

**Dietary habits and competitive interactions of
scavenging raptors in the Thar desert**

by

Manas Shukla

Enrollment no.: 50BB23A73010

Dissertation Thesis

Submitted to

Academy of Scientific and Innovative Research

For the partial fulfilment of the degree

Master of Science

in

Wildlife Science

Under the supervision of

Mr. Varun Kher, Scientist – C

Dr. Vishnupriya Kolipakam, Scientist - D



**भारतीय वन्यजीव संस्थान
Wildlife Institute of India**



June 2025



DECLARATION

I hereby declare that the work conducted under the thesis entitled “Dietary habits and competitive interactions of scavenging raptors in the Thar desert”, 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 **Mr. Varun Kher, Scientist - C**, and co-supervision of **Dr. Vishnupriya Kolipakam, Scientist - D**, of Wildlife Institute of India, Dehradun. 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 particulars given in it are true to the best of my knowledge.

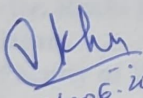
Manas

Manas Shukla

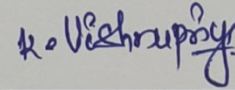
Enrolment No: 50BB23A73010

Place: Dehradun

Date: 24/06/2025


24.06.2025.

(Mr. Varun Kher)
Supervisor



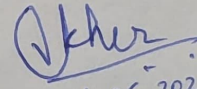
(Dr. Vishnupriya Kolipakam)
Co-supervisor



CERTIFICATE

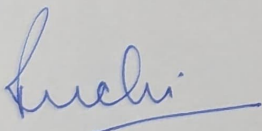
This is to certify that the thesis by **Mr. Manas Shukla** entitled “**Dietary habits and competitive interactions of scavenging raptors in the Thar desert**” is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master’s in Wildlife Science**.

Mr. Manas Shukla has put one semester of research work embodied 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.



24-06-2025

(**Mr. Varun Kher**)
Supervisor



(**Dr. Ruchi Badola**)
Dean
Faculty of Wildlife Science



भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE OF PLAGIARISM CHECK

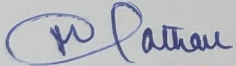
It is certified that the M.Sc. Dissertation titled “**Dietary habits and competitive interactions of scavenging raptors in the Thar desert.**” submitted by **Manas Shukla** has been examined by us for plagiarism check as per UGC (Promotion of Academic Integrity and Prevention of Plagiarism in Higher Educational Institutions) Regulations. The following inferences are drawn from this check:

- The Dissertation has significant new work/knowledge as compared to already published work or work under consideration for publication elsewhere.
- 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.
- The study 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 omitting data or results such that the research is not accurately represented.

Similarity index report are as follows:

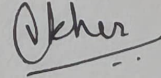
Software used	Date	Total Pages	Total word count	Drill bit similarity index
Drill bit	26/06/2025	75	13688	2%

The similarity index came as above. Scientific names, measuring units (SI) have been excluded from the document.



(Manohar Pathak)

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



(Sh. Varun Kher)

Scientist – C

पत्रपेटी सं० 18, चन्द्रबनी, देहरादून – 248 001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun - 248 001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स : +91-135-2640111 से 2640115 फैक्स : 0135-2640117
EPABX : +91-135-2640111 to 2640115 Fax : 0135-2640117
ई-मेल/E-mail : wii@wii.gov.in वेब/Website : www.wii.gov.in

TABLE OF CONTENTS

LIST OF TABLES.....	iv
LIST OF FIGURES.....	iv
ACKNOWLEDGMENT.....	1
EXECUTIVE SUMMARY.....	4
1. INTRODUCTION.....	6
1.1 <i>Literature review</i>	8
1.1.1 Introduction to Scavenging Raptors.....	8
1.1.2 Status of Vultures in the World.....	8
1.1.3 The Vulture Decline in the Indian Subcontinent.....	9
1.1.4 Restoration of Vulture Populations in India.....	10
1.1.5 The Persistent Threat of NSAIDs in India.....	11
1.1.6 Importance of Dietary Studies for Raptors.....	11
1.1.7 Studies on Raptor Diet.....	12
1.1.8 Studies on Competitive Interactions of Vultures.....	14
1.1.9 Knowledge Gaps.....	14
2. OBJECTIVES AND RESEARCH QUESTIONS.....	16
3. STUDY AREA.....	17
3.1 Site.....	17
3.2 Flora and fauna.....	18
CHAPTER I: DIETARY HABITS OF BREEDING AND MIGRATORY VULTURES.....	20
4.1 <i>Introduction</i>	21
4.2 <i>Methodology</i>	21
4.2.1 Field methods.....	21
4.2.2 Laboratory methods.....	22
4.2.3 Analytical methods.....	23

4.3 Results.....	24
4.4 Discussion.....	27
CHAPTER II: NSAID USAGE PATTERN OF LIVESTOCK HERDERS AND PASTORAL-ISTS	29
5.1 Introduction.....	30
5.2 Methodology.....	30
5.2.1 Field methods.....	30
5.2.2 Analytical methods.....	31
5.3 Results.....	31
5.4 Discussion.....	36
CHAPTER III: COMPETITIVE INTERACTIONS OF SCAVENGING RAPTORS	38
6.1 Introduction.....	39
6.2 Methodology.....	39
6.2.1 Field methods.....	39
6.2.2 Analytical methods.....	40
6.3 Results.....	42
6.4 Discussion.....	53
7. CONCLUSION.....	56
8. REFERENCES.....	58
9. APPENDICES.....	65

