Female Mate Sampling in a Blackbuck (*Antilope cervicapra*) Lek in Tal Chhapar Wildlife Sanctuary, Rajasthan, India

by

Akshay A. J.

Enrolment no: 50BB24A73015

Dissertation thesis

Submitted to

Academy of Scientific and Innovative Research

For partial fulfilment of the degree

Master of Science

in

Wildlife Science

Under the supervision of

Dr. Bilal Habib – Scientist F (Supervisor)

Dr. Akanksha Rathore (Co-supervisor)

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

AcSIR

July 2026

DECLARATION

I hereby declare that the work conducted under the thesis entitled "**Female Mate Sampling in a Blackbuck (*Antilope cervicapra*) Lek in Tal Chhapar Wildlife Sanctuary, Rajasthan, India**", is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master's in Wildlife Science** at the **Academy of Scientific and Innovative Research.** This research work has been carried out under the guidance and supervision of **Dr. Bilal Habib, Scientist – F** of Wildlife Institute of India, Dehradun, and co-supervision of **Dr. Akanksha Rathore,** Assistant Professor, Birla Institute of Technology and Science, Pilani, Hyderabad Campus. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the the particulars given in it are true to the best of my knowledge.

Akshay A. J.

Enrolment No: 50BB24A73015

Place: Dehradun

Date:

Dr. Bilal Habib

Supervisor

CERTIFICATE

This is to certify that the thesis by **Akshay A. J.** entitled "**Female Mate Sampling in a Blackbuck (*Antilope cervicapra*) Lek in Tal Chhapar Wildlife Sanctuary, Rajasthan, India**" is an original and independent research work submitted to the **Academy of Scientific and Innovative Research,** for the award of the degree of **Master's in Wildlife Science.**

Akshay A. J. has put one semester of research work embodies in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma, or distinction.

Dr. Bilal Habib
Scientist -F
Supervisor

Dr. Ruchi Badola
Dean

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE OF PLAGIARISM CHECK

It is certified that the Master's dissertation thesis titled **"Female Mate Sampling in a Blackbuck (Antilope cervicapra) Lek in Tal Chhapar Wildlife Sanctuary, Rajasthan, India."** submitted by **Akshay A. J.**has been examined by us for plagiarism check as per UGC (Promotion of Academic Integrity and Prevention of Plagiarism in Higher Educational Institutions) Regulations. The following inferences are drawn from this check:

a) Thesis has significant new work/knowledge as compared to already published work or work under consideration for publication elsewhere.
b) No sentence, equation, diagram, table, paragraph or section is found to have been copied verbatim from previous work unless it was placed under quotation marks and the source was duly cited.
c) The work presented is original work of the author (i.e., there is no plagiarism) and there is no fabrication of data or result by manipulating research materials, equipment or processes, or by changing or by omitting data or results such that the research is not accurately represented.

The similarity indices as reported by the software Drillbit are as follows:

Software used	Date	Total world count	Similarity index
Drillbit	15.07.2026	17085	8%

The similarity index came as above. Scientific names, measuring units (SI) and references have been excluded from documents.

15/7/26

Mr. Manohar Pathak
Librarian

मनोहर पाठक / Manohar Pathak
पुस्तकालयाध्यक्ष / (Librarian)
पुस्तकालय एवं प्रलेखन केन्द्र
Library and Documentation Centre
भारतीय वन्यजीव संस्थान
Wildlife Institute of India
चन्द्रबनी, देहरादून, उत्तराखंड
Chandrabani, Dehradun - 248 001

Dr. Bilal Habib
Supervisor

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

ACKNOWLEDGEMENT

I would like to start by quoting the words that "*If I have seen further, it is by standing on the shoulder of giants*." The completion of my thesis marks the culmination of a journey that would not have been possible without the support, guidance, and encouragement of many individuals and institutions. Firstly, I would like to thank my supervisor Dr. Bilal Habib for not only trusting me with the research idea, but also for placing your confidence in me by providing two brand-new drones for the project. Having the opportunity to take them to the field was both exciting and rewarding, and it added a unique dimension to the study. I am deeply grateful for your trust, support, and guidance throughout the course of work.

I would like to express my sincere gratitude to my co-supervisor Dr. Akanksha Rathore for your constant support throughout the study and in helping me integrate drone-based approaches in the study.

I would like to thank my course director, Dr. Sutirtha Dutta, for giving us a wonderful two years of experience and memory. Having you as our course director was one of the best parts of our M.Sc. life. I would also like to thank our assistant course director, Dr. Amit Kumar for the support, encouragement, and encyclopaedic knowledge of plants.

I would like to thank Shri. Umesh Bagotia, Range Forest Officer, Tal Chhapar Wildlife Sanctuary, for helping me in ways beyond my imagination. You played an indispensable role in the study and your generosity and hospitality were unwavering throughout my field work. I will always remember your reassuring words, "Main hu na", which invariably meant that a solution was at hand.

I would like to thank the Director, Dean, the Registrar and all the faculties of Wildlife Institute of India for the wealth of knowledge and the privilege to experience something truly unique and remarkable. I would like to thank Negi ji, Srikant ji, Hari Kishan ji, and all the administration staff of WII for a smooth processing of the logistical stuff.

I would like to thank the Chief Wildlife Warden of Rajasthan and the entire Rajasthan Forest department for granting me permission within a short period of time after the application.

I would like to thank my Lekk-arazi team, Anshul, Swathi, and Aneesha, for helping me out in the field. Over the course of study, you became much more than field interns – you were constant sources of encouragement, companionship, and emotional support during both challengeable and enjoyable moments.

I would like to thank Richpal ji, Narendra ji, Sarvan ji, and the late Somji for making the stay at Tal Chhapar as comfortable as possible and making it feel home.

I would like to thank Qamar sir and Dr. Jhala sir for their valuable suggestions.

I would like to thank Dipin for his insightful methodological suggestions, and endless willingness to discuss ideas. His encouragement, thoughtful inputs, and readiness to engage in scientific discussions played an important role in shaping this study.

I would like to thank Jyothi, Mayank, and Jayabharathy for replying to my enquiries and providing me their thesis to inspire me and think in new directions.

I would like to thank Dr. Aadil Kazi, Dr. Bimal Desai, and Dr. Rohit for their constant support and knowledge during my under graduation. It was the place where wildlife really caught up to me.

I would like to thank my batchmates, both wildlife and freshwater, for all the memories that were made and for the memories yet to come. I would like to thank Kiru for helping me with analysis, Ash for the stickers, and Ardra for the moist memories. I would like to thank my freshwater gangs who took my jokes as jokes and kept the spirit of humour alive.

I would like to thank my juniors and seniors, especially Isaka, Silambam master for helping in the study and being constant companions in the institute. I would like to thank Mohit anna, Abhishek anna, Ashish bayya, Ballu bayya, Abishek bayya, Rakshi, Ashik, Manyu, Shilpa di, and a Messi lover, and all the other bays and annas whom I have missed to mention the names, for the beautiful memories along with the side-by-side inputs.

I would like to thank team Swaeroes for being the best part of M.Sc. life. Long live Swaeroes.

I would like to thank Samil for lending his room and sacrificing his privacy for us to chill and sleep whenever we want.

I would like to thank my family for supporting me to pursue what I want without any hesitation.

I would also like to thank an anonymous girl for giving some memorable moments.

And finally, to all the female blackbuck who quietly demonstrated their tactics. Unaware of the answers they helped answer, they revealed a world of subtle decisions and complex behaviours that formed the heart of this study.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

LIST OF ABBREVIATIONS

AIC	Akaike Information Criteria
GLM	Generalized Linear Models
GLMM	Generalized Liner Mixed Effect Model
GPS	Global Positioning System
UAV	Unmanned Aerial Vehicle
WLS	Wildlife Sanctuary

EXECUTIVE SUMMARY

Mate choice is a fundamental component of sexual selection, and the behavioural mechanisms through which female sample males have been the focus of extensive theoretical research. Numerous mate sampling models have been proposed, including random mating, fixed-threshold, best-of-n, and Bayesian comparative tactics. However, the empirical evaluation of these frameworks remains limited in mammalian systems. Lekking species provide a unique opportunity to study female mate sampling behaviour because males aggregate spatially while females retain the freedom to sample and choose among multiple potential males. The blackbuck (*Antilope cervicapra*), one of the few mammals exhibiting a lek mating system, offers an ideal model for examining these processes.

This study was conducted at Tal Chhapar Wildlife Sanctuary, Rajasthan, India, between February 2026 and April 2026, during one of the peak mating seasons reported in India. Unmanned Aerial Vehicles (UAV) were used to track focal female movement and interactions within a mapped lek during a mate sampling bout. Female mate sampling bouts were defined as the period between a female's entry into and exit from the lek. Individual sampling trajectories on the lek were reconstructed to evaluate movement predictions under the theoretical mate sampling models and patterns of lek use.

Number female blackbucks on leks showed a seasonal increase, with peak activity occurring during late March and early April, tracking the patterns observed in number of males on lek. Both sexes exhibited significantly lower attendance during midday sessions compared to the morning and the evening sessions. Spatial analysis revealed that the centre of the lek received disproportionately higher female visits, and greater occurrence of mountings than the peripheral territories.

Most female mate sampling bouts involved visits to fewer than six territories despite substantially large number of available males, suggesting that females only sample a subset of potential males. The distribution of sampling strategies classified on the basis of movement patterns, did not differ significantly from a uniform distribution, indicating co-existence of multiple strategies within a population, such as whether to visit single or multiple males, or whether to revisit a previously sampled male within a sampling bout, etc. Patterns consistent with first encounter, sequential, and best-of-n mate sampling were observed.

Overall, this study provides one of the first detailed empirical examinations of mate sampling behaviour in a mammalian lekking species. By combining fine-scale movement observations of female blackbucks on leks with predictions of theoretical models, it offers an opportunity to evaluate how females sample mates under natural conditions. Specifically, the study quantified the movement parameters of female mate sampling behaviour, including the number of territories visited, the sequence and order of visits, time spent within territories and across the lek, and the occurrence of mounting attempts with a new methodological novelty. In doing so, it contributes to bridging the gap between theoretical models of mate choice and empirical evidence from free-ranging populations.

1 INTRODUCTION

Mating systems can have a significant effect on evolutionary and ecological processes (Klug, 2011). Thus, the study of mating systems is a core pillar of evolutionary research due to these effects (Clo et. al., 2025). Studies on animal mating systems have mainly focussed on describing and documenting variation in mating systems across and within animal groups, quantifying and describing such variation, understanding the factors that lead to and maintain these variations, and understanding the effect of mating systems on ecological and evolutionary dynamics (Klug 2011). Animal mating systems are incredibly diverse (Klug, 2011) and understanding the diversity of mating systems across taxa allows us to examine how ecological and social factors shape reproductive strategies and sexual selection pressures in different environments.

Mammals exhibit a wide array of mating systems (Clutton-Brock, 1989). Within mammals, ungulates exhibit diverse mating systems ranging from monogamous pairs to highly polygynous leks (Bowyer et. al., 2020). Leks have gained much attention where males compete for mating opportunities at display sites that offer no resources or parental care (Höglund & Alatalo, 1995). Leks have been reported for about 15 species of mammals and 35 species of birds out of which nine are ungulate species (Oring, 1982; Clutton-Brock et. al., 1993; Höglund & Alatalo, 1995; Isvaran, 2005a; Buzzard et. al., 2008). This breeding system is therefore not common (Davies et. al., 2012). Most studies on ungulate reproduction, especially leks, have focused on the covariates of male reproductive success, while there is much less information on female tactics of mate choice (Imperio et. al., 2020).

Although a substantial theoretical framework exists on female mate choice and mate sampling strategies (Janetos, 1980; Real, 1990; Luttbeg, 1996), empirical tests of these models remain comparatively limited and are heavily biased towards lower taxa (reviewed by Clutton-

Brock & McAuliffe, 2009). Studies evaluating mate sampling behaviour in mammals are particularly rare (reviewed by Clutton-Brock & McAuliffe, 2009). Consequently, lekking systems provide a valuable opportunity to examine the behavioural mechanisms underlying female mate choice in natural environment and to assess the applicability of theoretical predictions across taxa. Thus, the current study aims to bridge the gap between theoretical predictions and their validation.

1.1 LITERATURE REVIEW

1.1.1 Evolution of Ungulate Lekking

Several hypotheses have been proposed to explain ungulate lek evolution. These hypotheses are not necessarily mutually exclusive, and evidence from different species suggest that mechanisms promoting lek formation may vary among populations and taxa (Clutton-Brock et. al., 1993; Isvaran, 2020).

The "hotspot hypothesis" proposes that when females have large home ranges, males are expected to maximize their mating opportunities by establishing territories at locations where the probability of encountering females is highest, such as the intersection of multiple female home ranges (Balmford et. al., 1993; Isvaran, 2020). Consequently, leks emerge because several males independently select the same locations, or "hotspots," where female encounter rates are maximized, implying that lek formation arises as a consequence of male settlement patterns rather than active aggregation (Balmford et. al., 1993; Isvaran, 2020). However, the concept of a hotspot remains somewhat ambiguous. While most studies define hotspots as areas with high female encounter rates (Balmford et. al., 1993), alternative definitions have been proposed (Westcott, 1997). For example, Apollonio et. al. (1998) found that lek territories were established along female movement routes, where males experienced elevated encounter rates with females. Nevertheless, subsequent work suggested that although hotspot dynamics may

explain lek formation, they may not adequately explain lek persistence once established, contradicting the predictions of hotspot hypothesis (Apollonio et. al., 2014). Similarly, Gosling & Petrie (1990) reported findings consistent with the hotspot hypothesis, whereas Balmford et. al. (1993) highlighted several limitations of this hypothesis in fully explaining the evolution of lekking.

The "hotshot hypothesis" suggests that females are preferentially attracted to small number of exceptionally attractive or high-quality males, referred to as "hotshots" (Isvaran, 2020). Lower-quality males can increase their chances of encountering females by establishing territories close to highly preferred individuals (Isvaran, 2020). Consequently, leks emerge through the aggregation of poor-quality males around hotshots (Isvaran, 2020).

The "female preference hypothesis" proposes that males cluster their territories because females prefer to visit and mate within aggregations of males rather than with solitary males (Bro-Jørgensen, 2003b; Isvaran & Ponkshe, 2013; Isvaran, 2020). Several mechanisms have been suggested to explain these preferences. These include reduced harassment from males (Clutton-Brock et. al., 1993), and lower predation risk associated with visiting clustered males (Clutton-Brock et. al., 1993; Isvaran, 2020). In principle, each of these mechanisms could constitute an independent hypothesis explaining female preference for male aggregations. However empirical support for this hypothesis is mixed. Appolonio et. al. (2014) found evidence supporting both female preference and predation risk explanations, whereas Bro-Jørgensen (2002) rejected both the predation risk and harassment hypotheses. Gosling & Petrie (1990) also found little support for predation risk as direct driver of lek formation, although they suggested that females may benefit from reduced predation risk when congregating at hotspots.

Closely related to the female preference hypothesis is the "predation risk hypothesis", which proposes that males cluster their territories because aggregation reduces the risk of predation for one or both sexes (Balmford & Turyaho, 1992; Clutton-Brock et. al., 1993; Isvaran, 2020).

The "black-hole hypothesis" proposes that clusters of male territories are more effective in retaining females than solitary territories (Clutton-Brock et. al., 1992; Clutton-Brock et. al., 1993; Stillman et. al., 1993; Stillman et. al., 1996). According to this hypothesis, females entering a lek are less likely to leave before mating because the concentration of males encourages continued assessment within aggregations. Consequently, male clusters effectively function as "black holes" that capture and retain receptive females. Supporting this prediction, Clutton-Brock et. al. (1992) demonstrated that lek territories retained oestrous females more effectively than isolated territories.

1.1.2 General patterns in Ungulate Lekking Systems

Studies of lekking ungulates have revealed several recurring patterns that appear to characterize lek mating systems despite considerable variation among species.

One of the most consistent findings is the highly skewed distribution of mating success among males (Apollonio et. al., 1989a; Clutton-Brock et. al., 1988; Balmford et. al., 1992; Isvaran & Jhala, 2000; Bro-Jørgensen, 2003b). Only a small proportion of males obtain majority of matings, while most males achieve little or no copulatory success. This pattern has also been documented also in blackbuck, where matings are non-randomly distributed among males and concentrated in only a few territories (Isvaran & Jhala, 2000). A similar reproductive skew has been reported in Uganda kob, where only a few males account for most matings (Balmford et. al., 1992), and in fallow deer, where the majority of males failed to obtain any

matings (Apollonio et. al., 1989a; Clutton-Brock et. al., 1988). In topi, mating rates were also found to be distributed more in some territories (Bro-Jørgensen, 2003b).

