock python, monitor lizard, and bat species (Bhupathy and Ramesh, 2010). Keoladeo National Park is also known to have the highest density of near threatened Indian rock python in India (O' Shea, 2007) and it is presumed that the availability of many ICP burrows in the park is the major reason for such high density. Often Indian rock python is seen congregating in huge numbers (>10) around the burrows during winters (Krishnan et al., 2009; Bhupathy and Ramesh, 2010). The ICP burrows subsequently provide apposite microhabitat to canids including jackals and hyaenas during their breeding season and also to poikilothermic endangered Indian rock pythons, and therefore appear to be ecologically significant refuge sites in the region.

CHAPTER 3

Spatial Distribution of Burrows in KNP

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3.1. Introduction

Several physical, biological and ecological factors significantly influence the refuge site-selection by populations at various spatial scales (Endres and Smith, 1993). An understanding of these factors across a landscape is an imperative to manage the concerned species. For some mammals, burrows are a crucial form of engineered shelters (Reichman and Smith, 1990; Stromberg, 1978). The Indian crested porcupine is one of the major mammal inhabitants and apex ecosystem engineer in the park which occupies self-constructed permanent burrows (Gurung and Singh, 1996; Agrawal and Chakraborty, 1992; Mendelssohn and Yom-Tov, 1999), often showing site fidelity for years if not disturbed (Monetti et al., 2005). Their burrows (Fig. 3.1) are an important ecological niche as they are also co-occupied by golden jackal, striped hyaena, Indian rock python, monitor lizard, and bat species (Bhupathy and Ramesh, 2010). The high seasonal variation in the temperature and seasonal flooding makes the Keoladeo National park's ecosystem highly dynamic, thus an understanding of the spatial-occupancy and the site-selection for burrowing by porcupine was fundamental. The present chapter aims to examine the factors that are responsible for the spatial-occupancy and site-selection for permanent-occupancy of porcupine in Keoladeo National Park.

Figure 3.1. Indian crested porcupine *Hystrix indica* emerging from their burrows in Keoladeo National Park (Camera-trap image)

3.2. Methods

3.2.1. Identification of covariates

The Indian crested porcupine is a generalist species that cover long distances (up to 8km) from their permanent dwelling sites during foraging, (Arshad et al., 1990; Roberts, 1997; Sever and Mendelssohn, 1991) as shown for *Hystrix cristata* (Mori et al., 2014a). Thus, it was expected that the food resource availability will play important role in the occurrence of porcupine in the park. Soils that can be easily excavated for food resources were also expected to affect their habitat use. It was therefore expected that the vegetation parameters and the soil-type will influence the spatial-occupancy of porcupine in the park. The Indian crested porcupine is nocturnal in habit, and forage during the night resulting in negligible detections; and with an ease of detecting distinctive faecal dropping, it is the only visible and easily detectable sign of the species in the fields. Unlike other porcupines that have latrine sites near their burrows (Woods, 1973), the Indian crested porcupine is not reported to use any such sites for defecation and their faecal pellets (Fig. 3.2) were easily observed randomly. Faecal deposits have been used as an indirect indicator of species occurrence to assess habitat use by large mammals and their occupancy (Putman, 1984; Hines et al., 2010; Jain et al., 2011) including rodents (D' Adamo, 2000). Detecting the faecal deposits in the field is least expensive and easy, thus it was considered as an indicator of spatial-occupancy for the porcupine. Hence, five ground based covariates were identified: tree-density (TRDE), mean tree-height (TRHT), mean shrub-height (SHHT), shrub-density (SHDE) and soil-type (ST) which presumed to influence the occupancy of porcupine. The herb-density (HEDE) was used as a covariate to model detection probability that could influence the detection of indirect signs like faecal deposits.

Although the porcupine is a habitat generalist, in Keoladeo National Park with varying temperature, their burrows serve as surrogate for 'permanent-occupancy' of the species. The park experiences seasonal flooding causing inundation of certain parts of the park, which occasionally results in permanent damage to the burrow systems (Krishnan et al., 2009). Thus, it was predicted that the higher elevation and greater distance from the point of maximum level of water-stand would positively influence the likelihood of occurrence of the burrows, whereas, the percent water cover would have a negative influence. The park is also surrounded by vast agricultural fields having monoculture of seasonal crops like *Triticum aestivum*, *Brassica* *campestris*, *Sesamum indicum*, and tuberous vegetables like *Solanum tuberosum* and *Solanum melongena* which are reported to be part of Indian crested porcupine's diet (Hafeez, 2011). They are known to venture out to such nearby fields for regular foraging (Agrawal and Chakraborty, 1992; Mendelssohn and Yom-Tov, 1999). It was therefore predicted that the burrowing sites would likely be closer to the park's boundary surrounding the fields, thus making it easier for the porcupines to sneak out. Hence, greater distance from the park's boundary would negatively influence the likelihood of occurrence of the burrows. The available literature reveals that many species prefer soil types having clay and silt content with loamy texture due to their ability to hold molded form easily when wet. They have appeared to be vital constituents for construction of burrows in kangaroo rats (Carter, 1985; Laundré and Reynolds, 1993), pocket gophers (Sulentich, 1991), ground squirrels, deer mice, montane vole (Laundré and Reynolds, 1993) and prairie dogs (Reading and Matchett , 1997). The type of soil enhances durability of the burrows, which is also expected to play a role in site-selection for burrowing by the porcupine. This resulted in identification of one ground based covariates: soil-type (ST) and four remotely sensed covariates: grid with percent water-cover (WATER), mean elevation of the grid (ELE),

Figure 3.2. Distinctive faecal pellets of Indian crested porcupine *Hystrix indica* in Keoladeo National Park

distance from the park boundary(BOU) and distance from the point of maximum level of water-stand (DIWET) which presumed to influence occurrence of burrows. The duration of search (TIME) was used as a covariate to model detection probability that could influence the detection of burrows. The predicted response of the Indian crested porcupine to each of these covariates is shown in Table 3.1.

Table 3.1. Predicted species response to each covariate based on our a priori hypotheses for Indian crested porcupine

Type	**Covariates**	ψ	p
Droppings	TRDE	+	0
	TRHT	+	0
	SHHT	+	-
	SHDE	+	-
	HEDE	0	-
	ST	+	0
Burrows	WATER	-	0
	ST	+	0
	ELE	+	0
	TIME	0	+
	BOU	-	0
	DIWET	+	0

TRDE: tree density; TRHT: mean tree height; SHHT: mean shrub height; SHDE: shrub density; HEDE: herb density; ST: soil type; WATER: grid with percent water cover; ELE: mean elevation of the grid; TIME: duration of search; BOU: distance from park boundary; DIWET: distance from the point of maximum level of water-stand. '+' signifies a positive effect on the response variable, '-' signifies a negative effect on the response variable and '0' signifies that the covariate has no effect on the response variable. ψ: probability of occurrence; p: species detection probability

3.2.2. Survey design

The study area was overlaid with 25 ha grid layer with a total of 137 grids. To locate the faecal deposits of porcupine and to measure the habitat covariates, a diagonal line (707 m) was fixed for each grid as a sampling line for the assessment (Fig. 3.3). Sampling plots (20x20 m) were laid at a regular interval of 177 m on 10 m either side of the transect line inscribed as spatial replicates. Additionally, to locate their burrows, each grid (25 ha *i.e.* 500 x 500 m) was sub-divided into four (250 x 250 m) sub-grids (Fig. 3.3), and each sub-grid was considered as one spatial replicate. Spatial replicates suitable for single season survey (Krishna et al., 2008; Saracco et al., 2011; Das et al., 2014) were chosen to construct the detection histories due to limitation of manpower and logistics; nocturnal activity cycle of the species resulting in negligible detections and ease of detecting distinctive faecal deposits as the only detectable sign of the species in the field.

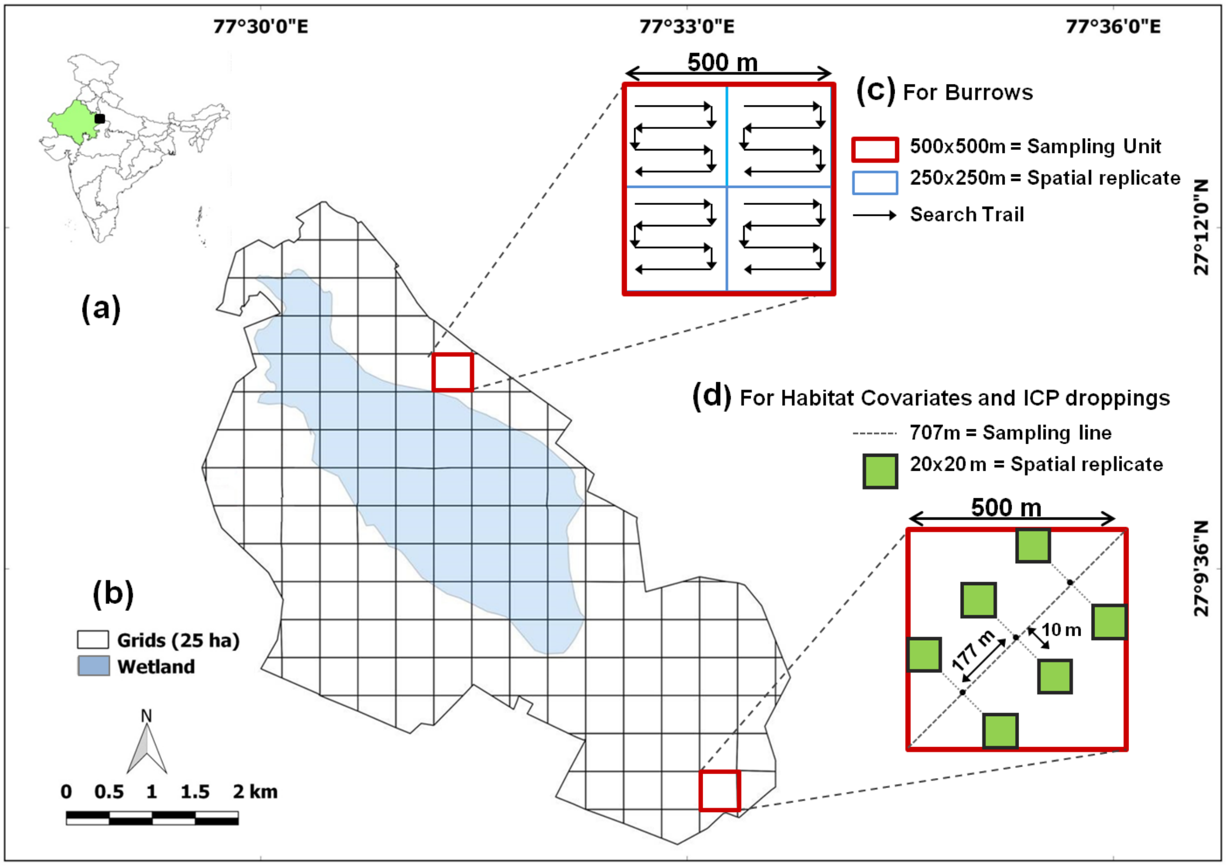

Figure 3.3. (a) The location of Keoladeo National Park in India. (b) Map of Keoladeo National Park overlaid with the sampling grids (25 ha). (c) Details of the sampling protocol in each grid for locating burrows. (d) Details of the sampling protocol for measuring habitat covariates and presence/absence of Indian crested porcupine faecal droppings

3.2.3. Field methods

Field surveys were conducted from September 2013-November 2014. Grids were realized on ground using a Global Positioning System, GPS (Garmin® eTrexVist™). Sampling for the burrow sites were carried out during the dry season to have access to majority of the landscape. Each grid which was further subdivided into four sub-grids was systematically walked to locate the burrows in a zigzag search trail with the help of two efficient local trackers. The geo-coordinates for all the detected burrows were recorded using handheld GPS. A sub-grid was recorded as 'occupied' if the burrow was detected (four spatial replicates).

The grids were overlaid on the shapefiles of the study area with maximum standing water, which was obtained from the Rajasthan Forest Department. The percent water standing area was calculated based on its proportion in each grid. ASTER-GDEM data was downloaded from the USGS Earth-Explorer followed by processing it in open source Quantum-GIS software (ver. 2.4.0). With this, the digital elevation map was built that helped determining the mean elevation of each grid. The distance covariates 'BOU' and 'DIWET' were digitally determined for each grid using measuring tool in Quantum-GIS software. Out of 137 grids, 91 grids formed the sampling unit for faecal deposits covering the terrestrial area of the park as others were either floodplains or outside park's jurisdiction. A straight diagonal line across each grid was chosen as a sampling line and the plots were laid on either side of the grids at fixed intervals. A full sized grid (25 ha) with complete accessibility had six such plots (spatial replicates). A total of 546 such plots were sampled for the presence of porcupine faecal deposits to determine its occupancy; to enumerate the vegetation parameters, and to collect the soil samples for assessing the soil-type. If plots or sub-grids could not be sampled, either due to inaccessibility resulted from water logging or due to logistic reasons such as areas falling outside the park's jurisdiction; the replicate was treated as a missing observation (MacKenzie et al., 2002).

For the enumeration of trees, shrubs and herbs, nested quadrates of 20 x 20 m (one), 5 x 5 m (one) and 1 x 1 m (four) were laid respectively within these plots. Species with GBH (Girth at Breast Height) >10 cm were considered as woody species. The plant species were recorded and their taxonomic identification was done following Prasad et al. (1996). Quantitative community characteristics including tree-height and the shrub-height was determined using Nikon-Forestry-Pro range-finder The stand density each for trees, shrubs and herbaceous layer *i.e.* total number of individuals per unit area was determined for each plots (Curtis and McIntosh, 1950; Philips, 1959; Muller-Dombois and Ellenberg, 1974). All the quantitative community characteristics assessed for each plots were then extrapolated to grid level which was further analysed as five habitat covariates namely, mean tree-height (TRHT), mean shrub-height (SHHT), tree-density (TRDE), shrub-density (SHDE) and herb-density (HEDE), influencing porcupine occupancy.

Apart from plots, soil samples were also collected from each burrow site and the soil-type was assessed using feel-analysis method (Thien, 1979). The soil types were classified based on the preference for burrowing by the porcupine. The soil types clay-loam (CL), silty-clay-loam (SCL) and silty-loam (SL) appeared to be the most preferred soil types in decreasing order. With this, a scoring of 0 to 10 was given to each grid considering the proportion of three preferred soil types (*Scores*- 0:None of the 3 soil types present; 1: Higher % of SL; 2: Higher % of SCL; 3: Equal % of all 3 soil types; 4: Higher % of CL; 5: 100% SL; 6: 50-75% CL/SCL; 7: >75% SCL+ others; 8: 100% SCL; 9: >75%CL+ others and 10: 100%CL) . Scoring was in a hierarchical order where a score of ‘10’ inferred that a grid has the highest probability of occurrence of the burrows whereas a score of ‘1’ inferred vice-versa.

3.2.4. Occupancy estimation

Detection histories of the porcupine faecal deposits and the burrows were constructed for each spatial replication (sub-grids and plots), where ‘1’indicates detection, ‘0’ indicates non-detection and ‘-’ indicates a missing observation. The data was z-transformed on covariates to rescale and normalized the data, prior to occupancy analysis. The two model parameters: the probability that a grid is occupied by the species (ψ) and the detection probability (p) were estimated using likelihood functions (MacKenzie et al., 2002). The data was analyzed using single season models in Program PRESENCE ver. 9.0 (MacKenzie et al., 2006; Hines, 2015) to derive maximum likelihood estimates of model parameters. Based on prior knowledge of Indian crested porcupine’s biology, it was speculated that the covariates indexing vegetation structure, soil-type, elevation and distance from the point of maximum level of water-stand would positively affect the occupancy and the burrow site-selection; whereas covariates indexing water-cover and distance from park boundary (agriculture fields) would negatively affect it. A step-wise approach was used to first model effects of covariates on detection (p), and then modelled (ψ). Three ground-based covariates: (1) SHHT, (2) SHDE and (3) HEDE affected the probability of detecting the droppings along the search trail; and (4) TIME covariate *i.e.* duration of search affected the probability of detecting the burrows. Hence, these covariates were used to model the detection probability (p). To avoid biased inferences resulting from multi co-linearity in predictor variables, Pearson-correlation analysis was done which did not identify autocorrelation among the covariates, and thus combination of covariates were used in one model and all selection models were uncorrelated. Subsequently a candidate set of 9 *a priori* models were formulated to investigate the influence of covariates on porcupine occurrence; whereas a candidate set of 10 *a priori* models were formulated to investigate the influence of covariates on burrow site-selection for permanent-occupancy. Model selection, computation of model weights and averaging of parameters followed Burnham and Anderson (1998). Models were ranked according to Akaike Information Criterion adjusted for a small sample size (AIC_c, Burnham and Anderson, 1998). Models were tabulated in ascending order of ΔAIC_c values. To establish the relative influence of each covariate on occurrence, computed model weights were summed over all models containing the particular covariate (Burnham and Anderson, 1998). We report the estimate of occupancy as mean ± standard error.

3.3. Results

3.3.1. Habitat factors affecting the occupancy of Indian crested porcupine

From 91 sites with 6 sampling occasions, the estimated species detection probability ($\hat{p}$) was $0.33 \pm 0.029_{SE}$. None of the covariates influenced detection probability (*wi* (SHDE) = 0, *wi* (HEDE) = 0, *wi* (SHHT) = 0; Table 3.2) so we ran subsequent models without SHDE, HEDE and SHHT as a function of p (Table 3.3). The naïve occupancy estimate was 0.64 and proportion of sites occupied (ψ) was 0.72. The model-averaged occupancy estimate from top ranked model $\psi(.),p(.)$ and the associated standard error was giving an estimate of $\hat{\psi}=0.71 \pm 0.06_{SE}$. Summed model weights of the covariates indicate SHHT (0.57), ST (0.57) and TRDE (0.48) are the major determinants of occupancy of porcupine over other covariates (Table 3.4). Further, the occupancy of porcupine was positively correlated to SHHT ($\beta_1 = 0.69 \pm 0.32$), ST ($\beta_1 = 0.17 \pm 0.07$) and TRDE ($\beta_1 = 0.60 \pm 0.31$).

3.3.2. Habitat factors affecting the burrow site-selection and permanent-occupancy of Indian crested porcupine

A total of 41 porcupine burrow systems were recorded in the park during the sampling (Fig. 3.4). From 137 sites with 4 sampling occasions, the estimated detection probability ($\hat{p}$) of burrow sites was 0.19 ± 0.05_{SE}. Since both null (.) and duration of search (TIME) equally influenced the detection probability (*wi* (.) = 0.50, *wi* (TIME) = 0.50; Table 3.2), we chose (.) over (TIME) and ran subsequent models without TIME as a function of *p* (Table 3.3). The naïve occupancy estimation for occurrence of burrows was 0.17 and proportion of sites occupied (ψ) for permanent-occupancy was 0.29. The model-averaged occupancy estimate from top ranked model ψ (WATER+BOU+ELE), *p*(.) and the associated standard error was giving an estimate of $\hat{\psi}$ = $0.61 \pm 0.18_{SE}$. The second 'best' model included ψ (WATER+BOU), *p*(.) and the associated standard error was giving an estimate of $\hat{\psi}$ = 0.59 ± 0.20_{SE}. Summed model weights (Table 3.4) for WATER (0.95), BOU (0.91) and ELE (0.86) were more than ST (0.004) and DIWET (0.00). Burrow site-selection for permanent-occupancy by porcupine was thus negatively correlated to both percent water-cover (WATER: β_1= -12.28 ± 9.94) and distance from the park boundary or nearest agricultural field (BOU: β_1 = 9.02 ± 4.52) and positively

Table 3.2. Summary of model selection procedure for factors affecting detection probability of Indian crested porcupine in Keoladeo National Park

Type	Model	$\hat{p}$	AIC$_c$	ΔAIC$_c$	w_i	*K*
Droppings	ψ (.), *p*(.)	0.33	558.54	0.00	1.00	2
	ψ (.), *p*(SHDE)	0.50	587.39	28.85	0	3
	ψ (.), *p*(HEDE)	0.50	589.73	31.19	0	3
	ψ (.), *p*(SHHT)	0.50	589.85	31.31	0	3
Burrows	ψ (.), *p*(.)	0.19	230.75	0.00	0.50	2
	ψ (.), *p*(TIME)	0.19	230.75	0.00	0.50	3

$\hat{p}$: is the estimated species detection probability; AIC$_c$: AIC corrected for small-sample bias; ΔAIC$_c$: difference in AIC$_c$ values between each model and the model with the lowest AIC$_c$; wi: AIC$_c$ model weight; K: number of parameters estimated by the model. SHHT: mean shrub height; DHDE: shrub density; HEDE: herb density; TIME: duration of search.

correlated to mean elevation (ELE: $\beta_1 = 8.57 \pm 5.10$). Site-selection for permanent-occupancy was mapped based on their occupancy estimates (Fig.3.4) for each grid based on best fit model. Overall 31.4%, 5.8%, and 65.0% of the sampled 137 grid cells were classified as low ($\hat{\psi}$ = 0.01–0.40), medium ($\hat{\psi}$ = 0.41 – 0.80), and high ($\hat{\psi}$ = 0.81 – 1.00) respectively.

Table 3.3. Summary of model selection procedure for Indian crested porcupine occupancy in Keoladeo National Park

	Model	$\hat{\psi}$	**(S$\hat{E}$)**	**AIC$_c$**	**ΔAIC$_c$**	w_i	*K*
Droppings	ψ (.), *p*(.)	0.71	0.06	558.54	0.00	0.40	2
	ψ (TRDE+SHHT+ST), *p*(.)	0.62	0.08	558.83	0.29	0.35	5
	ψ (TRDE+SHHT+SHDE+ST), *p*(.)	0.62	0.09	560.83	2.29	0.13	6
	ψ (SHHT+ST), *p*(.)	0.62	0.07	561.55	3.01	0.09	4
	ψ (SHHT), *p*(.)	0.49	0.04	565.76	7.22	0.01	3
	ψ (ST), *p*(.)	0.63	0.05	566.06	7.52	0.01	3
	ψ (TRDE), *p*(.)	0.49	0.04	567.09	8.55	5.60E-03	3
	ψ (TRHT), *p*(.)	0.50	0.04	569.75	11.21	1.50E-03	3
	ψ (SHDE), *p*(.)	0.49	0.03	570.45	11.91	1.00E-03	3
Burrows	ψ (WATER+BOU+ELE), *p*(.)	0.61	0.18	214.02	0.00	0.78	5
	ψ (WATER+BOU), *p*(.)	0.59	0.20	218.73	4.71	0.07	4
	ψ (WATER), *p*(.)	0.60	0.21	219.65	5.63	0.05	3
	ψ (WATER+ELE), *p*(.)	0.62	0.06	219.90	5.88	0.04	4
	ψ (BOU+ELE), *p*(.)	0.57	0.15	220.31	6.29	0.03	4
	ψ (BOU), *p*(.)	0.53	0.10	221.74	7.72	0.02	3
	ψ (ELE), *p*(.)	0.51	0.07	225.57	11.55	2.4E-03	3
	ψ (.), *p*(.)	0.28	0.05	230.75	16.73	2.0E-04	2
	ψ (ST), *p*(.)	0.60	0.19	233.84	19.35	0.00	3
	ψ (DIWET), *p*(.)	0.50	0.06	233.77	19.75	0.00	3

$\hat{\psi}$: Estimated occupancy parameter; S$\hat{E}$: Associated standard error; AICc: AIC corrected for small-sample bias; ΔAIC$_C$: difference in AICc values between each model and the model with the lowest AICc; wi: AIC$_c$ model weight; K: number of parameters estimated by the model.

Table 3.4. Covariates influencing the Indian crested porcupine occupancy ranked on the basis of summed model weights of covariates, with beta coefficient and associated standard error

	Covariate	Summed AIC$_c$ weights	β coefficients ($S\widehat{E}$)
Droppings	SHHT	0.58	0.69±0.32
	ST	0.58	0.17±0.07
	TRDE	0.48	0.60±0.31
	SHDE	0.13	0.12±0.27
	TRHT	1.50E-03	-0.32±0.23
Burrows	WATER	0.95	-12.28±9.94
	BOU	0.91	-9.02±4.52
	ELE	0.86	8.57 ±5.10
	ST	0.00	0.08±0.17
	DIWET	0.00	-0.09±0.35

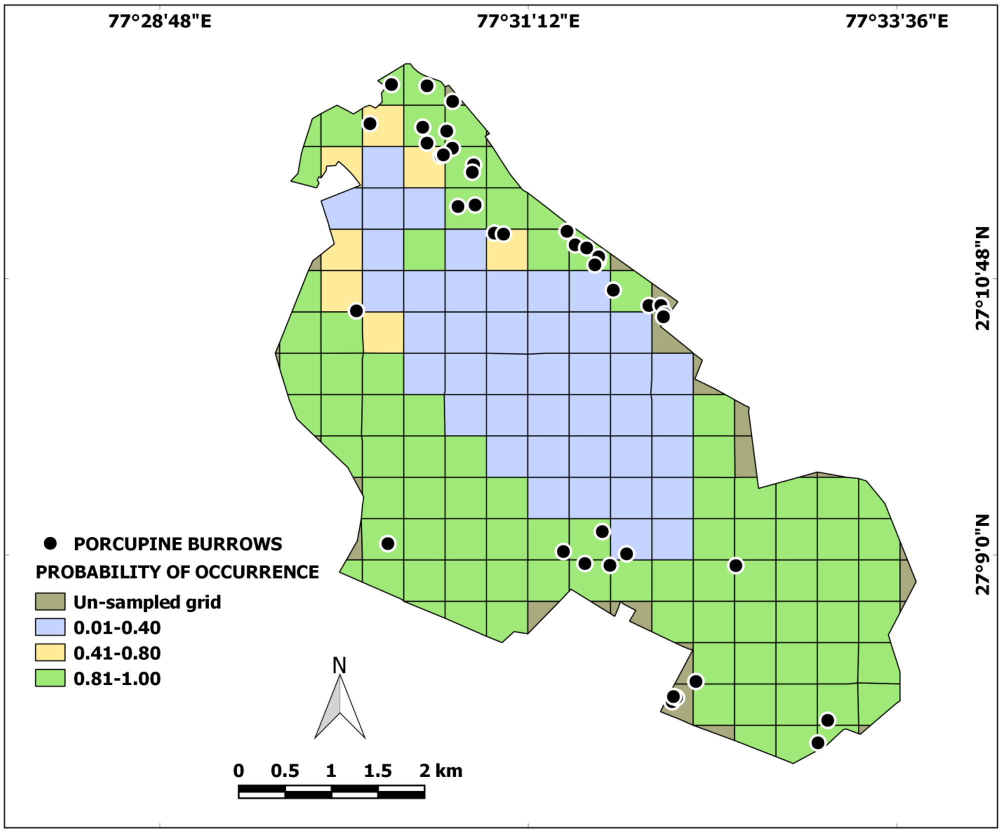

Figure 3.4. Estimated Indian crested porcupine burrow occupancy data generated for each grid, which were extracted from the best fitting model, [ψ (WATER+BOU+ELE), p(.)]. Un-sampled grid cells comprised those that were not sampled

3.4. Discussion

The detection probability (0.19 ± 0.05_{SE}) and occurrence (0.28 ± 0.05_{SE}) of Indian crested porcupine burrow sites is lower than the detection probability (0.33 ± 0.029_{SE}) and occupancy (0.71 ± 0.06_{SE}) of their faecal deposits, inferring that certain factors are responsible for their site-selection for permanent-occupancy irrespective of their uniform spatial-occupancy. The porcupine was found throughout the terrestrial area of the park (67 out of 91 sampled grids), however, percent water-cover, distance from the park boundary surrounded by agricultural fields and elevation of the landscape determined the selection for burrowing site. All the recorded 41 burrow systems (in 23 out of 137 sampled grids) were found confined to areas with non-floodplains, closer to the agricultural fields and at higher elevation than the average elevation of the park. The findings suggest that habitat in general and preferable feeding habits did not persuade shelter requirements or permanent-occupancy.