LIST OF TABLES

Table 1: Sampling effort for diet analysis.....	24
Table 2: Coefficients of predictor Distance of household from Jaisalmer (Distance_jsm) for the binomial response variable of presence of harmful NSAIDs for n = 128 pastoralists interviewed.....	33
Table 3: Effect size of significant predictors of scavenger visitation.....	44
Table 4: Raw Elo scores and dominance index (DI) of scavengers, based on n = 225 interactions involving scavenging raptors.....	49
Table 5: Untransformed coefficients of the best fitting model for efficiency index (EI), having scavenger species as the only significant predictor (Significance codes: * : 0.05, ** : 0.01).....	51
Table 6: Untransformed coefficients of the best fitting model for proportionate feeding duration of scavengers at a carcass site (Significance codes: ** : 0.01, *** : 0.0001).....	53

LIST OF FIGURES

Figure 1: Map of study area (Source of PA boundary: https://forest.rajasthan.gov.in).....	19
Figure 2: Diet composition of vultures as observed from Hellinger-transformed Relative Read Abundance (RRA).....	25
Figure 3: Hellinger-transformed RRA of livestock prey (summed RRA of Bos, Camelus, Capra and Ovis from Fig. 2).....	25
Figure 4: Pianka's index of niche overlap as reflected by Hellinger-transformed RRA.....	26
Figure 5: Resource spectrum of breeding and migratory vultures, based on information from DNA metabarcoding, camera traps and other field observations (coloured tiles signify presence).....	28
Figure 6: Source of NSAIDs used by surveyed pastoralists, categorised by their toxicity to vultures.....	33
Figure 7: Prevalence of harmful NSAID usage by pastoralists (n = 50).....	34
Figure 8: Usage of vulture toxic drugs in the study area.....	35
Figure 9: Number of sampled carcasses per species.....	43
Figure 10: Proportion of sampled size classes of carcasses.....	43

Figure 11: Predicted visitation probability of Red-headed vulture.....	45
Figure 12: Predicted visitation probability of Griffon.....	46
Figure 13: Predicted visitation probability of Tawny eagle.....	46
Figure 14: Predicted visitation probability of Fox.....	47
Figure 15: Predicted visitation probability of Dog.....	47
Figure 16: Dominance hierarchy of scavengers based on n = 225 aggressive encounters involving scavenging raptors. Species with DI above zero are winning more interactions than they are losing, and vice versa.....	50
Figure 17: Hierarchy of feeding efficiency in scavengers.....	52
Figure 18: Camera trap locations in the study area.....	67
Figure 19: A congregation of six vulture species: Cinereous vulture, Himalayan griffon, Eurasian griffon, Red-headed vulture, White-rumped vulture and Egyptian vulture.....	68
Figure 20: A White-rumped vulture with its unfledged chick.....	68
Figure 21: Nimesulide (L) and Meloxicam (R): The two major NSAIDs used by surveyed pastoralists.....	69
Figure 22: A free-ranging dog displacing a griffon congregation from a sheep carcass.....	69
Figure 23: Caught in the chaos: A White-rumped vulture struggles to find food in the midst of a griffon dominated feeding aggregation and an Egyptian vulture escaping with smaller carrion pieces.....	70
Figure 24: A pair of Red-headed vultures displaced off of a cattle carcass by Cinereous vulture and griffons.....	70

ACKNOWLEDGMENT

For the existence of this thesis, I firstly thank my supervisors, Varun Kher and Dr. Vishnupriya Kolipakam, for all their support and assistance. The furthest I can trace back the conception of this thesis is on a cold December night in Lal Dhang, where it was born next to a bonfire as a nascent idea that I shared with Varun. From entertaining my half-baked ideas to helping me with nest searches on field, he has provided tremendous support in brainstorming and refining the concept and design of this study, with his ecological and quantitative insights. Dr. Vishnupriya has been the backbone of the genetic component of this study and has provided her best support at all stages, in terms of both logistics and conceptual understanding.

I would like to thank the Director, Dean, Registrar, Course Director(s) and Assistant Course Director(s) of the XIX M.Sc. batch, and all the faculty members for facilitating this course and bringing to me some of the most mind boggling lectures I have ever attended.

My earnest thanks to Mr. Kiran Srivastava and Raptor Research and Conservation Foundation for generously providing me with the much needed financial aid for this Masters program, allowing me to put my love for vultures into practice.

My gratitude extends to the DCF, CCF and PCCF of Rajasthan, for allowing me to carry out this study to its fullest extent in Desert National Park, Jaisalmer.

For showing me around the landscape and helping me with field work, I thank Devendra Pandey. It was the peak of the 2024 summers when I first arrived in the desert for my recce survey, and I used to look forward to the morning and evening drives in Aradin's Thar with Dev, only to get knocked out to sleep by the heat and have my unconscious head bobbing around for half of the journey. When I started fieldwork in winters, I was also assisted by David Phineas, my senior turned colleague, who taught me a great deal about bird identification and with whom I have had the wildest natural history observations on field.

For the time I spent in Khuri, I thank Prabhu Singh Sodha, for his excellent spotting skills and untamed enthusiasm for wildlife, which helped me find quite a number of nests and carcasses used in this study. He was never hesitant to share his home-cooked meals whenever I gave up on cooking and resorted to starvation. The gratitude extends to Sawai Singh Sodha, who unfailingly turned up in his camper on time every day, and to Tosif Khan, with his own raptor-like eyesight and curiosity about wildlife, which helped me in fieldwork around Sam.

I thank Dr. Sutirtha Dutta, who has been supportive not just throughout my thesis, but also for a major part of the Master's course. I am extremely fortunate to have gained an extensive understanding of ecological statistics from the best. I am also grateful to his team at Project GIB, which accompanied me during my stay and welcomingly included me in the board/card games despite my social awkwardness.