A second widespread pattern is the importance of spatial position within a lek. Central territories generally experience higher mating success than peripheral leks (Fryxell, 1987; Gosling & Petrie, 1990; Balmford et. al., 1992; Clutton-Brock et. al., 1988; Isvaran & Jhala, 2000; Bro-Jørgensen, 2003b; Bro-Jørgensen & Durant, 2003). In blackbucks, mating activity is spatially aggregated, with central territories receiving a disproportionately high number of matings (Isvaran & Jhala, 2000). Similar patterns have been reported in Uganda kob (Balmford et. al., 1992), white-eared kob (Fryxell, 1987), fallow deer (Clutton-Brock et. al., 1988) and topi (Gosling & Petrie, 1990; Bro-Jørgensen, 2003), where both mating rates and female visitation were concentrated in central territories. Interestingly, the location of the lek centre itself may be dynamic, as shifts in the centre of the lek over time have been reported in Uganda kob (Buechner & Roth, 1974).

The association between male phenotype and mating success is another recurring feature of lekking systems. In topi, larger males obtain more matings than smaller males (Gosling & Petrie, 1990), and males occupying central territories are larger than those holding peripheral territories ((Bro-Jørgensen, 2002; Bro-Jørgensen & Durant, 2003). Similarly, mating success in fallow deer is influenced by both territory position and male phenotype (Clutton-Brock et. al., 1988). In Uganda kob, lekking has been proposed as a tactic adopted primarily by phenotypically superior males (Balmford et. al., 1992).

Several studies have demonstrated the fitness advantages associated with lekking. Male kafue lechwe participating in leks achieved higher mating rates than non-lekking males (Nefdt & Thirgood, 1997). In fallow deer, lek-holding males are more successful than males employing resource defence tactics (Clutton-Brock et. al., 1988), and majority of copulations

occurred within leks (Thirgood, 1991). Similarly, the lifetime reproductive success of lekking male topi exceeds that of males adopting alternative mating strategies (Bro-Jørgensen & Durant, 2003).

Despite the apparent advantages of lekking, males often exhibit considerable flexibility in mating tactics (Isvaran, 2005b). In topi, males adjust their reproductive strategies according to female movement patterns and social organizations (Gosling, 1981). While many males defend resource territories, some abandon territoriality to temporarily monopolize female groups, whereas others participate in lekking (Gosling et. al, 1987). Such behavioural flexibility suggests that lekking represents one of several alternative reproductive tactics available to males.

Patterns of female behaviour provide additional insights into lekking studies. In blackbucks, females continue to visit certain territories even after changes in territory ownership, suggesting that territory characteristics may influence female visitation independently of the identity of the resident male (Isvaran & Jhala, 2000). Females in topi populations have been reported to experience increased harassment within leks (Bro-Jørgensen, 2002), highlighting potential costs associated with lekking.

At a broader scale, lek occurrence appears to be influenced by ecological conditions. Blackbuck provide a particularly interesting example because lekking has been documented in only two populations despite the species being widely distributed across India (Ranjitsinh, 1989). This pattern may reflect the relatively large size of both leks examined, whereas smaller leks may have fewer males. In blackbucks, the degree of territorial clustering has been shown to be best predicted by female group size, which is influenced by habitat structure (Isvaran, 2005a). At finer scales, additional selective pressures such as female preference and male competition may further shape lek size and territory clustering (Isvaran, 2005a). Recently,

territory size within blackbuck leks was shown to decrease with increasing number of territorial males, indicating density-dependent effects on spatial organization (Isvaran, 2021).

Taken together, these studies suggest that lekking ungulates share several common characteristics, including extreme reproductive skew, increased mating success of central males, strong effects of male phenotype, and substantial fitness benefits of lek participation.

1.1.3 Male Behaviour and Reproductive Investment in Ungulate Leks

Studies of lekking ungulates consistently demonstrated that males incur substantial costs associated with territory defence and lek attendance. These costs include reduced foraging opportunities, increased energetic expenditure, elevated aggression rates, and a greater risk of injury. Nevertheless, such costs are often offset by the potential for disproportionately high reproductive success, particularly for males occupying central territories.

One of the most widespread patterns across lekking ungulates is the high degree of investment made by males in lek attendance (Buechner & Roth, 1974; Nefdt & Thirgood, 1997; Isvaran & Jhala, 2000; Jayabharathy, 2021). In Kafue lechwe, males that establish territories rarely leave them, spending 90-100 % of their time within the lek (Nefdt & Thirgood, 1997). Similarly, Uganda kob males spend most of their time in the vicinity of the lek (Buechner & Roth, 1974). Comparable patterns have been observed in blackbucks, where lek attendance varies with the intensity of rutting activity, and both lekking and non-lekking males alter their activity budgets according to reproductive conditions (Isvaran & Jhala, 2000; Jayabharathy, 2021).

Lek participation is often associated with substantial energetic costs. In blackbucks, males occupying central territories forage less, spend more time on lek, and engage in fights more frequently than males holding peripheral territories (Isvaran & Jhala, 2000; Jayabharathy, 2021). Similar costs have been reported in topi, where lek males experienced higher overall

costs than non-lekking males and devoted a greater proportion of their time to aggressive interactions (Gosling & Petrie, 1990; Bro-Jørgensen & Durant, 2003). These aggressive interactions can be severe, sometimes resulting in horn damage and other injuries (Gosling & Petrie, 1990). Fallow deer also show comparable behavioural trade-offs, with lek-holding males allocating little time to feeding during breeding season (Clutton-Brock et. al., 1988).

Despite these costs, males occupying central or highly contested territories often achieve greater reproductive success (Fryxell, 1987; Gosling & Petrie, 1990; Balmford et. al., 1992; Clutton-Brock et. al., 1988; Isvaran & Jhala, 2000; Bro-Jørgensen, 2003; Bro-Jørgensen & Durant, 2003). In blackbucks, the elevated costs incurred by central males are accompanied by substantially higher mating success, with the majority of matings occurring in central territories (Isvaran & Jhala, 2000; Jayabharathy, 2021).

Studies have also revealed behavioural adaptations that may increase the male's reproductive success. In fallow deer, successful males tend to arrive at leks earlier than the unsuccessful males, although early arrival alone does not guarantee mating success (Ciuti & Apollonio, 2016). In topi, males have been observed employing deceptive alarm snorts to delay departure of receptive females from their territories, thereby increasing mating opportunities (Bro-Jørgensen & Pangle, 2010). In topi, smaller peripheral males regularly shift their territories centripetally and, in this way, occasionally occupy central territories, thereby increasing their chances of female encounters within the lek (Bro-Jørgensen, 2011). Such behaviours illustrate the diversity of tactics that males may employ to maximize reproductive opportunities within highly competitive leks.

1.1.4 Female Behaviour in Ungulate Leks

Studies of lekking ungulates have revealed that females are active participants in the mating process and often exhibit complex behaviours associated with mate assessment. Across

species, females invest considerable time and effort in sampling males (Balmford et. al., 1992), utilize multiple sources of information during mate choice (Balmford et. al., 1992; Deutsch & Nefdt, 1992; Clutton-Brock & McComb, 1993; McComb & Clutton-Brock, 1994; Imperio et. al., 2020), and display substantial variation in mating tactics. These observations suggest that female behaviour plays a central role in shaping the structure and dynamics of lek mating systems.

In Uganda kob, female movement patterns within leks were consistent with repeated sampling of males, and females showed preferences for particular territories across visits (Balmford et. al., 1992). Similarly fallow deer does frequently move through several territories before settling temporarily in one, spending an average of over three hours on the lek before mating, although considerable variation exists among individuals (Clutton-Brock et. al., 1988). In blackbucks, females were observed visiting leks individually or in pairs and moving freely among territories despite attempts by males to herd them (Isvaran & Jhala, 2000).

Several studies have suggested that females use multiple sources of information when making mating decisions. Social information appears to be particularly important for some species. Female Uganda kob often joined larger groups of females already present within territories, indicating the use of conspecific cues during mate assessment (Balmford et. al., 1992). Similar patterns have been documented in fallow deer, where females copy the movements of other females on the lek (Clutton-Brock & McComb, 1993; McComb & Clutton-Brock, 1994; Imperio et. al., 2020). Females may also rely on direct cues from males and territories. Uganda kob females have been reported to use olfactory cues for mate choice (Deutsch & Nefdt, 1992). In blackbucks, females repeatedly investigate dung piles upon entering territories and frequently revisit them during their stay in a territory (Isvaran & Jhala, 2000), suggesting a potential role of olfactory signals in territory and mate quality assessment.

Some females were even observed resting on dung piles after repeated inspections (Isvaran & Jhala, 2000), highlighting the importance of dung piles and olfactory cues.

Evidence from several species further indicates that females are selective in their mate choice. Female Uganda kob preferentially mated with larger males (Balmford et. al., 1992), whereas female topi have been found to exhibit strong preferences for males occupying central territories (Bro-Jørgensen, 2002). Female topi often moved directly toward territories that regularly attracted large number of females (Gosling & Petrie, 1990). Female topi have been observed to compete aggressively for mating opportunities and exert dominance over other females, thereby disrupting their access to preferred males (Bro-Jørgensen, 2002). These observations demonstrate that sexual selection in lekking systems may involve competition among both females and males.

A common pattern across species is that females appear to visit leks primarily for mating rather than access to food resources (Clutton-Brock et. al., 1988; Isvaran & Jhala, 2000). In blackbucks, female and mixed herds did not move regularly through the lek, and herds passing near leks generally travelled around rather than through them (Isvaran & Jhala, 2000). Similar reports have been found in Uganda kob and fallow deer, where females spent less time feeding while on leks than when outside them, suggesting that lek visitation in primarily associated with reproductive activities rather than other resource acquisition (Clutton-Brock et. al., 1988; Isvaran & Jhala, 2000).

Detailed observations of fallow deer highlight the dynamic nature of female decision-making through mating sequences. Females often move between territories during courtship and mounting attempts, occasionally leaving and later returning to the same male before copulation occurrs (Clutton-Brock et. al., 1988). Females were also more likely to terminate mating sequence when males became distracted by rivals or non-territorial males, suggesting

that mating decisions may depend not only on male phenotype but also on male behavioural performance during courtship (Clutton-Brock et. al., 1988). Furthermore, when a mating sequence commenced, neighbouring females frequently moved toward the mating male's territory, resulting in a temporary increase in harem size (Clutton-Brock et. al., 1988). This behaviour may represent another form of social information use during mate assessment.

Finally, growing evidence suggests substantial variation in females mating tactics and sampling efforts. Studies in fallow deer indicate that females differ considerably in amount of time, energy, and risk they invest in mate assessment and may alter their tactics depending on age, experience, and ecological circumstances (Imperio et. al., 2020).

1.1.5 Mate sampling strategies

Theoretical studies of mate choice have long focused on how females sample potential males and make decisions within the constraints of their ecological environment. One of the earliest and most influential frameworks was proposed by Janetos (1980). Janetos (1980) described several mate sampling strategies, including random mating, fixed-threshold, best-of-n, and one-step decision processes, of which best-of-n was predicted to yield maximum benefits to the female. Subsequent studies, expanded these early models by incorporating search costs (Real, 1990) and compared the performance of sequential and best-of-n strategies. Later work examined how females acquire and update information, and how environmental dynamics and time constraints influence decision-making (Mazalov et. al., 1996).

Subsequent research has involved the prediction of strategies under variable conditions. Wiegmann et. al. (1996) examined at the predictions of the best-of-n and sequential search models under an expected distribution of mate quality. Wiegmann and Angeloni (2007) and Wiegmann et, al. (2010b) further evaluated how uncertainty in female decision-making affects the behaviour of best-of-n and sequential search models. Wiegmann et. al (2010a) examined

the fitness returns under sequential and best-of-n models and found that when search costs were included, sequential-search models outperformed best-of-n models, aligning with the results of Real (1990). Additional work explored the relationship between phenotypic traits and decision-making (Wiegmann & Mukhopadhyay, 1998).

Beyond these traditional strategies, Luttbeg (1996) introduced the Comparative Bayes tactic, which relaxed the assumptions of random encounter and perfect information, common assumptions in earlier models. Subsequent analysis has shown that the models can outperform each other under different circumstances (Luttbeg, 2002). Rosenthal (2017) classified all the mate sampling models discussed above into four broad categories: sequential static, sequential dynamic, simultaneous static, and simultaneous dynamic.

Despite the richness of theoretical work, empirical tests remain comparatively limited. Evidence consistent with best-of-n sampling has been reported in several taxa (Uy et, al., 2001; Locatello & Rasotto, 2007), while support for sequential search strategies has been documented in a range of species (Backwell & Passmore, 1996; Forsgren, 1997; Reid & Stamps, 1997; Ivy & Sakaluk, 2007; Lehmann, 2007; Beckers & Wagner, 2011). There is also evidence that multiple sampling strategies can coexist within the same population (Choudhary & Black, 1993). However, some theoretical studies remain debatable. For example, the feasibility of true simultaneous sampling in natural populations has been questioned (Wiegmann, 1999; Deb & Balakrishnan, 2014), highlighting the need for empirical studies that directly examine the behavioural mechanisms involved in mate sampling.

Although mate choice studies have been extensively conducted in birds, less attention has been given to mammals (reviewed by Clutton-Brock & McAuliffe, 2009). Lek mating systems are particularly valuable for investigating mate sampling behaviour because they create opportunities for females to sample multiple males within a confined spatial and

temporal context (Höglund, J., & Alatalo, 1995). Studies of lekking birds have provided evidence consistent with best-of-n sampling (Fiske & Kålås, 1995; Rintamäki et. al., 1995), and several studies have documented mate-choice copying in lekking species (Clutton-Brock & McComb, 1993; McComb & Clutton-Brock, 1994; Höglund et. al., 1995).

Gibson & Langen (1996) in their review argued that future research should move beyond documenting mating outcomes and instead focus on the processes by which females acquire and use information. Blackbuck leks provide an excellent opportunity to address this challenge. By allowing observations of fine-scale female movement, interactions, and mating events, blackbuck leks offers an opportunity to investigate behavioural mechanisms underlying mate sampling in a lekking mammal. Such studies not only test the predictions of theoretical models but also bridge the gap between extensive theoretical development and relatively limited empirical evidence in natural populations.

2 OBJECTIVES AND RESEARCH QUESTIONS

I. To understand the female mating behaviour in blackbuck leks

- **How do the number of female blackbucks on lek vary across the breeding season?**

  Specifically, how do daily count of males and females change over time, and do these patterns show consistent temporal trends (e.g., peaks) during the breeding season?

- **What are the behavioural patterns of female mate sampling during lek visits?**

  This includes quantifying key components of sampling behaviour such as the number of territories visited per bout, time spent within territories, and on the lek, and the frequency of mounting attempts as an indicator of mating outcomes.

- **How do female blackbucks use space within the lek during mate sampling visits?**

  In particular, do females show non-random spatial use of territories within the lek, and how does their movement relate to lek structure, including proximity to the lek.

- **What strategies do female blackbucks use to sample mates within leks?**

  This question examines the sequence and rules underlying mate sampling, such as whether females follow best-of-n, sequential, or first-encounter sampling strategies when visiting the male territories.

Hypotheses and predictions:

This study compares the movement patterns predicted under alternative mate sampling strategies used by female blackbuck during lek visits. Specifically, three alternative hypotheses are considered. Under the first-encounter hypothesis (H1), females are expected to assess the

first male encountered, resulting in visit to only a single territory during a sampling bout. This represents the pattern of random mating proposed by Janetos (1980). Under the sequential sampling hypothesis (H2), females are predicted to visit multiple male territories in a sequential manner without revisiting previously sampled males (Janetos, 1980; Real, 1990). In contrast, under the best-of-n hypothesis (H3), females are expected to sample multiple males, including revisits to previously visited territories (Janetos, 1980; Real, 1990). These hypotheses are compared by examining the female movement among territories, including the number of territories visited, occurrence of revisits, and the sequence of visits during mate sampling bouts within blackbuck leks.

3 STUDY AREA

3.1 Site

Current study was primarily conducted in Tal Chhapar Wildlife Sanctuary, located in Churu district of Rajasthan, India. The wildlife sanctuary falls within the biogeographic zone 3A – Thar Desert (Rodgers & Panwar, 1988). The wildlife sanctuary covers 7.2 km^2 and supports one of the largest blackbuck leks within the sanctuary and the country.