Null model $\psi(.)$, $p(.)$ remained as the top model with the lowest AIC_c value for occupancy of porcupine, and it is apparent that none of the habitat covariates played significant role in its occupancy. However, North American porcupine *Erethizon dorsatum* in Canada showed habitat selection pattern at tree levels as their bodies are modified for climbing and maneuvering in trees for resting, feeding on bark, fruit and leaves, and for avoiding predators (Griesemer et al., 1998; Morin et al., 2005). Similarly, concentration of preferred food items determined the habitat utilization of Indian crested porcupine in Israel (Saltz and Alkon, 1989) and Cape porcupine *Hystrix africaeaustralis* in South Africa (de Villiers et al., 1994). In Southern Tuscany, Italy, the crested porcupine *Hystrix cristata*, avoided cultivations and selected habitats with dense vegetation, providing cover and food within the study area (second order selection) and within home ranges (third order selection), in the warm period, porcupines selected agricultural areas representing a minor proportion of the study site (Mori et al., 2014a). Exceedingly generalist feeding behaviour of Indian crested porcupine (Hafeez et al., 2011); high abundance of resource material and lack of any fierce predator in Keoladeo National Park are possible reasons for them to cover long distances away from their permanent burrowing site for foraging and hence they occupy entire landscape.

Of the five covariates chosen to assess the burrow site-selection by porcupine, combination of percent water-cover, distance from the boundary and mean elevation had the highest model weight (w_i = 0.78), indicating an increase in the probability of permanent-occupancy with simultaneous decrease in area with water-cover, decrease in distance from the boundary and increase in mean elevation of the area. The park has a depression at the center forming a wetland and experiences post-monsoon flooding in low-lying areas due to release of water from nearby reservoirs. However, low lying water-logged areas are not suitable sites for burrowing, as seasonal flooding causes inundation which might result in permanent damage to the burrow systems. It was observed that even though the water cover reduced considerably during dry season, porcupines did not attempt to dig burrows for permanent settling in those regions. Another covariate: 'distance from the park boundary' had the second highest model weight (w_i = 0.07) which indicate the probability of permanent-occupancy increases with closer proximity of the park's boundary surrounded by the agricultural fields. This affirms previous findings highlighting Indian crested porcupine's affinity to the agricultural fields (Agrawal and Chakraborty, 1992; Mendelssohn and Yom-Tov, 1999). However, these findings were in contrast to a study in Drakensberg Midlands, South Africa (Ramesh and Downs, 2015), where the area available under cropland negatively influenced the occupancy and the extent of wetland area positively influenced it. Along with percent water-cover and distance from the boundary, mean elevation also influenced the probability of permanent-occupancy that increased with increase in mean elevation of an area. The park lies at an average elevation of 174m above sea level (asl) and digital elevation mapping of the area revealed the range of elevation between 148.2m–204.0m asl. Though there isn't much undulation in the area, even a minor elevation seemed to have influenced the placement of burrows by porcupine. All the 41 burrow systems were dug above an elevation of 170m which is also the maximum water level mark when the wetland is completely inundated to a depth of approximately 1.5m–2.0m. Burrow site-selection and location of the burrow systems on higher elevation thus protected them from permanent damage from surface run-off and inundation during monsoonal rains and post monsoon flooding. Another covariate: soil-type with lower summed model weight ($w_i = 0.00$; $\beta_1 = 0.08 \pm 0.17_{SE}$) did not come across as a good support for explaining the burrow site-selection and their occurrence, possibly because, there isn't much discrepancy between the use and availability of the most preferred soil types (clayey and silty) by the porcupine from the region. These soil types are the most widespread soil types found in the park and are also preferred by other burrowing rodents (Carter et al., 1985; Laundré and Reynolds, 1993; Sulentich, 1991; Reading and Matchett, 1997).

These results strongly support three of the five *a priori* hypotheses namely, 'percent water-cover' negatively influencing the permanent-occupancy and likelihood of "occurrence" of the burrows, farther 'distance from the boundary' surrounded by the agricultural fields negatively influencing the burrow site-selection and the 'elevation' positively influencing burrows' occurrence; whereas none of the covariates (vegetation, soil-type and distance from the point of maximum level of water-stand) were found to be significantly influencing the spatial-occupancy of porcupine. These results show that patterns of spatial-occupancy for a species at macro level not necessarily determine permanent-occupancy at micro level *i.e.* patterns observed at one scale are not necessarily good predictors of patterns obtained at other scales (McLoughlin et al., 2002; 2004) and conflicting demands at different scales lead to varied selection criteria (Fortin et al., 2003). Here, the Indian crested porcupines have been used as a study model to see how burrow site-selection by them have acted as a surrogate in determining their permanent-occupancy which otherwise is a generalist species with broader spatial-occupancy. This study highlights the factors determining the burrow site-selection by Indian crested porcupines for permanent-occupancy. The strategic locations of these earthen burrows are very significant since they also provide crucial ecological niche for various other co-occupants. Hence, it is critically important to conserve the natural habitats especially that of porcupines which is a primary excavator and a significant ecosystem engineer in extreme semi-arid conditions of Keoladeo National Park.

CHAPTER 4

Burrow Characteristics and Species Assemblage

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4.1. Introduction

Burrows in terrestrial habitats are one of the oldest forms of engineered shelters (Voorhies, 1974) reported as early as the Carboniferous Period (Olsen and Bolles, 1975). Three major categories of burrowing vertebrates have been identified by Kinlaw (1999) and have been broadly classified into: ‘primary excavators’ for whom digging burrows is an inevitable part of their life-cycle; ‘secondary modifiers’ that occupy and further transform the burrows of primary excavators and, the third category of ‘simple dwellers’ that take advantage of the existence of burrows and occupy them. In arid and semi-arid regions, rodents form the major group of burrowing mammals with elaborate multi-tier burrow systems (Prakash, 1997), which facilitates them to unload excessive heat due to high mean temperature during summer. Burrow inhabitants are even reported to be either in obligate and/or non-obligate commensal associations (Kiviat, 1978; Kinlaw, 1999). Several studies report vertebrate associates in the burrows of *Orycteropus afer* aardvark (20 vertebrate, Smithers, 1971), *Pedetes capensis* spring hare (7 vertebrates, Smithers, 1971), *Cynomys spp.* prairie dog (64 vertebrates, Campbell and Clark, 1981), *Gopherus agassizii* desert tortoise (23 vertebrates, Luckenbach, 1982), *Gopherus polyphemus* gopher tortoise (60 vertebrates, Jackson and Milstrey, 1989), *Dipodomys spp*. kangaroo rat (14 species of reptiles, Hawkins and Nicoletto, 1992)and *Meles meles* European badger (Eight mammal species, Mori et al., 2014b). In India, the burrow structure of Indian gerbil *Tatera indica* and Indian desert gerbil *Meriones hurrianae* have been excavated and seasonally examined in Thar Desert, wherein the burrow systems of *Tatera indica* was of simple ‘Y’ shaped type with one or two surface openings and with maximum depth of 35cm in winters to 45-50cm in summers whereas, burrow systems of *Meriones hurrianae* were complicated and extensive with numerous opening and with no significant seasonal change in burrow depth (Goyal and Ghosh, 1993). The burrows structure through excavation and the home range of Indian desert gerbil *Meriones hurrianae* has also been studied in Jaisalmer, Bikaner and Palsana districts of Rajasthan (Fitzwater and Prakash, 2009). In KNP, several species of vertebrates have been recorded inhabiting porcupine *Hystrix indica* burrows (Bhupathy, 1986, 1987). However, information pertaining to the architecture of burrows and burrow characteristics determining the occupancy of these burrowing vertebrates are unknown. The present chapter is an attempt to understand the external and internal burrow features and to identify the factors determining the animal assemblage and their co-occupancy in KNP. The objective involved non-invasive methods of camera trapping and the use of a burrow video camera to understand the burrow architecture and assemblage of animals dwelling inside.

4.2. Methods

4.2.1. Field Methods

Field surveys were conducted from September 2013 to February 2016. Upon locating the burrows, external burrow characteristics were recorded including number of openings in a burrow system, inter-opening distance, size of openings (in meters), orientation of openings (in cardinal degrees). For recording the internal burrow characteristics, nine burrow systems were randomly selected. A customised burrow video camera (BVC) was used attached with metered cable to determine the internal length and other burrow characteristics. To determine the internal dimensions of tunnels and chambers (Fig. 4.1), photographs were digitised with a reference scale (here the BVC was the measuring unit); at least five observations were taken for each chamber and tunnels for higher accuracy.

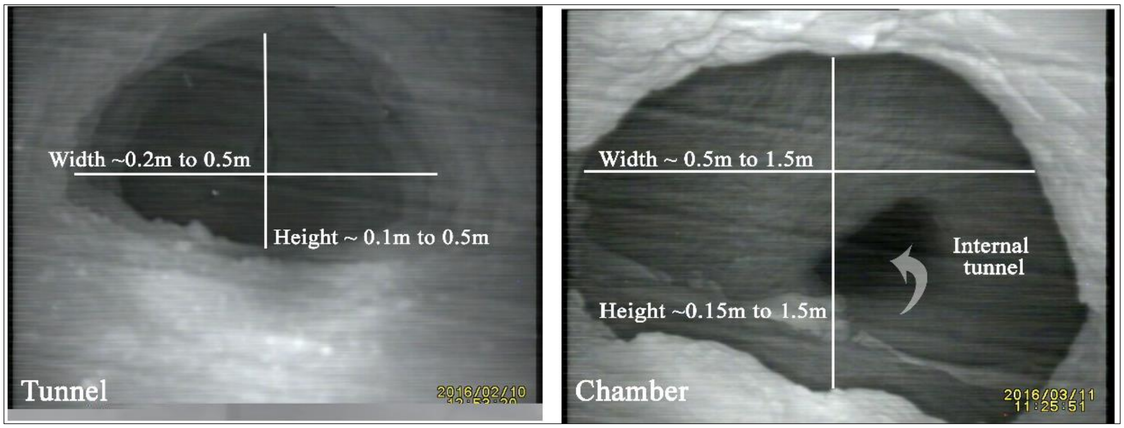

Figure 4.1. Dimensions (range in meters) of tunnels and chambers inside burrow system

As the BVC was manoeuvred inside, the internal structure of the burrow was graphically drawn along with recording internal dimensions including number of branches, number of chambers and internal surface types. The internal surface types (Fig. 4.2) were broadly characterised into three types, namely (a) flat undulating surface with rigid soil, (b) flat surface with loose soil and (c) irregular surface with loose soil and gravel. The total above-ground area covered by the burrow system was measured from the graphs using the minimum convex-polygon method (Southwood, 1978). The internal length and total above ground area of the burrow systems were recorded to measure the complexity and configuration of the burrow system. To record the presence of burrowing vertebrates, camera traps (Boskon Guard Scouting IR Camera, BG-520 series) were continuously deployed in front of the burrows and a burrow video camera were used once in five days.

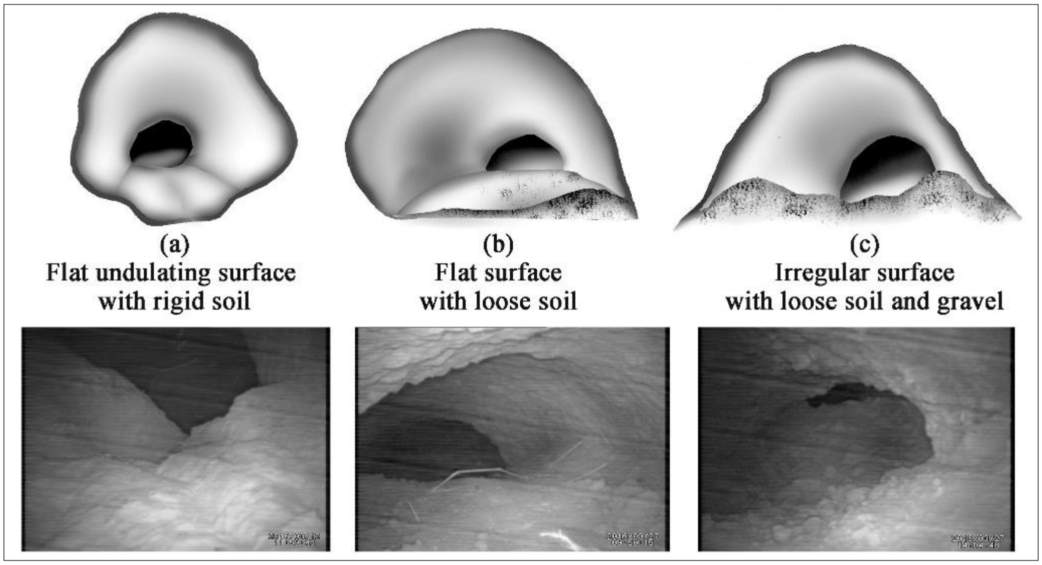

Figure 4.2. Schematic representation and photographic capture of internal surface types of burrow systems

4.2.2. Data analysis

To test the uniformity of compass orientation of the burrow openings, Rayleigh Z statistics (Zar, 1999) was computed in Oriana software ver. 4.01 (Kovach, 2009). The mean vector length 'r' represents the measure of dispersion of points around the mean angle 'μ' (Batschelet, 1965) and its length ($0 < r < 1$) varies according to the concentration of data around the mean angle, where $r = 1$ indicates minimum dispersion and $r = 0$ means maximum dispersion (Batschelet, 1965; Maia-Carneiro and Rocha, 2013). The 'degree of convolution' or complexity of each burrow system was quantified by dividing the total length of tunnels in the burrow system by its total above-ground area; a less convoluted system would have a smaller value for this index. In addition, the 'index of linearity' (Reichman et al., 1982) for a burrow system was computed as the ratio of the perimeter of the minimum convex polygon constructed around each burrow system to the circumference of a circle having the same area as the system. An index near 1.0 represented a circular system and indices more than 1.0 represented progressively more linear systems. After determining the external and internal burrow characteristics and indices, the relationship between burrow variables and occupancy of the burrowing vertebrates was analysed using Pearson's r two-tailed correlation test in SPSS ver. 16, to determine the burrow features influencing animal assemblage.

4.3. Results

4.3.1. External burrow features

A total of 44 burrow systems were recorded in KNP during the sampling. Of these, 40 burrow systems were included in analyses as four of them were found inundated during the study. The longest inter-burrow distance between two systems was 9.2 km, and the shortest was 0.02km (20m). A mean of 2.36 ± 1.4_{SD} openings per burrow system was recorded, which ranged from 1 to 8. Among them, 88 (84.61%) were found on elevated places (mounds) and the remaining 16 (15.39%) were present on flat terrain. Of the 40 burrow systems, 16 (36.36%) had a single opening and 24 (63.64%) burrows had multiple openings (13, 9, and 2 had two, three and more than three openings, respectively). The mean distance between two openings was 5.09 ± 3.00 $_{SD}$ m (range = 0.3- 14.0 m, n = 129). The openings were majorly within 6m from each other with a combined frequency of 68.99 % (n = 89), and 4.65 % (n = 6) of the openings were found over 10m from each other (Fig. 4.3).

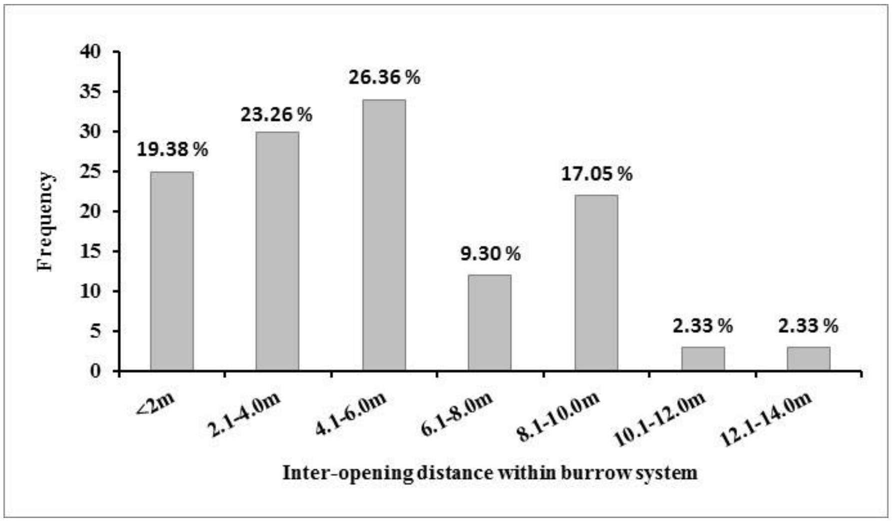

Figure 4.3. Distance between nearest openings in burrow systems in KNP

Mean radius and area of 64 burrow openings measured 17.40cm (range = 9.19 - 33.46 cm) and 952 cm^2 (range 266 cm^2- 3520 cm^2), respectively. The majority of burrow openings (n =38, 56%) had an area of 501-1000cm^2. Barring seven vertical or plunge holes, compass orientation of 97 openings were included in the analysis. These openings had a mean vector (μ) of 122° ± 111° (mean ± one circular standard deviation) with a mean vector length (r) of 0.15. The

Rayleigh Z-test showed that the orientations of burrow openings were randomly distributed, and did not show any trend in orientation ($Z = 0.722$; $p > 0.001$; Fig. 4.4).

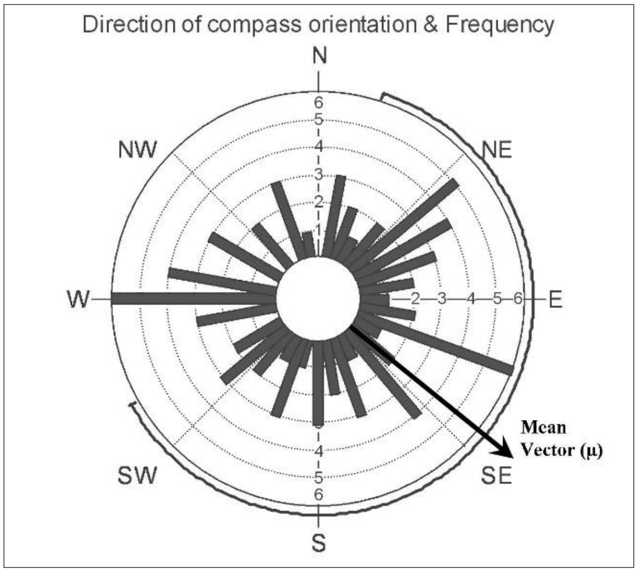

Figure 4.4. Frequency histogram showing circular distribution of opening orientation of 97 burrow openings

4.3.2. Internal burrow features

A total of nine burrows has been represented in the study to understand the internal burrow structure. Of nine burrow systems, four had the flat surface type with loose soil, three had an irregular surface with loose soil and gravel, and one had a flat undulating surface with rigid soil. The internal architecture of the burrow systems was characterised by tunnels interspersed with chambers at intervals. The mean internal width and height of tunnels was $0.40 \pm 0.09_{SD}$ (Range = 0.2 - 0.5m) and $0.30 \pm 0.09_{SD}$ (range = 0.1 - 0.5m) respectively. The chambers were comparatively larger with a mean internal width and height of $0.93 \pm 0.33_{SD}$ (Range = 0.5 – 1.5m) and $0.52 \pm 0.33_{SD}$ (Range = 0.15 to 1.5m), respectively.

The burrow systems had a looping structure (Fig 4.5). Burrow systems 2, 3, 5, and 6 were single-opening systems that continued for 6.5 to 8m in one stretch (Table 4.1). In contrast, burrow systems 1, 4, 7, 8, and 9 had multiple openings and sub-surface connections that continued for 5 to 16m in one stretch (Fig. 4.5, Table 4.1). For all systems combined, total length including all branches and above ground area of burrow system averaged $13.33 \pm 6.51_{SD}$ m and $18.81 \pm 9.92_{SD}$ m^2 respectively. The degree of convolution, which indicates the complexity of the structure, elucidated burrow 6 (B6) and 9 (B9) to be more complex, among single opening systems and multiple opening systems respectively (Table 4.1). The Reichman's Index of linearity indicated that all nine burrow systems showed circular configuration as none of the values were significantly higher than 1.0 (Table 4.1). Among all the burrow systems B4 was more circular followed by B1, B5, B9, B7, B3, B6, B2, and B8 .

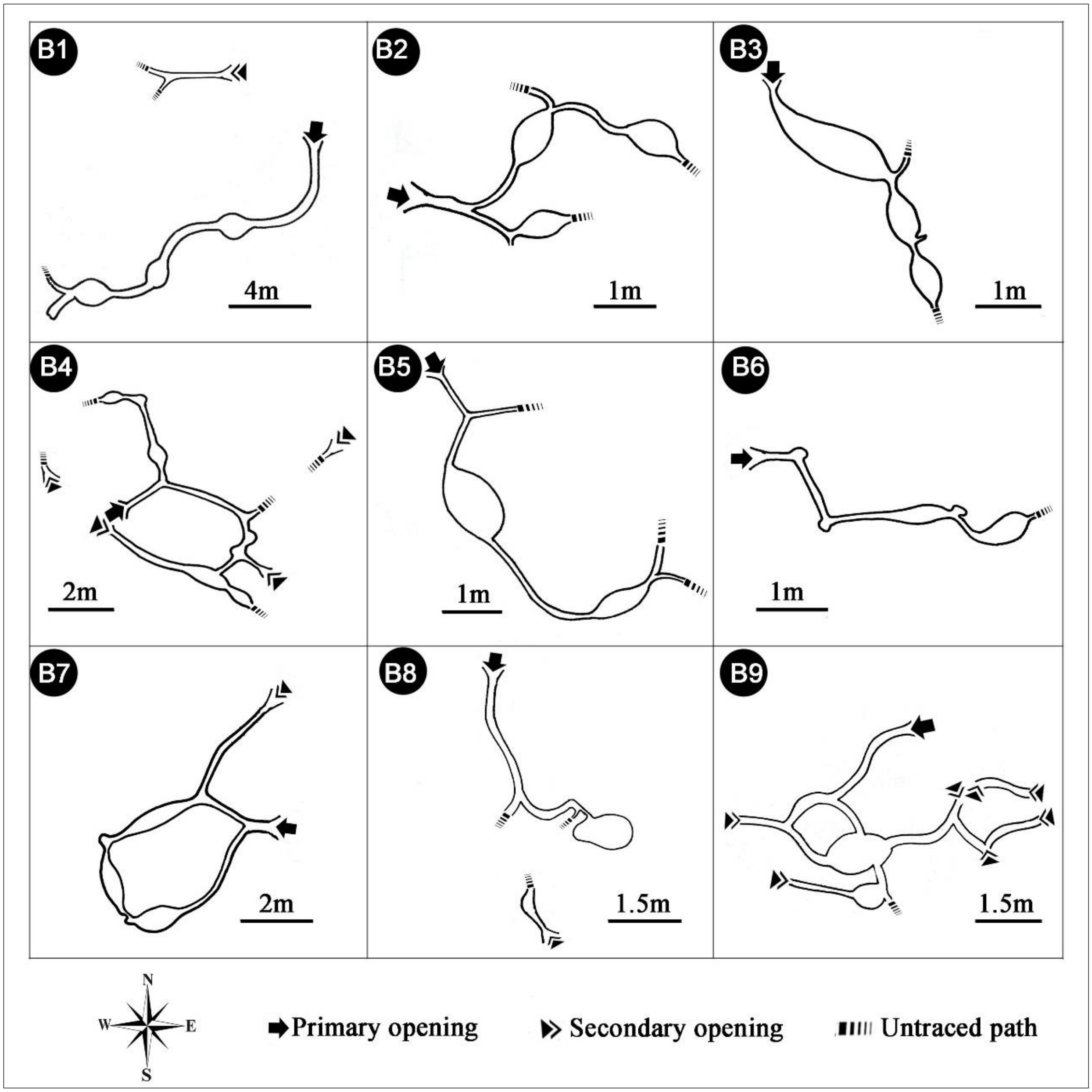

Figure 4.5. Schematic representation of burrow systems (n=9) from KNP

Table 4.1. Burrow system characteristics (n=9) of burrowing vertebrates from KNP

Burrow System type	**Single opening**				**Multiple opening**				
Burrow Id	**B6**	**B3**	**B5**	**B2**	**B9**	**B7**	**B8**	**B4**	**B1**
Total length (m)	6.50	6.50	8.50	11.00	22.0	19.00	7.50	19.50	19.50
Maximum length traced* (m)	6.50	6.50	8.00	8.00	5.50	11.00	5.00	7.00	16.00
Above ground area (m^2)	5.76	7.40	13.58	21.00	25.17	20.45	12.68	26.85	36.41
Number of openings	1.00	1.00	1.00	1.00	8.00	2.00	2.00	5.00	2.00
Number of branches	0.00	2.00	2.00	3.00	7.00	1.00	2.00	6.00	1.00
Number of chambers	2.00	3.00	2.00	3.00	2.00	3.00	1.00	4.00	3.00
Mean distance between chambers (Internally)	0.50	1.00	2.00	2.80	1.00	2.20	-	7.10	7.30
Mean tunnel width (m)	0.48	0.42	0.36	0.30	0.40	0.26	0.46	0.48	0.46
Mean tunnel height (m)	0.34	0.24	0.24	0.16	0.24	0.44	0.36	0.36	0.34
Mean chamber width (m)	0.80	0.90	0.75	0.87	1.15	0.53	1.50	1.40	0.73
Mean chamber height (m)	0.45	0.4	0.25	0.18	0.45	0.70	0.80	1.00	0.30
Degree of Convolution	1.13	0.88	0.63	0.52	1.19	0.93	0.79	0.73	0.44
Reichmann Index of Linearity	0.76	0.77	0.87	0.74	0.79	0.79	0.69	1.04	0.94

* This represents maximum length traced in one stretch irrespective of branching and turnings

4.3.3. Occupancy of burrowing vertebrates

All the nine burrows surveyed for understanding the internal structure were occupied by six burrowing vertebrate species including three mammal species, *Hystrix indica* Indian crested porcupine, *Canis aureus* golden jackal and *Hipposideros fulvus* leaf-nosed bat; and three reptile species, *Python molurus* Indian rock python, *Varanus bengalensis* Common Indian monitor, and an unidentified species of gecko (Fig. 4.6). The occupancy (Table 4.2) of Indian crested porcupine and gecko did not show any significant correlation with any of the internal burrow variables. In contrast, among mammals, occupancy of jackal showed a significant positive correlation ($r = 0.72$, $P < 0.05$) with mean chamber height; and bats showed a significant negative correlation with number of branches ($r = -0.69$, $P < 0.05$) and number of openings ($r = -0.85$, $P < 0.01$). Similarly among reptiles, occupancy of Indian rock python showed a strong negative correlation with mean chamber height ($r = -0.82$, $P < 0.01$) and mean chamber width ($r = -0.86$, $P < 0.01$).