I was greatly assisted by Himanshu Matta, Yashwanth Gowda, Shimontika Gupta, Bhavna Pant and others who guided me in my labwork and made me look at DNA extractions and PCRs as more than just sorcery. The efficiency and knowledge I gained during labwork in just a span of weeks would not have been possible without any of them.

The past two years with my batchmates of XIX MSc have definitely been one of the experiences I have ever had in my life. It began at a particular time and ended at another. The experience certainly involved multiple individuals talking at various points in time, and even breathing the same air. Without a doubt, there were many instances where information was exchanged. It was, undeniably, a part of my academic journey.

To Baks, for creating grounds of open communication and support which immensely helped my mental health and academics.

To Dr. Monideepa Mitra, who is blessed with the talent of nudging people in the right direction, akin to a medieval sage.

To Himani, for making both existence and genetics less scary.

Lastly, I express my deepest love and gratitude to Amma and Baba, whom I consider no less than my biological parents, for supporting my decision to pursue a career in wildlife and academia, even when it was not in our family's financial interests. Despite being from a generation which suppresses expression of emotions, they have always respected my ideas and individuality as a whole, and have loved me unconditionally.

Manas Shukla

June, 2025

EXECUTIVE SUMMARY

Scavenging raptors, especially vultures, play a crucial role in recycling nutrients and curbing pathogen prevalence in an ecosystem. Their populations in the Indian subcontinent have declined substantially in the past few decades, primarily due to the presence of toxic non-steroidal anti-inflammatory drugs (NSAIDs) in livestock carcasses. This problem worsens for vultures in the Thar desert landscapes, where large numbers of migratory vultures visit in the winter months and increase competition for resident vultures, reducing their access to resources in their critical breeding months. Therefore, understanding their dietary dependence on livestock and their interactions with other scavengers is essential for implementing targeted conservation measures. This study examines the dietary and competitive ecology of White-rumped vulture (*Gyps bengalensis*), other sympatric vultures, and mammalian scavengers in the Thar Desert, with additional focus on assessing risk from NSAID poisoned livestock carcasses and identifying ecological pressures from carcass use dynamics.

For dietary analysis, fecal samples of White-rumped vulture (n = 10) and other migratory vultures (n = 22) of the same foraging guild collected from their identified nesting and roosting sites respectively, and were analysed using DNA metabarcoding to assess dietary composition and overlap. Questionnaires (n = 128) with pastoralists and pharmacy surveys (n = 4) were used to evaluate NSAID usage patterns, along with a geographic hotspot analysis of toxic NSAIDs. Camera traps (n = 34) were opportunistically placed at carcasses to record scavenger presence, feeding time, and aggressive interspecific interactions. Interference and exploitative competition was quantified by developing dominance and efficiency indices, and constructing hierarchies of aggressive dominance and foraging efficiency, followed by the analysis of their ecological predictors using generalised linear models.

Dietary analysis revealed proportionately higher domestic prey in the diet of White-rumped vulture, with a high niche overlap with migratory vultures, creating ground for resource competition. Surveys showed NSAID usage was higher in isolated villages, with several hotspots near vulture nest sites and pharmacy locations. Camera trap analysis showed that distance from the village and size class of prey were the significant predictors for scavenger presence. The dominance of migratory vultures, feral pigs, and dogs at carcasses was also highlighted in the analysis, with them displacing resident vultures through aggressive interactions. Feeding efficiency was revealed to be the lowest for resident vultures. Analysis of ecological predictors revealed that highly efficient scavengers or group feeders tend to feed for a proportionately longer duration on carcasses.

This study highlights the need for mitigating accidental poisoning of scavenging raptors by curbing the use and supply of banned NSAIDs in the landscape, and implementing targeted conservation measures for scavenging raptors which will ensure equitable access to resources throughout the year, thereby restoring the resident vultures from the brink of local extinction and improving the conservation outlook of Indian scavenging raptors.

1. INTRODUCTION

Scavenging raptors, particularly *Gyps* vultures, were once the most ubiquitous birds of prey in the Indian subcontinent. The White-rumped vulture (*Gyps bengalensis*), notably, was thought to be probably the most abundant bird of prey in the world (Houston et al., 1984), to the extent where they were thought to be a severe threat to aircrafts (Pain et al., 2003) until their catastrophic decline in the past three decades (Prakash et al., 2004). *G. bengalensis* has been among the worst affected species with ~99% population decline (Pain et al., 2004), followed by Long-billed vulture (*G. indicus*) and Slender-billed vulture (*G. tenuirostris*). This severe population crash has been tightly linked to their diet, wherein they suffered from accidental poisoning by harmful NSAIDs (non-steroidal anti-inflammatory drugs) present in livestock carcasses which were commonly used by herders and pastoralists to treat pain and inflammation in livestock. Upon consumption by vultures, these NSAIDs disrupt kidney function, causing visceral gout and eventually leading to the death of the vulture within a few days of consuming a contaminated carcass (Oaks et al., 2004).

Being obligate scavengers, vultures largely depend on livestock as their primary food source, since they are the most commonly available mammal carrion in most parts of the country (Ghosh-Harihar,). This brings them in contact with harmful NSAIDs, which are used as painkillers for livestock. Though the government has taken legal actions to cut down the use of these drugs by imposing a ban on Diclofenac, Aceclofenac, Ketoprofen and Nimesulide, and promoting non-toxic alternatives such as Meloxicam and Tolfenamic acid, the illegal usage of Diclofenac in human formulation still prevails due to the high cost of safer alternatives (Kumar, 2006; Cuthbert et al., 2016).