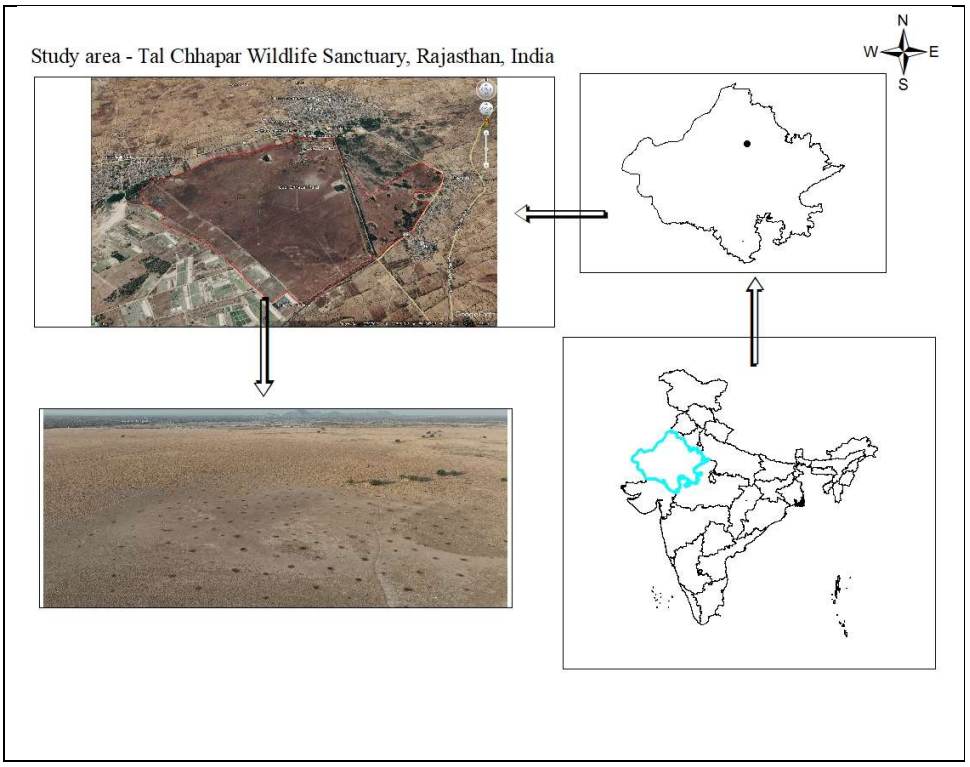


Figure 1: Map of the study area showing Tal Chhapar Wildlife Sanctuary and bird-eye view of the principal lek inside the sanctuary

3.2 Climate and Terrain

The wildlife sanctuary is characterized by a predominantly flat terrain interspersed with low lying depressions, surrounded by salt pans and open scrubs (Ojha, 2016). The open grassland with scattered *Acacia nilotica* trees gives the landscape a typical savannah-like

appearance. The region experiences extreme seasonal variation in temperature, with summer temperature reaching up to 48.5 ° C and winter temperatures dropping to as low as – 1.1 °C. Diurnal temperature fluctuations are also pronounced, and summer nights are often cooler than daytime conditions.

The climate is semi-arid, with an average annual rainfall of 363 mm. Most precipitation occurs during a short monsoon period extending from July to mid-September. Both soil and water bodies of Tal Chhapar are reported to be saline and alkaline (Mehtani et. al., 2013; Kaur et. al., 2023).

The area experiences four distinct seasons: summer (March - May), monsoon (June - September), post-monsoon (October - November), and winter (December - January) (Kaur et. al., 2023).

3.3 Flora

The vegetation of the study area is classified as Northern Tropical Thorn Forest (6B) and subclassifies as Desert Thorn Forest (6B/C1) according to Champion & Seth (1968). Among trees, *Acacia nilotica* dominates the landscape followed by *Prosopis cineraria* and *Capparis decidua*. *Sueda fruticose* leads among shrubs followed by *Haloxylon salicornicum* and *Boerhavia elegans* respectively. Among herbs, the major species present are *Corchorus depressus, Borhavia diffusa,* and *Aerva persica*. Among grasses and sedges, major species present are *Dichanthium annulatum, Lasiurus scindicus,* and *Desmostachya bipinnata.* (Kaur et. al., 2020).

3.3 Fauna

Blackbucks (*Antilope cervicapra*) are the dominant and characteristic mammalian fauna of the sanctuary along with chinkara (*Gazella bennettii*), blue bulls (*Boselaphus tragocamelus*), Indian fox (*Vulpes bengalensis*), desert fox (*Vulpes vulpes pusilla*), desert cat (*Felis sylvestris*

ornata), jungle cat (*Felis chaus*), and wild pigs (*Sus scrofa*). Herpetofauna includes desert monitor (*Varanus griseus*) and spiny tailed lizard (*Uromastyx hardwickii*). The sanctuary lies within migratory passage of birds with harriers being the major attraction. Other birds of prey found here are red-necked falcons (*Falco chicquera*), black-winged kite (*Elanus caeruleus*), eastern imperial eagle (*Aquila heliaca*), short-toed eagle (*Circaetus gallicus*), and tawny eagle (*Aquila rapax*). Largest vulture of India, Cinereous vulture (*Aegypius monachus*) is also found here (Ojha, 2016).

3.4 Study taxa

The Indian blackbuck (*Antilope cervicapra*), is an antelope endemic to Indian subcontinent, found in diverse habitats, ranging from shortgrass and savannas (Jhala & Isvaran, 2016). Primarily a grazer, the behaviour, nutrition, and demography of the blackbuck appear closely adapted to a stochastic low-resource environment and predation pressure (Jhala & Isvaran, 2016). Blackbucks show sexual dimorphism with adult males having a dark coat colour (Ranjitsinh, 1989). They live in groups ranging from two to several hundred individuals and exhibit a flexible mating system (Isvaran, 2005a). Blackbuck males have known to employ alternative mating tactics, with lekking and resource defence being the two mating tactics (Ranjitsinh, 1989; Jhala & Isvaran, 2016).

4 MATERIALS & METHODS

4.1 Study design

A comprehensive review of the mate sampling literature was undertaken to identify the principal theoretical models and to derive the movement predictions associated with each strategy. Based on these theoretical frameworks, the major mate sampling strategies described in the literature were grouped into a set of three operational categories that could be compared using field observations of movement patterns of females in the lek in the present study. The strategies considered and their corresponding predictive parameters are summarized in the *Table 1.* Present study adopted an event-based approach to investigate female-mate sampling behaviour. These operational categories differed in two aspects; whether to sample single or multiple males, and whether to revisit a previously sampled males within a same mate sampling bout.

Table 1: Details of theoretical mate sampling models and operational categories used in the current study

Sr.	Operational category	Strategy	Reference	Prediction on number of mates sampled	Prediction on revisits
1	First encounter	Random	Janetos (1980)	1	NO
2	Fixed threshold	Pure threshold	Janetos (1980)	≥ 1	NO
		Threshold with last option	Janetos (1980)	≥ 1	NO
		One step decision	Janetos (1980)	≥ 1	NO
		Sequential search	Real (1990)	≥ 1	NO
3	Best-of-n	Best-of-n	Janetos (1980)	> 1	YES

		Comparative Bayes tactic	Luttbeg (1996)	> 1	YES
		Fixed sample or pooled comparison	Wiegmann & Makhopadhyay (1998)	> 1	YES

4.2 **Field methods**

Present study was conducted from February 2026 to April 2026 at Tal Chhapar Wildlife Sanctuary, Rajasthan, India. Observations were carried out at the largest known lek within the sanctuary, encompassing the peak breeding season of blackbuck.

Each observation day was divided into three sampling sessions: morning (sunrise-11:00 h), midday (11:00 h-15:00 h), and evening (15:00 h-sunset). A team of four observers was stationed near the lek without causing any disturbance to the animals.

During each session, the lek was scanned for every 15-minutes. For every scan, the number of territorial males present on the lek and the number of females present on lek were recorded. Depending on the duration of daylight, each session consisted of approximately 14 to 16 scans.

Female mate sampling bouts were recorded using unmanned aerial vehicles (UAV). Because the females visited the lek unpredictably, tracking was initiated whenever a female entered the lek. Individual females were not uniquely identifiable; therefore, each tracking sequence was treated as an independent mate sampling bout.

Upon the entry of a female into the lek, a DJI Mavic 3 Enterprise UAV was launched and positioned at an altitude of 80 m above ground level. After locating the focal female, the camera gimbal was adjusted to a nadir position (90°), and continuous video recording was initiated. Throughout the observation period, the UAV was manoeuvred to keep the focal female at the centre of the frame.

A single battery typically provided 20-25 minutes of flight time. To maintain uninterrupted observations, a relay system involving a second UAV was employed. As the battery level of the first UAV approached the predefined return threshold (18 %), a second UAV was positioned directly above it at an attitude of approximately 100 m. Once the first UAV is returned to launch site, the second UAV was lowered to 80 m and the tracking was continued. This relay procedure was repeated until the focal female left the lek or all six available batteries were exhausted. Thus, a maximum uninterrupted tracking was possible for 2 hours and 5 minutes.

Tracking was primarily conducted during the morning and evening sessions and the scans were carried out throughout the day from sunrise to sunset. Whenever a the current focal female left the lek, the next female entering the lek was selected as the next focal female for observations.

To map the spatial structure of the lek, aerial imagery was collected periodically using the ortho-collection acquisition mode of DJI Mavic 3 Enterprise. Flights were conducted at an altitude of 80 m with a ground sampling distance of approximately 2.5 cm $pixel^{-1}$ and a flight speed of 6 m s^{-1}.

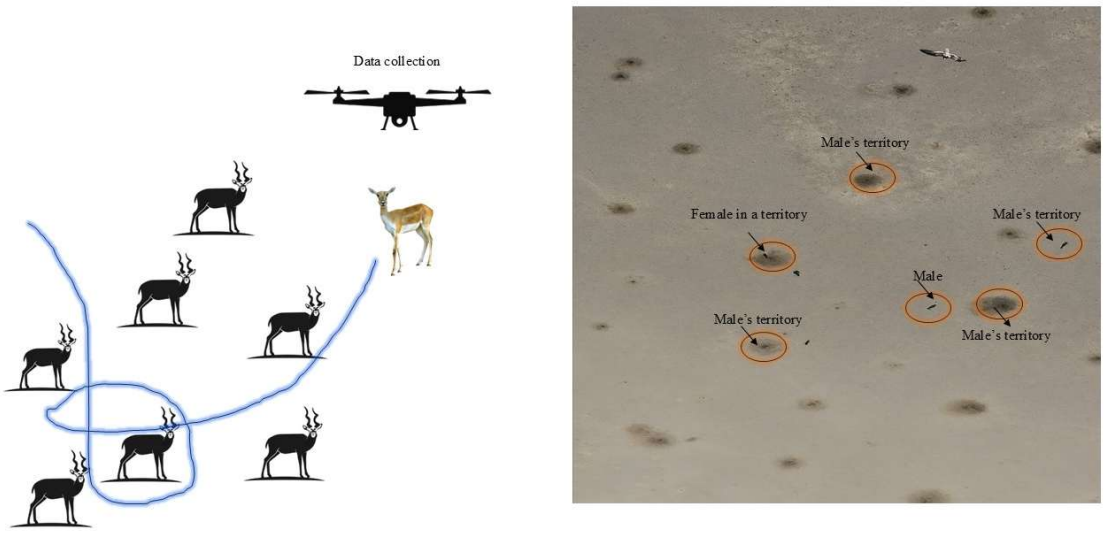


Figure 2: A schematic of the data collection strategy. The image displays top-down view of a blackbuck lek with male territories marked. Females were distinguishable males because of the contrasting colour. Individual territories could easily be identified using spatial features.

4.3 Data processing

Images collected were stitched using Microsoft Image Composite Editor (Gross & Heumann, 2016) to generate high-resolution ortho mosaic of the lek. These ortho mosaics were subsequently used to identify individual territories based on the central dung piles. Each central dung pile was assigned a unique identification number. Males were observed to repeatedly occupy pre-existing territories, although appearance of new territories and disappearance of new territories were documented using ortho mosaics acquired on different dates across the breeding season.

Because the focal female was maintained at the centre of the camera frame during UAV tracking, the GPS coordinates of the UAV were assumed to approximate the position of female on the lek. GPS coordinates associated with individual video frames were extracted and used to reconstruct movement trajectories in R (R Core Team, 2020). The resulting trajectories were imported into ArcMap and overlaid on the georeferenced ortho mosaic of the lek. Spatial

alignment was subsequently verified through manual review of video recordings to ensure consistency between mapped trajectories and observed female movements.

The recorded video sequences were then reviewed manually to create the visitation history of individual females within the lek. This visitation order was cross-verified with the earlier trajectory made using the GPS coordinates. A territory visit was recorded when a female stopped within a male's territory, often followed by sniffing the dung piles. Because most male-female interactions occurred on or in the vicinity of these dung piles, they provided a reliable spatial reference for assigning females to specific territories and minimized the ambiguity in territory identification (*Figure 2*). A revisit was defined as a female returning to a territory that had already been visited earlier within the same sequence. For each sequence, order of territory visits, revisits, total time spent on lek, and occurrence of mountings were recorded.

4.4 **Analytical Methods**

To quantify seasonal variation in lek attendance, the number of territorial males and female visits recorded during scan was averaged within each session to obtain a daily estimate. These daily values were subsequently plotted across the breeding season to examine temporal patterns in male attendance and female visits. Generalized Linear Mixed Effect Models (GLMM) (Nelder & Wedderburn, 1972) were used to explore the relation between male and female number on lek across sessions and days.

Geometric centre of the lek was calculated from the collected coordinates of all identifiable territories. A subset of territories was then plotted along with number of female visits, occurrence of mountings, and average time spent by a female on that territory, to visually plot the spatial use lek by the females.

GLM was used to test the relation between total time spent on lek and predictor variables.

Each sequence was classified into an operational category (*Table 1*) based on the following decision rules (*Table 2*). Chi-square test was used to test the ubiform distribution of strategies obtained using the decision rules among the sequences.

Table 2: Decision rules used to categorize each sequence recorded into mate sampling strategy

Operational category	**Number of territories visited**	**Revisits**
First encounter	1	NO
Sequential/fixed-threshold	> 1	NO
Best-of-n	> 1	YES

5 RESULTS

5.1 Temporal patterns in the number of male and females on lek

The principal lek within the sanctuary was scanned for a total of forty-one days in three sessions: morning (sunrise – 11:00 h), midday (11:00 h – 15:00 h), and evening (15:00 h – sunset) from 19th February 2026 to 5th April 2026.

Across the study period, the mean daily male attendance was 44.12 ± 21.12 individuals (*Table 3*). Across all the scans, the number of territorial males on lek ranged from 4 to 130 individuals. The mean number of territorial males on lek recorded per scan was highest in the evening (52.05 ± 23.62), followed by morning (44.24 ± 23.79), and lowest in the midday (35.89 ± 17.29) (*Table 3*).

Across the study period, the mean number of females visited the lek was 1.26 ± 1.26, and across the scans the number of females visiting the lek ranged from 0 to 13 individuals. The mean number of females recorded per scan was highest during the evening session (1.61±1.87), followed by morning session (1.37±1.65), and lowest during the midday session (0.70±0.77) (*Table 4*).