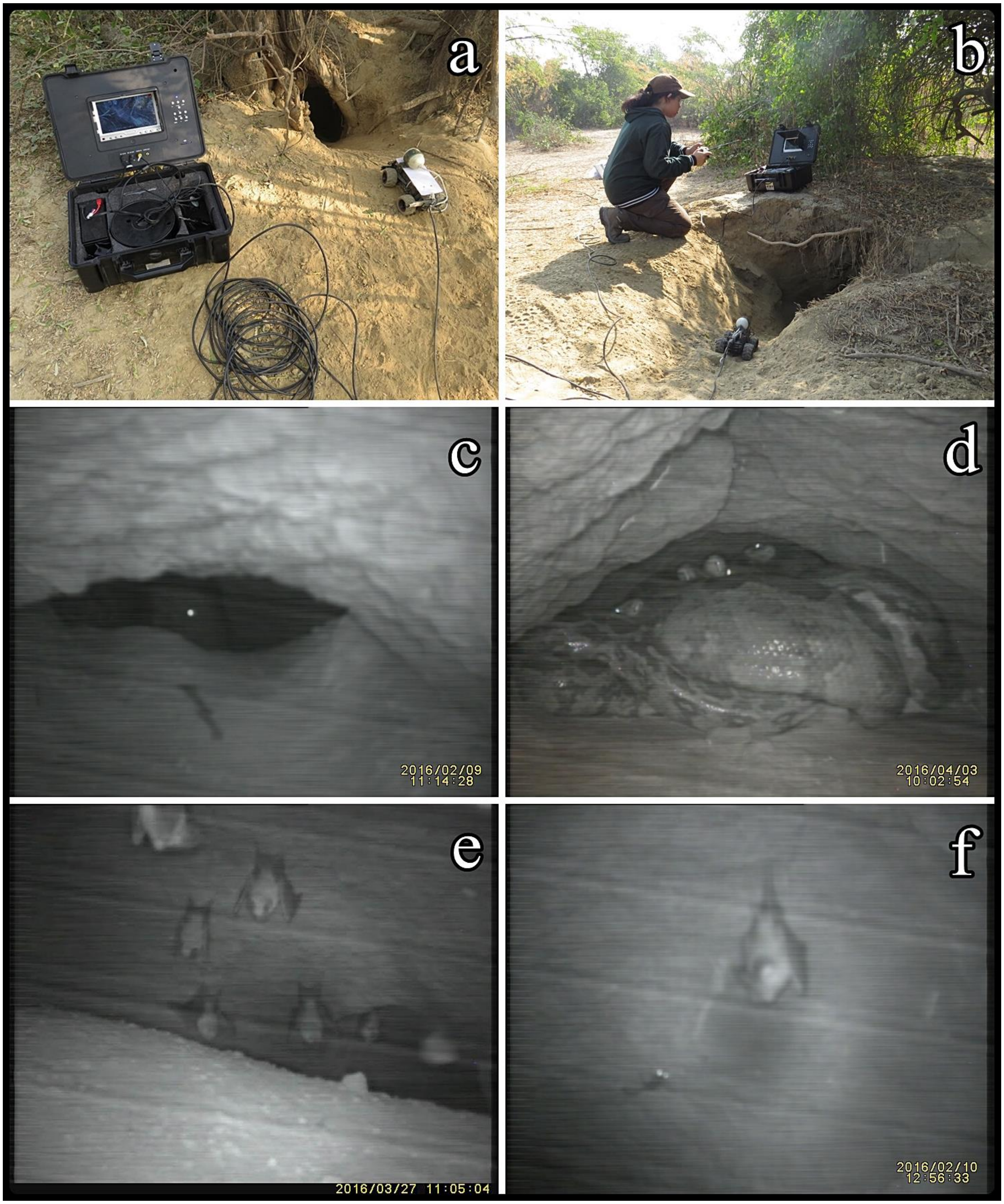

Figure 4.6. (a) Burrow video camera (BVC) unit; (b) BVC in operation; Photographic capture of burrowing vertebrate species by BVC: (c) *Hystrix indica* (Indian crested porcupine) inside its chamber with narrow opening; (d) *Python molurus* (Indian rock python), five individuals inter-coiled inside its curved chamber; (e and f) *Hipposideros spp.* (leaf-nosed bat) and a gecko occupying the ceiling of chamber and tunnel walls.

Table 4.2. Pearson's Correlation between burrow characteristics and occupancy of burrowing vertebrates in KNP

Burrow Characteristics	**Porcupine**		**Jackal**		**Python**		**Bat**	
	r	**P**	**r**	**P**	**r**	**P**	**r**	**P**
Total length (m)	-0.62	0.07	0.51	0.16	-0.01	0.97	-0.50	0.17
Above ground area (m^2)	-0.23	0.55	0.28	0.47	-0.05	0.89	-0.24	0.53
Number of branches	-0.32	0.40	0.20	0.60	-0.32	0.40	-0.69*	0.04
Number of openings	-0.58	0.10	0.22	0.56	-0.22	0.56	-0.85**	0.00
Number of chambers	0.04	0.93	0.61	0.08	0.04	0.93	0.24	0.54
Mean tunnel height (m)	-0.25	0.52	0.64	0.06	-0.38	0.32	0.27	0.48
Mean tunnel width (m)	0.51	0.16	-0.23	0.56	-0.48	0.19	0.01	0.98
Mean chamber height (m)	-0.15	0.70	0.72*	0.03	-0.82**	0.01	0.07	0.85
Mean chamber width (m)	0.21	0.59	0.01	0.98	-0.86**	0.00	-0.22	0.57
Mean chamber length (m)	-0.64	0.06	0.33	0.38	0.42	0.25	-0.15	0.71
Degree of Convolution	-0.57	0.11	0.06	0.89	0.10	0.80	-0.56	0.11
Index of Linearity	0.16	0.68	0.48	0.19	-0.23	0.56	0.11	0.79

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

Of nine, eight burrow systems were inhabited by three or more species at a time, which included presence of both prey and predators in a single burrow system, occupying different compartments (Table 4.3). Co-occupancy of porcupine (prey) and python (predator) showed a significant negative correlation with the number of openings ($r = -0.69$, $P < 0.05$) and mean chamber height ($r = -0.81$, $P < 0.01$). Similarly, co-occupancy of bat (prey) and python (predator) showed a significant negative correlation with number of branches ($r= -0.75$, $P < 0.05$), number of openings ($r = -0.76$, $P < 0.05$), mean chamber height ($r = -0.68$, $P < 0.05$) and mean chamber width ($r = -0.90$, $P < 0.01$). In contrast jackals have not been seeing co-occupying a burrow. The chambers (Fig. 4.6) of Indian crested porcupine were deeper inside and of distinctive character, wherein the entrance of the chambers was closed by loose dug out soil, leaving a narrow slit of ~ 0.05m. The pythons were seen coiled within concave caved-in chambers usually at the end of the tunnel branching not more than 5m inside. The active porcupine chambers and tunnels predominantly had loose and dug out soil, in contrast to active python chambers, which had a flat surface due to its serpentine movement. The leaf nosed bats and geckos gregariously occupied the ceilings and walls respectively. The bats were particularly seen roosting in groups in separate chambers other than porcupines and pythons.

Table 4.3. Co-occupying burrowing vertebrate species in nine burrow systems of KNP

Species	**Burrow Id.**									**Total number of burrows**
	B1	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	
Hystrix indica	+	+	+	+	+	+	-	+	-	7
Hipposideros fulvus	+	+	+	+	+	+	+	+	-	8
Canis aureus	-	+*	+*	-	-	-	-	-	-	2
Python molurus	+	+	+	-	+	+	+	-	+	7
Gecko (Unidentified)	+	+	+	+	+	+	+	+	+	9
Varanus bengalensis	-	-	+	-	-	-	-		-	1
Total number of co-occupying species	4	4	5	3	4	4	3	3	2	

* Jackals have eliminated others

4.4. Discussion

This study put forth the fundamentals of burrow architecture of burrowing vertebrates, to understand the occurrence and co-occupancy of several burrowing species in a semi-arid region of India. The present study has recorded 40 active burrow systems in the area with a mean number of openings and an inter-opening distance of 2.36 and 5.09 m respectively; with all the openings being randomly oriented. Internally, these systems were extending to a maximum length of 16.0 m (n=9) in one stretch, having looping structure interspersed with chambers twice the size of tunnels and with an overall circular configuration. The findings also suggested that porcupine, jackal, python and different bat species are the major co-occupants in these burrows. In the study area, *Hyaena hyaena* striped hyena was also observed as one of the burrow users during their breeding season. However, they are very rare and were not seen occupying the burrows that were sampled. All the animals, except porcupine, were observed to occupy burrows based on specific burrow characters, wherein jackal occupied burrows with larger chambers, python occurred in smaller compact chambers, and bats occupied burrows with less number of branching and openings. Findings of the present study indicate that Indian crested porcupine to be a major ecosystem engineer and a primary excavator constructing ecologically significant burrows in the study area.

External burrow characteristics recorded in the study are comparable to the burrows of Indian porcupine in similar habitat elsewhere. The burrow systems are usually known to have multiple openings (Greaves and Khan, 1978; Mendelssohn and Yom-Tov, 1999) and the mean number of openings recorded in the present study is 2.36 per burrow system; comparable to a mean of 1.3 to 6.0 in central Punjab, Pakistan (Kayani et al., 1990). Reasons for multiple openings in a burrow system could be natural, could be due to blockage of openings by larger animals inhabiting the burrow, to facilitate the escape from predators entering the burrows, or due to anthropogenic disturbances. Blocking of certain openings with boulders and directing water into burrows through channels made by a porcupine, hunters could be other reasons for digging hidden openings, which usually acts as emergency exits. Longest inter-opening distance within a burrow system recorded in this study was 15.2 m, which is analogous to that reported by Rabinovich and Horwitz (1994) and Greaves and Khan (1978), i.e. 8 m and 20 m, respectively. The burrows found in the present study have a mean width of 34.80 cm (n=64), similar to the burrows of Indian porcupines in central Punjab, Pakistan (51.9-56.1 cm; Kayani et al., 1990), northern Israel (30-40 cm; Mendelssohn and Yom-Tov, 1999), and in Bikaner district of Rajasthan, India (20-45 cm; Bhargava et al., 2001). The variation in opening size could be due to the varying size of animals of different age classes inhabiting these burrows, or could be due to the constant modification of the systems by Indian crested porcupine along with other reported cohabitants. In the present study, the burrow openings were randomly oriented and were not opening at any particular cardinal direction. The burrow architecture might be related to opening at any particular cardinal directions, e.g. animals might orient their burrow openings in certain directions to escape weather extremes like heavy torrential rain and high surface-wind velocity (Bihr and Smith, 1998; Torres et al., 2003). Preference for opening orientation has been studied on burrows of many taxa particularly in temperate regions where burrows open in a direction to maximize heat capture, e.g. burrows of gopher tortoise *Gopherus polyphemus* majorly faced southerly and westerly and was related to the amount of canopy cover at the site (McCoy et al., 1993). The portal orientation of red viscacha rat *Tympanoctomys barrerae* was such that burrows received direct sunlight in winter and indirect sunlight in summer (Torres et al., 2003). The burrows of giant armadillo *Priodontes maximus* had a westerly orientation that maximized the amount of heat reaching the entrance (Ceresolia and Duque, 2012). However, crested porcupine *Hystrix cristata* showed clear avoidance of a northern orientation, particularly to avoid muddy ground in winters in the Mediterranean coastal area, Italy (Monetti et al., 2005). It appears that porcupine in KNP with tropical climatic condition rely more on elevated areas and the dense vegetation cover around the burrow systems to escape variable weather conditions, rather than solely depending on the direction of orientation.

The present study employed non-invasive techniques of a burrow video camera to understand fundamentals of porcupine burrow architecture, including the configuration and degree of complexity of the burrow systems which were also simultaneously used by other occupants. The maximum total length of tunnels in a porcupine burrow system in our study was 22.0 m, which is slightly higher than 20 m reported from Punjab province of Pakistan (Greaves and Khan, 1978). All the nine burrows examined have looping structure with an overall circular configuration. As reported for other burrowing taxa (Cameron et al., 1988), burrow architecture may reflect adaptation to resource availability and population density or social structure. Hypothetically, clumped resource availability (Cameron et al., 1988; Williams, 1985) and to make efficient use of space and perimeter (Cameron et al., 1988), burrows have a looping structure which could also possibly be the reason in our study area. Also, Hickman (1977) suggested that burrow systems are looped with high population densities so as to avoid stressful interactions. Reichman et al. (1982) also suggested that burrow systems would become linear and highly branched with an increase in population density due to intraspecific avoidance. Contrastingly, in our study area, even though burrow systems were looping, they were also circular with mutual tolerance and co-occupancy of species.

As previously described, burrowing animals fall into three major categories (Kinlaw, 1999) and hypothetically in our study area, porcupines are the ‘primary excavator’, jackal and python are ‘secondary modifiers’ and bats are ‘simple dwellers’. Individually, different taxa occupied burrows with specific characteristics. In the case of porcupines, none of the burrow characters specifically influenced its presence, as all the burrow systems studied were virtually dug out by them. The occurrence of jackal on the other hand seemed to have been influenced by burrow systems with larger chambers. Jackal are not a permanent burrowing animal and majorly use burrows during the breeding season to rear young and to avoid any possible predation (Jhala and Moehlman, 2013) and therefore, requires burrows with larger chambers. Contrastingly, occupancy of python was significantly correlated to burrow systems with smaller chamber size. In the study area, the python is mostly seen congregating in large numbers during the winter season (November to March), which coincides with their breeding season. They bask outside the burrow systems in groups of 5 to 15 individual and seem to be thermoregulating their body temperature by intercoiling. In the present study, they have been observed inter-coiled inside their chamber in groups of 5 to 6 individuals and possibly because of this they prefer more compact chambers. Bats in the study area are cave or burrow dwelling micro-chiropterans that have mostly occupied burrows with less number of branches and openings. This possibly reduces disturbance and influx of external light inside the burrow system making the internal micro- habitat more comfortable for these nocturnal species. The study also reports the co-existence of prey and predator in single burrow system. It seems that python, porcupine and bat are mutually tolerant towards each other, which has also been observed previously from the same region (Bhupathy, 1986, 1987) and appears to be in a non-obligatory commensal association (Kinlaw, 1999). Inside burrows, there is however, a clear segregation of these individuals in separate chambers. Porcupine has been observed to block the chamber opening with dug out soil, similar to the descriptions of predator avoidance by Reichman and Smith (1990) where burrow inhabitants wall off segments of their burrow to avoid predators. However, in Italy (temperate areas and deciduous woodlands), crested porcupines *Hystrix cristata* may share their dens with predators such as red foxes *Vulpes vulpes* and European badgers, but, during the breeding period, they remain alone (Mori et al., 2013, 2014b).

In arid and semi-arid conditions, due to scanty rainfall and high fluctuations in temperature, it appears that earthen burrows act as important refugia for many species. The burrow systems have emerged to be ecologically very significant for several burrowing vertebrates for whom the burrows are crucial at least in certain stage of their life cycle, especially in extreme ambient conditions of any semi-arid region. Burrowing animals have been looked at as problem species for dams, reservoirs, and archaeological sites as their burrows weaken the embankments and other structures, reducing structural longevity (Bayoumi and Meguid, 2011; Blackham, 2000; Witmer et al., 2006). However, the ecological role of burrowing animals in terms of providing habitats for other animals and interaction among them are poorly studied and underappreciated. As pressures on natural ecosystems are on the rise, it is crucial to conserve the natural habitats of these burrowing vertebrates especially that of porcupines in wild environment as several animals appear to be dependent on this primary excavator, a significant ecosystem engineer.

CHAPTER 5

Burrow use pattern by Indian Crested Porcupine

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5.1. Introduction

Among the burrowing mammals, rodents are largely sedentary, possessing a home range for foraging, burrowing or constructing shelters to reproduce and avoid interactions with predators or other conspecifics (Gromov, 2017). The Indian crested porcupine (ICP) *Hystrix indica*, Kerr, 1792 from Hystricidae family, has permanent burrows within their territory along with several others which may be used in times of danger (Chakravarthy and Girish, 2007; Horwitz et al., 2012). The importance of burrows for new-born Cape porcupine *Hystrix africaeaustralis*, Peters 1852 for survival (decrease in vulnerability to predators), energy conservation and thermoregulation was reported (Haim et al. 1992). Burrow use by ICP has been observed during breeding, wherein the young ones are reared till the age of three months and then weaned (Horwitz et al. 2012). Despite its wide distribution, the information on temporal activity patterns of the ICP is available only from the sub-deserted area in Israel (Alkon and Saltz, 1985, 1986, 1988a 1988b; Server and Mendelssohn, 1989), Italy (Mori et al., 2016) and subtropical forest/grassland habitat in Nepal (Fattorini and Pokheral, 2012). In KNP, the burrows of ICP are located closer to the KNP boundary adjoining agricultural fields at a high elevation and away from the water bound areas (Chapter 3). In this semi-arid biogeographic region of India, the porcupines are apex ecosystem engineers, providing crucial ecological niche "burrows systems" for various other co-occupants including golden jackal *Canis aureus*, Linnaeus, 1758, Indian rock python *molurus*, Linnaeus, 1758 and bats *Hipposideros spp.*, Gray, 1838. (Bhupathy and Haque 1986, Bhupathy 1987). Understanding the activity patterns, time allocation for each activity and variations in activities with environmental alterations are necessary for understanding of the biology of any species (Pianka, 1988). Hence, in the current chapter, the relationship of micro-habitat and environmental conditions with seasonal and temporal activities of ICP around the burrows was investigated.

5.2. Methods

5.2.1. Field methods

The study was conducted from October 2013 to September 2016. A set of 37 burrows were selected for monitoring the population of ICP of the 47 burrow systems recorded in KNP. The sampling was done in quick succession in all the burrows in a short span of 10-15 days once in each season (winter, summer, and monsoon) in the year 2014-15. To study the activity pattern, 20 active burrows were selected, and they were sampled intensively during the first 24 months.

Each selected burrow was monitored for five consecutive days in a month. To understand the factors influencing the emergence, retreat and specific activity pattern, ten permanently occupied burrows were selected, and they were monitored from November 2015 to December 2016 (excluding June – July 2016).

The sampling was carried out using high sensitive passive infrared (PIR) motion sensor camera-traps (Boskon Guard Scouting, BG-520 series). The cameras were deployed at a minimum distance of 1.5 to 2.5 m at a height of 1.5 m. The camera-trap trigger gap was set to 10 seconds in case animals were continuously present in the camera view. With each trigger, a set of three pictures was captured, with date and time registered on each image. The photographs from the camera traps were downloaded on every fifth day and saved with the identity of burrow and month. After deployment of the camera traps, utmost care was taken to minimize the disturbance while changing the batteries every third day. The photographs were managed by filtering the undesired photographs with false trigger. The time of the initial trigger was considered, in cases when porcupines repeatedly triggered cameras without leaving the field of view. Only the photographs depicting the activities of ICP around the burrows including burrow-modification, exploring surrounding, feeding, guarding, marking, playing and resting were screened and used. The description of all these activities is provided in Table 5.1. The efforts varied between the months due to weather and malfunctioning of some of the camera traps. In a month, the trapping effort varied from 15 days (3 burrows for 5 days) to 300 (20 burrows for 5 days with repetition) with a total of 3254 days of camera-trap effort.

The data on sunrise, sunset, and lunar-phase were obtained from the official website of Indian Meteorological Department, Govt. of India (http://www.imd.gov.in). Temperature and Relative Humidity data (at 10-min interval x 24-h x 365 days) were recorded using Onset® Hobo^{TM} automatic data loggers. Four data loggers were deployed to spatially cover the entire KNP, and the data from the nearest logger was extracted for each burrow system. The data were recorded six times in an hour at the interval of 10-minutes. The hourly-mean of the logged data was then used for further analysis.

Table 5.1. Ethogram of the behaviors by Indian crested porcupine recorded around the burrows in KNP

Activities	Description
Burrow modification	To break up and dig in front of burrow opening with the long claws, remove dug up loose soil around the burrows
Marking	To urinate after investigating the burrow; squatting and evacuation of urine
Emergence	Coming out from the burrow
Retreat	Entering the burrow
Exploring surroundings	To meander around the burrows; sniffing (olfactory investigation); whisking (tactile investigation)
Feeding	Gnawing leaves, grasses etc.
Guarding	Staying close to the burrow opening and monitor when litters are either inside or outside
Playing	Litters leaping on each other; interacting with an inanimate object (bones, twigs)
Resting	Sitting and lying down in a relaxed manner; Lying on the belly with hands extended; hind legs bent and resting close to the body on each respective side

5.2.2. Data Analysis

To understand the population structure of the ICP in KNP, the percentage of burrows occupied in each season was calculated based on the number of burrows occupied per sampled burrows. This was further used to determine the expected number of burrows occupied of the 47 burrows recorded from KNP. The mean group size, and mean number of adults, juvenile and litters were calculated for each season. The population size was then computed as a product of mean group size and the expected number of burrows occupied in each season. Further, a minimum population size of ICP was determined for the terrestrial area of 20.5 km^2 from the calculated population size in each season.

The frequency data of each activity by ICP was pooled across 12 months and standardized as per sampled burrow per camera-trap days in each month as the efforts varied across the months. For determining the specific circadian activity patterns by the ICP and the litters outside the burrows, data across the months was analyzed using Rayleigh Z statistics (Batschelet, 1965; Zar, 1999) in Oriana software ver. 4.01 (Kovach, 2009). We calculated the mean number of detections per day using SPSS v.16.0 (SPSS Inc., 2007) and compared it across all the months using G-test of independence (McDonald, 2009). For analyzing the daily emergence and retreat (mean ± standard deviation) pattern of ICP, the frequency of each event was summed into bi-hourly intervals across all the months and the trend was compared across three seasons using Friedman test.

To determine the relationship between sunrise and sunset on retreat and emergence timings respectively, mean daily difference for each event was computed and then compared across seasons using ANOVA. To ascertain the relationship of temperature and relative humidity with each of the activities, Pearson's correlation test was performed in SPSS. To determine the relationship between the intensity of moonlight and ICP activity (if any), the emergence and retreat events were analyzed across eight lunar phases in Oriana software.

To analyze the activity pattern of ICP around burrows, we selected the permanently occupied burrows. The data from those burrows were pooled and the mean time spent on each activity (in seconds) was computed and compared across the months using Kruskal Wallis H test. All the data was tested for normality and appropriate parametric or nonparametric statistics was employed.

5.3. Results

5.3.1. Indian crested porcupine abundance and demography

Of the 39 sampled burrows, 58.97 %, 38.46% and 83.78% burrows were occupied by the ICP in winter, summer, and monsoon respectively (Table 5.2) and these seasonal differences were significant (χ^2 = 13.88, df =2, p = 0.001). The mean group size for the sampled burrows was highest in monsoon (2.45 ± 2.06_{SD}), followed by summer (2.47 ± 1.33_{SD}) and winter (2.04 ± 1.33_{SD}). In monsoon, the mean number of adults (1.55 ± 0.72_{SD}) and juveniles (2.55 ± 1.44_{SD}) was highest (Table 5.2), followed by 1.43 ± 0.51_{SD} adults and 2.00 ± 0.82_{SD} juveniles in winter, and 1.20 ± 0.56_{SD} adults and 1.50 ± 0.84_{SD} juveniles in summer. The ICP litters were recorded only in summer with a mean litter size of 2.00 ± 0.00_{SD} litters per burrow. The time of first appearance of litters was around first week of April 2016 and a total of ten litters were recorded from six burrows in that season. The estimated density of ICP was 3.21 ± 1.32_{SD}

individuals/km^2, accounting to a population size of 65.89 ± 27.15_{SD} ICP in KNP. However, the density and the corresponding population size ranged between 2.18 to 4.71 individual/km^2, and 44.65 to 96.48 ICP respectively across seasons.

Table 5.2. Burrow use and demography of Indian crested porcupine across different seasons in KNP

	Winter	Summer	Monsoon
Total number of burrows present	47.00	47.00	47.00
Number of burrows sampled	39.00	39.00	37.00
Number burrows occupied	23.00 (58.97 %)	15.00 (38.46 %)	31.00 (83.78 %)
Expected no. of burrows occupied (out of 47)	28.00	18.00	39.00
Mean group size ($\bar{x}$ ± SD)	2.04 ± 1.33	2.47 ± 1.33	2.45 ± 2.06
Mean number of adults ($\bar{x}$ ± SD)	1.43 ± 0.51	1.20 ± 0.56	1.55 ± 0.72
Mean number of juveniles ($\bar{x}$ ± SD)	2.00 ± 0.82	1.50 ± 0.84	2.55 ± 1.44
Mean number of litters ($\bar{x}$ ± SD)	0.00	2.00 ± 0.00	0.00
Population size	56.54	44.65	96.48
Density (Individual/km^2)	2.76	2.18	4.71

5.3.2. Major activity pattern around the burrows

A total of 3254 camera-trap days produced 3346 activity records of Indian crested porcupine around the burrows. Daily activity records (Fig. 5.1) of adult porcupine outside burrow showed a significant peak in January (Z = 6.89, p < 0.001), whereas that of litter was significantly high during May (Z = 12.99, p < 0.001; Table 5.3).

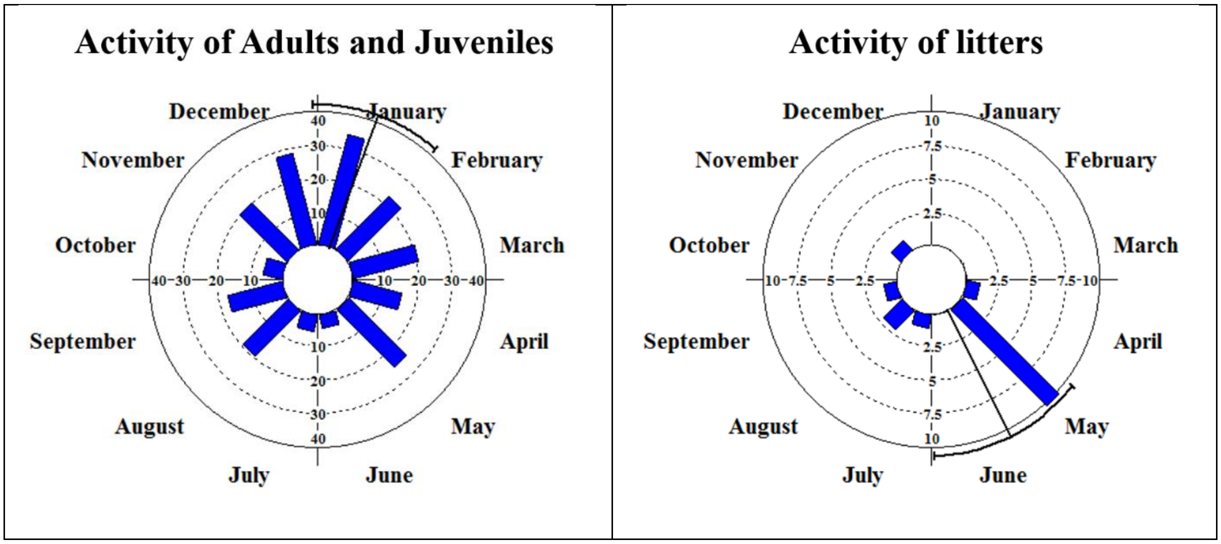

Figure 5.1. Daily activity records of Indian crested porcupine activity outside burrows KNP. Bar represents the individual records and the line represents the mean vector and its circular standard deviation.

Table 5.3. Activity outside burrows by Indian crested porcupine across months in KNP.

	Activity of adults and juveniles	Activity of litters
Number of Observations	3343	169
Mean Vector (µ)	20.03°	153.14°
Mean Group	January	May
Length of Mean Vector (r)	0.25	0.66
Circular Standard Deviation	95.93°	52.58°
Standard Error of Mean	11.08°	13.31°
Rayleigh Test (Z)	12.99	6.89
Rayleigh Test (p)	0.000	0.000

The mean detections per day (Table 5.4) was significantly highest in the month of May for ‘playing’ (0.66 ± 1.44 $_{SD}$; G = 327.99, df = 11, $p < 0.001$) and ‘exploring surrounding’ (0.48 ± 1.20 $_{SD}$; G = 151.62, df = 11, $p < 0.001$). The ‘feeding’ activity around the burrows was significantly high in the months of April and June (0.30 ± 1.07 $_{SD}$ and 0.30 ± 0.80 $_{SD}$ respectively; G = 101.67, df = 11, $p < 0.001$). The mean detections per day for other activities such as ‘guarding’ (0.23 ± 1.36 $_{SD}$; G = 109.89, df = 11, $p < 0.001$), ‘burrow modification’ (0.20 ± 0.79 $_{SD}$; G = 130.69, df = 11, $p < 0.001$) and ‘resting’ (0.06 ± 0.39 $_{SD}$; G = 37.65, df = 11, $p < 0.001$) was significantly high in the months of August, February and July respectively.

Table 5.4. The mean number of detections per day in a month for major activities throughout year by Indian crested porcupine around the burrow systems in KNP from 2013-2016. [N=2186 Camera Trap (CT) days; F = Frequency].