Aside from NSAID poisoning, availability of food resources has been highlighted as a major concern for *Gyps* vultures, with the increasing trend of carcass disposal by burial or incarceration (Clements et. al., 2013) being a key driver for the reduction in available food resource. Moreover,

the breeding period of many resident vultures coincides with the arrival of migrant scavenging raptors in winter months, who come in relatively larger numbers, further reducing the food availability to the resident vultures in their critical breeding stages. This can pose a direct threat to their breeding success and population growth.

Although having cultural and religious significance historically in the Indian subcontinent, *Gyps* vultures have gained an ill human perception of being “unclean” and a threat to human health due to their foraging style. On the contrary, they have coexisted with humans for centuries without being linked to any major spread of disease and their obligate scavenging habits have made them the most efficient scavengers. They assist in keeping a check on a plethora of dangerous zoonotic diseases, such as anthrax and rabies. Despite their seemingly unclean foraging habits, they have evolved a number of adaptations which keeps them clean and rid of pathogens, such as their bald head and necks, their incredibly strong gastric acid and their Clostridia and Fusobacteria dominated gut-microbiome which eliminates any harmful pathogens ingested.

Since the fall of vulture populations in India, their scavenging niche has been taken over by a number of other facultative scavengers, especially feral dogs and rats, which are linked to increase in risk of fatal diseases such as rabies (Markandya et al., 2008). Further, the lack of efficient carcass offtake is expected to facilitated spread of other diseases like foot-and-mouth disease, which leads to livestock mortality and financial loss to pastoralists. Other scavengers like wild pigs have also had a population boost, which has led to a substantial increase in human-wildlife conflict in rural areas owing to their crop raids, the economic loss of which has to be further incurred by farmers. All the aforementioned facts are just a few of many reasons why the presence of obligate scavengers like vultures is crucial for a healthy ecosystem, beneficial to human society.

With that in perspective, this study was conducted to investigate the threats faced by the low population of *Gyps bengalensis* in the Thar desert landscape, especially related to their diet. In par-

ticular, I look into their diet composition to understand their dependency on livestock and niche overlap with other scavengers in the same foraging guild, the looming threat of NSAID usage by the livestock herder and pastoralist community, and their competitive interactions with migratory scavengers which become a barrier to food availability in breeding months.

1.1 LITERATURE REVIEW

1.1.1 INTRODUCTION TO SCAVENGING RAPTORS

Scavenging raptors are a polyphyletic group of birds, characterised by their diet which is predominantly composed of carrion. Their role in the ecosystem is critical, as they facilitate the decomposition of carrion and curb the spread of zoonotic diseases (Ogada et al., 2012). These scavenging raptors are known to be highly efficient at carcass consumption and recycling of nutrients, thereby playing a crucial role in prevention of the accumulation of decaying organic matter that would otherwise encourage the breeding of many harmful pathogens (Houston, 2001). The foraging nature of obligate scavenging in the vertebrate community is only known to be exhibited by Old World vultures, belonging to the family Accipitridae, and New World vultures from the family Cathartidae, which imparts them with special adaptations, including a sharp eyesight to locate carcasses, powerful beaks to tear open flesh, and stomach acids of extremely low pH (~1.0) which helps them neutralise deadly pathogens like *Bacillus anthracis*, *Aphovirus*, *Lyssavirus*, etc.

1.1.2 STATUS OF VULTURES IN THE WORLD

Today, almost half of the world's raptors are currently showing population declines, and around 20% are classified as threatened by the IUCN (McClure et. al., 2018). Out of these, obligate scavenging raptors, or vultures, have been one of the worst affected groups of species. New World vultures like the California condors have faced tremendous declines

linked to their diet, as they would die from lead poisoning from spread ammunition (Finkelstein et al., 2012). Similarly, the Old-World vultures in Africa have also seen sharp population declines by deliberate poisoning, which was linked to poaching activities as poachers would lace carrion with toxic contaminants to prevent inviting swarms of vultures on their illegally hunted animals (Ogada et al., 2016). In South Asia, *Gyps* vultures, which were once thought of as the most common birds of prey in the world, came very close to extinction in the past three decades due to NSAID poisoning. The IUCN now classifies the White-rumped vulture (*G. bengalensis*), Long-billed vulture (*G. indicus*), Slender-billed vulture (*G. tenuirostris*) and Red-headed vulture (*Sarcogyps calvus*) as critically endangered. Other threats to their populations have been noted to be habitat destruction, reduced availability of carrion, and electrocution from power infrastructure (Selvaraj et al., 2021, Uddin et al., 2021).

1.1.3 THE VULTURE DECLINE IN THE INDIAN SUBCONTINENT

Between 1992 and 2007, the numbers of *Gyps bengalensis* declined by 99.9%, whereas *G. indicus* and *G. tenuirostris* declined by 96.8%, with an average annual decline rate of 43.9% and 16% respectively (Prakash et al., 2007). The primary reason for these sudden vulture deaths and population crashes was delineated as kidney failures and visceral gout, wherein crystals of uric acid would get deposited in large amounts on the inner organs. This was caused by the veterinary use of Diclofenac, a NSAID (non-steroidal anti-inflammatory drug) which was widely used for cattle treatment across the Indian subcontinent (Green et al. 2004; Oaks et al. 2004; Shultz et al. 2004). Up until the early 1990s, the vulture population in India was presumed to be somewhere between 3-5 crore individuals. They coexisted with humans in urban areas, depending primarily on livestock carcasses. The 16th Livestock Census for the year 1997 reports an estimate of about 28.9 crore bovines and 44.5 crore livestock present

in the country, which clearly outnumbered the abundance of wild ungulates. Furthermore, as protected areas support higher densities of wild ungulates (Karanth et al., 2004), loss of habitat of wild ungulates and increased grazing within protected areas also had a role to play in increasing the dependency of vultures on human-supplemented prey, amplifying their risk to NSAID exposure (Ghosh-Harihar et al., 2024).