Table 3: Number of males holding territories on the lek at different times of the day. For each observation session, the number of males seen on the lek, averaged across scans, was used as measure of the number of males on the lek for that session

Session	**No. of sessions**	**Mean number of males**	**SD**	**SE**	**95% CI**
Morning	39	44.24	23.79	3.81	36.53 – 51.96
Midday	36	35.89	17.29	2.88	30.04 – 41.74
Evening	37	52.05	23.62	3.88	44.17 – 59.92

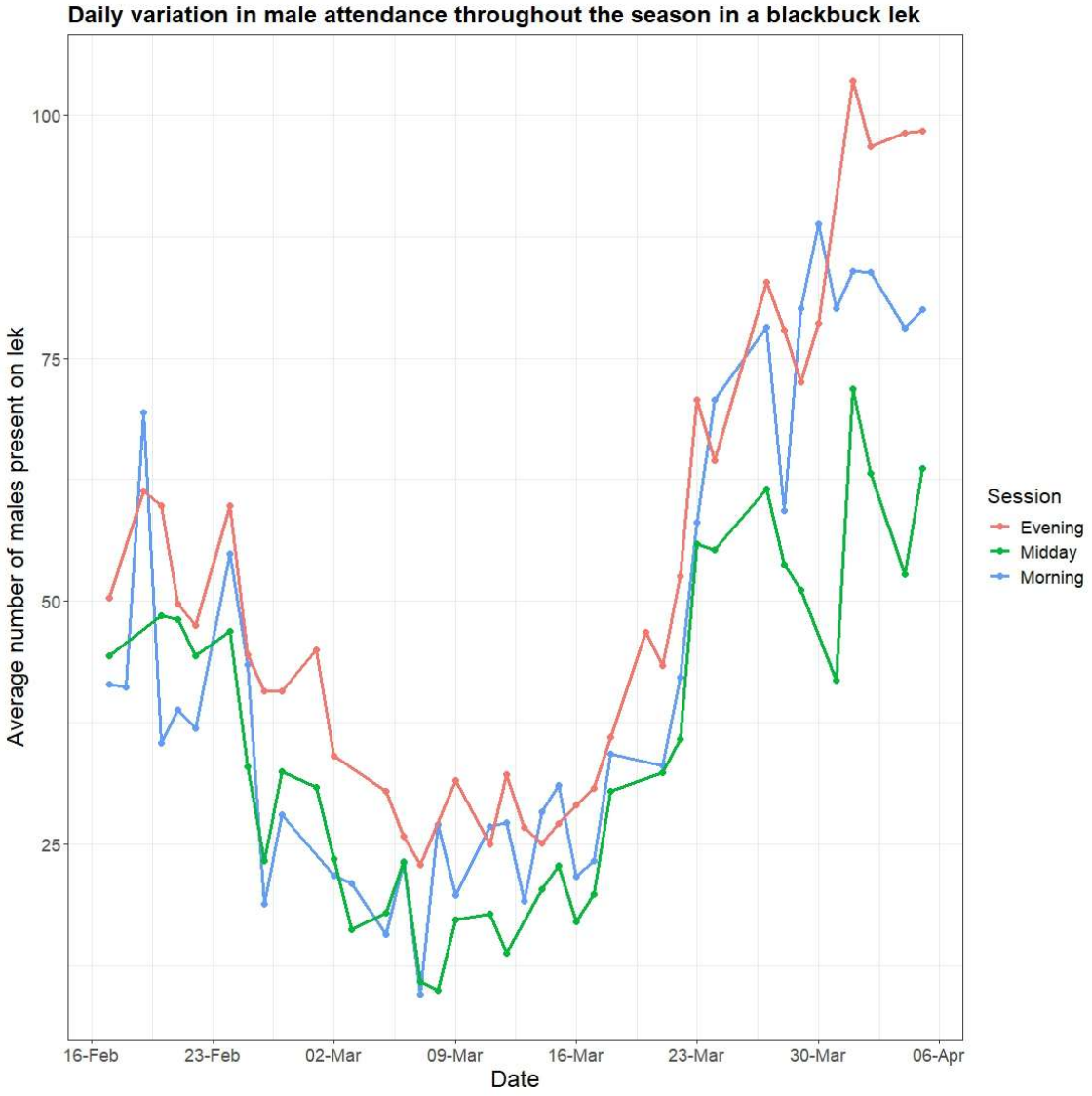


Figure 3: Number of males on the lek per scan per session during 41 days from 19th February 2026 to 5th April 2026 in a blackbuck lek in Tal Chhapar WLS, Rajasthan, India

For the purpose of plotting the male attendance across the breeding season, scan-level counts of males were averaged within each session to obtain a single representative value per session per day. These session-wise means were the plotted across the total study duration to examine the pattern in male attendance over time (*Figure 3*).

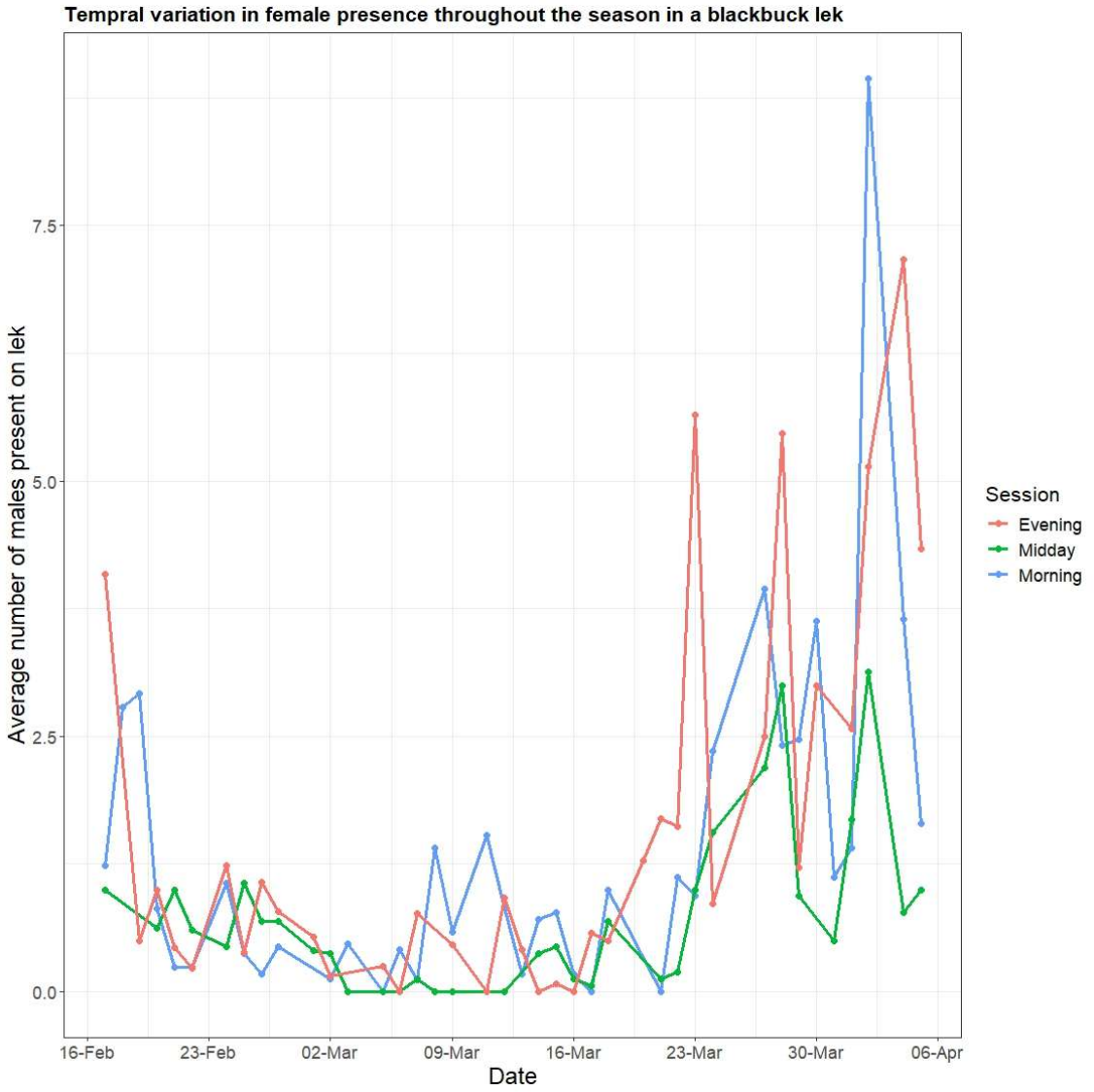


Figure 4: Number of females on the lek per scan per session during 41 days from 19th February 2026 to 5th April 2026 in a blackbuck lek in Tal Chhapar WLS, Rajasthan, India

For the purpose of plotting the female attendance across the breeding season, scan-level counts of female visits were averaged within each session to obtain a single representative value per session per day. These session-wise means were the plotted across the total study duration to examine the pattern in female visits over time.

Table 4: An index of the number of females visiting the lek at different times of the day. For each observation session, the number of females seen on the lek, averaged across scans, was used as an index of the number of females visiting the lek for that session

Session	**No. of sessions**	**Mean number of males**	**SD**	**SE**	**95% CI**
Morning	39	1.37	1.65	0.26	0.83 – 1.90
Midday	36	0.70	0.77	0.12	0.44 – 0.96
Evening	37	1.61	1.87	0.30	0.99 – 2.24

Number of males on lek varied significantly among the three sessions. Compared with morning, significantly fewer males were present during the evening session ($\beta = -0.187 \pm 0.037$, $z = -5.03$, $p < 0.001$), whereas significantly more males were present during the evening session ($\beta = 0.169 \pm 0.034$, $z = 5.03$, $p < 0.001$). Number of males on lek also varied significantly across weeks. Relative to week 1, male number was lower during weeks 2 to 4 (*Table 6*). In contrast, number of males on lek significantly increased during week 5 and 6.

Table 5: Model selection results from GLMMs examining factors influencing the number of males on a lek. Models are ranked according to AIC, with lower values indicating better model support

Model	**Distribution family**	**Variables used**	**df**	**AIC**	**ΔAIC**
nm ~ session + week + day (random effect)	Poisson	Session and week	103	785.1	0
nm ~ session + day (random effect)	Poisson	Session	108	862.3	77.2
nm ~ week + day (random effect)	Poisson	Week	105	877.5	15.2

Table 6: Parameter estimates, standard errors, test statistics, and significance levels for predictors included in the best-supported model explaining the variation in number of males on lek

Predictor	**Coefficient value**	**SE**	**z**	**p**
intercept	3.87	0.06	63.19	< 2e-16
midday session	-0.19	0.04	-5.02	4.99e-07
evening session	0.17	0.03	5.03	4.80e-07
week 2	-0.49	0.09	-5.68	1.37e-08
week 3	-0.81	0.09	-8.95	< 2e-16
week 4	-0.51	0.09	-5.88	3.93e-09
week 5	0.23	0.08	2.86	0.004
week 6	0.49	0.08	5.90	3.73e-09

The number of females on lek also differed significantly among sessions. Compared with morning, significantly fewer females were present during the midday session ($\beta = -0.555 \pm 0.241$, $z = -2.30$, $p = 0.021$). Although the number of females on lek was higher during the evening than in the morning, this difference was not statistically significant. Relative to week 1, significantly fewer females were recorded during weeks 2 to 4. The number of females on lek increased significantly during week 5 and 6 (*Table 8*).

Table 7: Model selection results from GLMMs examining factors influencing the number of females on a lek. Models are ranked according to AIC, with lower values indicating better model support

Model	**Distribution family**	**Variables used**	**df**	**AIC**	**ΔAIC**
fn ~ session + week + day (random effect)	Poisson	Session and day	103	281.4	0
fn ~ session + week	Poisson	Session and day	105	290.1	8.7
fn ~ session	Poisson	Day	108	315.5	25.4

Table 8: Parameter estimates, standard errors, test statistics, and significance levels for predictors included in the best-supported model explaining the variation in number of females on lek

Predictor	**Coefficient value**	**SE**	**z**	**p**
intercept	0.12	0.26	0.47	0.64
midday session	-0.55	0.24	-2.30	0.02
evening session	0.24	0.19	1.29	0.19
week 2	-1.22	0.48	-2.55	0.01
week 3	-1.09	0.45	-2.41	0.01
week 4	-0.85	0.41	-2.05	0.04
week 5	0.65	0.29	2.24	0.02
week 6	1.06	0.29	3.67	0.0002

5.2 Spatial structure of lek and patterns of lek use by blackbuck females

Figure 5 depicts the spatial arrangement of all male territories recorded during the study period and the location of the lek centre. The map represents the cumulative territorial structure of the lek across the breeding season rather than a single temporal snapshot. Territory occupancy was dynamic, with some territories remaining active throughout the season, others becoming inactive or abandoned, and new territories being established over time. Consequently, the mapped territories encompass the full range of territorial positions observed during the study. Territories varied in their distance from lek centre and in their spatial configuration, providing the spatial framework for subsequent analysis of female visitation patterns and mating activity within the lek.

The cumulative time spent by females varied among territories (*Figure 6*). Female activity was not distributed uniformly across the lek, with some territories receiving greater cumulative visitation time than others. The spatial distribution of their activity hotspots is illustrated relative to the lek centre in *Figure 6*.

Patterns of female visits and occurrence of mounting also differed among territories (*Figure 7)*. The number of unique female visits and the number of unique matings and the occurrence of mountings were unevenly distributed over lek. Territories that received a greater number of female visits generally also experienced higher occurrence of mountings, although the magnitude of these measures varied among territories.

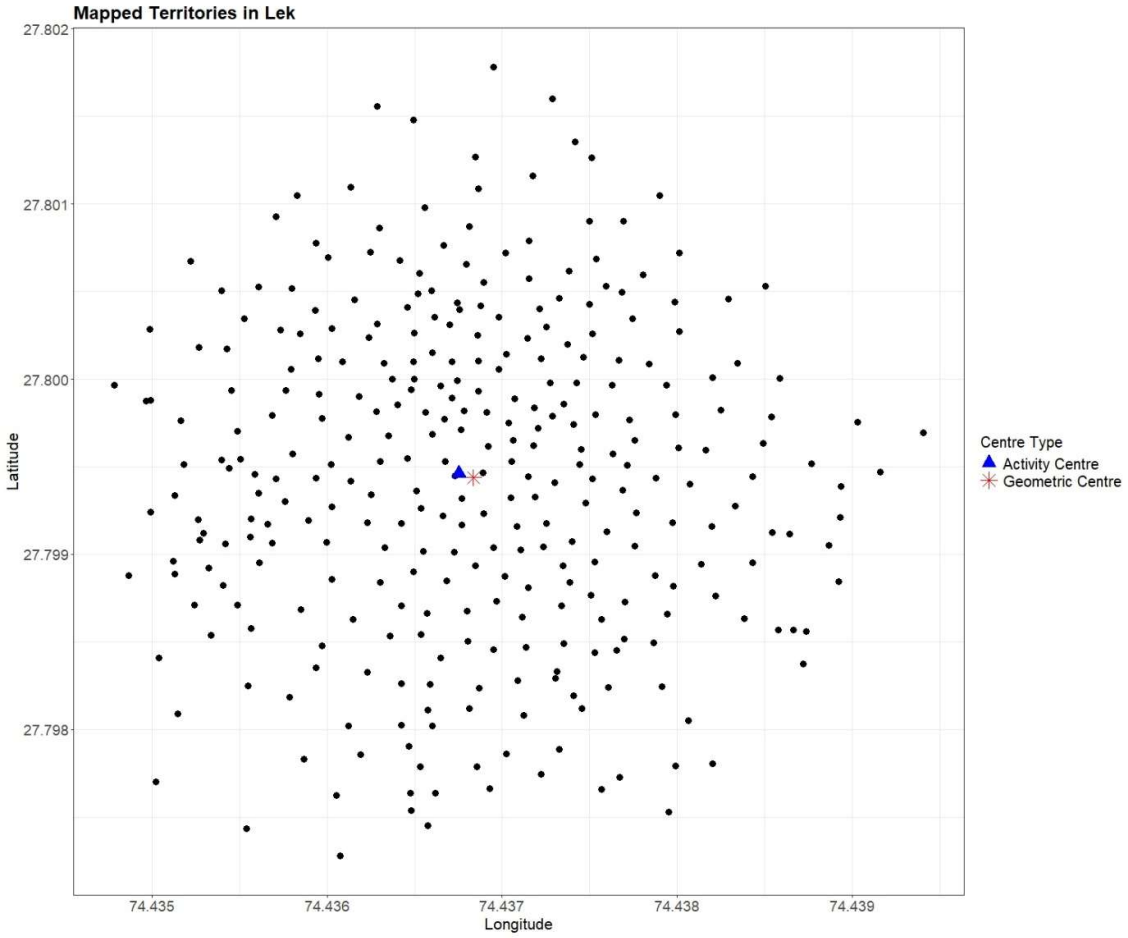


Figure 5: Map of the lek territories (April 2026) denoting the geometric centre and activity centre (defined as the territory with maximum clustering) of the lek. The calculation was made with all the identifiable territories on the lek which may or may not be actively defended by males on lek

More than 300 central dung piles were recordedcomprising both active territorial dung piles from the current lekking season and inactive dung piles remaining from the previous lekking season. The centre of the lek was determined as the geometric centre of the spatial distribution of all recorded dung piles.