Month	**Sampled burrows**	**CT days**	**Modifying burrow**		**Exploring surrounding**		**Feeding**		**Guarding**		**Marking**		**Playing**		**Resting**	
			F	**$\overline{X}$ ± SD**	**F**	**$\overline{X}$ ± SD**	**F**	**$\overline{X}$ ± SD**	**F**	**$\overline{X}$ ± SD**	**F**	**$\overline{X}$ ± SD**	**F**	**$\overline{X}$ ± SD**	**F**	**$\overline{X}$ ± SD**
Jan	13	273	21	0.08 ± 0.48	27	0.10 ± 0.40	28	0.10 ± 0.45	8	0.03 ± 0.19	0	0.00	0	0.00	1	0.00 ± 0.06
Feb	21	249	51	**0.20 ± 0.79**	20	0.08 ± 0.35	50	0.20 ± 0.81	9	0.04 ± 0.21	0	0.00	0	0.00	10	0.04 ± 0.20
Mar	19	225	3	0.01 ± 0.15	14	0.06 ± 0.31	35	0.16 ± 0.72	32	0.14 ± 0.99	1	0.00 ± 0.07	1	0.00 ± 0.07	1	0.00 ± 0.07
Apr	18	215	3	0.01 ± 0.15	14	0.07 ± 0.25	64	**0.30 ± 1.07**	6	0.03 ± 0.17	0	0.00	4	0.02 ± 0.14	2	0.01 ± 0.10
May	8	80	0	0.00	38	**0.48 ± 1.20**	6	0.08 ± 0.41	13	0.16 ± 0.65	0	0.00	53	**0.66 ± 1.44**	4	0.05 ± 0.45
Jun	8	40	2	0.05 ± 0.22	1	0.03 ± 0.16	12	**0.30 ± 0.80**	0	0.00	0	0.00	0	0.00	0	0.00
Jul	13	65	1	0.02 ± 0.12	12	0.18 ± 0.68	16	0.25 ± 0.66	2	0.03 ± 0.17	0	0.00	0	0.00	4	**0.06 ± 0.39**
Aug	18	168	9	0.05 ± 0.41	53	0.32 ± 1.37	43	0.26 ± 0.65	38	**0.23 ± 1.36**	0	0.00	0	0.00	4	0.02 ± 0.15
Sep	8	90	1	0.01 ± 0.11	28	0.31 ± 0.70	24	0.27 ± 0.56	2	0.00	1	0.01 ± 0.10	0	0.00	0	0.00
Oct	11	117	4	0.03 ± 0.18	10	0.08 ± 0.31	16	0.14 ± 0.66	2	0.02 ± 0.13	3	**0.03 ± 0.16**	0	0.00	0	0.00
Nov	20	278	27	0.10 ± 0.56	17	0.06 ± 0.34	123	0.44 ± 1.37	5	0.02 ± 0.13	5	0.02 ± 0.19	0	0.00	5	0.02 ± 0.16
Dec	20	386	64	0.17 ± 0.94	25	0.06 ± 0.34	67	0.17 ± 0.69	27	0.07 ± 0.68	5	0.01 ± 0.13	1	0.04 ± 0.26	16	0.01 ± 0.11

5.3.3. Emergence and retreat pattern

The overall daily emergence and retreat of Indian crested porcupine (Fig. 5.2) peaked between 1800 to 2000 hours and 0400 to 0600 hours respectively.

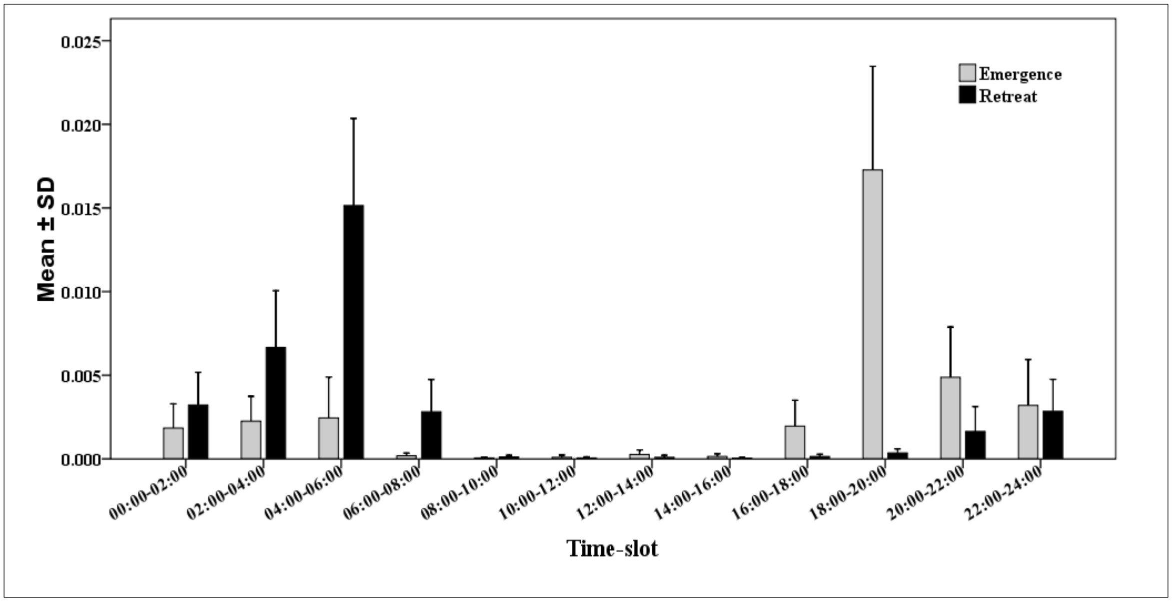

Figure 5.2. Daily emergence and retreat pattern into burrows by Indian crested porcupine in KNP. (N=2186 camera trap day; Emergence = 1156 captures, Retreat = 1232 captures)

The porcupines emerged (Table 5.5) earlier in monsoon and winter (1600 – 1800 hours) than in summers (1800 – 2000 hours) though, the seasonal shift was not significant (χ^2 = 4.89, df=2, p = 0.09). The rate of retreat (Table 5.5) significantly varied across seasons (χ^2 = 22.33, df = 2, p < 0.000), wherein the porcupines retreated late in winter (0600 to 0800 hours) than in monsoon and summer (0400 to 0600 hours).

Table 5.5. Rate of emergence and retreat (mean ± SD) from the burrows in different season by Indian crested porcupine in KNP.

Time-slot	Monsoon	Summer	Winter
Rate of emergence (Mean ± SD)			
00:00-02:00	0.001 ± 0.001	0.003 ± 0.004	0.001 ± 0.001
02:00-04:00	0.002 ± 0.002	0.003 ± 0.004	0.002 ± 0
04:00-06:00	0.001 ± 0.001	0.005 ± 0.007	0.002 ± 0.001
06:00-08:00	0	0	0
08:00-10:00	0	0	0
10:00-12:00	0	0	0
12:00-14:00	0	0	0
14:00-16:00	0	0	0
16:00-18:00	0.001 ± 0.001	0	0.005 ± 0.003
18:00-20:00	**0.009 ± 0.004**	**0.023 ± 0.014**	**0.02 ± 0.008**
20:00-22:00	0.005 ± 0.005	0.008 ± 0.007	0.002 ± 0.001
22:00-24:00	0.002 ± 0.002	0.007 ± 0.007	0.001 ± 0.001
Rate of emergence (Mean ± SD)			
00:00-02:00	0.001 ± 0.001	0.004 ± 0.004	0.005 ± 0.003
02:00-04:00	0.003 ± 0.002	0.007 ± 0.007	0.01 ± 0.007
04:00-06:00	**0.009 ± 0.005**	**0.022 ± 0.012**	**0.014 ± 0.005**
06:00-08:00	0	0	0.006 ± 0.002
08:00-10:00	0	0	0
10:00-12:00	0	0	0
12:00-14:00	0	0	0
14:00-16:00	0	0	0
16:00-18:00	0	0	0
18:00-20:00	0	0	0.001 ± 0
20:00-22:00	0.001 ± 0.001	0.003 ± 0.004	0.001 ± 0.001
22:00-24:00	0.001 ± 0.001	0.005 ± 0.005	0.002 ± 0.001

A total of 312 emergence event timings were compared with the sunset timings. The median emergence time of porcupines (Fig. 5.3a) was 3.13 minutes after sunset in monsoon (n = 86, range = 142 minutes before sunset to 98 minutes after sunset), 28.83 minutes after sunset in summer (n = 92, range = 52 minutes before sunset to 254 minutes after sunset), and 29.63 minutes after sunset in winter (n = 134, range = 38 minutes before sunset to 152 minutes after sunset), with a significant seasonal variation (ANOVA, $F_{2, 309} = 19.65$, $p < 0.001$). Similarly, a total of 311 retreat event timings were compared with the sunrise timings. The median retreat time of porcupines (Fig. 5.3b) was 62 minutes before sunrise in monsoon (n = 49, range = 270 minutes before sunrise to 68 minutes after sunrise), 58 minutes before sunrise in summer (n = 114, range = 353 minutes before sunrise to 10 minutes after sunrise), and 132 minutes before sunrise in winter (n = 148, range = 426 minutes before sunrise to 50 minutes after sunrise) with a significant seasonal variation (ANOVA, $F_{2, 308} = 15.29$, $p < 0.001$). Few outliers were also recorded in emergence timings during summer and winter.

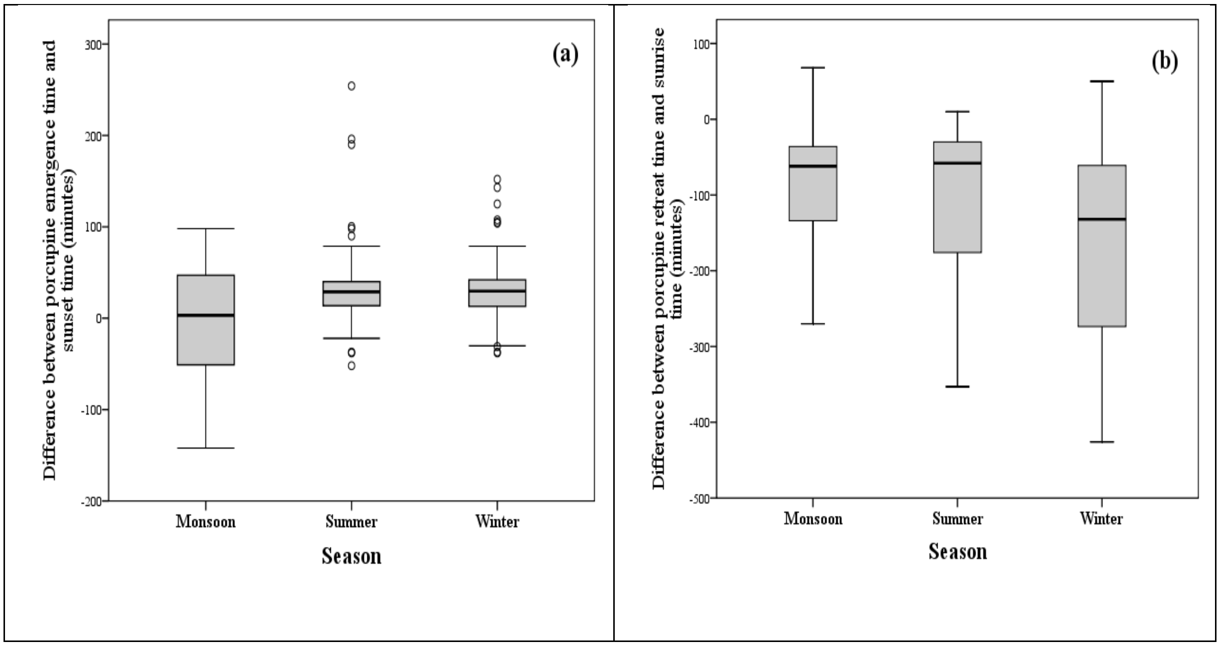

Figure 5.3. Seasonal variation in (a) emergence time with sunset time; and (b) retreat time with sunrise time for Indian crested porcupine in KNP.

5.3.4. Variables affecting the activity pattern

Low temperature and high humidity significantly influenced (Table 5.6) the frequency of retreat ($R_T = -0.66$, $p < 0.001$; $R_{RH} = 0.70$, $p < 0.001$) into the burrow. The frequency of emergence peaked at lower temperature and high humidity, but was insignificant ($n = 12$; $R_T = -0.21$, $p = 0.19$; $R_{RH} = 0.29$, $p = 0.06$). None of the activities were influenced by changes in temperature and humidity, except 'burrow modification' wherein low temperature and high humidity significantly influenced (Table 5.6) the rate of digging ($R_T = -0.66$, $p < 0.001$; $R_{RH} = 0.63$, $p < 0.001$).

Table 5.6. Pearson's Correlation between temperature/humidity influencing Indian crested porcupine activities around the burrow system in KNP.

Activities (2013-2016)	**Temperature (°C); n=40**	**Relative Humidity (%); n=40**
Emergence	$R_T = -0.21$, $p = 0.19$	$R_{RH} = 0.29$, $p = 0.06$
Retreat	$R_T = -0.66$, $p < 0.001$**	$R_{RH} = 0.70$, $p < 0.001$**
Burrow modification	$R_T = -0.66$, $p < 0.001$**	$R_{RH} = 0.63$, $p < 0.001$**
Exploring surroundings	$R_T = 0.01$, $p = 0.96$	$R_{RH} = 0.15$, $p = 0.34$
Feeding	$R_T = -0.21$, $p = 0.19$	$R_{RH} = 0.30$, $p = 0.06$
Guarding	$R_T = -0.02$, $p = 0.91$	$R_{RH} = 0.13$, $p = 0.43$
Marking	$R_T = -0.08$, $p = 0.63$	$R_{RH} = 0.15$, $p = 0.35$
Playing	$R_T = 0.25$, $p = 0.12$	$R_{RH} = -0.08$, $p = 0.64$
Resting	$R_T = -0.22$, $p = 0.17$	$R_{RH} = 0.29$, $p = 0.07$

** Correlation is significant at the 0.01 level (2-tailed).

The porcupine was observed to be active across all lunar phases (Fig. 5.4), however a significant peak (Z = 11.95, $p < 0.001$; Table 5.7) was recorded between first quarter and waxing gibbous phase ($\mu = 110.52° \pm 131.62°$ CSD).

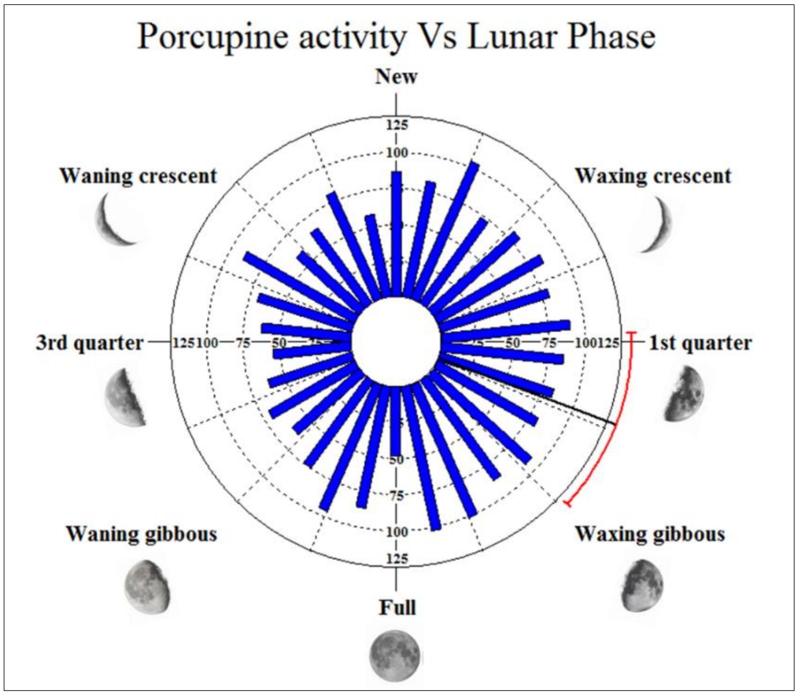

Figure 5.4. Nocturnal activity of Indian crested porcupine during corresponding lunar-phase. Bar represents the individual records and the line represents the mean vector and its circular standard deviation.

Table 5.7. Nocturnal activity of Indian crested porcupine during different lunar phase in KNP.

Circular Parameters and Statistics	Porcupine activity
Number of Observations	2340
Mean Vector (μ)	110.52°
Mean Group	Waxing gibbous
Length of Mean Vector (r)	0.07
Circular Standard Deviation	131.62°
Standard Error of Mean	11.70°
Rayleigh Test (Z)	11.95
Rayleigh Test (p)	0.000

5.3.5. Intensity of activity around the burrow

A total of 1060 activity records were captured in 2186 camera trap days (Table 5.8). Porcupines spent an average time on 'burrow modification' (168.16 ± 566.34 $_{SD}$ sec; $\chi^2 = 81.84$, df = 11, $p < 0.001$) per 24 hours followed by 'guarding' (112.02 ± 553.79 $_{SD}$ sec; $\chi2 = 11.01$, df = 11, p = 0.44), 'exploring surrounding' (94.31 ± 456.23 $_{SD}$ sec; $\chi2 = 24.16$, df = 11, p = 0.01), 'playing' (87.14 ± 476.64 $_{SD}$ sec; $\chi2 = 201.6$, df = 11, $p < 0.001$), 'feeding' (83.27 ± 261.95 $_{SD}$ sec; $\chi2 = 89.64$, df = 11, $p < 0.001$), 'resting' (31.43 ± 233.33 $_{SD}$ sec; $\chi2 = 38.52$, df = 11, $p < 0.001$) and 'marking'(1.58 ± 20.09 $_{SD}$ sec; $\chi2 = 31.10$, df = 11, p = 0.001), which varied significantly across the timings of the day.

Table 5.8. The mean time spent on various activities outside burrow by Indian crested porcupine in 24 hours across different months. (N=2186 camera trap days; Total snapshots = 1060).

Activity	Frequency of occurrence	Duration of activity in seconds	Mean duration ± SD (sec)	Kruskal Wallis Test
Burrow modification	184	78700.64	168.16 ± 566.34	$\chi^2 = 81.84$, df = 11, $p < 0.001$
Exploring surroundings	227	44135.3	94.31 ± 456.23	$\chi^2 = 24.16$, df = 11, p = 0.01
Feeding	457	38968.36	83.27 ± 261.95	$\chi^2 = 89.64$, df = 11, $p < 0.001$
Guarding	71	52424.13	112.02 ± 553.79	$\chi^2 = 11.01$, df = 11, p = 0.44
Marking	15	740.00	1.58 ± 20.09	$\chi^2 = 31.10$, df = 11, p = 0.001
Playing	59	40781.43	87.14 ± 476.64	$\chi^2 = 201.6$, df = 11, $p < 0.001$
Resting	47	14710.00	31.43 ± 233.33	$\chi^2 = 38.52$, df = 11, $p < 0.001$

5.4. Discussion

In KNP, ICP occupied 58.97 %, 38.46% and 83.78% of the 39 sampled burrows in winter, summer, and monsoon respectively. The estimated density of ICP was 3.21 ± 1.32$_{SD}$ individuals/ km^2, accounting for a population size of 65.89 ± 27.15$_{SD}$ individuals for the entire KNP. A seasonal shift in the rate of emergence was observed in monsoon and winter, when ICP emerged earlier than summers. This was also significantly correlated with the sunset timings when emergence was delayed by 28.83 minutes after sunset in summer correlating with lower temperature. The ICP returned long before the sunrise time (132 minutes) in winters, thereby with a reduced duration of activity outside the burrows. The ICP showed a trend of moonlight avoidance as their temporal activity significantly reduced in the full moon nights and peaked between first and the third quarter.

In the present study, the density of ICP was lowest in summer 2.18 individuals/km^2, whereas in monsoon it was 4.71individuals/ km^2. The density was comparable to that of 4 individuals/km^2 on the Mediterranean coastal plains (Server and Mendelssohn, 1991), 2.10 individuals/km^2 in the Negev desert (Alkon, 1999), and 2.35 individuals/km^2 in scrubland of semi-arid Sariska Tiger Reserve, Rajasthan (Sharma, 2001). The difference in the density can be attributed to food availability (Horwitz et al., 2012). For example, in the natural areas of Negev desert, the density of ICP was 2.10 individuals/ km^2, while the density attained 7.50 individuals/ km^2 at the localities with potato crops *Solanum spp*. in the same desert (Alkon, 1999). The entire KNP used to dry up in summers and ICP might be sneaking out to agricultural fields to raid the tuberous vegetable crops like *Solanum tuberosum* and *Solanum melongena*, which are part of its diet (Gutterman, 1982; Arshad 1990; Hafeez et al., 2011). This possibly has lead to the lower density of ICP in the KNP.

ICP seasonally adjusted its emergence, retreat and duration activity outside the burrow. The increased activity in summers was in concurrence with those of ICP in the Negev desert (Alkon and Saltz, 1988a) and crested porcupine in central Italy (Corsini et al., 1995). The heavy rain days curtailed their activities in monsoon, as also observed in ICP of the Negev desert (Alkon and Saltz, 1988a). Some sporadic late emergence and continued presence around the immediate surroundings of the burrows corresponded with the presence of litters in the burrow, where probably the parent would have chosen favorable conditions to emerge and forage near the burrows, along with guarding the burrows.

The daily activities of adult ICP peaked in January-February, wherein mostly they were engaged in digging and modifying the burrow. This is just prior to their breeding season in March (Prater, 1965; Prakash, 1997), when ICP prepares the burrows for the gestation period of 90 – 112 days (Khaliq et al., 1991; Kadhim, 1997), followed by the rearing of the young. The litter activity significantly increased during May, i.e. ~40-55 days after their birth. This was in concurrence with the crested porcupine in Italy (Mori et al., 2016), wherein the adult porcupines were mostly observed in the immediate surrounding either feeding or digging, and the litters left the den for the first time when about 45–60 days old, assuming that litters were born when parents started alternating in the burrow.

The pattern of moonlight avoidance by ICP in KNP was similar to that of ICP in the Negev desert (Alkon and Saltz, 1988a) and also to that of crested porcupines in Tuscany (Mori et al., 2014a). The avoidance of moonlight can be an anti-predator behavior, presuming that more moonlight increases the visibility and subsequently favors detections by the predators (Alkon and Saltz, 1988a; Server and Mendelssohn, 1991; Corsini et al., 1995; Mori et al., 2014a).

The ICP having a widespread distribution with broad habitat tolerance (Amori et al., 2016), is often considered an agricultural pest (Greaves and Khan, 1978; Alkon and Saltz, 1985; Khan et al., 2000; Hafeez et al., 2011). However, in natural conditions, ICP significantly contributes to the ecosystem functions especially by being an ‘allogenic engineer’ by providing significant refuge sites for other species. High seasonal variation in the temperature makes the KNP’s ecosystem highly dynamic. Thus, an understanding of the various environmental factors determining the biology of this essential ‘ecosystem engineer’ (Gutterman et al., 1990) was necessary. The present study affirms that weather parameters, timings of sunrise, sunset and lunar phase influence the variations in activity patterns including the timing of emergence and retreat from the burrows as a response to predator avoidance in the nocturnal ICP.

PLATE 5.1

(a) Adult porcupine emerging at night; (b) Adult porcupine active in day; (c) Diurnal activity of porcupines; (d) Burrow modification (Digging); (e) Adult with litters and (f) Suckling litters.

CHAPTER 6

Burrow use pattern by Golden Jackal

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6.1. Introduction

The golden jackal (*Canis aureus*) is one of the most common canids in its ranges of Asia and Europe (Macdonald and Sillero-Zubiri, 2004; Giannatos et al., 2005; Jhala and Moehlman, 2008). Golden jackals are monogamous (Kleiman, 1977; Moehlman, 1987; 1989; Asa and Valdespino, 1998; Admasu et al., 2004) with rare observations of mate change (Moehlman, 2014). They demonstrate elaborate pre-copulatory sequences (Golani and Mendelssohn, 1971), followed by making or occupying burrows at the onset of the breeding season (Sharma, 1998). During the breeding season, golden jackals use burrows for rearing the pups, therefore, selection of suitable burrowing habitat is essential for the successful persistence of their population (Golani and Keller, 1975).

In India, golden jackals search for suitable natal sites commences from February to March (Golani and Keller, 1975) often preceded by scent marking through urination and defecation around burrows (Jhala and Moehlman, 2008) from November through January. Favorable shelter sites for golden jackal include natural or human-modified sites, for e.g. golden jackal selected open deciduous forests often with areas of sandy soil to build the burrows in Saurashtra region, Gujarat (Soni et al., 1995). They also prefer grassland, medium *Prosopis*, dense *Prosopis*, village outskirts, saline wasteland, halophytic scrub, fallow fields, mud flat, road edges and canal as potential habitat types in Bhal region, Gujarat (Aiyadurai and Jhala, 2006; Patil and Jhala, 2008). The golden jackal as typical ‘secondary modifiers’ has been observed to modify and use the existing burrows of Indian fox (*Vulpes bengalensis*), Asiatic grey wolf (*Canis lupus*) and Indian crested porcupines (*Hystrix indica*) (Jhala and Moehlman, 2008).

While there are biological data on golden jackals from previous studies in India, these studies have been conducted on small populations and over short durations. However, long-term assessment and quantification of their activity pattern when they live in a high density and in different habitat condition will provide detailed insights into the biology of the species. Keoladeo National Park (hereafter KNP) has recorded highest density of golden jackal (14.84 individuals/km^2) ever reported from any protected area around the world (Singh et al., 2016). It is, therefore, an imperative to understand the factors influencing the golden jackals to select appropriate natal burrows, which in turn influences their propagation. The present chapter attempts to understand the pattern of habitat preference for burrow-site selection by golden jackals in case of a large population of KNP over a span of three years, wherein the existing conditions of habitat availability, social organization and level of competition varies. In view of this, the biotic or abiotic elements influencing the golden jackals in selecting specific burrows during the breeding season in KNP were explored. The results describes the site-specific habitat characteristics and physical characteristics of these natal sites; and the micro-habitat conditions, the environmental conditions and the presence of conspecifics playing role in site selection by a golden jackal. The breeding season of the golden jackal was also compared with the seasonality of other canids across different geographical regions to comprehend the possibility of any specific pattern in their breeding seasonality. The findings also explores the burrow-specific activities particularly during the breeding season and the possible factors affecting the activities of the cathemeral canid in its native range of semi-arid conditions.

6.2. Methods

6.2.1. Identification of covariates

The golden jackal population in Gujarat preferred scrub habitat for burrowing with one to three openings (Jhala and Moehlman, 2013) as also shown for Coyotes (*Canis latrans*) preferring bush-covered south-facing slopes and thicket cover (Gier, 1968). In KNP, jackals are known to occupy existing burrows of Indian crested porcupine co-occupied by pythons. Therefore, we expected the vegetation parameters around the burrows; the external burrow structural features; and the presence of both porcupine and python would determine the selection of burrows by golden jackal in KNP. Hence, we identified *five habitat covariates*: Soil Type (ST), Percent Ground Cover (GC), Percent Canopy Cover (CC), Percent Wood Cover around Burrow (WC), Percent Herb Cover Over Burrow opening (WC); *four burrow structure covariates*: Slope of Burrow Mound (SL), Orientation of Burrow Opening (OR), Number of Openings (NOP), Area of Primary Opening (APM) along with *abundance of* porcupine (POR) and python (PYT), which were presumed to determine the burrow selection by jackals. The predicted response of the golden jackal to each of these covariates is shown in Table 6.1.

Table 6.1. Predicted species response to each covariate based on our a priori hypotheses for selection of burrows by golden jackal in KNP.

Independent variables	**Covariates**	**Hypothesis for burrow selection**
Habitat variables	Soil Type (ST)	Will prefer specific soil type (+)
	Percent Ground Cover (GC)	Will prefer open area (-)
	Percent Canopy Cover (CC)	Will prefer overall shady area (+)
	Percent Wood Cover around Burrow (WC)	Will prefer more wood cover to avoid disturbance (+)
	Percent Herb Cover Over Burrow opening (HC)	Will prefer clear openings (-)
Burrow Structure variables	Slope of Burrow Mound (SL)	Will prefer higher mounds (+)
	Orientation of Burrow Opening (OR)	Will prefer specific cardinal direction (+)
	Number of Openings (NOP)	Will prefer less opening to reduce disturbance (-)
	Area of Primary Opening (APM)	Will prefer smaller openings to reduce predation pressure (-)
Presence of Other species	Abundance of Porcupine (POR)	Avoid competition (-)
	Abundance of Python (PYT)	Avoid competition (-)

‘+’ signifies a positive effect on the dependent variable, ‘-’ signifies a negative effect on the dependent variable.