1.1.4 RESTORATION OF VULTURE POPULATIONS IN INDIA

India has been one of the leading nations in vulture conservation efforts, ever since their decline in recent decades. Following the ban of Diclofenac by the Indian government in 2008 (Gazette notification vide GSR No. 499 (E) dated 4th July, 2008), more studies emerged highlighting the toxicity of other NSAIDs such as Aceclofenac, Ketoprofen and Nimesulide (Chandramohan et al., 2022, Naidoo et al., 2010, Bohra et al., 2023), leading to their consequent ban in 2023 (Gazette notifications S.O. 3448(E) dated 31st July, 2023; S.O. 5633(E) dated 30th December, 2024). This was also backed up by ex-situ conservation efforts launched by the Bombay Natural History Society (BNHS) in collaboration with the government, under which captive breeding centers were established in Haryana, West Bengal and Assam, prioritising breeding and reintroduction of *Gyps bengalensis*, *G. indicus* and *G. tenuirostris* (Prakash et al., 2012). Moreover, the concept of Vulture Safe Zones (VSZs) has started to popularise in several Indian states, including Madhya Pradesh, Jharkhand, Assam and Uttar Pradesh. These VSZs refer to 100 km radius zones with absolutely no trace of toxic NSAIDs to ensure a safe environment for vultures (Chaudhary et al., 2012). “Vulture restaurants” or supplementary feeding sites have also been set up in some areas where vulture-safe carcasses are provided for consumption (Gilbert et al., 2007).

1.1.5 THE PERSISTENT THREAT OF NSAIDS IN INDIA

Despite the ban on Diclofenac and other harmful NSAIDs in India, the looming threat of NSAID poisoning still exists for vultures as Diclofenac is still being used illegally in human formulations to treat livestock (Cuthbert et al., 2016), even though safer alternatives like Meloxicam are widely available. This is due to the significantly cheaper prices of human formulations of Diclofenac than veterinary grade Meloxicam. The pharmacies continue to offer them, although with a decreasing trend (Galligan et al., 2020). In Bikaner, Rajasthan, pharmacies in high vulture presence areas like Jorbeer were also known to be selling Nimesulide and Ketoprofen (Khatri, 2015). Covert surveys of pharmacies have proven to be useful to extract information about supply of illegal drugs. As the pharmacies are in a public sphere, the staff accepts the responsibility of their actions and public observation is allowed (Spicker et al. 2011), and concealing true identity to gather information on illegal activities is not an unethical practice in science (Galligan et al., 2020). As of 2017, covert surveys revealed that a significant proportion of pharmacies in regions of Central Gujarat, Southern Gujarat, Madhya Pradesh and Uttar Pradesh continue the supply of Diclofenac (46.2%, 37.5%, 25.2%, and 20.3% respectively) along with other harmful NSAIDs like Nimesulide.

1.1.6 IMPORTANCE OF DIETARY STUDIES FOR RAPTORS

Most raptors lie at the top of the food chain and require large, good-quality habitats to satisfy their dietary needs (Demerdzhiev et al., 2023). This, coupled with the risk of poisoning, makes them particularly vulnerable to increasing anthropogenic pressures and changes in land-use patterns. These risks are further amplified in the fragmented human-dominated landscapes of the developing world, where exposure to threats is much higher.

Assessing the diet composition of these threatened birds (especially *Gyps* vultures) can assist in planning targeted conservation measures (Liu et al., 2018), by understanding their degree of dependency on human supplemented prey. Dietary information will also provide insights on niche overlap with other raptors of the same guild. This has important conservation implications, as communities with lower overlap can promote greater biodiversity (Pianka et al., 1974). Thus, in order to achieve a better understanding on the ecology of raptors, dietary studies across time and space are essential as they not only highlight the spectra of resources used but also allow for inferences on habitat use, anthropogenic impacts, demography, evolutionary adaptations and trophic interactions (Newton, 1979; Buij et al., 2011; O'Bryan et al., 2022).

1.1.7 STUDIES ON RAPTOR DIET

Assessment of raptor diet can be methodologically challenging as it can involve a series of intricate steps, such as locating, collecting, preserving and identification of undigested prey (Resano-Mayor et al., 2014; Marti CD et al., 2007), each of which are prone to their individual biases. There exist a variety of methods for raptor diet assessment, with their own degrees of suitability as per the species, the research question, and resource feasibility.

Using camera traps for diet observations has been a fairly common method because of its cost effectiveness, better prey identification and allows for monitoring for longer time periods (Rogers et al., 2005; Margalida et al., 2005; Delaney et al., 1998). There are also notable disadvantages to this, such as technical problems like battery depletion and camera or memory card failure which can create gaps in data collection. Image capture and analysis also does not work with equal efficiency for all species, as they may not use the same ground for foraging (Swan et al., 2011). Moreover, the rate of prey identification from camera traps is

usually lower than prey identification from pellets and faecal matter, especially for small sized prey species (Booms et al., 2003; Reif et al., 2006).

Popular means for diet analysis using indirect methods include identification of prey from remains in nests, examination of regurgitated pellets or faecal matter, conducting stable isotope analysis, and using metagenomics to amplify and sequence prey DNA present in the sample. Analysing prey remains and pellets for diet assessment involves the collection of identification of prey remains from nest sites, and is often deemed advantageous as it allows collection of larger samples which provide robust results (Marti, 1987). Although, they bias diet estimates in favour of different prey types, as some species digest prey more thoroughly than others, and a combination of pellets and prey remains may be required to eliminate this bias (Simmons et al., 1991).