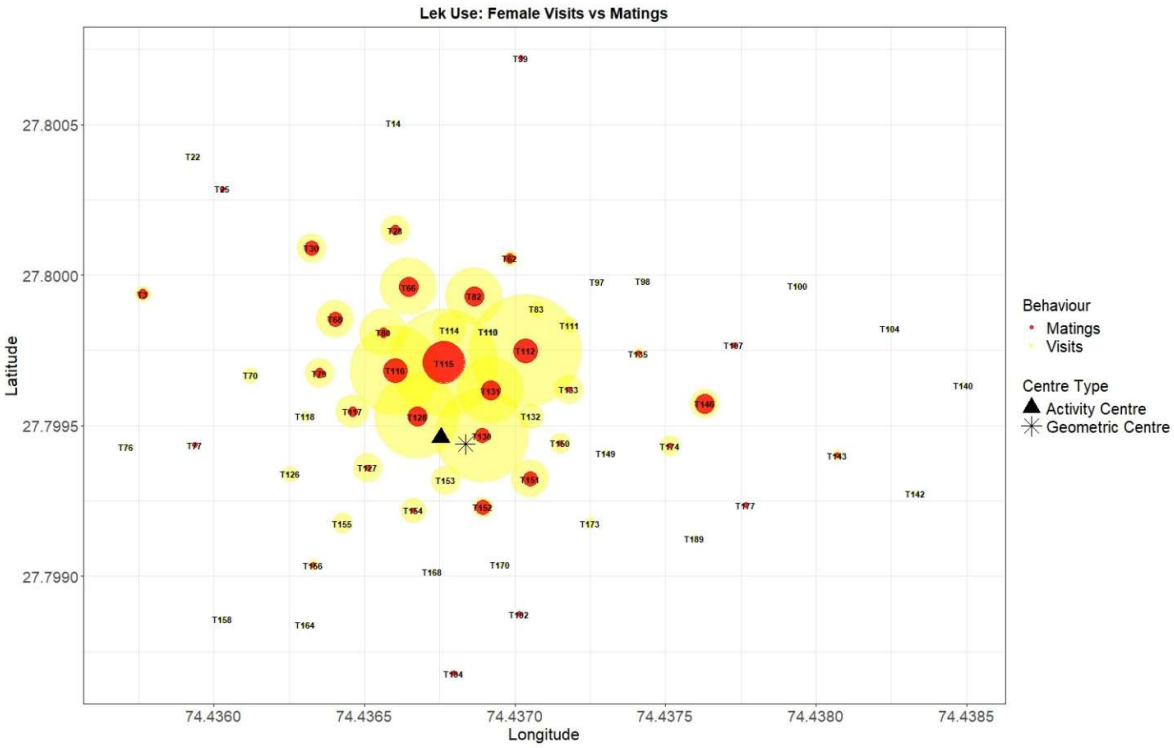


Figure 7: Subset of territories with lek centre showing the unique female visits and number of unique mountings observed. Larger circles indicate larger values

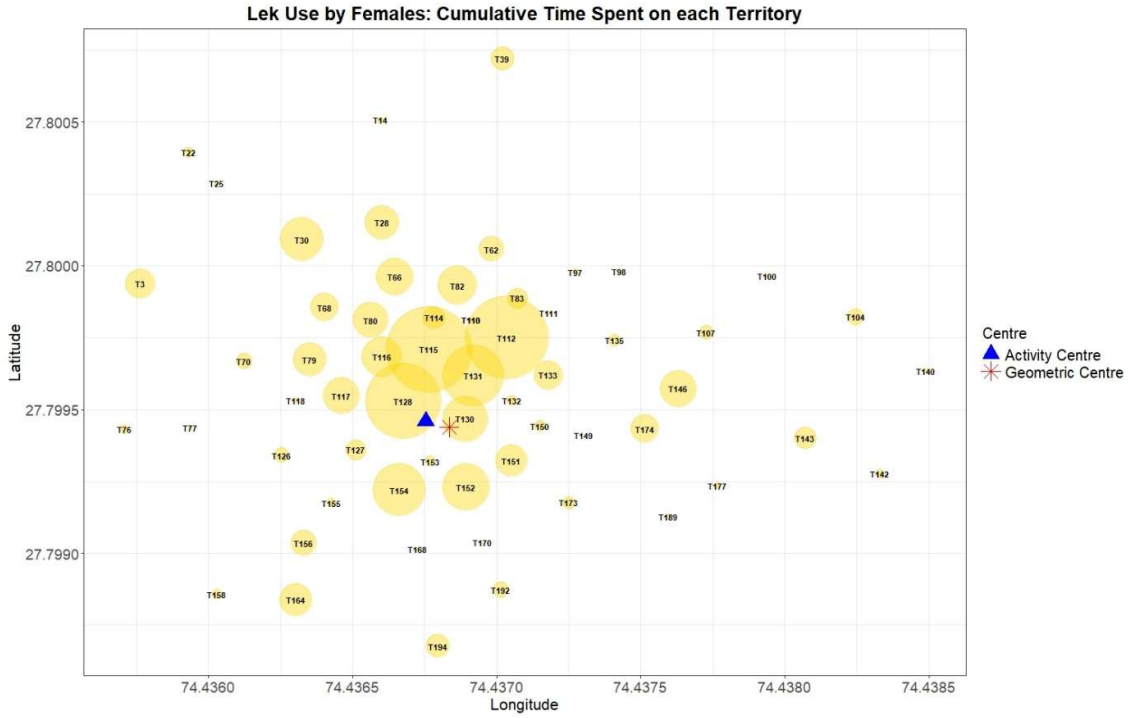


Figure 6: Subset of territories with the lek centre representing the cumulative time accumulated on the territory by females. Size of the circle indicates more time accumulated

5.3 General patterns of mate sampling behaviour of blackbuck females

A total of 97 mate sampling bout sequences were recorded over the entire study period. Of these, 5 sequences were incomplete due to loss of focal females during tracking. An additional 23 sequences were truncated because the drone battery depleted before either entry or exit of the focal female could be fully documented. Consequently, 69 complete sequences, in which both entry to exit were clearly observed, were retained for further analysis. In total, 66 hours of focal observations were obtained.

All subsequent analyses, except those estimating the proportion of revisits (which included incomplete sequences that included at least one revisit to a previously sampled territory). Were based exclusively on these 69 complete sequences to ensure consistency in behavioural metrics derived from fully observed sampling bouts.

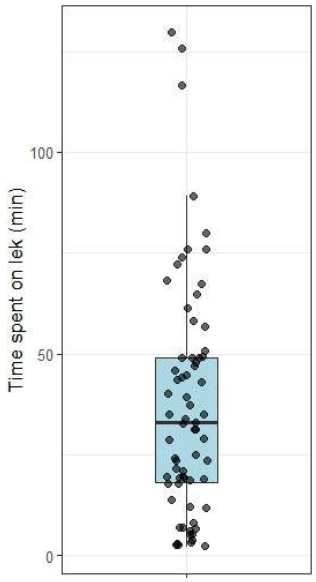


Figure 8: Variation in time spent by blackbuck females during the sampling bout (n = 69 sequences)

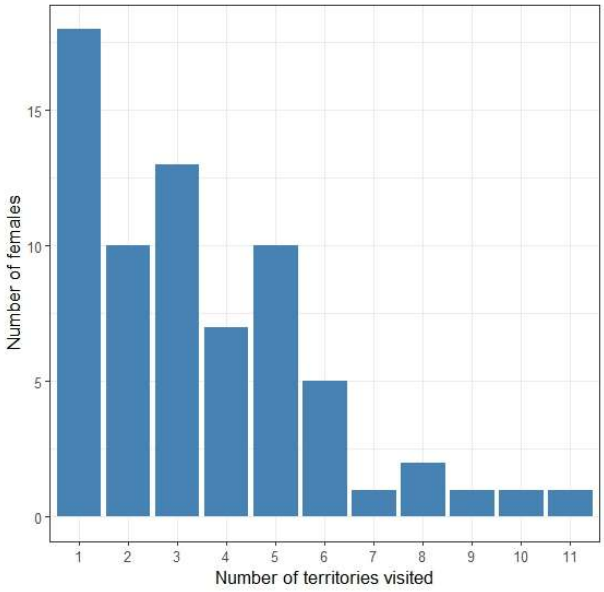


Figure 9: Frequency distribution of number of territories visited by blackbuck females during the sampling bout (n = 69 sequences)

Females visited 3.45 ± 2.35 (median = 3) unique male territories during a single mate sampling bout (*Figure 9*). However, the number of unique territories visited showed considerable variation among single mate sampling bouts, ranging from a single territory to a maximum of 11 territories. This indicates substantial variation in sampling effort among females

The duration of mate sampling bouts also exhibited wide variation. The time spent by female on lek ranged from as little as 2 minutes to as long as 130 minutes per bout, with mean duration of 37.38 ± 29.14 minutes and a median of 33 minutes (*Figure 8*). In additional to UAV-based observations, a focal observation conducted outside the drone tracking sessions recorded an extended visit lasting 3 hours and 45 minutes on lek, highlighting that exceptionally long sampling bouts can occur.

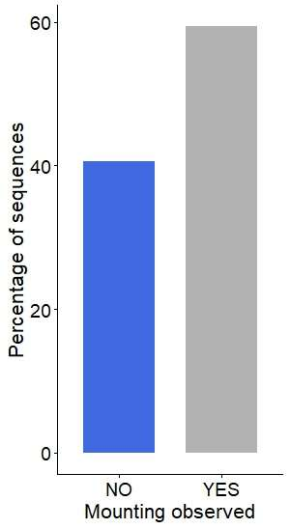


Figure 10: Proportion of sequences which observed mounting in at least one territory and sequences that recorded no mountings (n = 69 sequences)

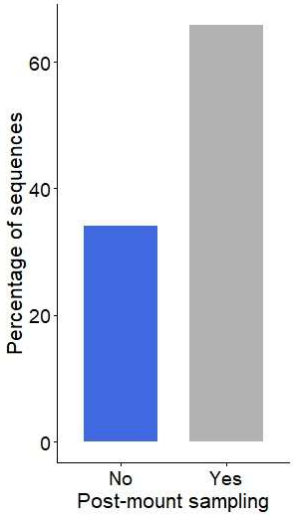


Figure 11: Proportion of sequences in which the female continued sampling after the first mount (n = 41 sequences)

Out of 69 mate sampling bouts (entry to exit), 41 (59.42%) sequences included occurrence of mountings within the bout (*Figure 10*). Within these 41 sequences, 27 (65.85%) recorded continued sampling after the first occurrence of mounting (*Figure 11*), suggesting that mounting did not always terminate the sampling process and that females often continued to visit additional territories even after an initial mounting event.

Further, among these 41 sequences, 17 (41.46%) included occurrence of mountings in more than one territory within a bout (*Figure 12*), indicating that the occurrence of mountings was sometimes distributed across multiple males within a single bout. Across a total 79 sequences, 35 (44.30%) included at least one revisit to a previously sampled territory (*Figure 13*).

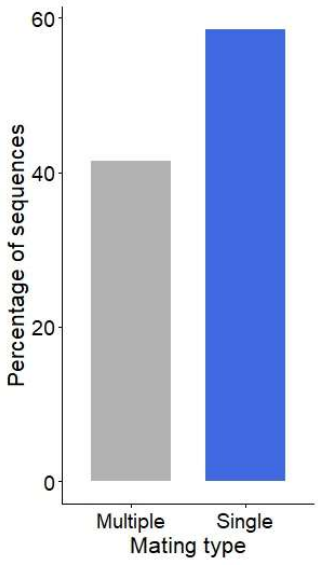


Figure 12 Proportion of sequences that recorded multiple matings (n = 41 sequences)

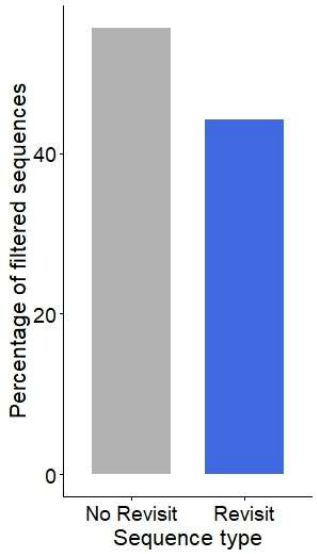


Figure 13: Proportion of sequences that recorded revisits (n = 75 sequences)

5.4 **Mate sampling strategies of female blackbucks**

The observed distribution of sampling strategies based on the decision rules does not significantly differ from a uniform distribution (X-squared = 1.8261, df = 2, p-value = 0.4013). Thus, no single strategy was represented disproportionately higher relative to the others, and the distribution of individuals across strategies was broadly even (*Figure 14*).

The likelihood of observing occurrence of mountings varies among the three sequences types. Of the 24 best-of-n sequences, 20 (83.3%) recorded occurrence of mountings. In contrast, occurrence of mounting was recorded in 14 of 27 sequential sampling sequences (51.9%). The lowest occurrence of mounting was observed in first-encounter sequences, where only 7 of the 18 sequences (38.9%). Thus, occurrence of mountings was more frequently associated with best-of-n sequences, intermediate in sequential sequences, and, least frequent in first-encounter sequences (*Figure 14*).

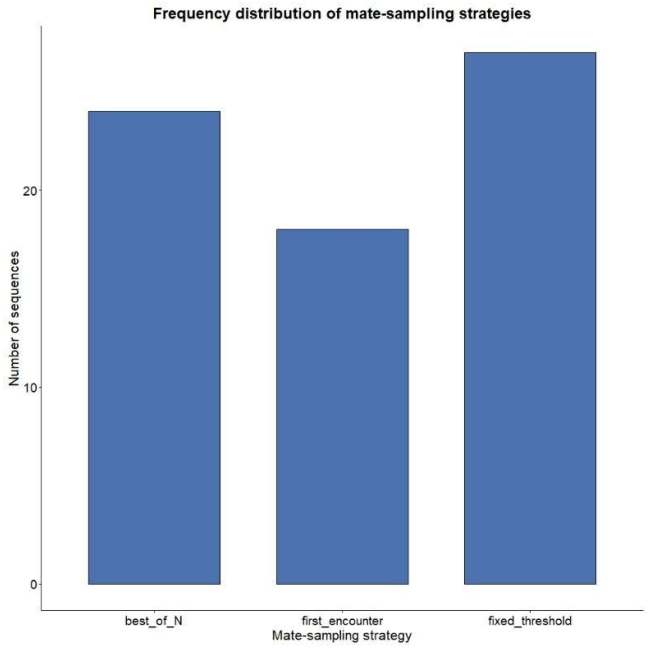


Figure 14: Distribution of strategies among the recorded sequences (n = 69 sequences)

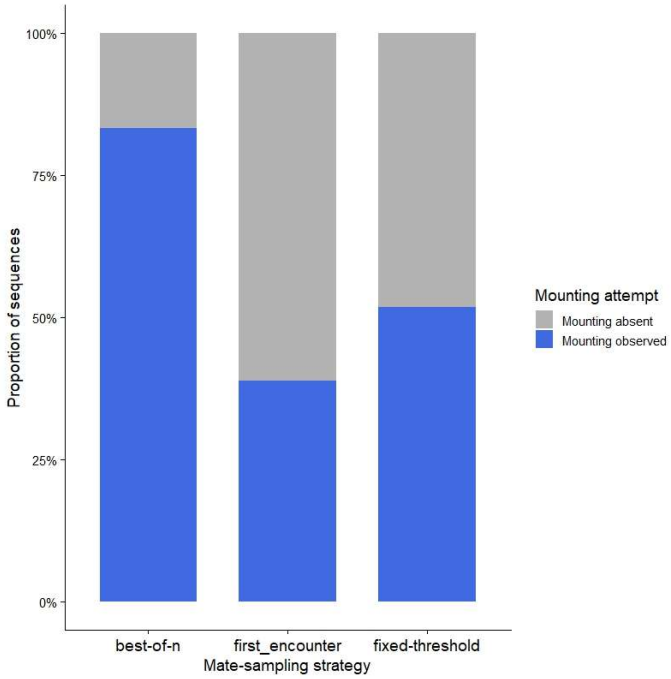


Figure 16: Proportion under each strategy that recorded mounting in at least one territory or no mounting (n – 69 sequences)

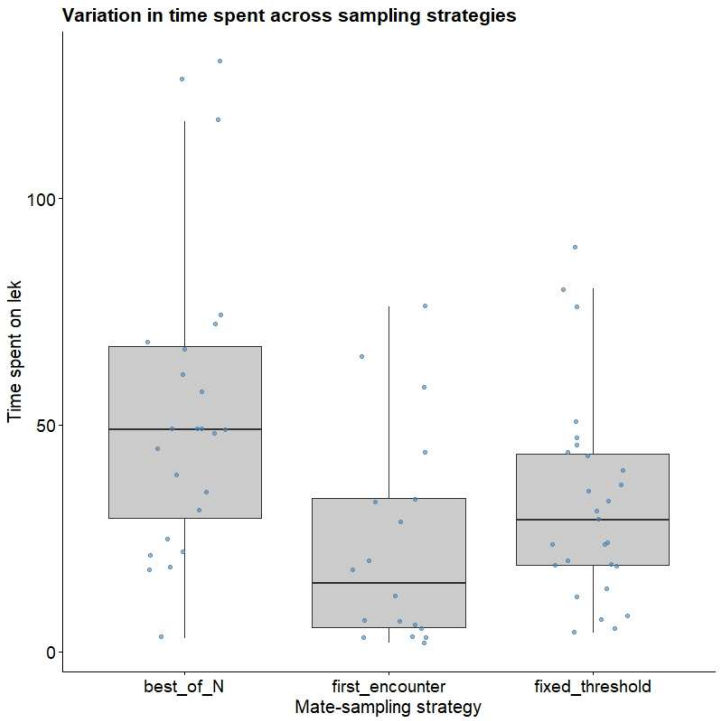


Figure 15: Comparison of time spent by a blackbuck female on the lek adopting different strategies (n = 69 sequences)

Total time spent on the lek differed significantly among strategies (*Figure 16*). Females with movement patterns consistent with first encounter ($\beta = -29.47 \pm 8.39$, $t = -3.51$, $p = 0.0008$) and sequential sampling strategy ($\beta = -20.49 \pm 7.55$, $t = -2.71$, $p = 0.008$), significantly spent less time compared to the female movement patterns consistent with best-of-n strategy.