6.2.2. Field methods

To understand the natal-site selection of burrows by golden jackal, the geo-coordinates for all the detected burrows (n = 47, Fig. 6.1) were recorded using handheld GPS and information about all identified variables (ST, GC, CC, WC, HC, SL, OR, NOP, APM, POR, PYT) were

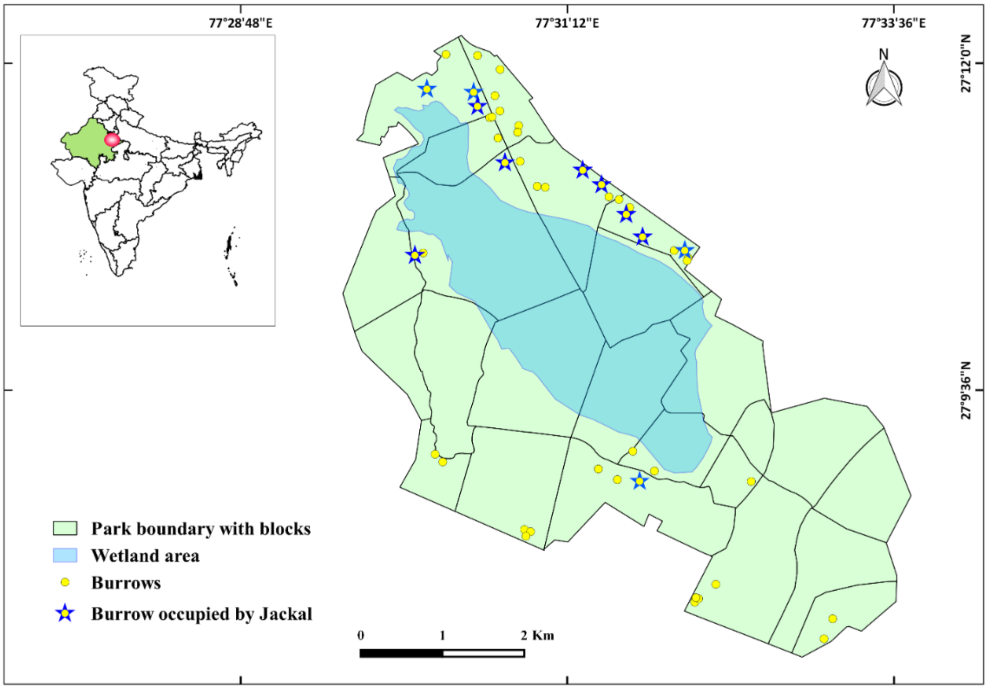


Figure 6.1. The location of KNP in India (Inset). Map showing all burrows occupied by golden jackal during three years of study.

collected from these sites. Circular plots of the 10-m radius were laid keeping the burrows in the center to assess the percent ground cover, canopy cover and wood cover around the burrow. Soil samples were collected from each burrow site and the soil type was assessed using feel-analysis method (Thien, 1979), and classified into six soil types i.e. clay, clay loam, sandy clay, sandy clay loam, silty clay loam, and silty loam. External burrow characteristics were recorded including slope of burrow mound, the number of openings in a burrow system, the size of openings (in square -meter), and orientation of openings (in cardinal degrees). The number of porcupines and pythons present prior to jackal's permanent occupancy of the burrow was recorded using camera trap images and also by a visual encounter of the animal.

Among the 47 recorded burrows, a subset of 20 random burrows were selected for intensive monitoring of the major activities around the burrows over three years. A total of 11 high sensitive passive infrared (PIR) motion sensor camera-traps (Boskon Guard Scouting, BG-520 series) were deployed in 20 selected random burrows. The camera-trap trigger gap was set to 10 s in case animals are continuously present in camera view. With each trigger, a set of three pictures were captured. The sampling effort for 20 burrows was systematically divided through the months. The camera-traps were placed for five consecutive days in 5-10 burrows depending upon the number of openings and then were shifted to the next set of remaining 20 burrows for another 5 days. This deploying method was repeated for the first 24 months continuously. The efforts have varied for some months due to weather constraints, and malfunctioning of some camera traps. In a month, the trapping effort varied from 15 (3 burrows for 5 days) to 300 camera trapping sessions (20 burrows for 5 days with repetition) with a total of 3254 days of camera-trap effort.

Every fifth day, the photographs were downloaded and saved with the identity of burrow and month. The photographs were screened and managed for further analysis. The time of the initial trigger was considered, in cases, jackals repeatedly triggered cameras without leaving the field of view. The major activities around the burrows were recorded as burrow-inspection, marking, burrow-modification and occupancy during the breeding season. The definition of each of the activities is provided in Table 6.2.

To understand the specific activity pattern, a pair of jackal was tracked until they chose to select a burrow during the breeding season in 2016 (April-May; dry season). Upon their permanent occupancy, camera traps were deployed and utmost care was taken to minimize the disturbance while changing the traps every third day. The activity of the pack (adults and pups) outside the burrow was continuously monitored until they leave the burrow.

Along with recording the activities of golden jackal, data on environmental parameters were simultaneously collected. The information on lunar-phase was obtained from the official website of Indian Meteorological Department, Govt. of India. The ambient temperature and relative humidity data (at 10-min interval x 24-hour x 365 days) were recorded using Onset® Hobo^{TM} automatic data loggers, to determine whether any of these values influence the activities of a jackal. Four data loggers were deployed to spatially cover the entire KNP. The data from the nearest logger was extracted for each burrow system. The data were recorded six times in an hour at the interval of 10-minutes. The hourly-mean of the logged data was then used for further analyzing the effect of temperature and humidity on each activity event recorded in a particular hour of the day.

Table 6.2. Ethogram of the behaviors by golden jackal recorded around the burrows in KNP

Events	**Activities**	**Description**
Major events around the burrow through the year	Inspection	To meander about, sniffing the ground surrounding burrow and peeping into burrow
	Marking	To urinate after investigating the burrow; stretching and/or lifting a hind leg while urinating; squatting and evacuation of urine
	Burrow modification	To break up and dig in front of burrow opening with the paws, remove dug up loose soil around the burrows
	Rearing Litters	Parental care; pups' activity (following specific activities)
Specific events during litter rearing; after occupancy of the burrow	Emergence	Coming out from the burrow
	Retreat	Entering the burrow
	Exploring surroundings	Pups meander around the burrows; nose-nudging performed toward any inanimate object (wood, stone, bone, stick), touching and sniffing
	Feeding	Nursing of the pups; regurgitate for the pups, starting when the pups are about 3 weeks old
	Grooming	Self-nibbling by pups; parents grooming fur or other body part by nibbling gently with the incisors, interspersed with wiping and licking; act performed to eliminate flea or other irritation
	Guarding	Either parent staying close to the burrow opening and monitor when pups are inside; staying close with ears forward (alert) when pups are outside
	Huddling	Parent curling around pups; lying in a curled posture, legs tucked in close, head tucked, often with the tail covering the nose
	Playing	Holding an object (bone, stick) in the mouth while standing or moving around; chasing and blowing leaves, pups leaping on each other; interacting with an inanimate object (trees, twigs); pawing among pups.
	Resting	Sitting and lying down in a relaxed manner; Lying on the belly with forelegs extended; hind legs bent and resting close to the body on each respective side; body twisted and both hind legs to one side, head up/lowered to rest on the forelegs or the ground between them)

6.2.3. Data analysis

To ascertain the effects of various habitat variables on the likelihood of burrow selection by the golden jackal, binomial logistic regression was performed using SPSS v.16.0 (SPSS Inc., 2007) on the data from 47 burrows. A binary response variable (y) was defined for each observation, such that y = 1 if jackal selected and used the burrow and y = 0 if it did not. Binomial logistic regression estimates the probability of an event (in this case, jackal occurrence in a burrow) occurring (Keating and Cherry, 2004). If the estimated probability of the event occurring was greater than or equal to 0.5 (better than even chance), the event was classified as 'occurring' and if the probability was less than 0.5, the event was classified as 'not occurring'. To predict the response of our dependent variable (DV, here jackal occurrence) on other explanatory variables (ST, GC, CC, WC, HC, SL, OR, NOP, APM, POR, PYT), combination of several models were tested in the form of the equation: $Y = A + Bx_1 + Cx_2 + \dots$¸ where Y is the response variable, A is the β-coefficient of the constant, B, C are the β-coefficients of the predictor variables and x_1, x_2 are odds ratio. The product of odds ratio and predictor determines the value of the response variable which changes according to the odds ratios. The models were defined based on the β-coefficients and Predicted Group Response (PGR) for each of the models. Usually, the R^2 (Cox and Snell R^2 or Nagelkerke R^2 values) derived in logistic regression are pseudo R^2 values. Hence, an approach of bivariate correlation between DV and PGR was considered for obtaining the real R^2 values. Different models were tested with different independent variables, followed by step by step removal of variables according to their significance, and finally, the model with highest R^2 value was considered the best. R^2 gives how much percentage of DV is predicted by the explanatory variables and hence the best model is the one with the highest value (Hosmer and Lemeshow, 2000).

Conceptually jackals recorded by camera traps are considered active only when they move out of the refuge and their activity records were defined as the times of day at which cameras were triggered (Rowcliffe et al., 2014). Frequency data of each activity from the subset of 20 burrows were pooled across 12 months from 20 randomly selected burrows and standardized as per sampled burrow per camera-trap days in each month; as the efforts varied across the months. We calculated the mean number of detections per day and compared it across all the months using G-test of independence (McDonald, 2009).

The specific circadian activity patterns were determined during the breeding season of 2016, wherein the activities of one pack (adults and pups) from one burrow were continuously monitored for 40 days. The data on 24 h timescale was analyzed by using Rayleigh Z statistics (Batschelet, 1965; Zar, 1999) in Oriana software ver. 4.01 (Kovach, 2009). In circular statistic, the mean vector length ‘r’ represents the measure of dispersion of points around the mean vector ‘µ’ (Batschelet, 1965) and its length ($0 < r < 1$) varies according to the concentration of data around the mean angle, where $r = 1$ indicates minimum dispersion and $r = 0$ means maximum dispersion (Batschelet, 1965). To ascertain the effect of temperature and relative humidity on each of the activities, Pearson's correlation test was performed in SPSS. To determine the relationship between the intensity of moonlight and jackal’s activity (if any), the activity data was screened only for the night (1900 h to 0600 h) hours and then analyzed across eight lunar phases in Oriana software. The mean of each specific activity (in minutes) was analyzed across 24 h time scale and Kruskal-Wallis H test was performed to determine if there are statistically significant differences between the intensity of specific activities across six weeks of continuous burrow use by the jackal pack. All the data were tested for normality and appropriate parametric or nonparametric statistics was employed.

6.3. Results

6.3.1. Natal-site selection of burrows by golden jackal

Of the known 47 burrow system (2013-2014), golden jackal occupied 11 of these burrow systems (Fig. 6.1). The binary logistic regression suggested *Model Y = A + BxAPM + CxWC + DxHC* statistically significant (Walds $\chi^2 = 11.84$, $p < 0.001$), with highest R^2 value (Table 6.3). The model explained 78.0% (Table 6.3) of the variance in different covariate suitability in selecting burrows and correctly classified 95.7% of cases. Jackals were 1.12 times more likely (Table 6.4) to choose an area with more wood cover ($\beta = 0.12$; Walds $\chi^2 = 4.18$, df = 1, $p = 0.04$). Area of primary opening negatively affected ($\beta = -0.03$) and herb cover positively affected ($\beta = 0.03$) the burrow selection by a jackal. However, the responses of jackal selecting the burrow in corresponding to the latter variables in the model were statistically insignificant (Table 6.4).

Table 6.3. Summary of model selection procedure for golden jackal burrow choice in KNP based on correlation between Predicted Group Response (obtained from Binary Logistic Regression) and Dependent variable.

Model	β Coefficient of (Constant + variables)	R^2
APM+WC+HC	Model = 7.701 + 0.122* (WC)	**0.78**
GC+CC+WC+HC	Model = -5.365 + 0.098* (WC)	0.67
NOP+APM+WC	Model = 9.671 + 0.165* (WC)	0.67
GC+NOP+APM+WC	Model = 9.393 + 0.161* (WC)	0.67
ST+GC+CC+WC+HC	Model = -5.405 + 0.098*(WC)	0.67
CC+WC+HC	Model = -6.162 +0.091* (WC) + 0.097* (HC)	0.58
APM+HC	Model = 8.354 - 0.021* (APM) + 0.092* (HC)	0.58
WC+HC+POR	Model = -5.299 + 0.119* (WC)	0.48
APM+WC	Model = 8.045 + 0.140* (WC)	0.48
SL+OR+NOP+APM	Model = 14.184 - 0.029*(APM)	0.48
HC	Model = -3.124 + 0.042* (HC)	0.38
WC	Model = -4.710 + 0.095* (WC)	0.28
APM	Model = 9.096 - 0.019* (APM)	0.15

* Significant at 0.05 level

Table 6.4. Best-fit model parameters, β coefficient of each determinant variable with their statistical significance and odds of selecting burrows by golden jackal in KNP.

Covariates	β Coefficient ± S.E.	Walds χ^2 Test	Exp(β)	95% 0f CI for Exp(β)	
				Lower Limit	Upper limit
APM	-0.03 ± 0.02	χ^2 = 4.44, df = 1, p = 0.11	0.97	0.94	1.01
WC	0.12 ± 0.06	χ^2 = 4.18, df = 1, p = 0.04*	1.12	1.01	1.27
HC	0.03 ± 0.04	χ^2 = 0.62, df = 1, p = 0.43	1.03	0.95	1.12

* Significant at 0.05 level

6.3.2. Major activity pattern around the burrows

A total of 3254 camera-trap days' effort produced 2074 activity records of golden jackal around the subset of 20 burrows. The activities namely, 'burrow modification' and 'rearing pups' were restricted to the months of March-July and April-May respectively (Fig. 6.2). The mean detections per day (Table 6.5) were significantly highest in the month of May for 'rearing pups' ($5.81 \pm 16.31_{\text{SD}}$; $G = 5741.00$, $df = 11$, $p < 0.001$) and 'burrow inspection' ($1.45 \pm 3.75_{\text{SD}}$; $G = 1131.30$, $df = 11$, $p < 0.001$). This was followed by 'burrow modification' ($0.13 \pm 1.08_{\text{SD}}$; $G = 161.70$, $df = 11$, $p < 0.001$) and 'marking' ($0.10 \pm 0.63_{\text{SD}}$; $G = 51.47$, $df = 11$, $p < 0.001$) in the month of April.

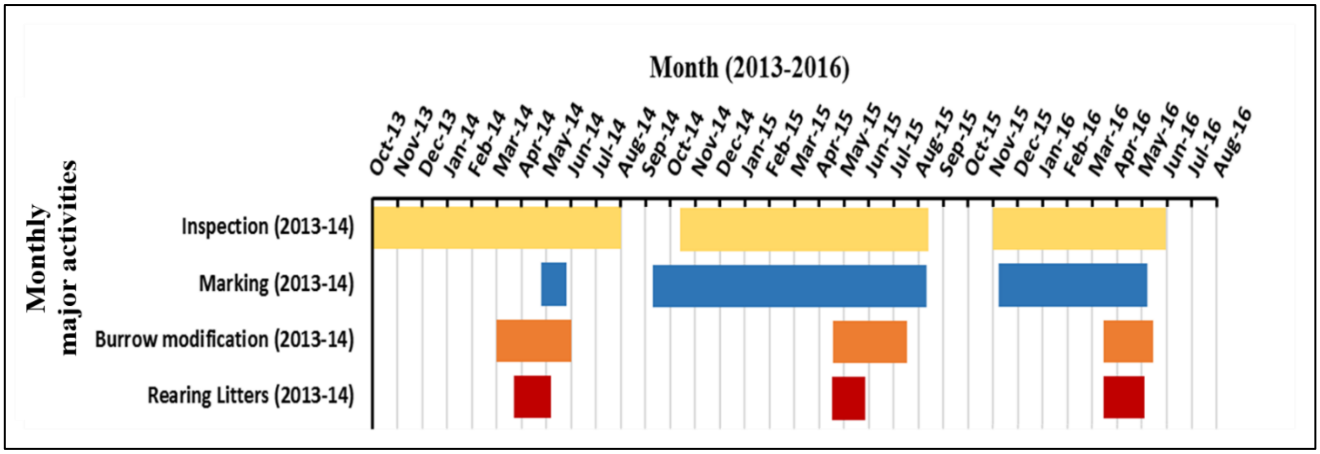


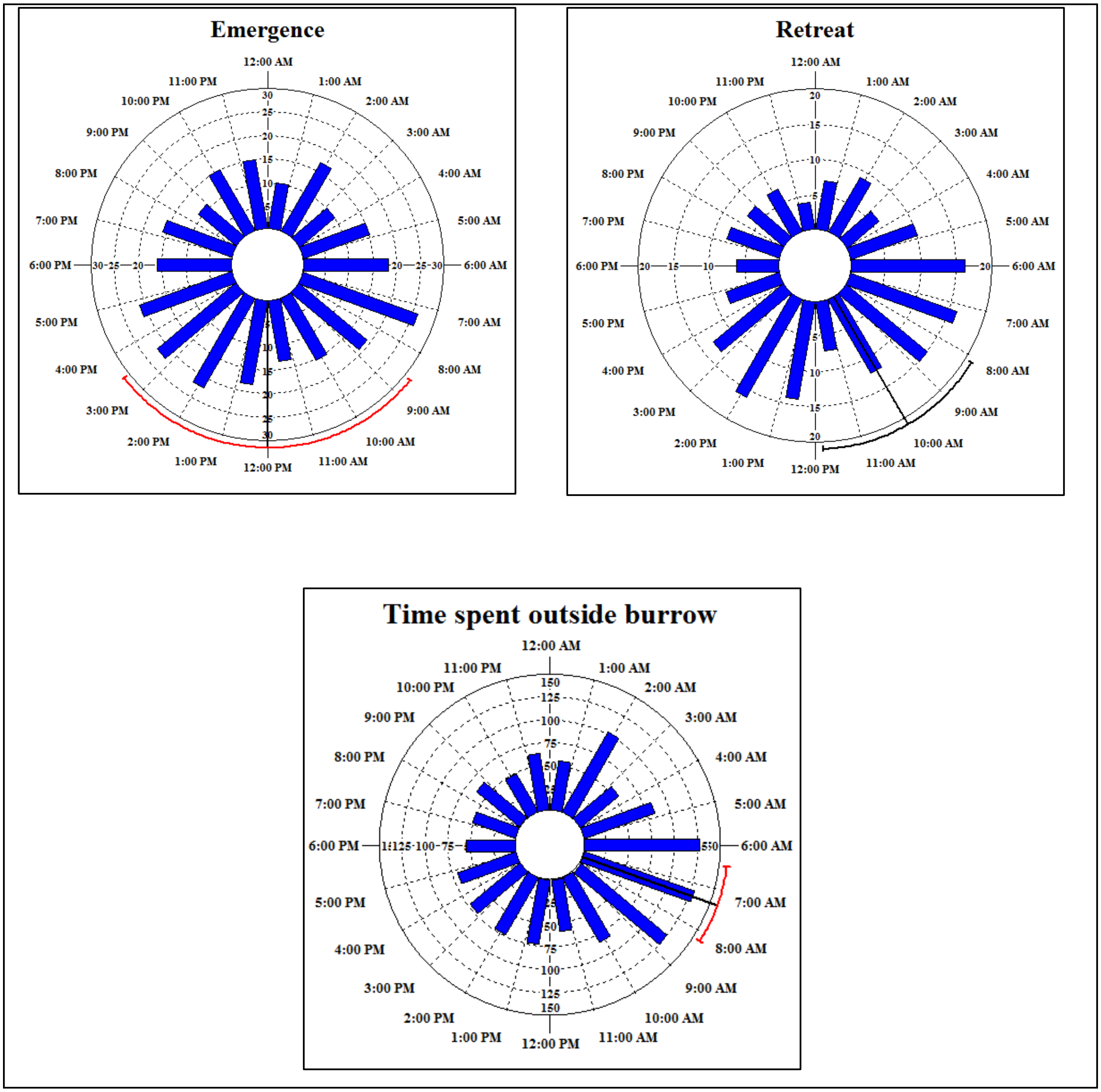
Figure 6.2. Monthly of major activities by golden jackal around the burrow system from 2013 to 2016 in KNP.

6.3.3. Specific activity pattern after occupancy

The occupied burrow by the jackal pack (a pair with pups) was continuously monitored (N= 40 days) and was found active throughout the day with specific activities peaking at a particular period. The time spent outside (Fig. 6.3) the burrow significantly peaked between 0600 to 0800 h ($Z = 37.50$, $p < 0.001$, Table 6.6). The emergence of jackal from the burrow was not significant for a particular time. However, the retreat into the burrow significantly peaked between 0800 to 1200 h ($Z = 7.96$, $p < 0.001$).

Table 6.5. The mean detections per day for major activities throughout year by golden jackal around the burrow systems in KNP from 2013-2016. [N=3254 Camera Trap (CT) days; F = Frequency].

Month	**No. of sampled burrows**	**No. of CT days**	**Inspecting**		**Marking**		**Modifying burrow**		**Rearing Litters**	
			F	**$\bar{x}$ ± SD**	**F**	**$\bar{x}$ ± SD**	**F**	**$\bar{x}$ ± SD**	**F**	**$\bar{x}$ ± SD**
Jan	19	381	80	0.21 ± 0.84	15	0.04 ± 0.23	0	0.00	0	0.00
Feb	30	414	24	0.06 ± 0.30	0	0.00	0	0.00	0	0.00
Mar	27	369	14	0.04 ± 0.33	1	0.00 ± 0.05	3	0.01 ± 0.12	0	0.00
Apr	31	355	219	0.62 ± 2.00	3	**0.10 ± 0.63**	35	**0.13 ± 1.08**	444	1.13 ± 6.46
May	23	155	225	**1.45 ± 3.75**	7	0.05 ± 0.31	12	0.08 ± 0.46	900	**5.81 ± 16.31**
Jun	25	125	5	0.04 ± 0.30	0	0.00	0	0.00	0	0.00
Jul	22	110	8	0.07 ± 0.35	4	0.04 ± 0.23	2	0.02 ± 0.19	0	0.00
Aug	29	249	11	0.04 ± 0.31	1	0.00 ± 0.06	0	0.00	0	0.00
Sep	17	185	1	0.01 ± 0.07	0	0.00	0	0.00	0	0.00
Oct	14	167	5	0.03 ± 0.20	1	0.01 ± 0.08	0	0.00	0	0.00
Nov	27	333	8	0.02 ± 0.15	3	0.01 ± 0.09	0	0.00	0	0.00
Dec	25	411	36	0.09 ± 0.40	7	0.02 ± 0.13	0	0.00	0	0.00



Emergence

Retreat

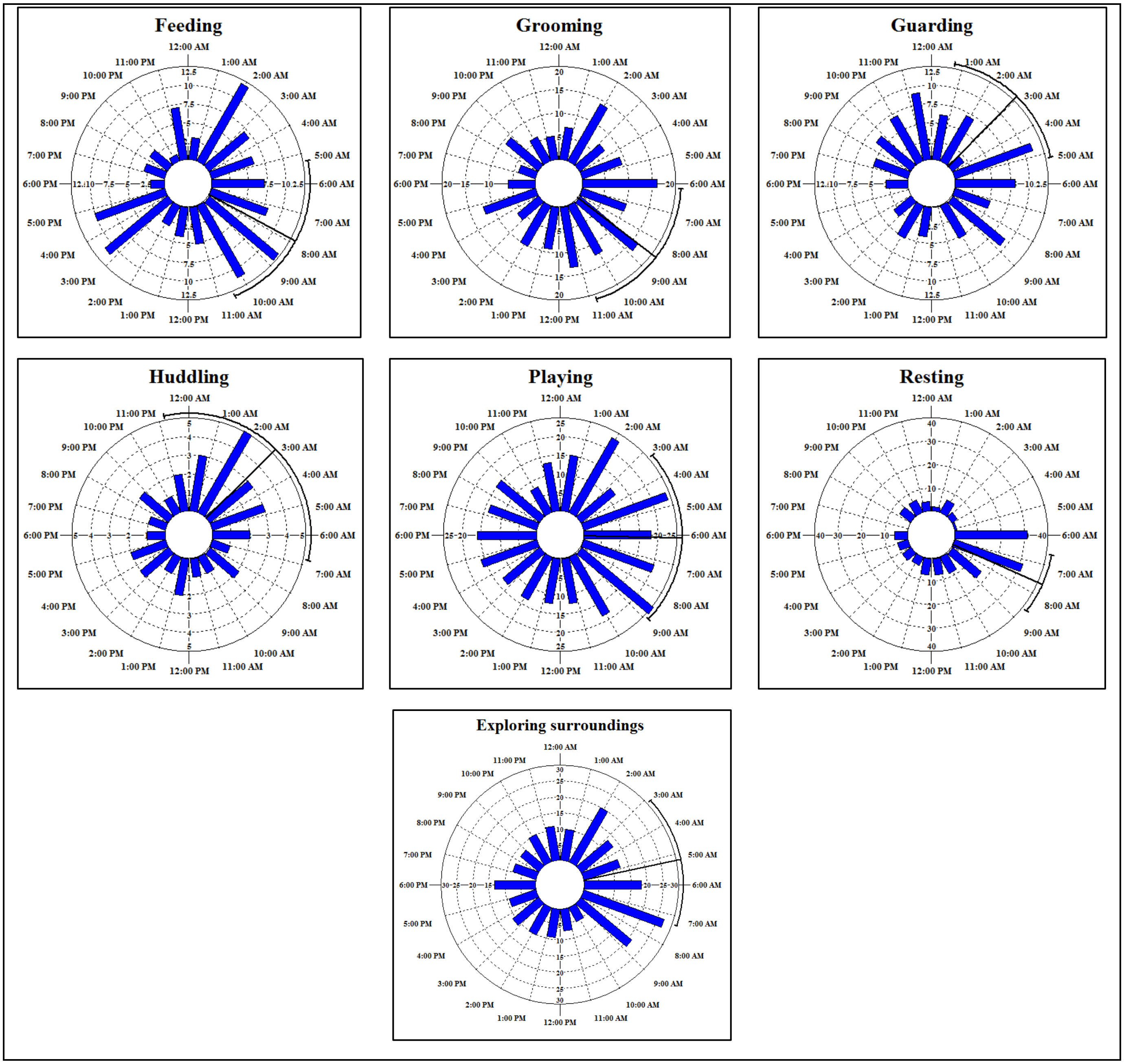
Time spent outside burrow

Figure 6.3. Daily records of emergence, retreat and time spent outside burrows after permanent occupancy by golden jackal in KNP. Bar represents the individual records and the line represents the mean vector and its circular standard deviation.

Table 6.6. Daily emergence, retreat pattern and peak time spent outside burrows after permanent occupancy; circadian activity patterns outside the burrows, and nocturnal activity of golden jackal during different lunar phase in KNP.

	Daily emergence, retreat and peak time pattern			**Activity outside burrow**							**Lunar phase**
	Emergence	Retreat	Time spent outside	Feed	Groom	Play	Rest	Explore	Guard	Huddle	Nocturnal activity
Number of observations	299	181	1346	115	171	287	148	222	95	35	681
Mean vector (μ)	180.40°	149.71°	109.80°	118.37°	127.29°	91.42°	114.07°	78.15°	44.18°	45.10°	283.42°
Mean time (Mean Group)	12:01 PM	9:58 AM	7:19 AM	7:53 AM	8:28 AM	6:05 AM	7:36 AM	5:12 AM	2:56 AM	3:00 AM	Waning crescent
Length of mean vector (r)	0.09	0.21	0.17	0.19	0.17	0.11	0.43	0.17	0.24	0.23	0.48
Circular standard deviation	125.96°	101.28°	108.69°	104.87°	107.31°	120.25°	74.62°	107.84°	96.60°	97.96°	75.68°
Standard error of mean	26.20°	14.20°	6.57°	19.99°	17.76°	21.57°	7.40°	15.87°	16.95°	29.13°	3.54°
Rayleigh test (Z)	2.38	7.96	37.50	4.04	5.13	3.51	27.14	6.43	5.54	1.89	118.96
Rayleigh test (p)	0.092	0.00035	<0.0001	0.018	0.006	0.03	<0.0001	0.002	0.004	0.15	0

Other activities (Fig. 6.4) like feeding, grooming, playing, resting, exploring the surrounding and guarding significantly peaked between 0500 to 1000 h ($Z = 4.04$, $p = 0.02$), 0600 to 1100 h ($Z = 5.13$, $p = 0.01$), 0300 to 0900 h ($Z = 3.51$, $p = 0.03$), 0630 to 0830 h ($Z = 27.14$, $p < 0.001$), 0300 to 0700 h ($Z = 6.43$, $p = 0.002$) and 0030 to 0500 h ($Z = 5.54$, $p = 0.004$) respectively (Table 6.6). Frequency histogram of feeding activity also projected three peak time-slots, namely 0130 to 0230 h, 0830 to 1000 h and 1530 to 1630 h (Fig. 6.4).