Stable isotope analysis has developed over the years as a prevalent non-invasive dietary assessment method (Katzenberg et al., 2018), as it can predictably reflect the birds diet using isotopic ratios in bird tissue at the time of tissue synthesis. Isotopic analysis also provides diet estimates using assimilated rather than ingested prey, which can potentially overlook short term dietary shifts (Jones et al., 2024). Also, it relies on baseline isotopic values from prey, which can vary spatially and temporally, introducing uncertainty if prey samples are not adequately characterized across the raptor's foraging range (Redpath et al., 2001).

Metagenomic technologies like DNA metabarcoding have been the most recent revolutionisation to understand dietary ecology of species (Pompanon et al. 2012; Taberlet et al. 2012), by bringing forth the possibility of identifying prey non-invasively from all available DNA in the faecal matter or pellets, which would otherwise not be identifiable using other traditional methods. It provides flexibility to identify prey down to species level, and can help to reveal spatial patterns in diet (Ghosh-Harihar et al., 2024). Despite its advantages, it has its own set

of biases involved which might hinder with ecological inferences by giving false negatives, false positives and lower taxonomic resolution due to incorrect design of primers or choice of targeted metabarcode region (Pompanon et al. 2012, Ficetola et al. 2016; Galan et al. 2018).

1.1.8 STUDIES ON COMPETITIVE INTERACTIONS OF VULTURES

Studying competition among vultures has been instrumental in highlighting factors like species dominance, foraging efficiency and dietary niche partitioning. Competitive interactions among African vultures was first described by Houston (1974), where the dominance pattern was different based on size of the species and their numbers. Species which are larger in size and higher in numbers, tend to dominate the feeding site. Donázar et al. (1999) also found that arrival order and group size influence the feeding success of vultures in Spain. Remote camera traps have been proven to be efficient to monitor scavenger behaviour at a carcass in a non-invasive manner, without incurring the bias in behavioural change when direct observations are done by humans (Caravaggi et al., 2017).

1.1.9 KNOWLEDGE GAPS

Although the vulture population crash has been thoroughly studied, there still is an absence of robust information on the diet of vultures across the subcontinent, and their competitive interactions with other scavenging raptors, especially in the ecologically fragile landscape of the Thar desert where there is an absence of large mammalian predators, and constitutes a major gap in our understanding of this ecosystem. By addressing these two critical aspects, this study can potentially contribute to the long-term survival and recovery of raptor populations in the Thar Desert and beyond. The NSAID usage information from this landscape will reveal how effectively the ban on toxic NSAIDs is manifesting in remote villages of India, and will be important in planning species-targeted conservation measures. Moreover, the re-

gion is currently undergoing rapid changes in land-use patterns, and the information generated through this study will serve as a vital baseline for upcoming studies to compare with. There is also a critical gap in understanding how these dynamics influence population trends and ecosystem stability, underscoring the need for integrated studies using tools like DNA metabarcoding and camera trapping at carcass sites to explore niche overlaps and competitive hierarchies.

2. OBJECTIVES AND RESEARCH QUESTIONS

I. TO UNDERSTAND THE DIETARY HABITS OF WHITE-RUMPED VULTURE

- *What is the diet composition of the study species?*
- *What is their dependency on human-supplemented prey?*
- *Is there an overlap in prey selection with migrant scavengers?*

II. TO UNDERSTAND THE PATTERN OF NSAID USAGE AMONG PASTORALISTS

- *What is the prevalence of NSAIDs in the landscape?*
- *Does NSAID prevalence increase with the remoteness of villages?*
- *What are the NSAIDs available to the public in local pharmacies?*

III. TO ASSESS CARCASS UTILISATION DYNAMICS AND COMPETITIVE INTERACTIONS IN SCAVENGERS

- *What are the factors that drive carcass visitation by different scavenger species?*
- *Are resident vultures outcompeted by other scavengers at feeding sites?*
- *Are resident vultures less efficient at feeding than other scavengers?*

3. STUDY AREA

3.1 SITE

The study was primarily conducted in and around Desert National Park (DNP) in the Jaisalmer district, falling in the Thar desert of Western Rajasthan and within the Desert Biogeographic Zone (Rodgers et al., 1988). While 1837 km² of the PA lies in Jaisalmer district, the boundary is also shared with Barmer district, making the park span across a large area of 3162 km². The landscape hosts some of the largest Open Natural Ecosystems (ONEs) in the Indian subcontinent, making it a critical region for wildlife conservation in South Asia (Madhusudan et al., 2023). DNP encompasses diverse habitats including protected grasslands, community rangelands, agricultural fields, sand dunes, and over 100 settlements (IUCN PA). It is the largest protected area in the Thar-Cholisthan Desert complex and has been designated as an Important Bird and Biodiversity Area (IBA) by BirdLife International. The sanctuary serves as a key stopover site for migratory birds on the Central Asian Flyway (Ram et al. 2024) and a vital breeding ground for many threatened species, including the study species. The climate is characterised by scarce and erratic rainfall, at mean annual quanta of 100-300 mm. Droughts are common in the region, and ambient temperatures can reach up to 50°C in the summer. The study area is topographically composed of stabilised sand dunes with wide and flat interdunal valleys. The flat areas are intensively farmed, and almost the entire landscape is subjected to some form of livestock grazing. Agriculture is mostly seasonal, and land is generally left fallow between cropping cycles. There is also an absence of large mammalian predators in the region, which opens up a wide niche for terrestrial and avian scavengers to exploit.