Table 9: Model selection results from GLMs examining the effect of candidate predictor variables on the total time spent by a female on lek. Models are ranked according to AIC, with lower AIC values indicating better models.

Model	**Family distribution**	**Variables used**	**df**	**AIC**	**ΔAIC**
time_spent ~ date + strategy + mounting_yes_no + available_males	Gaussian	Date, strategy used, whether mated or not, available number of males on lek during the visit	7	636.730	0
time_spent ~ strategy + mounting_yes_no + available_males	Gaussian	Strategy used, whether mated or not, available number of males on lek during the visit	6	638.047	1.317
time_spent ~	Gaussian	Date, number of territories visited, whether mated or not, available number of	8	638.206	0.159

		males on lek during the visit, and strategy used			
time_spent ~ date + territories_visited + mounting_yes_no + available_males	Gaussian	Date, number of territories visited, whether mated or not, available number of males on lek during the visit	6	638.702	0.496
time_spent ~ territories_visited + mounting_yes_no + available_males	Gaussian	Number of territories visited, whether mated or not, available number of males on lek during the visit	5	639.581	0.879

Table 10: Parameter estimates from the best-fit GLM explaining variation in total time spent by females on the lek during mate sampling bouts. Shown are model coefficients (β), standard errors (SE), test statistics, and associated p-values.

Predictor	**Coefficient value**	**SE**	**t**	**P**
intercept	-9517.0338	5433.685	-1.751	0.084
date	0.466	0.264	1.762	0.082
strategy_first_encounter	-20.964	7.881	-2.660	0.009
strategy_fixed_threshold	-15.0918	7.002	-2.155	0.034
mounting_yes_no	20.5958	6.654	3.095	0.002

available_males	-0.4391	0.147	-2.969	0.004

The occurrence of mounting had a significant positive effect on total time spent by the female on lek ($\beta = 20.6$, $t = 3.095$, $p = 0.002$), with females involved in mounting events spending more time on the lek than females for which no mounting was observed. In contrast, the average number of available males present on the lek during a sampling bout was negatively associated with times spent by a female on lek ($\beta = -0.44$, $t = -2.969$, $p = 0.004$). Female therefore tended to spend less time on lek when male number was higher (*Table 10*).

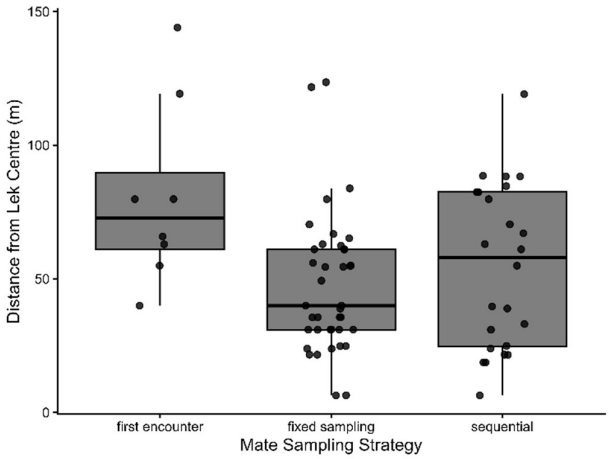


Figure 17: Distribution of territories in which mounting was observed under each strategy in relation to the lek centre

The distance of territories in which mounting was recorded from the lek centre under each strategy were significantly different (Kruskal-Wallis: $\chi^2 = 7.06$, $df = 2$, $p = 0.029$). Pairwise comparison showed a significant difference in the distance of territories where mounting was observed from the lek centre between the first encounter and best-of-n sampling (adjusted $p = 0.014$). In contrast, no significant difference was detected between first encounter and sequential sampling (adjusted $p = 0.208$) or between sequential and best-of-n sampling (adjusted $p = 0.372$).

6 DISCUSSIONS

6.1 Temporal patterns in the number of males and females on lek

The number of males on the lek were considerably high in the late February, declined throughout March, and surged again in the late March to April first week. Female visits to lek also tracked this variation. Blackbucks are reported to show two seasonal peaks of lekking in India, although they are capable of breeding throughout the year (Schaller, 1967; Ranjitsinh, 1989). Schaller (1967) documented two peaks, a minor peak during March-April, and a major peak during August-October. However, in arid regions of Rajasthan, Ranjitsinh (1989) proposed that reproductive timing is likely adapted to maximise offspring survival following monsoon rainfall, when forage availability is highest, and consequently December to March may pose as the optimal period. Present study provides support to this argument, with peak numbers of both male and females recorded in late March and early April, despite males being present on lek from as early as December.

Both male and female number on lek were significantly lower during the midday sessions. This aligns with previous studies (Isvaran & Jhala, 2000). Blackbucks exhibit peak activity during dawn and dusk and reduced activity during midday and late afternoon resting periods (Mungall, 1978). This behavioural rhythm might explain the observed session-wise differences. Additionally, in the open habitats, blackbuck activity is known to affected by heat, wind, and wetness (Mungall, 1978), suggesting environmental constraints may influence daily patterns of lek attendance. Male attendance has also known to be sensitive to weather conditions in other lekking species, such as the sage grouse (Fremgen et. al., 2019). Incorporating environment variables in future analyses would help to answer the effects of environment variables.

High ambient temperature can impose physiological constraints on reproduction, mainly affecting parts such as cremaster muscles and reducing the production of sperm (Casady et. al., 1953; Glover and Young, 1963). Spermatogenesis may then require approximately 7-8 weeks for the production of viable sperm following thermal sterility (White, 1968), and range animals like blackbucks are known to be vulnerable to thermal sterility (Mungall, 1978). Nonetheless, there was never an occasion where the lek was completely empty.

Female visits to lek followed a similar pattern of male number on lek. However, there was a pronounced increase in female numbers during peak periods. Although females are capable of reproducing throughout the year (Ranjitsinh, 1989), the presence of short, pronounced peaks in visitation may indicate synchronisation of estrous within the population. Estrous synchrony in ruminants have benefits such as predator dilution of newborns (Rutberg, 1987). In blackbucks, such synchrony may be influenced by local ecological conditions, particularly seasonal resource availability, where aligning reproduction with periods of optimal forage availability may enhance their and newborn's survival (Mungall, 1978; Ranjitsinh, 1989).

6.2 **Spatial structure of lek and patterns of lek use by blackbuck females**

Across all observed sequences, the centre of the lek consistently received higher numbers of visits, longer cumulative time spent by females, and higher occurrence of mountings. This pattern aligns with the findings of several other ungulate lekking systems, where central territories typically gained higher mating success and conferred reproductive advantages to males holding them (Fryxell, 1987; Gosling & Petrie, 1990; Balmford et. al., 1992; Clutton-Brock et. al., 1988; Isvaran & Jhala, 2000; Bro-Jørgensen, 2003; Bro-Jørgensen & Durant, 2003).

In blackbucks, females are known to respond to volatile compounds such as meta-cresol present in male urine and dung, which may function as a chemical cue in attracting them

(Jyothi, 2023). Additionally, the occurrence of female visits even after the changes in ownership (Isvaran & Jhala, 2000), suggests that stable territorial features may be an important parameter influencing female decision making.

6.3 General patterns of mate sampling behaviour of blackbuck females

There was substantial variation in the time spent by females during mate sampling bouts on the lek. Similar variation has been reported in other lekking ungulates, including fallow deer (*Dama dama*) (Clutton-Brock et. al., 1988; Imperio et. al., 2020). Such variation could be because of multiple factors. In fallow deer, age and experience have shown to shape the sampling effort of females, with younger females investing more time on lek compared to older females (Imperio et. al., 2020). However, age-class information for the focal females in this study was not available to test these differences.

Despite the high number of available males, more than 80% of sampling sequences involved visits to fewer than six territories. This supports the theoretical prediction proposed by Janetos (1980) that the marginal benefit of sampling decreases with increased number of mates sampled. Similar patterns have been documented in other lekking species, including satin bowerbird (*Ptilonorhynchus violaceus*) (Uy et. al., 2001), great snipe (*Gallinago media)* (Fiske & Kålås, 1995), and black grouse (*Tetrao tetrix*) (Rintamäki et. al., 1995), where females typically sampled only a subset of available males. Is this because of females using prior information – such as centrality of lek (Bro-Jørgensen, 2002) to reduce further sampling? In the present study, females often entered the lek directly towards central areas and initiated sampling without as systematic peripheral to central progression. Given the spatial clustering of territories in the centre, sampling a limited subset of males may reduce the sampling costs that may have incurred if such an information was not available (Reynolds & Gross, 1990).

Interestingly, total time spent on lek decreased with increasing number of males, suggesting that larger leks may impose higher costs on females. This pattern may reflect increased harassment, chasings, and interference as male density increases (Bro-Jørgensen, 2003a). As sampling costs increases, females may restrict their search to a subset of males and reduce total time spent on lek.

Several sequences involved occurrence of mountings across different territories within a single bout. Multiple matings may arise from suboptimal choice (Rivers & DuVal, 2019) or from female preferences for certain males (Petrie et. al., 1992). Multiple matings provide certain benefits like fertilisation assurance, increased genetic diversity, avoidance of male infertility, and access to direct and indirect benefits (reviewed by Petrie et. al., 1992). Multiple mating is widely reported in lekking systems (Balmford et. al., 1992), suggesting it may be a common outcome in lek systems.

In contrast, some sequences did not record any occurrence of mountings. This is consistent with the idea that females may sample prior to mating, sometimes across multiple sampling bouts, to gather information about potential males (Dale & Slagsvold, 1996; Uy et. al., 2001). Such information may include male phenotype (Gosling & Petrie, 1990), display quality, territory characteristics (Deutsch & Nefdt, 1992), or competitive interactions as these parameters have found to be correlated with a male's mating success (Appolonio et. al., 1992; Festa-bianchet et. al. 1990; San José & Braza, 1997; Balmford et. al., 1992). Alternatively, non-mating visits may occur when preferred males are absent or when no encountered males exceed a female's acceptance threshold (Janetos, 1980). This could be questionable in leks, especially if central males are indeed better-quality males than peripheral males. Because one can expect a greater number of available males near the centre of lek and the decision of not mating may require further investigations apart from the traditional threshold acceptance and social context point of view (Bro-Jørgensen, 2002).

Social interactions may also shape sampling outcomes. Female-female competition has been shown to influence a female's access to preferred males in topi leks (Bro-Jørgensen, 2002). In such contexts, dominant females may displace others from high-quality territories, thereby altering sampling decisions. The presence of multiple females can also affect female mating opportunities (Mayank, 2019). In blackbuck leks, males often continue mounting attempts with a focal female despite interruptions, while other females may be forced to wait, increasing their vulnerability to herding attempts by other males and female-female competition. Similar observations have been made in fallow deer leks, where female does were more likely to terminate a bout by leaving if the buck became distracted by the presence of young bucks around the periphery (Clutton-Brock, et. al., 1988). Consequently, sampling without mating carries both energetic and opportunity costs (Byers et. al., 2005; Real, 1990), particularly given the short duration of female receptivity (approximately 24 hours within a 5-6 days estrous cycle; Mungall et. al., 1978) and short duration of peaks, where the maximum number of high-quality males are supposed to be available. But, in leks, these costs may be considerably low as leks almost guarantee mates to the females (Höglund & Alatalo, 1995).

6.4 **Mate sampling strategies of female blackbucks**

The distribution of mate sampling strategies did not deviate significantly from a uniform expectation, suggesting that females do not employ a fixed strategy but instead exhibit a mixture of co-existing tactics. Such co-existence of alternative behavioural strategies has been reported in several animal populations (Dale & Slagsvold, 1996; Choudhury & Black, 1993). However, it is important to note that present analysis is based on single mate sampling bout events rather than lifetime or seasonal decisions. Consequently, the inferred strategy reflects behaviour within discrete sampling bouts rather than long term individual-level decision rules. Scale of analysis is therefore critically influences inference. If strategies were defined across the entire rutting period, rather than individual bouts, both classification and predicted

outcomes would likely differ. This highlights a key limitation in mapping theoretical sampling models onto empirical bout-level observations. Most importantly, this distribution represents the operational categories defined according to the decision rules presented on *Table 2*. Comparison with *Table 1* indicates that these movement patterns may correspond to multiple mate sampling strategies within each operational category. Therefore, the interpretations and conclusions drawn from this study pertains to these broader operational categories, as inferred from the female movement patterns within lek, rather than specific mate sampling strategies in their strict theoretical sense.

A substantial proportion of sequences involved revisits to previously sampled territories. Among theoretical models, revisitation is primarily predicted under best-of-n and Bayesian comparative tactics (Janetos, 1980; Luttbeg, 1996). In contrast, sequences involving visits to only one territory correspond to most closely to the first-encounter or random mating model (Janetos, 1980), while sequences involving multiple territories without revisits are consistent with pure threshold or one-step decision rules (Janetos, 1980).

However, distinguishing these strategies empirically with movement patterns alone remains challenging. For example, first-encounter may arise under multiple, non-exclusive scenarios: (i) strong time constraint limiting sampling, (ii) immediate acceptance of an internal threshold, or (iii) a default strategy in environment where encounters are rare or costly. In the present study, classification is solely based on visitation order and number of territories visited; therefore, it is not possible to distinguish true first-encounter decisions from conditional fixed-threshold decisions. Another explanation could be that a female could have multiple sampling bouts prior to mating (Uy et. al., 2001). In an initial bout, a female may visit several territories and identify one as favourable, and in a later bout she may spend most or all of her time in that chosen territory.

Similarly, best-of-n and Bayesian comparative tactics are difficult to separate because both predicts revisits (Janetos, 1980; Luttbeg, 1996). Bayesian models, in particular, allow for directed movement based on prior information (Luttbeg, 1996), which may be consistent with the observed tendency of females to move directly towards central lek areas (Gosling & Petrie, 1990; personal observations). This raises possibility that females may possess prior spatial information about mate quality, reducing the need for extensive sampling. Robust discrimination among these strategies therefore requires additional behavioural or state-level predictions beyond spatial visitation sequences that can be tested empirically.

For example, most models assume perfect knowledge about mate quality distributions (Janetos, 1980; Real, 1990). Let us consider the first-encounter sequences. When spatial structure of territories was considered, out of the 7 sequences that recorded mounting in at least one territory, only two where on the centre of the lek. If centrality is assumed to be correlated with mate quality, then sequences classified as first-encounter but occurring in central territories may instead reflect threshold decisions, where the first encountered male already exceeds the acceptance threshold. However, without direct information on male quality or female thresholds, these strategies remain statistically indistinguishable. A further complication arises from the definition of "encounter" in lek systems. Females may pass multiple males during the entry without engaging in sampling, implying that not all encounter events constitute sampling. This highlights the limitation of inferring cognitive decision rules solely from the movement trajectories.