Feeding

Grooming

Guarding

Huddling

Playing

Resting

Exploring surroundings

Figure 6.4. Circadian activity by golden jackal and the litters outside the burrows in KNP. Bar represents the individual records and the line represents the mean vector and its circular standard deviation.

The lunar phase was associated with the nocturnal activity of jackal, which was observed to be higher between ‘third quarter’ to ‘new moon’ phase (Fig. 6.5) with a significant peak ($Z = 118.96$, $p < 0.001$, Table 6.6) during the waning crescent phase.

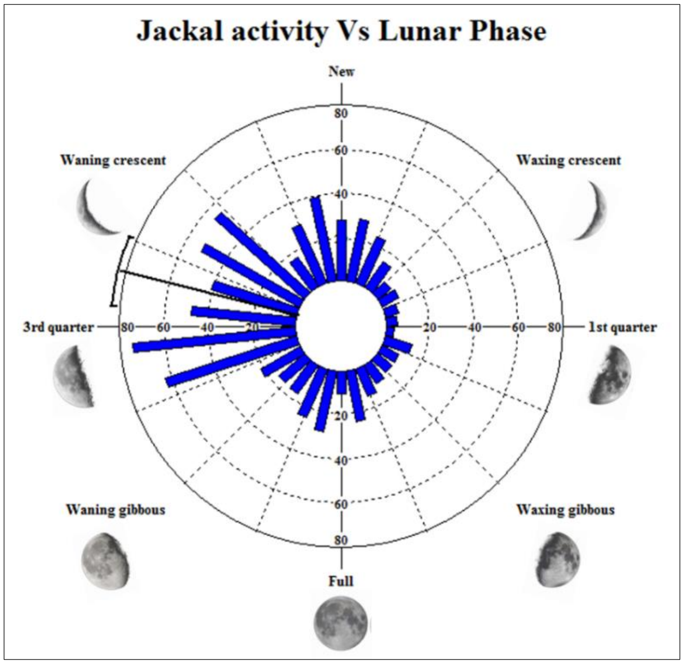


Figure 6.5. Nocturnal activity of golden jackals during corresponding lunar-phase (One burrow; N=40 days; Total snapshots = 696; Bar represents the individual records and the line represents the mean vector and its circular standard deviation).

Major activities including ‘burrow inspection’ and ‘burrow modification’ was significantly associated with increasing temperature and decreasing humidity. ‘Marking’ however was associated with neither. Low temperature and corresponding high humidity was significantly associated with (Table 6.7) specific activities like feeding ($R_T = -0.47$, $p = 0.02$; $R_{RH} = 0.45$, $p = 0.03$), grooming ($R_T = -0.52$, $p = 0.01$; $R_{RH} = 0.46$, $p = 0.03$), playing ($R_T = -0.48$, $p = 0.02$; $R_{RH} = 0.46$, $p = 0.03$) and guarding ($R = -0.67$, $p < 0.001$; $R_{RH} = 0.66$, $p < 0.001$). Any change in temperature or humidity did not significantly affected other activities including, emergence, retreat, exploring surrounding, huddling and resting.

Table 6.7. Pearson's correlation between temperature (RT) and humidity (RH) influencing the activities of golden jackals around the burrow system in KNP.

Major Activities	Temperature (°C)	Relative humidity (%)
2013-2016 (n = 48)		
Inspection	$R_T = 0.50, p < 0.001$**	$R_{RH} = -0.58, p < 0.001$**
Marking	$R_T = 0.01, p = 0.93$	$R_{RH} = 0.12, p = 0.24$
Burrow modification	$R_T = 0.34, p = 0.02$*	$R_{RH} = -0.30, p < 0.001$**
Breeding season (n = 23)		
Overall activities	$R_T = -0.45, p = 0.03$*	$R_{RH} = 0.44, p = 0.04$*
Emergence	$R_T = -0.25, p = 0.24$	$R_{RH} = 0.24, p = 0.26$
Retreat	$R_T = -0.31, p = 0.15$	$R_{RH} = 0.30, p = 0.16$
Exploring surroundings	$R_T = -0.31, p = 0.15$	$R_{RH} = 0.32, p = 0.13$
Feeding	$R_T = -0.47, p = 0.02$*	$R_{RH} = 0.45, p = 0.03$*
Grooming	$R_T = -0.52, p = 0.01$*	$R_{RH} = 0.46, p = 0.03$*
Guarding	$R_T = -0.67, p < 0.001$**	$R_{RH} = 0.66, p < 0.001$**
Huddling	$R_T = -0.05, p = 0.81$	$R_{RH} = 0.02, p = 0.93$
Playing	$R_T = -0.48, p = 0.02$*	$R_{RH} = 0.46, p = 0.03$*
Resting	$R_T = -0.25, p = 0.25$	$R_{RH} = 0.27, p = 0.21$

6.3.4. Intensity of activity around the burrow

A total of 696 activity records were captured during the breeding season of a jackal that lasted for 40 days. The intensity of each activity was analyzed across six weeks (Fig. 6.6). The activities including feeding ($\chi^2 = 30.76$, $p < 0.001$), grooming $\chi^2 = 33.85$, $p < 0.001$), guarding ($\chi^2 = 28.91$, $p < 0.001$) and playing ($\chi^2 = 34.65$, df = 5, $p < 0.001$) significantly occurred between fourth and sixth weeks (Table 6.8). However, 'exploring surroundings' and 'resting' were not significantly restricted to any week. Jackals spent an average of 103.60 min (± 154.74_{SD}) per 24 h on playing, followed by guarding (36.13 min), grooming (20.18 min), feeding (6.95 min), resting (3.74 min) and exploring the surroundings (1.17 min).

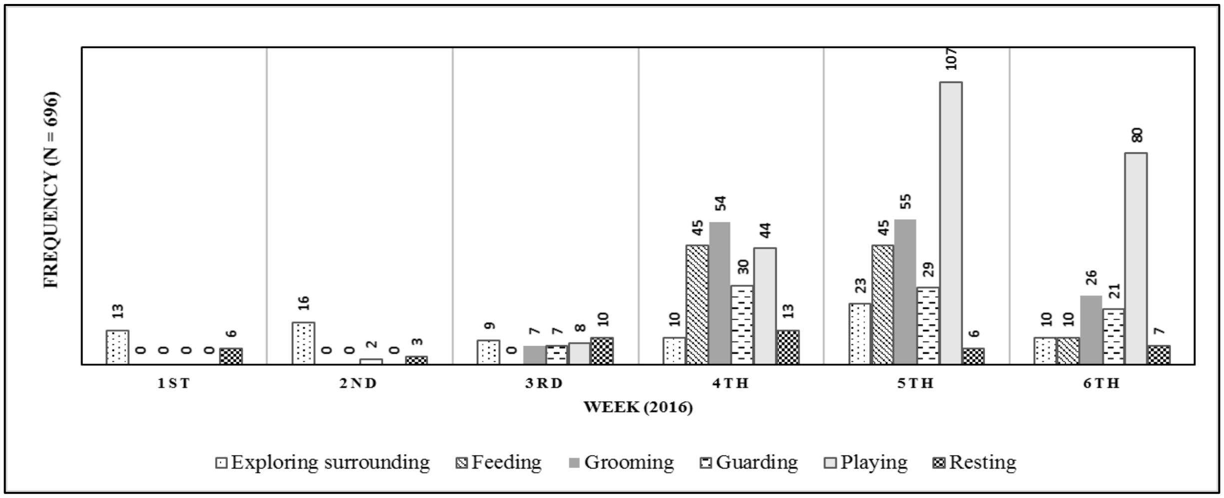


Figure 6.6 Frequency of activities outside the burrow across six weeks during the breeding season of the golden jackals in the year 2016 in KNP (One burrow; N=40 days; Total snapshots = 696)

Table 6.8. The mean time spent on various activities outside the burrow by the golden jackal breeding pair and the pups in 24 hours during the breeding season of 2016. (N=40 days; Total snapshots = 696).

Activity	Frequency of occurrence	Duration of activity (min)	Mean duration ± SD (min)	Kruskal Wallis test
Explore	81	46.75	1.17 ± 1.27	$\chi^2 = 6.39$, df = 5, p = 0.27
Feed	100	278.00	6.95 ± 16.40	$\chi^2 = 30.76$, df = 5, $p < 0.001$
Groom	142	807.00	20.18 ± 28.54	$\chi^2 = 33.85$, df = 5, $p < 0.001$
Guard	89	1445.00	36.13 ± 56.18	$\chi^2 = 28.91$, df = 5, $p < 0.001$
Play	239	4143.83	103.60 ± 154.74	$\chi^2 = 34.65$, df = 5, $p < 0.001$
Rest	45	149.67	3.74 ± 6.29	$\chi^2 = 1.51$, df = 5, p = 0.91

6.4. Discussion

Suitable and safe natal burrow site is important for the survival of golden jackal populations wherein they give birth and rear their young ones. The results of the study indicate that the golden jackals in KNP frequently visited the burrows throughout the year. The general activities around the burrows begin with ‘inspection’ of the burrow sites and scent ‘marking’; followed by specific activities such as, ‘burrow modification’ and ‘rearing of pups’ restricted to March-July and April-May respectively. The jackal in KNP occupied 23.4 % of the 47 burrows and selected natal sites with more vegetation cover and small openings. During the pup rearing season, jackals were found active outside the burrow throughout the day, executing specific activities around the burrows. These include feeding, grooming, playing, resting, exploring the surroundings and guarding. The burrow-specific activities during pup rearing season lasted for six weeks.

Though the golden jackals were frequently seen around the burrows, their nocturnal activity significantly peaked between 'third quarter' and 'new moon' phase in KNP. Similarly, other canids have also shown this peak in activity, for e.g. crab-eating fox (Yanosky and Mercolli, 1990; Faria-Corrêa et al., 2009) and maned wolf in Brazil, wherein the latter traveled significantly more on nights of the new moon than compared to the full moon (Sábato et al., 2006). It is likely that the increased activity in the last quarter and new moon nights could be associated with a circumvention behavior including possible detection by prey and protection from predators (Yanosky and Mercolli, 1990; Sábato et al., 2006).

In KNP, interspecific burrow sharing and facilitative interaction have been observed between the primary burrower i.e. Indian crested porcupines, and non-obligatory commensals i.e. golden jackals, leaf-nosed bats and Indian rock pythons (Chapter 4). In the present study, the jackal as 'secondary modifiers' (Kinlaw, 1999; Sillero-Zubiri et al., 2004) has occupied only 20 to 25% of the existing porcupine burrows in KNP during April- May. The present data is similar to the previous findings on several other canids which are also secondary excavators. For example, raccoon dogs, used 8% of the Eurasian badger burrows in Žemaitija National Park, Lithuania (Ulevičius, 1997); raccoon dogs and red foxes occupied 33% and 20% of the burrows of Eurasian badgers respectively during the breeding season in Białowieża Primeval Forest, Poland (Kowalczyk et al., 2008). Likewise, kit fox, dingo, crab-eating fox, short-eared dog and bush dog were also known to use existing burrows of prairie dog, wombat, armadillo, and paca (Sillero-Zubiri et al., 2004; Faria-Corrêa et al., 2009). Since jackals inhabit the burrows only for a short period during their breeding season (Jhala and Moehlman, 2004), they seem to have opportunistically selected the existing burrows to avoid energetic cost in digging new burrows (Vleck, 1979; Frafjord, 2003; Zelovà et al., 2010). In addition to regular visits to burrow sites, the jackals selected abandoned Indian crested porcupine burrows as the natal sites in locations with more wood cover and entrances with small opening with more herb cover. The thick cover at burrow sites of golden jackal reduces the predation risk of vulnerable pups as also observed by Saad et al. (2015) in Jhelum district of Pakistan. Similarly, other canids such as female red wolf (*Canis rufus*) in eastern North Carolina, USA, seek shelter in shallow surface depressions located in dense vegetation (Kelly et al., 2004). Likewise, the natal burrows of kit foxes in

Tooele County, Utah had small entrances with high vegetation cover. The physical burrow characteristics and the surrounding habitat are critical for the successful rearing and propagation of the young ones (Bekoff and Wells, 1982).

The mean detections of the pups and rearing of pups peaked during April-May corresponding to the rearing season of golden jackal in Israel (Golani and Keller, 1975), and India (Jhala and Moehlman, 2008). Most of the canids are seasonal breeders (Holt et al., 2014), albeit canids such as bush dog exhibiting no seasonality. The breeding timings of different canid species differed across the globe, however, the season of the breeding remained during the dry season. For example, the short-eared dog in Peru (Leite Pitman and Williams, 2004), maned wolves (*Chrysocyon brachyurus*) in South America (Rodden et al., 1996; 2004), the Indian fox (Acharjyo and Misra, 1976; Johnsingh, 1978; Johnsingh and Jhala, 2004), and the dholes (*Cuon alpinus*) (Davidar, 1973; Johnsingh, 1982; Venkataraman, 1998) in India, are all breeding during the dry spell. In India, the dry spell is followed by the monsoon and several of these abiotic factors affect the breeding onset and subsequent birth of young ones (Lehman et al., 1997; Prendergast, 2005; Holt et al., 2014). Thus, optimizing the survival of the young ones, due to factors such as appropriate ambient temperature; abundant nutrition and water availability; and probable variations in the predation activities of other species (Moehlman, 1979; 1983; 1987).

The specific activities of jackal around the burrows are throughout 24 h during breeding and rearing season, which is in concordance with jackal’s cathemeral behavior (Sharma et al., 2013). Specific activities like feeding, grooming, playing, resting and exploring the surroundings significantly peaked during early hours of the day in concurrence with lower temperatures. Increased temperature with the day’s progress significantly reduced the activities of the jackal around the burrows and they were observed retreating around 1200 h. Guarding of the burrows by adults significantly increased during night hours (0030 to 0500 h), when the pups are more susceptible to predation. Some predators like striped hyena can be a threat to the unattended pups. Similarly, pup-guarding by adults was observed in other canids e.g. African wild dog (*Lycaon pictus*) (Courchamp et al., 2002), hoary fox (*Lycalopex vetulus*) (Dalponte and Courtenay, 2004), and pampas fox (*Lycalopex gymnocercus*) (Lucherini et al., 2004). The pups were suckling every eight hours, around 0200, 0900 and 1500 h; and when the pups were about three weeks old, in addition to milk, regurgitated food also became part of the diet. This was similar to the golden jackals in Serengeti (Estes, 1991) where the pups suckle at least five times a day and twice at night for the first month followed by consuming disgorged food by the end of the month.

It was observed in the present study that both the sexes participated in parental care activities, taking turns to guard the burrow, grooming and playing with the pups. The male exhibited female care, including food supplementation prior to birth and throughout nursing, which is similar to male parental care in few other canids (Moehlman, 1978; Moehlman, 1989; Sillero-Zubiri et al., 2004; Dalponte and Courtenay, 2004; Lucherini et al., 2004; Bothma, 2013). In few quantitative field studies of jackals (Moehlman, 1978; Malcolm, 1985), the female attendance around the burrows dropped to ~ 35% of the time from the third week onwards as they were engrossed in extensive foraging after the first two weeks of confinement, with subsequent increase in paternal attendance to almost twice the time from the second to the fourth week.

The breeding success of all species depends on several factors, of which availability of a suitable natal site and a microhabitat as a refuge for rearing the young is a vital factor. Except in Antarctica, canids occur across the globe (Sillero-Zubiri et al., 2004), and hence the availability and use of an appropriate burrowing site for rearing their young ones are highly significant for the propagation of their population. Despite prominence in their range and some of them being highly generalist, they still prefer to select safe shelter for breeding to avoid running into the risk of predation (Tannerfeldt et al., 2003). In view of this, the study is relevant as it delivers a collective and detailed account of the use of the sub-surface earthen refuge by the golden jackal in semi-arid conditions of KNP. The present study affirms that the jackals are highly selective of their natal sites with a preference for appropriate cover. The burrow usage is largely restricted during the breeding season, corresponding to the dry season prevailing in the region. The rearing of the pups around the burrows lasted for six weeks, wherein the adults and the pups exhibited true cathemeral behavior and remained active throughout the day. The low temperature conditions and changes in lunar phase influenced the variations in burrow specific activity patterns including the timing of emergence and retreat from the burrows. All the comprehensive information thus provides noteworthy inferences for further understanding of the biology of this cathemeral canid.

PLATE 6.1

(a) Marking; (b) Burrow modification (Digging); (c) Guarding; (d) Grooming; (e) Suckling pups and (f) Regurgitating.

CHAPTER 7

Burrow use pattern by Indian Rock Python

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7.1. Introduction

The physiological performances of all organisms whether an ectotherm or an endotherm is vastly temperature dependent (Huey, 1979; Geiser, 1985; Angilletta, 2010). All organisms have evolved and adapted to virtually all possible thermal environment of the earth (Johnston and Bennett, 2008). Particularly in terrestrial ectotherms, adaptive behavioral thermoregulation is an essential proximate factor influencing their physiology (Strelnikov, 1934; Sergeyev, 1939; Cowles and Bogart, 1944; Reinert, 1993). The evolution of thermoregulation in poikilothermic reptiles particularly arose because environments thermally fluctuate both on a daily and seasonal basis with irregular heat disseminations within environments (Bogert, 1949). Consequently, reptiles attempt to attain physiological optimum body temperatures by exploiting the thermal distribution patterns in the environment (Shine, 1980; Huey et al., 1989; Adolph, 1990). Thermoregulatory behavior in reptiles is a critical mechanism that enables them to enhance physiological performance including running speeds, growth, reproduction and digestion (Huey and Slatkin, 1976; Saint Girons, 1980; Shine, 1980; Huey, 1991). In the temperate areas, reptiles largely rely upon behavioral thermoregulation for maintaining their body temperature within a specific range (Bulté and Blouin-Demers, 2010). The behavioral thermoregulation commonly includes behavior such as selecting appropriate activity times (Crawford et al., 1983; Sinervo and Adolph, 1994) as well as postural adjustments (Boyer, 1965; Seebacher, 1999). Several studies on thermoregulatory behavior have been recorded in many snake species including the free ranging water snake *Natrix fasciata* and *N. taxispilota* in the United States (Osgood, 1970), the captive Indian rock python *Python molurus* (Vinegar, 1973, 1974; Vyas, 1996, 1998; Walsh and Murphy, 2003), the captive Burmese python *P molurus bivitattus* (Van Mierop and Barnard, 1976a, 1976b; Brashears and DeNardo, 2013), the ball python *Python regius* (Ellis and Chappell, 1987), the free ranging diamond python *Morelia spilota* (Sup and Shine, 1988), the Brazilian boid snakes (Pizzatto and Marques, 2007), the Children's python *Antaresia children* (Lourdais et al., 2008; Lorioux et al., 2012) and the water python *Liasis fuscus* (Stahlschmidt et al., 2012).

Of all the thermoregulatory behaviors, ‘basking’ is the most conspicuous, wherein the animal exposes whole or at least a part of their body to thermal radiation while being immobile (Bulté and Blouin-Demers, 2010). Some reptiles spend up to 80 % of their time inside their burrows or other microrefugia in cold climates, which is also a thermoregulatory behavior where the primary function is avoiding critically low body temperatures (Pearson and Bradford, 1976). Upon favorable ambient conditions, the reptiles then emerge from their burrows and spend long and frequent basking periods acquiring appropriate body temperatures (Boyer, 1965; Hammond et al., 1988; Janzen et al., 1992). In arid and semi-arid regions, burrows appear to be crucial micro-refuges to several species of reptiles, providing protection against temperature extremes and predation (Kinlaw, 1999). The chapter investigate the adaptive strategies of a poikilothermic Indian rock python in extreme weather condition that prevails in the arid and semi-arid region of northern India. The Indian rock python of Pythonidae family is found in many tropic and sub-tropic areas of southern and southeast Asia ranging from Pakistan, India, southern Nepal, Sri Lanka, Bhutan, Bangladesh and probably in the north of Myanmar (Whitaker and Captain, 2004). It is listed as ‘Schedule I’ species in Wildlife Protection Act of India, 1972. The Indian rock python is one of the large bodied charismatic non-venomous species and they often use the burrows in the winter in arid and semi-arid regions as a refuge site (Bhupathy and Haque, 1986). However, they often come out of the burrows and bask to regulate their body temperature (Bhupathy and Haque, 1986). When several individuals come out for basking, they are more easily visible and often highly disturbed by people (Daniel, 1983).

Keoladeo National Park (hereafter, KNP) is known to have one of the highest populations of India rock python in India (O’ Shea, 2007). Only short-term assessment of Indian rock python population is available for KNP where Bhupathy and Vijayan (1989) reported 105 individuals and Krishnan et al. (2009) reported 112 individuals. The species in its range is recorded to have unimodal diurnal activity pattern during winter and a bimodal crepuscular activity pattern during the summer (Bhatt and Choudhury, 1993). Daniel (1983) reported increased nocturnal activity with an increased level of disturbance. The cost-benefit model of thermoregulation (Huey and Slatkin, 1976) which has support from numerous studies on lizards and snakes (Blouin-Demers and Weatherhead, 2002) predicts that ectotherms should invest more in thermoregulation when the costs of doing so are low in a thermally superior habitat (Huey and Slatkin, 1976). In KNP, the open basking grounds provide the desired high quality of thermal habitat to the thermoregulating pythons during the winters. However, despite the availability of such superior conditions, the continuous disturbance caused by the tourists can differ the central prediction of the cost-benefit model. Hence the chapter also investigates whether any anthropogenic disturbance set fundamental limits on behavioral repertoires, including patterns of emergence and retreat into the burrow and basking periods by Indian rock python.

7.2. Methods

7.2.1. Field Methods

A total of 41, 43, and 47 burrows were visited in the year 2013-14, 2014-15 and 2015-16 respectively, to determine the minimum population size of Indian rock python in KNP. Of the 47 burrows in 2015-16, six burrows were continuously monitored from October 2015 to May 2016 to understand the daily emergence, retreat and basking pattern of the Indian rock python. Due to high the influx of tourists to the KNP, the disturbance level was categorized as (1) disturbed burrow with more than 15 visits by tourists per day at a proximity of less than 20 m from the burrow, (2) semi-disturbed burrows with 1 to 14 visits by tourists per day at a proximity of less than 20 m, and (3) undisturbed burrow with no tourist footfall. According to this disturbance level, three separate burrows were selected (Fig. 7.1) to determine the level of disturbance by tourists on the activity pattern of India rock python, and they were monitored from October 2015 to May 2016.

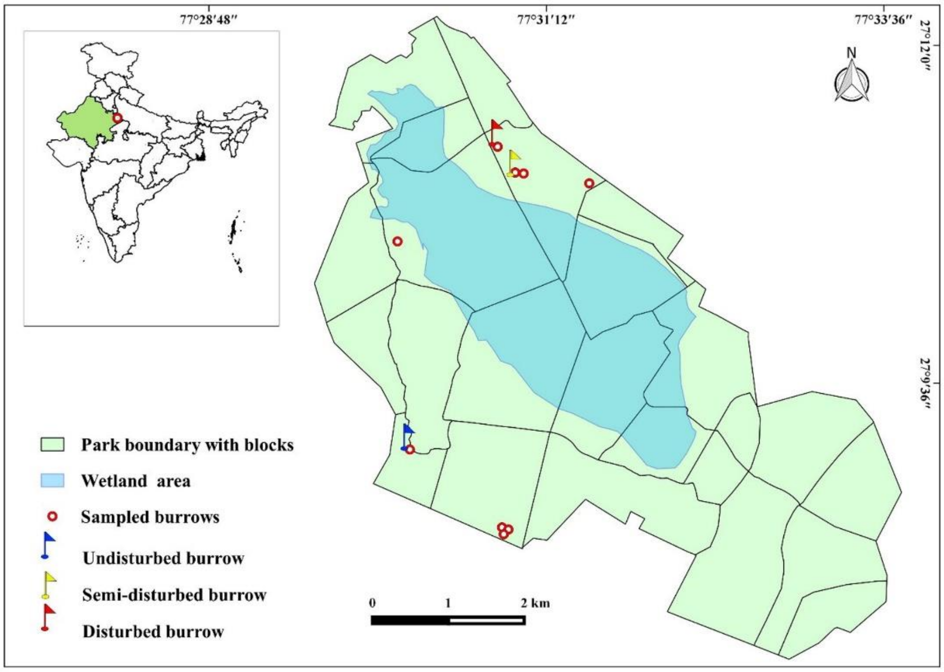


Figure 7.1. The location of KNP in Rajasthan state of India (Inset). Map showing burrows monitored for quantifying the burrow-use activity by Indian rock python during the study period. The flagged burrows were chosen to determine the level of disturbance by tourists on the activity pattern of python

For determining the minimum population size of India rock python in KNP, fortnightly observations were carried out at the burrow sites from November 2013 to October 2016, wherein the number of individuals present outside the burrows was counted from about 50 to 100 m using binoculars to avoid any disturbance to the basking pythons. The fortnightly counts were conducted on a clear weather between 1000 h– 1400 h, presuming that all individuals would emerge for basking. At each burrow site, a scan sampling of 15 min was conducted. The counts were simultaneously repeated for four days in quick succession on all the burrow sites and the maximum number of sightings of pythons at a given burrow was then considered for the analysis.

To understand the daily emergence, retreat and basking pattern of Indian rock python, intensive monitoring of six burrows was carried out using high sensitive passive infrared (PIR) motion sensor camera-traps (Boskon Guard Scouting, BG-520 series) investing a total effort of 1092 camera-trap days. The three burrows selected for determining the impact of tourist’s disturbance was monitored using camera traps for 137 days from 0700 h to 2000 h, comprising a total of 411 camera-trap days. Furthermore, each of the burrows selected in disturbed, semi-disturbed and undisturbed areas had an equal number of pythons (n = 8) to avoid discrepancies in the analysis.

The camera traps were deployed at six active burrows for investigating the overall basking and burrowing behavior. Another set of three burrows were selected, one in each disturbed, semi-disturbed and undisturbed areas. The cameras were in continuous ‘on’-mode with a trigger gap of 10 sec. The extremely sluggish movement of India rock python would often cause failure of camera trigger; hence the cameras were deployed in continuous on mode. With each trigger, a set of three pictures were captured, with date and time registered on each image. Every third day, the photographs were downloaded and saved with the identity of burrow and month. The photographs were screened and managed by filtering faulty photographs. The time of the initial trigger was considered, in cases, pythons repeatedly triggered cameras without leaving the field of view. After deployment of the camera traps, utmost care was taken to minimize the disturbance while changing the batteries every third day, by visiting the burrow either before 0700 h or after 1800 h. We presumed that different environmental variables might influence the activity of India rock python around the burrow. To ascertain this presumption, the data on sunrise and sunset obtained from the official website of Indian Meteorological Department, Govt. of India. The ambient temperature was recorded using Onset® Hobo^{TM} automatic data loggers. Four data loggers were deployed to spatially cover the entire KNP, and the data from the nearest logger was extracted for each burrow system. The data were recorded six times in an hour at the interval of 10 min. The hourly-mean of the logged data was then used for further analysis.

7.2.2. Data Analysis

To determine the minimum population size of Indian rock python in the KNP, the percentage of burrows occupied in each year was determined based on a number of burrows occupied per sampled burrows. This was further used to determine the expected number of burrows occupied and the mean group size in each year. The population size was then computed as a product of mean group size with the expected number of burrows occupied in each year.

The duration of time spent outside the burrows by India rock python was pooled across the months of October 2015 to May 2016, and the data across the months were analyzed using Rayleigh Z statistics (Batschelet, 1965; Zar, 1999) in Oriana software ver. 4.01 (Kovach, 2009). The frequency of emergence and retreat, and duration of basking time by India rock python was pooled across one-hour intervals and standardized as per the number of individuals present in each burrow; as the number varied across the burrows. The mean emergence and retreat rate at hourly intervals were calculated using SPSS v.16.0 (SPSS Inc., 2007). The mean duration of basking time (in min) was calculated for each hour per day and hourly variation in basking time is compared using Kruskal Wallis test.

Similarly, in the case of disturbed, semi-disturbed and undisturbed burrows, the mean of emergence rate, retreat rate and duration of basking time (in min) at hourly intervals per day was calculated and the variations across different burrow types were compared using Friedman test.