3.2 FLORA AND FAUNA

The park's woody vegetation primarily consists of drought-resistant tree species such as *Prosopis cineraria*, *Ziziphus mauritiana*, *Capparis decidua* and *Vachellia tortilis* which provide nesting and roosting sites for raptors as they tend to be the tallest trees in the landscape. DNP is home to a diverse array of wildlife, including flagship species like the Great Indian Bustard (*Ardeotis nigriceps*), Indian Fox (*Vulpes bengalensis*), and Desert Cat (*Felis lybica*). The park is particularly significant for scavenging raptors, hosting resident species such as the White-rumped Vulture (*Gyps bengalensis*), Red-headed Vulture (*Sarcogyps calvus*), Tawny eagle (*Aquila rapax*) and Egyptian vulture (*Neophron percnopterus*). Since the park is dominated by human presence, there is a high availability of human-supplemented prey (Cattle, goat, sheep and camel) ubiquitously. This site also serves as a critical wintering ground for migratory vultures like the Cinereous Vulture (*Aegyptius monachus*), Eurasian Griffon (*Gyps fulvus*), and Himalayan Griffon (*Gyps himalayensis*) (Prakash et al., 2003; Saran et al., 2021), which arrive as early as October and leave by March.

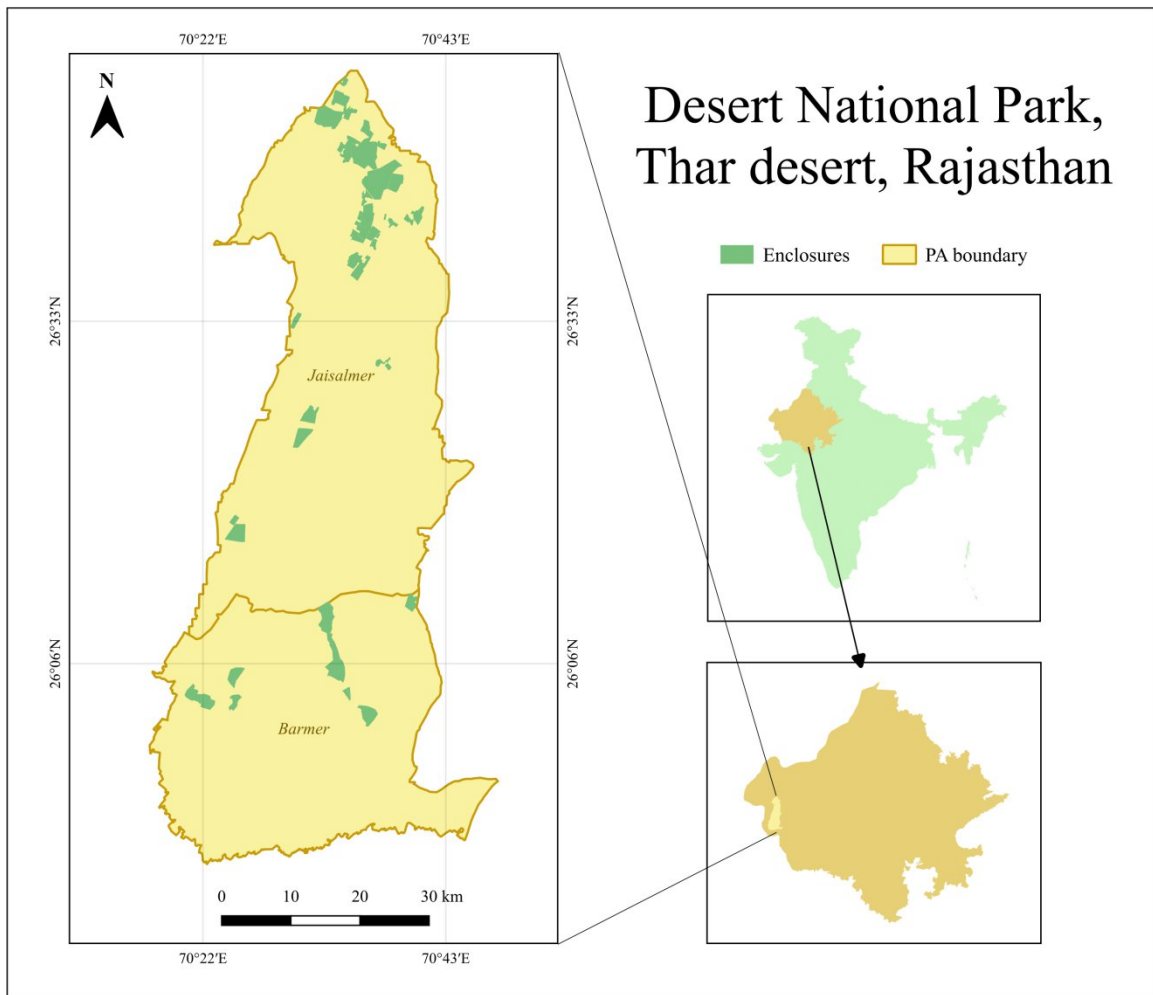


Figure 1: Map of study area (Source of PA boundary: <https://forest.rajasthan.gov.in>)

CHAPTER I

DI-

ETARY HABITS OF BREED-
ING AND MIGRATORY VUL-
TURES

4.1 INTRODUCTION

Despite the thorough investigative research on their population crash, the information on dietary habits of vultures and the threats posed by harmful NSAID usage are not well understood across the Indian subcontinent. The uncertainty amplifies in the Thar desert ecosystem, which experiences a high influx of migratory vultures in winters, coinciding with the breeding season of *G. bengalensis*. These migrants are usually larger in size than the resident vultures, often outnumbering them by a significant margin on animal carcasses, therefore posing a stark risk of outcompeting them. This might create an acute shortage in the food availability for these obligate scavengers, notably in their critical breeding stages when the nutritional demand is high (Morant et al., 2023, Tapia et al., 2018), threatening nest failures when the population is already struggling to stabilise. Therefore, insights into their dependency on human-supplemented prey, their resource spectrum and their niche overlap with migrant vultures of the same foraging guild with the use of dietary studies will be crucial in planning and implementing species-targeted conservation measures in the landscape.