Another concern is that leks are highly dynamic, it can be considered as a spatial collective phenomenon arising from local interactions between individuals interacting at various spatio-temporal scales (Rathore et. al., 2023). For example, a simple interaction might propagate in their neighbourhood and thus, in turn affect the behaviour of other individuals (Rathore et. al., 2023). Consequently, movement patterns observed at the level of an individual female may not

always reflect independent sampling decisions, but rather cumulative effects of interactions occurring within her local environment.

In blackbuck leks, for example, a female is often subjected to herding attempts by nearby territorial males. When a territory-holding male leaves a female unattended to chase away the intruder males or sub-adults on lek, neighbouring males frequently attempt to herd her into their own territories. Although such attempts are often unsuccessful, they may occasionally prompt the female to leave her current territory and move to another neighbouring territory or any territory located at another part of the lek. In this sense, one can argue that the female movement can arise indirectly from male movement and interactions across the lek during the sampling bout.

At the same time, observations indicate that females frequently move independently despite herding attempts (Isvaran & Jhala, 2000; personal observations), and in some cases actively evade males through body-feinting. This creates a conceptual challenge in classifying movement trajectories within the framework of mate sampling strategies. For instance, if a female leaves a territory following a herding attempt by a neighbouring male but subsequently returns to the same territory without visiting or assessing another territory, should this movement be considered a revisit? From strict sampling perspective, no comparison among males has occurred. Nevertheless, the behaviour still may require the female to retain information about the location of the previously encountered male, a key assumption underlying best-of-n strategy (Janetos, 1980). Such examples highlight the difficulty of mapping observed movement trajectories onto discrete theoretical mate-choice strategies.

Despite these limitations, patterns observed in this study suggests that best-of-n-like sampling often involving revisits may be highly rewardable, with over 80% of sequences under this broad classification resulted in the occurrence of mounting. In contrast, more than half of

first-encounter sequences wherein only one territory was visited did not lead to mating. This also corresponds to the search effort as females classified under best-of-n comparatively spent more time in lek compared to others.

Overall, our results indicate that blackbuck female movement patterns within a lek during a mate sampling bout are consistent with mixed sampling strategies, rather than adhering to a single fixed rule. Future work should incorporate additional behavioural predictors to better discriminate among competing theoretical models. Incorporating alternative frameworks such as female-copying (Clutton-Brock & McComb, 1993; McComb & Clutton-Brock, 1994; Imperio et. al., 2020) may further improve the theoretical models.

6.5 Limitations

Several limitations should be considered while interpreting the findings of the study.

Firstly, individual females could not be identified throughout the study period. Consequently, the dataset may contain repeated observations of the same female across multiple mate sampling bout sequences, limiting the ability to infer consistent sampling strategies at an individual level. For instance, a hypothetical female may undertake several sampling bouts prior to mating (Uy et. al., 2001). During an initial bout, she may sample several males, whereas subsequent bout may involve visit to only the preferred male chosen during the initial bout (Uy et. al., 2001). Treating these bouts as independent observations thus limit the classification of strategies at an individual level.

Secondly, theoretical models of mate sampling assume variation in mate quality and perfect information about the distribution of potential males (Janetos, 1980; Real, 1990). However, the present study could not quantify direct measures of mate quality. The only variable that could potentially serve as a proxy for male quality was distance of a territory from lek centre, assuming that centrally located territories are occupied by superior males (Bro-

Jørgensen, 2002). This limits the examination of step-wise rejection and acceptance decisions of females during the mate sampling bout.

A further limitation is the inability to identify successful matings. Occurrence of mountings could be used as a proxy for mating, but it cannot be interpreted as definitive evidence of female mate choice. In sequences where mounting occurred in multiple territories, it is not possible to determine the territory at which successful copulation ultimately occurred. Although certain behaviours have been used in previous studies (Isvaran & Jhala, 2000) as indicators of successful copulation, the reliability of such behavioural proxies remain uncertain.

Finally, current study assumes that females sample males sequentially by visiting territories one after another. This assumption underpins the classification of sampling strategies. However, lekking systems may also permit simultaneous sampling (Rosenthal, 2017), whereby females evaluate males without physically visiting every territory. If females employ such simultaneous sampling, movement trajectories alone might not accurately reflect the complete sampling process, potentially influencing the inferred strategy. Although the ecological prevalence of simultaneous sampling remains debated (Wiegmann, 1999; Deb & Balakrishnan, 2014), its potential occurrence in blackbuck lek cannot be excluded.

Collectively, these limitations indicate that the operational categories defined in this study should be interpreted as movement-based representations of female sampling behaviour rather than definitive evidence underlying theoretical mate sampling strategies.

7 REFERENCES

Apollonio, M., De Cena, F., Bongi, P., & Ciuti, S. (2014). Female preference and predation risk models can explain the maintenance of a fallow deer (Dama dama) lek and its 'handy'location. *PLoS One*, *9*(3), e89852. https://doi.org/10.1371/journal.pone.0089852

Apollonio, M., Festa-Bianchet, M., & Mari, F. (1989a). Correlates of copulatory success in a fallow deer lek. *Behavioral Ecology and Sociobiology*, *25*(2), 89-97. https://doi.org/10.1007/BF00302925

Apollonio, M., Festa-Bianchet, M., Mari, F., Bruno, E., & Locati, M. (1998). Habitat manipulation modifies lek use in fallow deer. *Ethology*, *104*(7), 603-612. https://doi.org/10.1111/j.1439-0310.1998.tb00095.x

Apollonio, M., Festa-Bianchet, M., Mari, F., Mattioli, S., & Sarno, B. (1992). To lek or not to lek: mating strategies of male fallow deer. Behavioral Ecology, 3(1), 25-31. https://doi.org/10.1093/beheco/3.1.25

Rutberg, A. T. (1987). Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *The American Naturalist*, *130*(5), 692-710. https://doi.org/10.1086/284739

Backwell, P. R., & Passmore, N. I. (1996). Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, Uca annulipes. *Behavioral Ecology and Sociobiology*, *38*(6), 407-416. https://doi.org/10.1007/s002650050258

Balmford, A., & Turyaho, M. (1992). Predation risk and lek-breeding in Uganda kob. *Animal behaviour*, *44*(1), 117-127. https://doi.org/10.1016/S0003-3472(05)80761-4

Balmford, A., Albon, S., & Blakeman, S. (1992). Correlates of male mating success and female choice in a lek-breeding antelope. *Behavioral Ecology*, *3*(2), 112-123. https://doi.org/10.1093/beheco/3.2.112

Balmford, A., Deutsch, J. C., Nefdt, R. J., & Clutton-Brock, T. (1993). Testing hotspot models of lek evolution: data from three species of ungulates. Behavioral Ecology and Sociobiology, 33(1), 57-65. https://doi.org/10.1007/BF00164347

Beckers, O. M., & Wagner Jr, W. E. (2011). Mate sampling strategy in a field cricket: evidence for a fixed threshold strategy with last chance option. *Animal Behaviour*, *81*(3), 519-527. https://doi.org/10.1016/j.anbehav.2010.11.022

Bowyer, R. T., McCullough, D. R., Rachlow, J. L., Ciuti, S., Whiting, J. C., 2020. Evolution of ungulate mating systems: integrating social and environmental factors. Ecol. Evol. 10(11), 5160-5178. https://doi.org/10.1002/ece3.6246

Bro-Jørgensen, J. (2002). Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences*, *99*(14), 9290-9293. https://doi.org/10.1073/pnas.142125899

Bro-Jørgensen, J. (2003a). No peace for estrous topi cows on leks. *Behavioral Ecology*, *14*(4), 521-525. https://doi.org/10.1093/beheco/arg026

Bro-Jørgensen, J. (2003b). The significance of hotspots to lekking topi antelopes (Damaliscus lunatus). *Behavioral Ecology and Sociobiology*, *53*(5), 324-331. https://doi.org/10.1007/s00265-002-0573-0

Bro-Jørgensen, J. (2011). Queuing in space and time reduces the lek paradox on an antelope lek. *Evolutionary ecology*, *25*(6), 1385-1395. https://doi.org/10.1007/s10682-011-9523-5

Bro-Jørgensen, J., & Durant, S. M. (2003). Mating strategies of topi bulls: getting in the centre of attention. *Animal Behaviour*, *65*(3), 585-594. https://doi.org/10.1006/anbe.2003.2077

Bro-Jørgensen, J., & Pangle, W. M. (2010). Male topi antelopes alarm snort deceptively to retain females for mating. *The American Naturalist*, *176*(1), E33-E39. https://doi.org/10.1086/653078

Buechner, H. K., & Daniel Roth, H. (1974). The lek system in Uganda kob antelope. *American Zoologist*, *14*(1), 145-162. https://doi.org/10.1093/icb/14.1.145

Buzzard, P. J., Bleisch, W. V., Xü, D., & Zhang, H. (2008). Evidence for lekking in chiru. Journal of Zoology, 276(4), 330-335. **https://doi.org/10.1111/j.1469-7998.2008.00493.x**

Byers, J. A., Wiseman, P. A., Jones, L., & Roffe, T. J. (2005). A large cost of female mate sampling in pronghorn. *The American Naturalist*, *166*(6), 661-668. https://doi.org/10.1086/497401

Casady, R. B., Myers, R. M., & Legates, J. E. (1953). The effect of exposure to high ambient temperature on spermatogenesis in the dairy bull. **DOI: 10.3168/jds.S0022-0302(53)91449-0**

Champion, H. G., & Seth, S. K. (1968). *A revised survey of the forest types of India*. Manager of publications.

Choudhury, S., & Black, J. M. (1993). Mate-selection behaviour and sampling strategies in geese. *Animal Behaviour*, *46*(4), 747-757. https://doi.org/10.1006/anbe.1993.1252

Ciuti, S., & Apollonio, M. (2016). Reproductive timing in a lekking mammal: male fallow deer getting ready for female estrus. *Behavioral Ecology*, *27*(5), 1522-1532. https://doi.org/10.1093/beheco/arw076

Clo, J., Abu Awad, D., Bilde, T., Bocedi, G., Haag, C. R., Pannell, J., & Hartfield, M. (2025). Perspectives on mating–system evolution: comparing concepts in plants and animals. Journal of evolutionary biology, voaf009. https://doi.org/10.1093/jeb/voaf009

Clutton-Brock, T. H. (1989). Review lecture: mammalian mating systems. *Proceedings of the Royal Society of London. B. Biological Sciences*, *236*(1285), 339-372. https://doi.org/10.1098/rspb.1989.0027

Clutton-Brock, T. H., Deutsch, J. C., & Nefdt, R. J. C. (1993). The evolution of ungulate leks. *Animal Behaviour*, *46*(6), 1121-1138. https://doi.org/10.1006/anbe.1993.1302

Clutton-Brock, T. H., Green, D., Hiraiwa-Hasegawa, M., & Albon, S. D. (1988). Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behavioral Ecology and Sociobiology*, *23*(5), 281-296 https://doi.org/10.1007/BF00300575

Clutton-Brock, T. H., Price, O. F., & MacColl, A. C. (1992). Mate retention, harassment, and the evolution of ungulate leks. *Behavioral Ecology*, *3*(3), 234-242. https://doi.org/10.1093/beheco/3.3.234

Clutton-Brock, T., & McAuliffe, K. (2009). Female mate choice in mammals. *The Quarterly review of biology*, *84*(1), 3-27. https://doi.org/10.1086/596461

Clutton-Brock, T., & McComb, K. (1993). Experimental tests of copying and mate choice in fallow deer (Dama dama). *Behavioral Ecology*, *4*(3), 191-193. https://doi.org/10.1093/beheco/4.3.191

Dale, S., & Slagsvold, T. (1996). Mate choice on multiple cues, decision rules and sampling strategies in female pied flycatchers. *Behaviour*, *133*(11-12), 903-944. https://doi.org/10.1163/156853996X00305

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology*. John Wiley & Sons.

Deb, R., & Balakrishnan, R. (2014). The opportunity for sampling: the ecological context of female mate choice. *Behavioral Ecology*, *25*(4), 967-974. https://doi.org/10.1093/beheco/aru072

Deutsch, J. C., & Nefdt, R. J. (1992). Olfactory cues influence female choice in two lek-breeding antelopes. *Nature*, *356*(6370), 596-598. https://doi.org/10.1038/356596a0

Festa-Bianchet, M., Apollonio, M., Mari, F., & Rasola, G. (1990). Aggression among lekking male fallow deer (Dama dama): territory effects and relationship with copulatory success. Ethology, 85(3), 236-246. https://doi.org/10.1111/j.1439-0310.1990.tb00403.x

Fiske, P., & Kålås, J. A. (1995). Mate sampling and copulation behaviour of great snipe females. *Animal Behaviour*, *49*(1), 209-219. https://doi.org/10.1016/0003-3472(95)80169-3

Forsgren, E. (1997). Mate sampling in a population of sand gobies. *Animal Behaviour*, *53*(2), 267-276. https://doi.org/10.1006/anbe.1996.0374

Fremgen, A. L., Hansen, C. P., Rumble, M. A., Gamo, R. S., & Millspaugh, J. J. (2019). Weather conditions and date influence male Sage Grouse attendance rates at leks. *Ibis*, *161*(1), 35-49. https://doi.org/10.1111/ibi.12598

Fryxell, J. M. (1987). Lek breeding and territorial aggression in white-eared kob. *Ethology*, *75*(3), 211-220. https://doi.org/10.1111/j.1439-0310.1987.tb00654.x

Gibson, R. M., & Langen, T. A. (1996). How do animals choose their mates?. *Trends in Ecology & Evolution*, *11*(11), 468-470. DOI: 10.1016/0169-5347(96)10050-1

Glover, T. D., & Young, D. H. (1963). Temperature and the production of spermatozoa. *Fertility and Sterility*, *14*(4), 441-450. https://doi.org/10.1016/S0015-0282(16)34929-9

Gosling, L. M., & Petrie, M. (1990). Lekking in topi: a consequence of satellite behaviour by small males at hotspots. *Animal Behaviour*, *40*(2), 272-287. https://doi.org/10.1016/S0003-3472(05)80922-4

Gosling, L. M., Petrie, M., & Rainy, M. E. (1987). Lekking in topi: A high cost, specialist strategy. *Animal Behaviour*.

Gross, J. W., & Heumann, B. W. (2016). A statistical examination of image stitching software packages for use with unmanned aerial systems. *Photogrammetric Engineering & Remote Sensing*, *82*(6), 419-425. https://doi.org/10.14358/PERS.82.6.419

Höglund, J., & Alatalo, R. V. (1995). *Leks*. Princeton University Press.

Höglund, J., Alatalo, R. V., Gibson, R. M., & Lundberg, A. (1995). Mate-choice copying in black grouse. *Animal Behaviour*, *49*(6), 1627-1633. https://doi.org/10.1016/0003-3472(95)90085-3

Imperio, S., Lombardi, S., De Marinis, A., Ronchi, F., Santini, G., & Focardi, S. (2020). Female mating tactics in lekking fallow deer (Dama dama): experience explains inter-individual variability more than costs. *Scientific Reports*, *10*(1), 3598. https://doi.org/10.1038/s41598-020-58681-5

Isvaran, K. (2005a). Female grouping best predicts lekking in blackbuck (Antilope cervicapra). *Behavioral Ecology and Sociobiology*, *57*(3), 283-294. https://doi.org/10.1007/s00265-004-0844-z

Isvaran, K. (2005b). Variation in male mating behaviour within ungulate populations: patterns and processes. *Current Science*, 1192-1199. https://www.jstor.org/stable/24110971

Isvaran, K. (2020). The lekking puzzle: The evolution of costly mating behaviour. *Resonance*, *25*(3), 353-362. https://doi.org/10.1007/s12045-020-0950-x

Isvaran, K., & Jhala, Y. (2000). Variation in lekking costs in blackbuck (Antilope cervicapra): relationship to lek-territory location and female mating patterns. *Behaviour*, *137*(5), 547-563. https://doi.org/10.1163/156853900502204

Isvaran, K., & Ponkshe, A. (2013). How general is a female mating preference for clustered males in lekking species? A meta-analysis. *Animal behaviour*, *86*(2), 417-425. https://doi.org/10.1016/j.anbehav.2013.05.036

Ivy, T. M., & Sakaluk, S. K. (2007). Sequential mate choice in decorated crickets: females use a fixed internal threshold in pre-and postcopulatory choice. *Animal Behaviour*, *74*(4), 1065-1072. https://doi.org/10.1016/j.anbehav.2007.01.017

Janetos, A. C. (1980). Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology*, *7*(2), 107-112. https://doi.org/10.1007/BF00299515

Jayabharathy, R. (2021). *Territorial and mating strategies of males in a lekking population of blackbuck Antilope cervicapra* (Doctoral dissertation).