The hourly mean of the logged temperature data was used for further analyzing the effect of temperature on emergence, retreat and basking events recorded in a particular hour of the day. To determine the relationship between sunrise and sunset on retreat and emergence pattern respectively, the daily difference for each event (in hours) was calculated and the median value with range was obtained. To ascertain the influence of sunrise time on emergence time, sunset time on retreat time and that of temperature on emergence, retreat and basking duration, Pearson's correlation test was performed in SPSS. For this, all the ‘time’ values were formatted to ‘decimal’ values in excel using the formula: hour (cell number) + minute (same cell number) / 60 + second (same cell number) / 3600.

7.3. Results

7.3.1. Indian rock python population size

Of the 41 burrows in 2013-14, 43 burrows in 2014-15 and 47 burrows in 2015-16, 73.2%, 69.8% and 66.0% burrows were occupied by pythons, respectively (Table 7.1). The mean group size per burrow ranged from 2.4 to 3.0 individuals. The estimated minimum population size of the India rock python was 79.8 ± 10.3_{SD} individuals’ in KNP. s

Table 7.1. Burrow use and estimated minimum population size of Indian rock python in KNP

	2013-14	**2014-15**	**2015-16**
Total Burrows sampled	41.0	43.0	47.0
Burrows occupied	30.0	30.0	31.0
% Burrow occupied	73.2	69.8	66.0
Mean group size (SD)	2.6 ± 2.1	2.4 ± 1.5	3.0 ± 2.5
Population size	77.1	71.1	91.1

7.3.2. Activity across different months

A total of 1092 camera-trap days produced 1104 activity records of Indian rock python around the burrows. The activity of pythons around the burrows was confined between November and April. Daily activity records (Fig. 7.2) of India rock python outside burrow showed a significant peak in February ($Z = 100.4$, $p < 0.001$; Table 7.2) spending a mean time of 45.0± 18.3_{SD} min per day. In April, January and March, pythons spent a mean time of 41.8 ± 10.8_{SD} min, 39.6 ± 11.1_{SD} min and 38.4 ± 7.2_{SD} min outside burrow per day respectively. However, mean time spent per day outside the burrow was less in the months of November (22.3 ± 16.7_{SD} min) and December (13.2 ± 8.5_{SD} min).

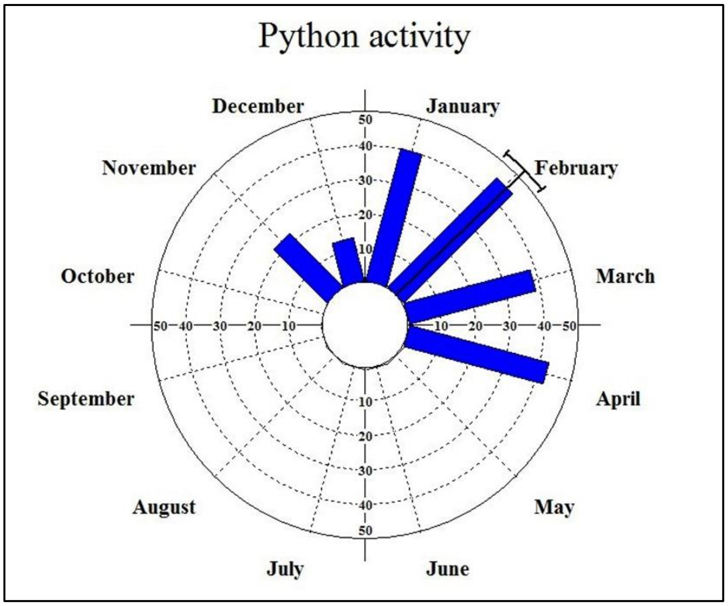


Figure 7.2. Duration of the daily activity of Indian rock python outside burrows across different months of the year (Nov 2015 to October 2016) in KNP. Bar represents the individual records and the line represents the mean vector and its circular standard deviation

Table 7.2. Activity outside burrows across different months of the year by Indian rock python in KNP.

Circular Parameters and Statistics	Python activity
Number of Observations	681
Mean Vector (µ)	45.9°
Mean Group	February
Length of Mean Vector (r)	0.7
Circular Standard Deviation	47.6°
Standard Error of Mean	3.4°
Rayleigh Test (Z)	100.4
Rayleigh Test (p)	0.000

7.3.3. Overall emergence, retreat and basking pattern

The pythons were active outside burrow from 0800 to 1800 h. The overall daily emergence and retreat rate of Indian rock python (Table 7.3) peaked between 0900 to 1000 h and 1700 to 1800 h respectively. A significant difference was observed in the basking time at different h of the day ($\chi^2 = 50.9$, df = 9, $p < 0.001$). The mean basking time during morning 0800 to 0900 h (20.0

± 12.8 $_{SD}$ min) and evening 1700 to 1800 h (23.8 ± 19.1 $_{SD}$ min) was relatively lesser than in post-noon. The mean basking time per day reached a peak in the post-noon h (Fig. 7.3) between 1200 to 1500 h (mean basking time ranged from 47.2 to 49.3 min).

Table 7.3. Rate of emergence and retreat in different time-intervals of the day by Indian rock python in KNP. (N= 1092 camera trap day; Emergence = 185 captures, Retreat = 166 captures)

Time-slot	**Emergence (Mean ± SD)**	**Retreat (Mean ± SD)**
08:00-09:00	0.143 ± 0.00	-
09:00-10:00	**0.156 ± 0.01**	**-**
10:00-11:00	0.142 ± 0.02	-
11:00-12:00	0.139 ± 0.02	-
12:00-13:00	0.144 ± 0.03	0.140 ± 0.02
13:00-14:00	0.143 ± 0.02	0.139 ± 0.02
14:00-15:00	0.146 ± 0.02	0.141 ± 0.03
15:00-16:00	**-**	0.136 ± 0.01
16:00-17:00	**-**	0.147 ± 0.03
17:00-18:00	**-**	**0.149 ± 0.02**

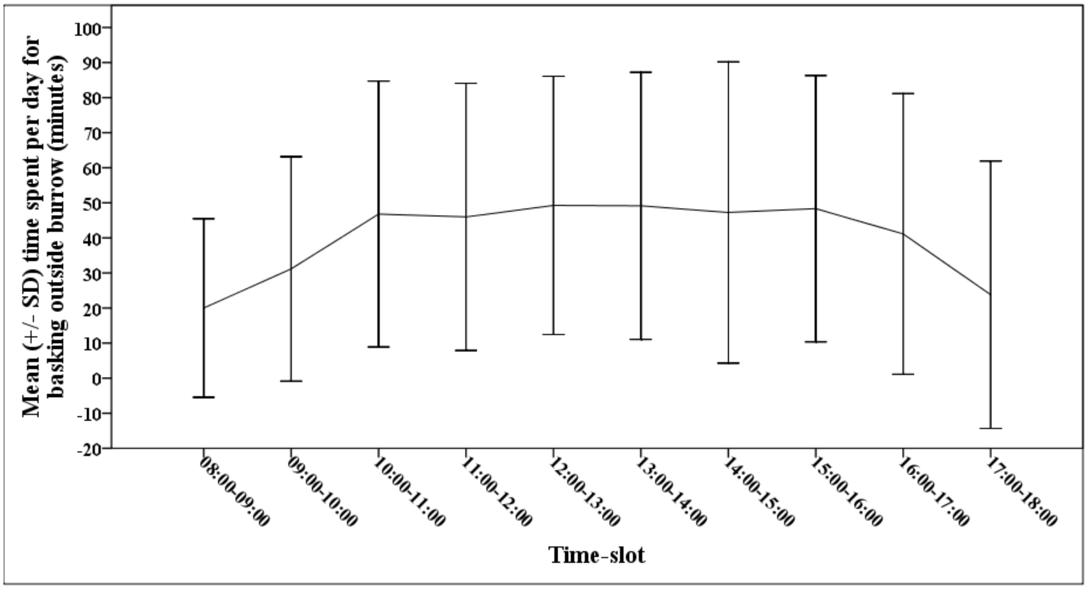


Figure 7.3. Duration (in min) spent per day for basking outside burrow in different time-intervals of the day by Indian rock python in KNP

The pythons mostly basked around the burrow within 5 m of the openings. In few instances, they were observed to move away from the burrows and basked under the bushes at proximity of 5 to 10 m from the burrow openings. They exhibited limited movements and basked by placing part of their body in the shade or by coiling to reduce the exposed surface area of the body. Apart from basking on ground, some individuals were also recorded basking on tree branches. Some of the burrows were present 0.5 to 1m from the *Salvadora persica* trees on which pythons would spend the entire basking period. Pythons would mostly bask in individually in linear position exposing their full body, at times with few individuals linearly inter-coiling. During periods of low light and on the cold winter days with less sunlight, the individuals would mostly bask just at the entrance without any movement.

7.3.4. Different disturbance gradient and activity pattern

The difference in the rate of emergence ($\chi^2 = 13.0$, df = 2, p = 0.002) and retreat ($\chi^2 = 6.9$, df =2, p = 0.03) was significant across disturbed, semi-disturbed and undisturbed burrows in different h of the day. In undisturbed burrows, the emergence rate peaked during 1000 to 1100 h ($0.1 \pm 0.0_{SD}$), whereas, it peaked during 1100 to 1200 h ($0.4 \pm 0.1_{SD}$) and 1400-1500 ($0.3 \pm 0.2_{SD}$) in semi-disturbed and disturbed burrows respectively (Table 7.4). Similarly, in undisturbed burrows, the retreat rate peaked during 1600 to 1700 h ($0.1 \pm 0.0_{SD}$), whereas, it peaked during 1700 to 1800 h ($0.2 \pm 0.1_{SD}$) and 1300-1400 ($0.2 \pm 0.1_{SD}$) in semi-disturbed and disturbed burrows respectively (Table 7.4).

The time spent for basking significantly varied ($\chi^2 = 14.9$, df = 2, $p < 0.001$) between disturbed, semi-disturbed and undisturbed burrows across different time-slots. The time spent for basking doubled in the undisturbed burrows compared with the disturbed burrows across all time intervals of the day (Fig. 7.4). The mean basking time per day reached a peak during 1300 to 1400 h for undisturbed ($59.4 \pm 02.8_{SD}$ min), semi-disturbed ($39.0 \pm 22.0_{SD}$ min) and disturbed ($36.2 \pm 26.7_{SD}$ min) burrows. The pythons in semi-disturbed ($08.0 \pm 07.0_{SD}$ min) and undisturbed burrows ($30.8 \pm 14.7_{SD}$ min) continued basking even during 1700 to 1800 h, but was never recorded in disturbed burrows in the same time interval.

Table 7.4. Daily emergence and retreat rate into burrows by Indian rock python in Disturbed (D), Semi-disturbed (S) and Undisturbed (U) burrows in KNP. (N= 137 days; Emergence$_{(D)}$ = 160 captures, Emergence$_{(S)}$ = 71 captures, Emergence$_{(U)}$ = 50 captures; Retreat$_{(D)}$ = 60 captures, Retreat$_{(S)}$ = 83 captures, Retreat$_{(U)}$ = 54 captures)

Time-slot	Emergence (Mean ± SD)			Retreat (Mean ± SD)		
	Disturbed	Semi-Disturbed	Undisturbed	Disturbed	Semi-Disturbed	Undisturbed
08:00-09:00	-	-	-	0.20 ± 0.00	-	-
09:00-10:00	0.20 ± 0.00	-	0.11 ± 0.00	0.20 ± 0.00	-	-
10:00-11:00	0.23 ± 0.07	0.25 ± 0.00	**0.13 ± 0.03**	0.20 ± 0.00	-	-
11:00-12:00	0.21 ± 0.05	**0.35 ± 0.05**	0.11 ± 0.00	0.20 ± 0.00	0.17 ± 0.00	-
12:00-13:00	0.26 ± 0.18	0.31 ± 0.00	0.12 ± 0.00	0.20 ± 0.00	0.17 ± 0.00	0.12 ± 0.00
13:00-14:00	0.25 ± 0.1	0.30 ± 0.00	0.11 ± 0.00	**0.24 ± 0.09**	0.17 ± 0.00	0.11 ± 0.00
14:00-15:00	**0.28 ± 0.15**	0.25 ± 0.00	0.11 ± 0.00	0.23 ± 0.08	0.17 ± 0.00	0.12 ± 0.00
15:00-16:00	0.20 ± 0.00	0.25 ± 0.00	-	0.20 ± 0.00	0.17 ± 0.00	0.13 ± 0.00
16:00-17:00	0.20 ± 0.00	0.17 ± 0.00	-	-	0.17 ± 0.00	**0.14 ± 0.00**
17:00-18:00	-	-	-	-	**0.20 ± 0.07**	0.13 ± 0.00

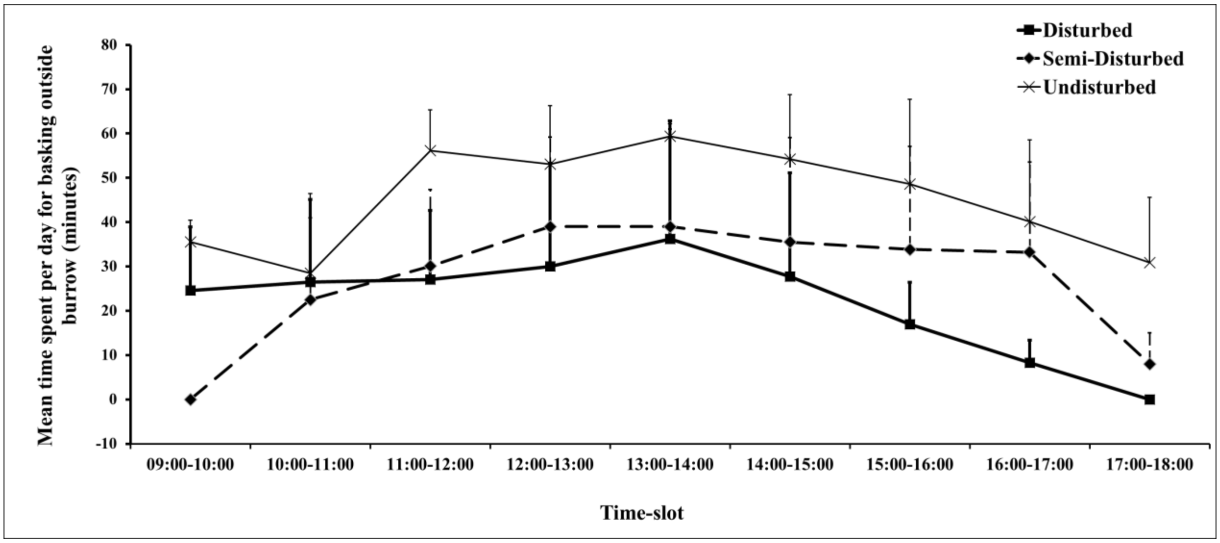


Figure 7.4. Duration (in min) spent per day for basking outside burrows in disturbed, semi-disturbed and undisturbed state by the Indian rock python in KNP

7.3.5. Variables affecting the activity pattern

A total of 313 emergence event timings were compared with the sunrise timings. The median emergence time of India rock python (Fig. 7.5) was 4 h 48 min after sunrise (range = 1 h 15 min to 7 h 18 min after sunrise). Similarly, a total of 103 retreat event timings were compared with the sunset timings. The median retreat time of India rock python (Fig. 7.5) was 2 h 1 min before sunset (range = 2 h 57 min to 0 h 43 min before sunset). Also, the emergence timings positively correlated with the sunrise timing ($R = 0.1$, $p = 0.02$) and increasing temperature ($R = 0.4$, $p = 0.02$). Whereas, the retreat timings positively correlated with the sunset timing ($R = 0.4$, $p < 0.001$) but not with increasing temperature ($R = 0.2$, $p = 0.25$).

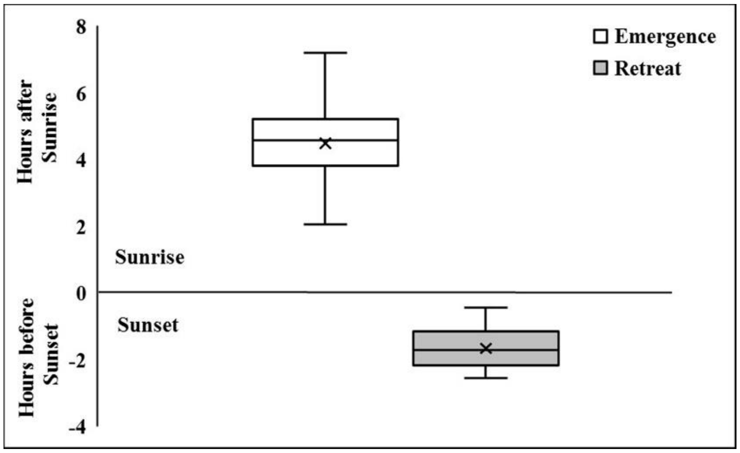


Figure 7.5. Variation in emergence time with sunrise time; and retreat time with sunset time for Indian rock python in KNP.

The pythons emerged from the burrows in an ambient temperature range of 4°C to 45°C (n = 411). The mean ambient temperature during emergence from the burrow was 25.5°C ± 11.4°C $_{SD}$. The peak in emergence rate was observed at 24.3°C ± 2.1°C $_{SD}$. The emergence rate decreased with temperatures below 13°C (n = 26) and above 35°C (n = 35). The retreat rate of India rock python occurred between the ambient temperature range of 8°C to 45°C (n = 273). The mean ambient temperature during the retreat from the burrow was 25.7°C ± 11.1°C$_{SD}$. Only a few retreats were observed at temperatures below 9°C (n = 2) and above 40°C (n = 9).

7.4. Discussion

The estimated minimum population size of India rock python in KNP was 79.8 ± 10.3$_{SD}$ individuals. During the active months of November to April, a general pattern of India rock python activity was observed wherein pythons emerged at 0900 to 1000, with a peak in mean basking time during 1200 to 1300 h following retreat at 1700 to 1800 h. In undisturbed burrow, pythons emerged at 1000 to 1100 h, with a peak in mean basking time of $59.4 \pm 02.8_{SD}$ min per day. However, in disturbed burrows, a significant change in the emergence, retreat and basking duration was observed with only $36.2 \pm 26.7_{SD}$ min of mean basking time.

The method of estimating the population size of the pythons by computing the product of mean group size with the expected number of burrows occupied in each year was also effectively used to estimate the population of various reptile species such as Alligator *Alligator mississippiensis* (Thompson and Gidden, 1972), European pond turtle *Emys orbicularis* (Lebboroni and Cecchini, 2005), and Massasauga rattlesnake *Sistrurus catenatus* (Shoemaker and Gibbs, 2010). In India, the India rock python population in KNP is the only one subjected to monitoring (Bhupathy and Vijayan, 1989). The previous estimation of India rock python population in KNP was 105 individuals in 1986 -87 (Bhupathy and Vijayan, 1989) and 112 individuals in 1999- 2000 (Krishnan et al., 2009). The earlier estimation was based on individual identification using variations in the natural markings (Bhupathy, 1990). Since individual identification was not possible in camera traps, the present finding reports the minimum population size based on a maximum number of individuals emerged per burrow in the winter season. The previous findings suggest that all individuals residing in the burrow would not emerge daily for basking (Krishnan et al., 2009), hence, the actual count of India rock python number could have been underestimated even in case different individuals had emerged.

In the present study, pythons were found congregating in large numbers around the burrows during the winters of November to March. Similarly, in the plain forests of northern Bengal and Sikkim (Shaw et al., 1939) and Darjeeling foothills of northern India (Pope, 1961), Indian rock python are often seen congregating from October to December, facilitating mating in these months (Pope, 1937). The Indian rock python in KNP basked continuously for 4 to 5 h a day, peaking between 1000 to 1600 h. Similarly, diamond python *Morelia spilota*, in southeastern Australia, spent an average of 3 to 4 h a day in basking (Slip and Shine, 1988). The basking India rock pythons in KNP were usually lying folded laterally on one another similar to the large bodied *Boa constrictor imperator* in Mexico (Myres and Eells, 1968), ensuring maximum body exposure to the sun.

The emergence and retreat regimes and the prolonged basking periods by Indian rock python confirm their need to thermoregulate at elevated temperatures for a minimum amount of time per day during cold climates to reach optimum body temperature for carrying out physiological activities, especially reproduction (Saint Girons, 1980; 1982). This behavioral adaptation is in affirmation with the Huey and Slatkin's (1976) cost-benefit model of thermoregulation, which predicts that the time spent in thermoregulation will be more when the costs of thermoregulating are low. The cost of thermoregulating by Indian rock python is absolutely nil, as they have to just come out from their burrows in order to bask. Our comparisons between the disturbed, semi-disturbed and undisturbed burrows highlight the differences in Indian rock python activity across the burrows. In KNP, disturbance by tourists has been previously reported and was considered as threats to the pythons in KNP (Bhupathy and Vijayan, 1989; Krishnan et al., 2009). The pythons remained in basking habit throughout the day in undisturbed burrows. Once preferred body temperature was obtained, they exhibited limited body movements by placing part of its body in the shade or by coiling to reduce the exposed surface area of the body similar to the observation in large bodied carpet python *Morelia spilota imbricata* in southwestern Australia (Pearson et al., 2003). However, in this study, the exact assumption of the optimum body temperature has not been quantified for further affirmation. In the case of disturbed burrows, the continuous approach of tourists resulted in repeated failed emergence attempts in all time-slots of the day. The mean basking time spent in disturbed burrows was almost half of the time spent on basking in undisturbed burrows. The semi-disturbed burrow recorded fewer tourist visits after 1500 h, and the basking period by India rock python was observed to be extended to 1800 h, conceivably to compensate for the disturbance in continuous basking regime in other time-slots of tourist visits before 1500 h. This change observed in the basking behavior ascertains that, despite the utmost favorable conditions, the continuous approach of tourist is disrupting the cost-benefit model of thermoregulation wherein the reptile must thermoregulate maximum under superior thermal environment.

Reptiles are ectothermic producing limited metabolic heat and essentially depending on ambient temperature to regulate their body heat (Saint Girons, 1980). Thus, affirming the importance of basking durations even in the case of Indian rock python during their breeding season from November to egg laying season in May (Smith, 1935; Bhupathy, 1993; Ramesh and Bhupathy, 2010). The observations on breeding thermoregulatory behavior in reptiles suggests that gravid females spend more time basking than do non-gravid females, for at least three reasons: (i) higher body mass corresponds to slower heating rates in gravid females, therefore taking longer to attain preferred body temperatures; (ii) females select higher temperatures to speed up embryonic development; and (iii) females may select higher temperatures to compensate for their lowered mobility when gravid (Shine, 1980). Basking periods are equally important in the case of male reptiles (Saint Girons, 1982) wherein the spermatogenesis occurs only at a particular temperature, for example in European adder *Vipera berus* in Europe, spermatogenesis cannot occur below 21-22°C (Joly and Saint Girons, 1975). Apart from reproduction, the ambient temperature affecting the body temperature of reptiles ultimately affects the intensity oxygen consumption (Saint Girons, 1980). For example, in reptiles every 10°C rise temperature increases the oxygen consumption by a factor of 2.4 (Bennett and Dawson, 1976), similarly, in the case of python, brooding females require 9.3 times more oxygen compared to non-brooding females (Hutchison and Maness, 1979).

Pertaining to the importance of thermoregulation in Indian rock python, the burrows appear to be crucial thermal micro-refugia, especially during the cold periods in the semi-arid region of KNP. Pythons are oviparous snakes that show distinct thermoregulatory behavior (Shine and Madsen, 1996), wherein temperature affects the dynamics of all physiological processes, thereby influencing many facets of its breeding life. The present study highlights the change in basking regime of Indian rock python in disturbed and undisturbed habitats. KNP, being one of the important wintering grounds for migratory birds, witnesses an enormous number of tourists during October to April each year. During the present study, it was observed that a few burrows were repeatedly visited by tourists at the proximity of less than 10 m, forcing pythons to retreat and emerge more frequently. The continued disturbance of the burrows by tourist forces pythons to retreat without basking for the optimum period repeatedly. It eventually might lead to lower breeding rates (Bulté and Blouin-Demers, 2010; Huey and Slatkin, 1976; Huey, 1991), thereby affecting the natural physiology of the python and its population size in KNP. It is therefore suggested for the formulation of effective management plans to reduce the anthropogenic pressure on the India rock python population, in addition to continuous monitoring of their population.

PLATE 7.1

(a) Emergence; (b) Retreat; (c) Basking in group; (d) Disturbance 1; (e) Disturbance 2 and (f) Disturbance 3.

CHAPTER 8

Synthesis

"Nonconformity is the highest evolutionary attainment of social animals"

‡ *Aldo Leopold* ‡

Findings at a glance

Keoladeo National Park in India is an eminent ‘World Heritage Site’ renowned for large congregation of migratory waterfowl and heronry species, especially during the winter migratory season, commencing from November up to March. Apart from the 8.5 km^2 of wetland area, the terra firma area of 20.5 km^2 is a mosaic of woodland, scrubland, grassland and mixed thickets of a semi-arid region. In such mosaic habitat, animals adjust themselves to diverse ecological conditions and occupy virtually all possible habitats. The foremost prerequisite for the persistence of any organism is the presence and selection of appropriate refuge sites. KNP, which faces extreme tropical weather conditions, *Burrow Systems* are crucial micro-refuge supporting for many dependent life forms. These burrow systems in KNP might recurrently face the threat of inundation during heavy monsoonal rains resulting in variations in park’s water level. Hence, it was perceived that the area of burrow site selection could not be random. The Indian crested porcupine is the most conspicuous ‘primary’ burrow architect in selecting appropriate areas for burrowing. The porcupines avoided areas with water-cover, and selected areas closer to the boundary nearby agricultural fields at higher elevation as burrow sites. Thus, porcupines were observed to strategically create burrows at appropriate sites and as apex ecosystem engineers in this region that also provides favorable micro habitats for other co-occupants.

The exploration of the architecture of burrows using non-invasive methods of camera trapping and burrow video camera revealed the species assemblage in each burrow system. The burrow systems were majorly co-occupied by four vertebrate species; Indian crested porcupine, golden jackal, leaf-nosed bat and Indian rock python. All the animals except porcupine occupied burrows with specific burrow characters; wherein jackals occupied burrows with larger chambers, pythons occurred in smaller compact chambers and bats occupied burrows with fewer branching and openings. The choice of burrows for inhabitation by python increased with reduced chamber height. Internally, the animals occupied different positions of the burrow. The chambers of porcupines were deeper inside and of distinctive character, wherein the entrance of the chambers was closed by loose dug out soil, leaving a narrow slit for minimum air circulation. The pythons were coiled within concave caved-in chambers usually at the end of the tunnel branching not more than 5 m inside. The active porcupine chambers and tunnels predominantly had loose and dug out soil, in contrast to active python chambers having flat surface due to its serpentine movement. The bats gregariously occupied the ceilings and particularly roosted in groups in separate chambers other than that of porcupines and pythons.

The density of porcupine was $3.21 \pm 1.32_{SD}$ individuals/ km^2 with a population size of $65.89 \pm 27.15_{SD}$ individuals in KNP. Porcupine emerged earlier in winter and monsoon than in summers. In summers they emerged after sunset, once the temperature reduced to comfortable levels. In winters, the porcupines returned long before the sunrise. In monsoon, heavy rain days curtailed porcupine activity and they adjusted their emergence and retreat accordingly. The daily activity of adult porcupine outside burrow peaked in January-February, wherein they were regularly involved in digging and modifying the burrow. It was just before their breeding season, when porcupine prepares the burrows for the gestation period of 90 -112 days. The litter activity increased nearly 40-55 days after their birth during the month of May.

The golden jackal, a predominant 'secondary' burrower in the park occupied 23% of the existing burrows in the park during the breeding season, to avoid energetic cost in digging new burrows. Jackals selected the burrows in an area with more wood cover and burrows with small opening with more herb cover, thereby reducing the predation risk of vulnerable pups. The major activity around the burrow was high in the months of April and May which also corresponds to the breeding season of golden jackal. The continuous activity of jackal around the burrows throughout 24 hours is in concordance with jackal's cathemeral behavior. Specific activities like feeding, grooming, playing, resting and exploring the surrounding peaked during early hours of the day in concurrence with lower temperatures. Higher temperature with the day's progress reduced the activities of the jackal around the burrows and they retreated around 1200 hour. Guarding of burrows by adults increased during night hours (0030 to 0500), presumably the pups are more susceptible to predators like striped hyena occurring in the region and are active at night. The pups were suckled at every eight hours, around 0200, 0900 and 1500 hours. When the pups were about three weeks old, regurgitated food became part of the diet along with the mother's milk. The male golden jackal exhibited a high degree of participation during the breeding season that includes supplementation of food to females prior to the birth of pups and throughout nursing, and equally participated in by taking turns in guarding the burrow, grooming and playing with the pups.