Jhala, Y. V., & Isvaran, K. (2016). Behavioural ecology of a grassland antelope, the blackbuck Antilope cervicapra: linking habitat, ecology and behaviour. In *The ecology of large herbivores in South and Southeast Asia* (pp. 151-176). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-94-017-7570-0_6

Jyothi (2023) Factors affecting variation in mating success of males in a blackbuck lek http://hdl.handle.net/10603/535784

Kaur, M., Das, S. K., & Sarma, K. (2023). Water quality assessment of Tal Chhapar Wildlife Sanctuary using water quality index (CCME WQI). Acta Ecologica Sinica, 43(1), 82-88.

Kaur, M., Joshi, P., Sarma, K., & Das, S. K. (2020). Assessment of plant community structure in Tal Chhapar wildlife sanctuary, Rajasthan, India. Species, 21(67), 126-139.

Klug, H. (2011). Animal mating systems. *eLS*.

Lehmann, G. U. (2007). Density-dependent plasticity of sequential mate choice in a bushcricket (Orthoptera: Tettigoniidae). *Australian Journal of Zoology*, *55*(2), 123-130. https://doi.org/10.1071/ZO06105

Locatello, L., & Rasotto, M. B. (2017). Females' sampling strategy to comparatively evaluate prospective mates in the peacock blenny Salaria pavo. *The Science of Nature*, *104*(7), 57. https://doi.org/10.1007/s00114-017-1483-3

Luttbeg, B. (1996). A comparative Bayes tactic for mate assessment and choice. *Behavioral Ecology*, *7*(4), 451-460. https://doi.org/10.1093/beheco/7.4.451

Luttbeg, B. (2002). Assessing the robustness and optimality of alternative decision rules with varying assumptions. *Animal Behaviour*, *63*(4), 805-814. https://doi.org/10.1006/anbe.2001.1979

Mayank (2019). Variation in behaviour of male and female blackbuck with respect to the number of females on the same lek. (Master thesis)

Mazalov, V., Perrin, N., & Dombrovsky, Y. (1996). Adaptive search and information updating in sequential mate choice. *The American Naturalist*, *148*(1), 123-137. https://doi.org/10.1086/285914

Mccomb, K., & Clutton-Brock, T. H. (1994). Is mate choice copying or aggregation responsible for skewed distributions of females on leks?. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *255*(1342), 13-19. https://doi.org/10.1098/rspb.1994.0003

Mehtani, P., Sharma C., Chatterjee, S., & Bhatnagar, P. (2013). Evaluation of halophilic nature of soil and water from Tal Chhapar black buck sanctuary, Churu, Rajasthan, India. Int J Bio-Technol Res, 3, 101-104.

Mungall, E. C. (1978). The Indian blackbuck antelope: a Texas view.

Nefdt, R. J., & Thirgood, S. J. (1997). Lekking, resource defense, and harassment in two subspecies of lechwe antelope. *Behavioral Ecology*, *8*(1), 1-9. https://doi.org/10.1093/beheco/8.1.1

Nelder, J. A., & Wedderburn, R. W. (1972). Generalized linear models. *Journal of the Royal Statistical Society Series A: Statistics in Society*, *135*(3), 370-384. https://doi.org/10.2307/2344614

Ojha, A. (2016). Ecological study of Tal Chhapar Sanctuary, Churu (Rajasthan). J. Glob Res, 3, 27-31.

Oring, L. W. (1982). Avian mating systems. *Avian Biology*. Vol. VI, 1-92.

Petrie, M., Hall, M., Halliday, T., Budgey, H., & Pierpoint, C. (1992). Multiple mating in a lekking bird: why do peahens mate with more than one male and with the same male

more than once?. *Behavioral Ecology and Sociobiology*, *31*(5), 349-358. https://doi.org/10.1007/BF00177775

Ranjitsinh, M. K. (1989). *The Indian Blackbuck*. Natraj Publishers.

Rathore, A., Isvaran, K., & Guttal, V. (2023). Lekking as collective behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1874), 20220066. doi: 10.1098/rstb.2022.0066

R Core Team. (2020). R: A language and environment for statistical computing [Computer software]. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Real, L. (1990). Search theory and mate choice. I. Models of single-sex discrimination. *The American Naturalist*, *136*(3), 376-405. https://www.jstor.org/stable/2462150

Reid, M. L., & Stamps, J. A. (1997). Female mate choice tactics in a resource-based mating system: field tests of alternative models. *The American Naturalist*, *150*(1), 98-121. https://doi.org/10.1086/286058

Reynolds, J. D., & Gross, M. R. (1990). Costs and benefits of female mate choice: is there a lek paradox?. *The American Naturalist*, *136*(2), 230-243. https://doi.org/10.1086/285093

Rintamäki, P. T., Alatalo, R. V., Höglund, J., & Lundberg, A. (1995). Mate sampling behaviour of black grouse females (Tetrao tetrix). *Behavioral Ecology and Sociobiology*, *37*(3), 209-215. https://doi.org/10.1007/BF00176719

Rivers, P. R., & DuVal, E. H. (2020). Multiple paternity in a lek mating system: Females mate multiply when they choose inexperienced sires. *Journal of Animal Ecology*, *89*(5), 1142-1152. https://doi.org/10.1111/1365-2656.13158

Rodgers, W. A., & Panwar, H. S. (1988). Planning a wildlife protected area network in India.

Rosenthal, G. G. (2017). *Mate choice: the evolution of sexual decision making from microbes to humans*. Princeton University Press.

San José, C., & Braza, F. (1997). Ecological and behavioural variables affecting the fallow deer mating system in Doñana. *Ethology Ecology & Evolution*, *9*(2), 133-148. https://doi.org/10.1080/08927014.1997.9522892

Schaller, G. B. (1967). *The deer and the tiger*. University of Chicago Press.

Stillman, R. A., Cutton-Brock, T. H., & Sutherland, W. J. (1993). Black holes, mate retention, and the evolution of ungulate leks. *Behavioral Ecology*, *4*(1), 1-6. https://doi.org/10.1093/beheco/4.1.1

Stillman, R. A., Deutsch, J. C., Clutton-Brock, T. H., & Sutherland, W. J. (1996). Black hole models of ungulate lek size and distribution. *Animal Behaviour*, *52*(5), 891-902. https://doi.org/10.1006/anbe.1996.0237

Thirgood, S. J. (1991). Alternative mating strategies and reproductive success in fallow deer. *Behaviour*, 1-10. https://www.jstor.org/stable/4534906

Westcott, D. A. (1997). Lek locations and patterns of female movement and distribution in a Neotropical frugivorous bird. *Animal Behaviour*, *53*(2), 235-247. https://doi.org/10.1006/anbe.1996.0294

Uy, J. A. C., Patricelli, G. L., & Borgia, G. (2001). Complex mate searching in the satin bowerbird Ptilonorhynchus violaceus. *The American Naturalist*, *158*(5), 530-542. https://doi.org/10.1093/beheco/arm031

White, I. G. (1968). Mammalian semen. *In*: E. S. E. Hafez, ed. Reproduction in farm animals, 2nd ed. Lea and Febiger, Philadelphia. Pp. 39-59

Wiegmann, D. D. (1999). Search behaviour and mate choice by female field crickets, Gryllus integer. *Animal behaviour*, *58*(6), 1293-1298. https://doi.org/10.1006/anbe.1999.1243

Wiegmann, D. D., & Angeloni, L. M. (2007). Mate choice and uncertainty in the decision process. *Journal of Theoretical Biology*, *249*(4), 654-666. https://doi.org/10.1016/j.jtbi.2007.08.027

Wiegmann, D. D., & Makhopadhyay, K. (1998). The fixed sample search rule and use of an indicator character to evaluate mate quality. *Journal of theoretical biology*, *193*(4), 709-715.

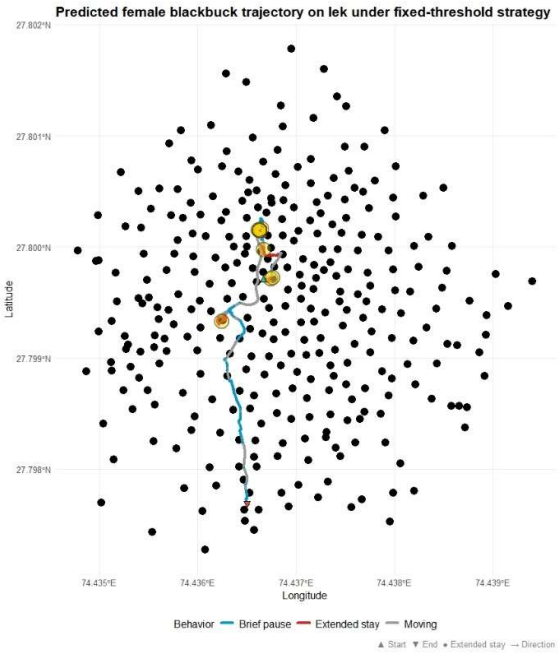
Wiegmann, D. D., Real, L. A., Capone, T. A., & Ellner, S. (1996). Some distinguishing features of models of search behavior and mate choice. *The American Naturalist*, *147*(2), 188-204. https://doi.org/10.1086/285846

Wiegmann, D. D., Seubert, S. M., & Wade, G. A. (2010). Mate choice and optimal search behavior: fitness returns under the fixed sample and sequential search strategies. *Journal of theoretical biology*, *262*(4), 596-600. https://doi.org/10.1016/j.jtbi.2009.08.033

Wiegmann, D. D., Weinersmith, K. L., & Seubert, S. M. (2010). Multi-attribute mate choice decisions and uncertainty in the decision process: a generalized sequential search strategy. *Journal of mathematical biology*, *60*(4), 543-572. https://doi.org/10.1007/s00285-009-0274-7

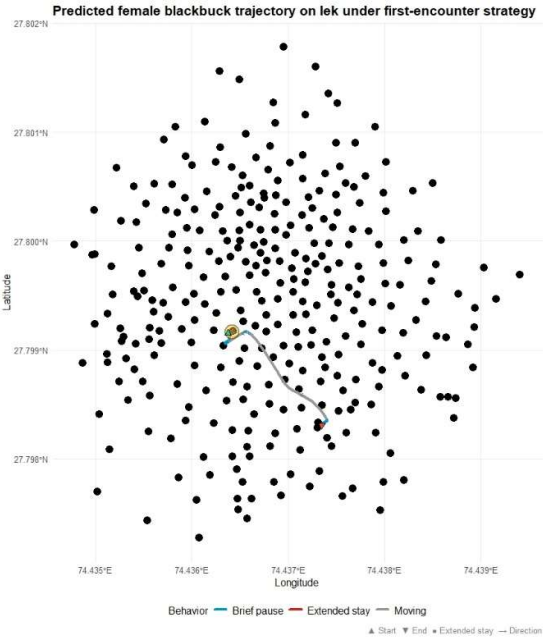
APPENDICES

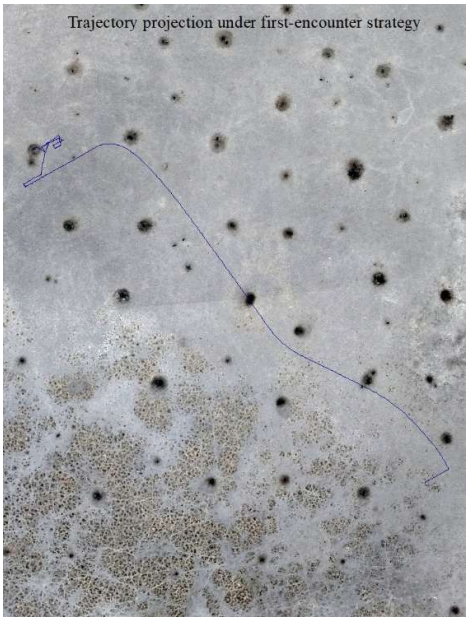
Appendix 1: Conceptual representation of female movement trajectories under alternative mate sampling strategies and their projection onto a georeferenced lek map. For each sampling strategy, left panel represents a conceptual representation of the movement pattern, whereas right panel shows the same trajectory projected onto the spatial configuration of territories mapped within the lek. Golden circles indicate the points where she spent considerably more time along her trajectory. a) Fixed-threshold sampling: females sequentially assess multiple males or territories until an acceptance threshold is reached, resulting in visits to several territories with no revisits. b) First-encounter: females sample only one male or territory, resulting in limited movement and prolonged residence within a single point. c)Best-of-n sampling: females compare multiple males or territories, leading to repeated assessment and greater concentration of residence time within some criss-crossing points along the trajectory. Note: The mapped territories represent the cumulative set of territories recorded during the study. Some may have disappeared, and some may be inactive for the season. Owing to close spatial clustering of territories within lek and positional uncertainty associated with GPS, some points may appear overlapping. Visitation sequences and territory assignments were manually reviewed and cross-validated using the original tracking data.


Predicted female blackbuck trajectory on lek under fixed-threshold strategy
27.802°N
27.801°N
27.800°N
27.799°N
27.798°N
Latitude
74.435°E
74.436°E
74.437°E
74.438°E
74.439°E
Longitude
Behavior Brief pause Extended stay Moving
▲ Start ▼ End ● Extended stay → Direction

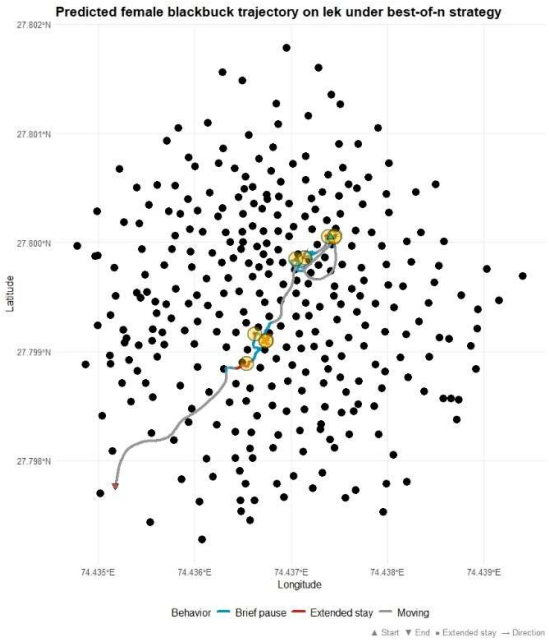

Trajectory projection under fixed-threshold strategy

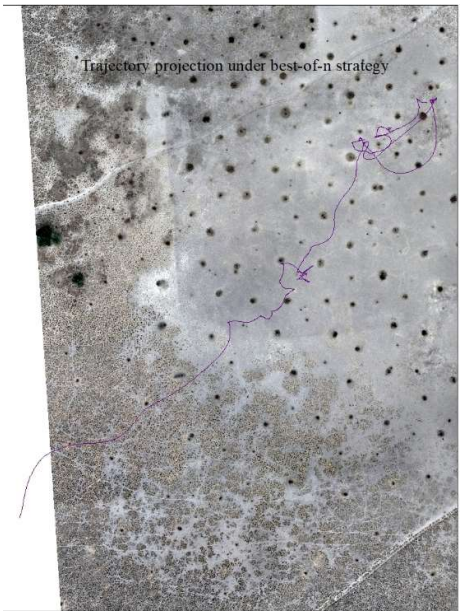
a)


Predicted female blackbuck trajectory on lek under first-encounter strategy
27.802°N
27.801°N
27.800°N
27.799°N
27.798°N
Latitude
74.435°E
74.436°E
74.437°E
74.438°E
74.439°E
Longitude
Behavior Brief pause Extended stay Moving
▲ Start ▼ End ● Extended stay → Direction


Trajectory projection under first-encounter strategy

b)


Predicted female blackbuck trajectory on lek under best-of-n strategy
27.802°N
27.801°N
27.800°N
27.799°N
27.798°N
Latitude
74.435°E
74.436°E
74.437°E
74.438°E
74.439°E
Longitude
Behavior Brief pause Extended stay Moving
▲ Start ▼ End ● Extended stay → Direction


Trajectory projection under best-of-n strategy

c)