KNP harbour one of the known highest populations of Indian rock python in India. These serpents are highly dependent on the already existing porcupine burrows in the park during the winter. They are largely 'tertiary' burrow occupants and exploit the existing burrows as significant refuge sites. The minimum population size of python based on a maximum number of individuals emerged per burrow in the winter was $79.78 \pm 10.29_{SD}$ individuals in the park. Pythons are ectothermic oviparous snakes that show distinct thermoregulatory behavior wherein temperature affects the dynamics of all physiological processes, thereby influencing many facets of its breeding life. Hence, any change in basking regime is presumed to have probable implication on the biology of python. The study highlights the probable behavioral variations in basking and burrow use pattern by python in vicinity of anthropogenic disturbances. In undisturbed burrows, pythons emerged at 1000 to 1100 hours, with a peak in mean basking time of $59.36 \pm 02.81_{SD}$ minutes per day during 1300 to 1400 hours following retreat at 1600 to 1700 hours. The pythons remained in basking for throughout the day in undisturbed burrows. In disturbed burrows, the continuous approach of tourists resulted in repeated failed emergence attempts. The emergence rate in disturbed burrows peaked only at 1400 to 1500 hours with a mean basking time of $36.24 \pm 26.65_{SD}$ minutes, almost half of the hours spent for basking in undisturbed burrows. The semi-disturbed burrow was visited less by tourists after 1500 hour, and thus the basking period by python extended till 1800 hours, conceivably to compensate for the disturbance in continuous basking regime in other time-slots of tourist visits before 1500 hour. Pertaining to the importance of thermoregulation in Indian rock python, the burrows are crucial thermal micro-refugia, especially during cold periods.

Burrows for all – Some as occupants and other as visitors

Three major burrow users of KNP are Indian crested porcupine, golden jackal, and Indian rock python. However, during the study several species were observed exploiting the resources from the existing burrows. Observations from 32 burrows show a total of 22 species (Table 8.1) utilizing the burrows in some on the other form. Amongst 22, ten were mammals, eight birds, three reptiles and one amphibia.

Table 8.1. Animals recorded around the burrows in Keoladeo National Park.

Taxa	Species	Scientific name	Burrow numbers
Mammals	Indian crested porcupine	*Hystrix indica*	32
	Golden jackal	*Canis aureus*	23
	Bat	*Hipposideros spp.*	21
	Indian grey mongoose	*Herpestes edwardsii*	9
	Rat	*Rattus spp.*	8
	Squirrel	*Funambulus spp.*	8
	Hare	*Lepus spp.*	7
	Striped hyaena	*Hyaena hyaena*	5 (1*)
	Jungle cat	*Felis chaus*	5
	Small Indian Civet	*Viverricula indica*	3
Reptiles	Indian rock python	*Python molurus molurus*	16
	Monitor Lizard	*Varanus bengalensis*	10
	Gecko	unidentified	9
Amphibians	Toad	unidentified	4
Aves	Indian peafowl	*Pavo cristatus*	28
	Indian robin	*Saxicoloides fulicatus*	23
	Grey francolin	*Francolinus pondicerianus*	12
	Greater coucal	*Centropus sinensis*	7
	Laughing dove	*Spilopelia spp.*	4
	Magpie robin	*Copsychus saularis*	4
	Jungle babbler	*Turdoides striata*	3
	Hoopoe	*Upupa epops*	3

*Number in parenthesis- Burrow occupied by striped hyaena for littering and pup rearing

Amongst mammals, the porcupine was present in all burrows, followed by jackal predominately using the burrow during breeding season and bats. The most persistently visiting mammals were mongoose, rat, squirrel, hare, jungle cat, and small Indian civet in order of their visits to the number of burrows (Table 8.1; PLATE 8.2). They mostly seen peeping into the burrow, sometimes entering possibly in search of food or for temporary shelter. The only carnivore other than jackal in KNP is striped hyaena, which was recorded visiting five burrows, but occupied only one during the breeding season (February and May), corresponding with the breeding season of porcupine, jackal and python. The hyaena population in KNP is restricted to three to four pairs and because of their elusive nature, they were often not seen and hence the burrow use pattern by them was excluded from the study. Amongst reptiles, python was recorded in 16 burrows of 32, which they primarily occupied during the entire winter season. Monitor lizard was recorded in 10 burrows, their burrow openings were typical vertical plunge hole and were separate from the ones used by porcupines or pythons. They were mostly seen seeking temporary shelter during the day time. Geckos gregariously occupied burrows and recorded in nine burrows, and were observed to emerge daily at night for feeding on small invertebrates, owing to their nocturnal feeding habit. Seldom, toads were recorded during monsoon season, seeking shelter at the entrance of the burrow opening. Apart from reptiles and mammals that were occasionally seeking shelter in the burrows, eight species of birds were the frequent visitors (PLATE 9.3). Amongst them, the Indian peafowl was a regular visitor which was recorded in 28 burrows. They were often in groups of more than ten individuals peeping into the burrow and feeding on small invertebrates. Indian robin also regularly visited 23 of 32 burrows primarily for feeding on insects. Interesting behavior was observed in robin, wherein they were always seen in a pair and each took turns to go inside the burrow for feeding, meanwhile other was perching outside and gave alarm call in case of any lurking danger. During an inspection of the internal architecture of the burrows using burrow video camera, several insects were observed approaching the camera lens. These insects and other invertebrates would have probably lured the insectivorous bird species towards the burrow systems for feeding. Similar observation of burrow sharing was observed in case of European badger *Meles meles* which shared their burrows with a total of eight mammal species: crested porcupine *Hystrix cristata*, Eastern cottontail *Sylvilagus floridanus*, red fox *Vulpes vulpes*, pine marten *Martes martes*, stone marten *Martes foina*, wood mouse *Apodemus spp*., brown rat *Rattus norvegicus* and coypu *Myocastor coypus*. Den sharing was observed throughout the year, with a significant reduction of sharing during winter, when badgers were probably induced to move to alternative setts to avoid breeding porcupines (Mori et al., 2014b).

Interaction among burrow occupants

When animals or groups of animals in their habitats come close to each other within a defined distance, it is termed as an association (Erinjery et al., 2016). All the occurrences of animals in and around the burrow system in KNP were recorded as independent events, where interspecific interaction or competition was observed between Indian crested porcupine, golden jackal and Indian rock python. The probability distribution function (PDF) was estimated to assess the differences in annual burrow use pattern by Indian rock python, Indian crested porcupine and golden jackal; and daily activity patterns of by Indian rock python and Indian crested porcupine. For this, the data for activity outside burrows during the day for Indian rock python and Indian crested porcupine was arranged by converting time to proportion of 24 h. Similarly, annual data for burrow use by species, was converted to proportion of year by dividing the day of the year by 365 (366 for a leap year). Both these proportion of the day and proportion of the year data were converted to circular radian time format by multiplying them by a factor of 2π, so that the circular variable statistics could be employed. PDF was estimated for each species through circular Kernel Density Estimation (KDE) using the package 'activity' (Rowcliff, 2016) in R statistical language (R Core Team, 2017). Wald test (W) was used to compare the difference in the activity pattern of the species. Proportion of overlap in daily activity and annual burrow use patterns was estimated as the true coefficients of overlap (Δ) using the package 'overlap' (Meredith and Rideout, 2017).

In case of burrow use pattern by porcupine and python, the true coefficient of overlap (Δ) throughout the year is relatively higher than their respective overlaps with jackal (Table 8.2). The annual occupancy of the burrows across the months also significantly differed between each species (Table 8.2).

Table 8.2. Annual distribution pattern of burrow use between Indian crested porcupine (ICP), Indian rock python (IRP) and golden jackal (JK) in Keoladeo National Park. (Δ - true coefficient of overlap, SE – standard error, W – Wald test, p – statistical significance)

	Δ	Difference	SE	W	p
ICP vs IRP	0.512	0.300	0.014	418.88	0.00
ICP vs JK	0.283	0.342	0.014	563.56	0.00
IRP vs JK	0.177	0.041	0.004	105.27	0.00

It is projected under the kernel density estimation curve that the porcupines use burrows throughout the year whereas python occupies it from late December to April; and jackals particularly occupy during their breeding season, i.e., from April to June (Fig. 8.1).

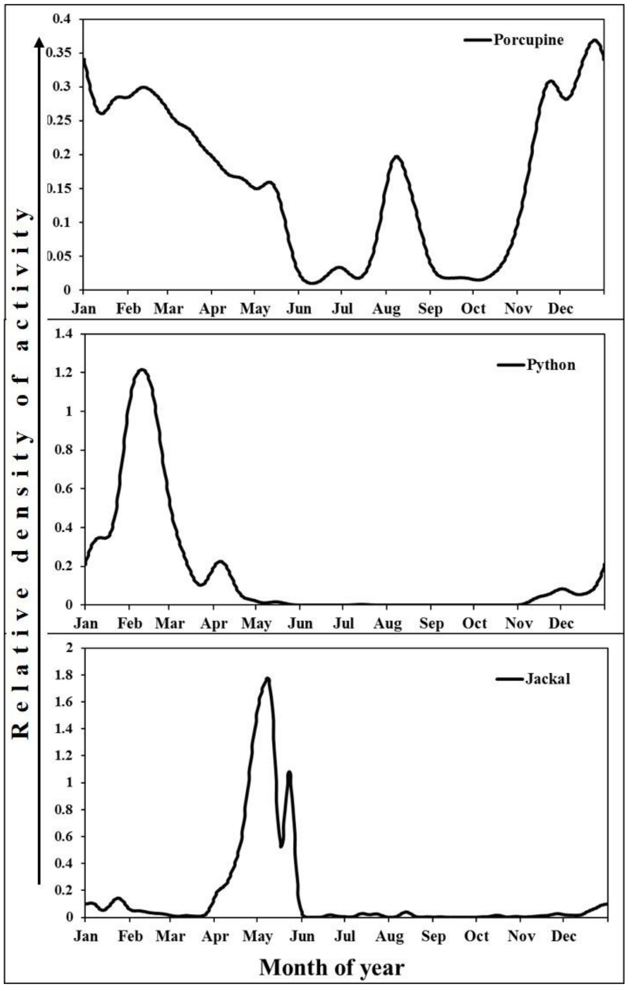


Figure 8.1. Density estimates of the monthly activity patterns of Indian crested porcupine (ICP), Indian rock python (IRP) and golden jackal (JK) in Keoladeo National Park. The solid lines are kernel-density estimates**.**

The study witnessed antagonistic interaction by golden jackal with both python and porcupine. The jackal was observed to visit 23 of 32 burrows, and the direct interaction was observed in seven burrows with python, wherein the jackal was able to eliminate python from four burrows (Table 8.3.). Similarly, jackal interacted with porcupine in five burrows, and was efficacious in eliminating porcupines from four burrows (Table 8.3). Jackal also burrow in several micro-habitats like rock crevices, thickets, culverts and similar hideouts, but can also use other animal burrows to reduce their energy cost in digging.

Table 8.3. Number of burrows with co-occupancy and antagonistic interaction between the major inhabitants of burrows in KNP

Co-occupancy	**No. of burrows with association**
Porcupine	7
Porcupine - Python	6
Porcupine - Bat	9
Porcupine – Python - Bat	10
Antagonistic Interaction	**No. of burrows with interaction**
Jackal - Porcupine	5 (4)
Jackal - Python	7 (4)

*Number in parenthesis- Number of burrows occupied by golden jackal after elimination of the respective competitor

The elimination of porcupine and python confirms the dominance of jackal, especially when there is a chance of exploiting the existing burrows. Similar observation was recorded for warthogs for access to the burrows which rely mostly on aardvark excavations (Cumming, 1975), and also compete intra-specifically with several other species including hyaenas, wild dogs and porcupine (Somers, 1992; Somers et al., 1994). Interestingly, all the burrows which were used by jackal in the study during their breeding season were regularly visited by porcupine and were re-occupied by the upon abandonment by jackal.

The types of interactions were classified into three classes ‘Non- aggressive’, ‘Aggressive – without contact’ and ‘Aggressive - with direct contact’ in order to understand the types and intensity of dyadic interactions between Jackal- Porcupine and Jackal- Python (Table 8.4). With porcupines, jackal exhibited ‘aggressive’ interaction without any direct contact, wherein the animals would intimidate each other. A total of 10 events of interactions (Table 8.5) were observed and at all the instances, the jackals were guarding their burrows from approaching porcupines. The interaction between them were recorded outside the burrow opening at a mean closest distance of 2.57 ± 0.61_{SD} m. The incidences occurred at an average time of 0228 h (range 0110 h to 0537 h) and the mean time spent/ interactions was 17.86 ± 5.67_{SD} s (Table 8.5). In case of jackals and python, a total of 22 events of interactions were observed between them, of that all the interactions happened in the burrows occupied by the python. Of the 22 interactions between jackal and python, 45.45 % of the interactions were 'non-aggressive' and 54.55 % was 'aggressive'. Amongst 'aggressive' interaction, 10 events (83.33%) were aggressive but without contact, and only two (16.67 %) were aggressive with direct contact. The proximity (Table 8.5) of the animals decreased with increased aggression, wherein the mean closest distance between the animals involved in non-aggressive interaction was 2.70 ± 0.82_{SD} m and in case of aggressive interaction without any direct contact was 1.10 ± 0.57_{SD} m. All the incidences occurred at an average time of 1405 h (ranges 1150 h to1559 h) and the mean duration of interactions was highest for aggressive interaction without any contact between the animals (347.00 ± 306.52_{SD} s), followed by 170.00 ± 98.99_{SD} s for aggressive interaction involving direct contact and lowest for non-aggressive interaction (27.00 ± 10.55_{SD} s; Table 8.5). A single account of interaction was observed between a python and jackals were in the latter was the burrow occupant. Camera traps were deployed at that burrow upon realizing that the jackals had given birth. There were 4 pups and 2 adult individuals. After 10 days of camera deployment, on May 13th, 2015 at 0742 h, a python was observed coiling at about 5 m from the burrow opening. Initially, the python did not show any movement for about 15 min. The jackals, even though aggressive, kept themselves at a safe distance from the python and were observed to guard their pups. The pups on the other hand showed inquisitive behavior, at times approached python, and came as close as 2 m. Upon their approach towards the python, the adults pulled the pups away and forced them inside the burrows. However, there was one pup, which was repeatedly coming out, but was constantly guarded by an adult. Seeing the python not moving, the adult jackals started growling at it and in response the python started to 'hiss' and puffed its body. At several occasions the python made attacking gestures towards jackals. This aggressive interaction continued till 0816 h until the python moved away from the burrow. The entire interaction took place without any physical contact between the two species and lasted for 34 min.

Table 8.4. Description of different categories of interactions between golden jackal, Indian rock python and Indian crested porcupine around the burrows in Keoladeo National Park

Interaction	Description
Non- aggressive	The approaching animal avoided any aggressive tactics and would pass by. The other animal upon detecting the approaching animal silently retreated into the burrow, thus terminating the interaction
Aggressive - without contact	The approaching animal moved towards the other animals with aggressive displays such as restless movement, visual contact, canine flash and growl (in case of jackal), rattling and shaking of quills (in case of porcupine) and hissing, puffing and rubbing of body (in case of python). Occasionally chased without any physical interaction. Encounter was terminated with either animals moving away.
Aggressive - with direct contact	The approaching animal moved towards the other animals, both showing aggressive behaviour. The aggression culminating in severe physical intimidation, including biting. The severe agonistic interactions continue, until one animal retreats, thus terminating the encounter.

Table 8.5. Frequency and mean time spent on neutral different categories of interactions between golden jackal, Indian rock python and Indian crested porcupine around the burrows in Keoladeo National Park

Python as burrow occupant approached by jackal			
	Non-aggressive	Aggressive without contact	Aggressive - with direct contact
Frequency of interaction	10	10	2
Overall rate of interactions	45.45	45.45	9.09
Mean Approach Distance (m)	2.7 ± 0.82	1.1 ± 0.57	0
Total duration of interaction (s)	265	3470	340
mean time spent (s)/ interactions	27 ± 10.55	347 ± 306.52	170 ± 98.99
Jackal as burrow occupant approached by porcupine			
Frequency	-	10	-
Rate	-	100	-
Mean closest Distance (m)	-	2.57 ± 0.61	-
Total duration of interaction (s)	-	125	-
mean time spent (s)/ interactions	-	17.86 ± 5.67	-

It was observed that Indian crested porcupine and Indian rock python showed association amongst each other while cohabiting in the same burrow. Even though, python is considered a predator of porcupine, no incidence of passive interaction and antagonism was observed. The possible reason is the temporal segregation of diurnal nature of python and nocturnal nature of porcupine, wherein the daily activity pattern (Fig. 8.2) outside the burrow differed significantly ($W = 20.91$, $p < 0.001$) with minimal overlap ($\Delta = 0.065$).

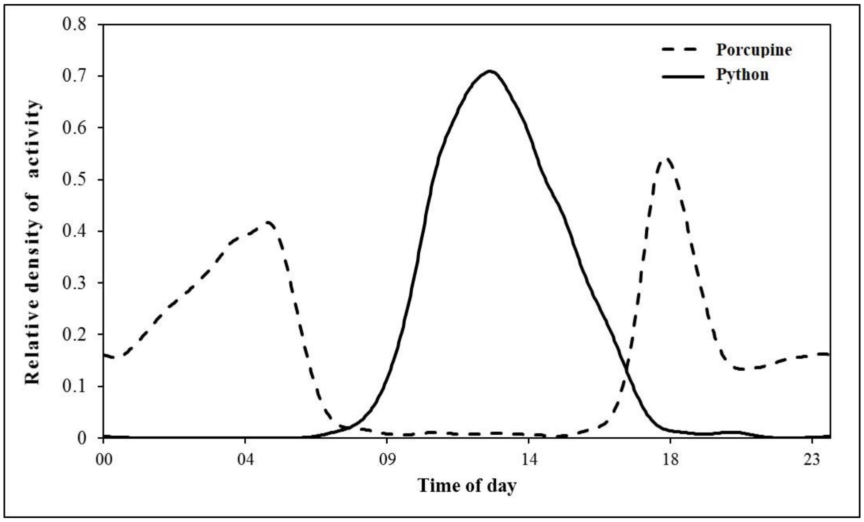
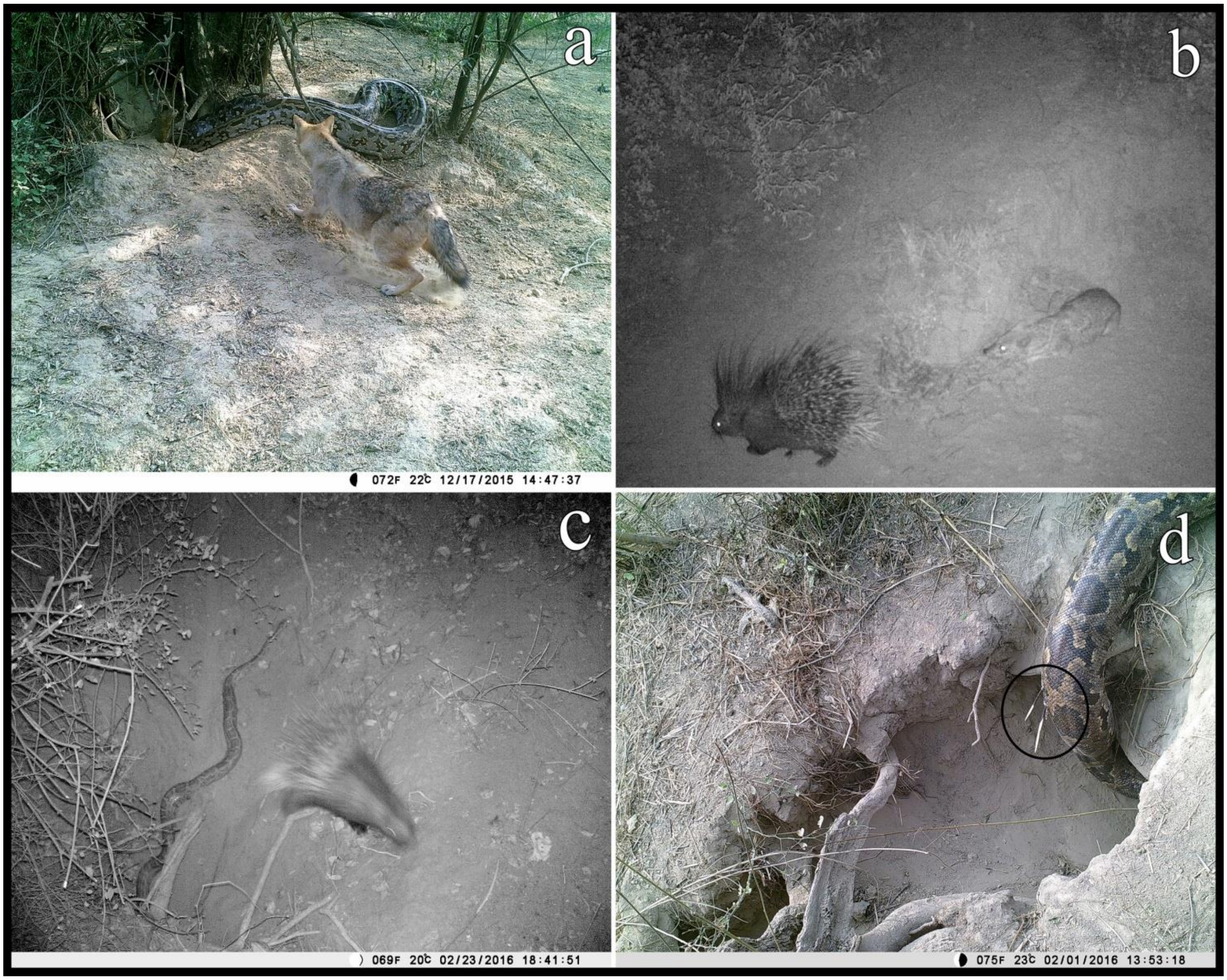


Figure 8.2. Density estimates of the daily activity patterns of Indian crested porcupine and Indian rock python in Keoladeo National Park. The solid lines are kernel-density estimates.

Similar temporal segregation in burrow use was observed between Warthogs *Phacochoerus africanus* and its competitors hyaenas *Crocuta crocuta*, wild dogs *Lycaon pictus*, and porcupine *Hysrix cristata* in KwaZulu-Natal, South Africa (White and Cameron, 2009). Another reason of python not predating on porcupines, could be attributed to the months of its burrow use. The burrow use by python is restricted between November and March corresponding with its breeding season, when they cease to feed during this period, resulting in reduced metabolic rate. In one incidence, python was observed to emerge from the burrow at midnight 0004 hours, with porcupine in the vicinity (PLATE – 9.1). The porcupine was alert with its raised quills, considered as defense strategy (Mori et al., 2013), but did not portray any aggression. In another incidence, porcupine quills were pierced into python body (PLATE – 9.1). Hence, chances of antagonistic interaction between porcupine and python cannot be completely ruled out.

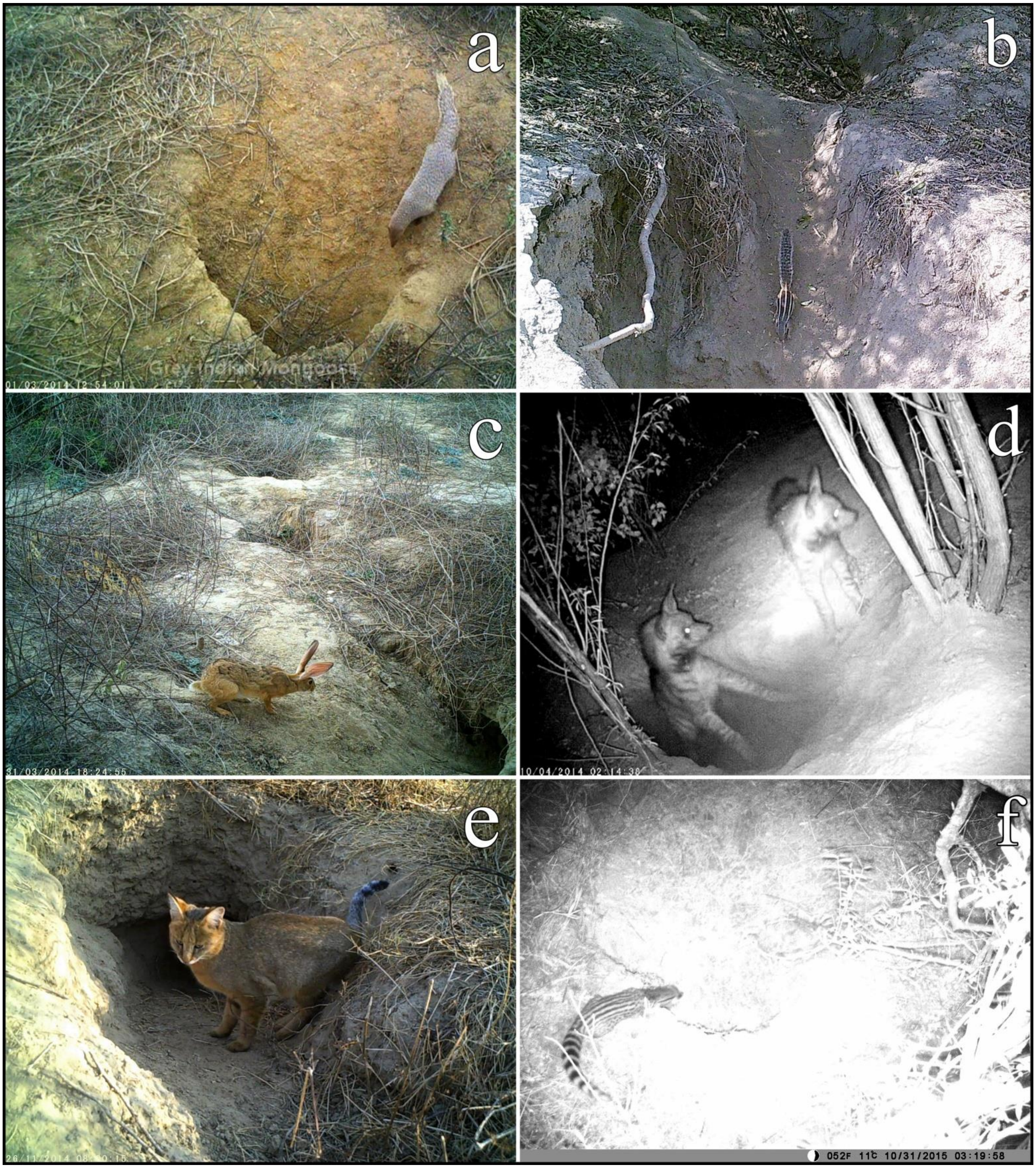
The usage of Indian crested burrows by numerous species in the featureless landscape of KNP explains the functional role of these rodents, often considered as pests (Alkon and Saltz, 1985; Khan et al., 2000). The range of species and their association always determines the ecological health of any habitat or microhabitat (Legendre, 2005), whereby there is an accentuated need of conservation and management of such species capable of creating significant refugia. The study provided a detailed and comprehensive account of the factors governing the burrowing behaviors and sub-surface burrow use pattern by numerous vertebrates, including their assemblage, specific activity at spatiotemporal scales, and their interactions. The observed assembly pattern of micro-communities has therefore established the importance of Indian crested porcupine and their burrows as ‘keystone’ structures in the semi-arid regions.

PLATE 8.1



Interactions between (a) Jackal and Python; (b) Jackal and Porcupine; (c) Python and Porcupine and (d) Python with quill.

PLATE 8.2



Burrow visiting mammals: (a) Indian grey mongoose; (b) Squirrel; (c) Hare; (d) Striped hyena pups; (e) Jungle cat and (f) Small Indian civet.

PLATE 8.3

Burrow visiting birds: (a) Indian peafowl; (b) Indian robin; (c) Gray francolin; (d) Greater coucal; (e) Laughing dove and (f) Magpie robin.

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