4.2 METHODOLOGY

To evaluate the diet composition of vultures, two complementary approaches were employed: DNA metabarcoding of freshly collected fecal samples, and direct dietary observations from camera traps at animal carcasses.

4.2.1 FIELD METHODS

Camera traps on opportunistically detected carcasses were placed to get direct observations of dietary data. For DNA metabarcoding, fresh fecal samples of *Gyps bengalensis* (White-rumped vulture), *Gyps fulvus* (Eurasian griffon), *Gyps himalayensis* (Himalayan griffon) and *Aegypius monachus* (Cinereous vulture) were collected opportunistically from nesting

and roosting sites which were identified through vehicle surveys of about 4000 km. The sampling was done during the breeding season (December 2024 to February 2025) when the visitation of *G. bengalensis* at nests was maximum by both parents, and migrant vultures (*G. fulvus*, *G. himalaensis*, and *A. monachus*) were present in higher abundance. Samples were immediately placed in 5mL sterile tubes containing DNA/RNA shield to prevent DNA degradation, and were refrigerated until DNA isolation.

4.2.2 LABORATORY METHODS

DNA extraction and metabarcoding:

DNA was extracted from approximately 150-200 mg of fecal matter sample using the QIAmp Fast DNA Stool Mini Kit (Qiagen), following a standardised protocol to get maximum output. For amplification, the 16S region of the DNA was targeted using the universal vertebrate primer described by Kitano et al (2007). Library preparation was performed using the MGI Easy Universal DNA Library Prep Set in combination with MGI Dual Barcode Kits, following the manufacturer's protocol. 100–200 ng of high-quality genomic DNA was enzymatically fragmented and end-repaired, followed by adapter ligation using dual-index bar-coded adapters to enable multiplexing. Post-ligation cleanup and PCR amplification steps were carried out to enrich adapter-ligated fragments, and libraries were quantified using Qubit and assessed for fragment size distribution using a Bioanalyzer (Agilent Technologies). Equimolar amounts of each library were pooled and subjected to paired-end sequencing (2×250 bp) on the MGI DNBSEQ platform G99, using patterned flow cells and DNA nanoball technology for high-throughput data generation.

Bioinformatics pipeline:

A reference database was built using the available checklist of animals in the DNP management plan (2017-2027) and field observations, including domesticated species like cattle, camel, goat, sheep and chicken, and wild species like fox, chinkara and nilgai along with free-ranging dogs, cats and pigs. The database was created by downloading sequences from GenBank (NCBI) and using the NCBI BLAST+ tool. Paired-end reads were quality filtered by using Trimmomatic with scores encoded in Phred+33 and removing sequences shorter than 20 bp. Paired reads were then merged using PEAR, followed by conversion of sequences from FASTQ to FASTA format and filtering out sequences shorter than 80 bp. Clustering of sequences was done at 99% similarity using CD-HIT to reduce redundancy and over-representation. BLASTn was then used to match the final sequences against the provided reference database, retaining hits with 95% identity up to the best 5 matches. The final results were filtered based on identity, bit-score and e-value with detailed logs. This streamlined pipeline ensured a robust region-specific sequence identification.

4.2.3 ANALYTICAL METHODS

All analyses and visualisations were done in R version 4.5.0. The raw DNA sequence reads were converted into relative read abundance (RRA), which was calculated for each prey taxon by expressing the number of reads of a taxon as percentage for that sample. Furthermore, any RRA below 2% was trimmed to reduce noise in the dataset and improve the precision. To enhance the visualisation of diet structure by deflating dominant taxa, Hellinger transformation (Legendre et al., 2001) was done to RRA using the `vegan()` package. In order to assess relative livestock dependence of vultures, RRA for domestic prey (including cattle, goat, sheep, camel and poultry) was visualised for the White-rumped vulture, Cinereous vulture and Himalayan/Eurasian griffon. Dietary overlap between these species was evaluated using Pianka's niche overlap index (Pianka, 1974). To capture the broader spectra

of resources utilised by these vultures, ancillary observations and camera trap records were taken into account to construct a binary matrix of prey taxa.

4.3 RESULTS

The sampling effort for diet analysis of vultures is listed as follows:

Table 1: Sampling effort for diet analysis

Vulture species	Nesting sites	Roosting sites	Fecal samples collected	Samples with adequate DNA concentration
White-rumped vulture	19	-	10	7
Cinereous vulture	-	4	15	13
Griffon	-	5	7	6

Out of the 32 fecal samples collected, 26 samples had DNA presence and were pooled for each of the three species (White-rumped vulture = 7, Cinereous vulture =13, Griffon = 6) While RRA does not reflect actual biomass consumed due to several biases such as prey DNA persistence, amplification efficiency, DNA degradation, etc., comparing relative differences in proportions reveal meaningful information (Skelton et al., 2023, Deagle et al., 2019), especially when using sequences derived from the same sequencing run as it makes systematic biases consistent across all samples in the dataset. The disproportionately high RRA of pigs and foxes (Fig. 2) could also be a result of fecal matter contamination. Though the limited sample size makes any inference about prey species selection unreliable, for White-rumped vulture, the Hellinger-transformed RRA (Fig. 3) of livestock (summed RRA of *Bos*, *Camelus*, *Capra*, *Ovis*) was notably higher than that for Cinereous vulture and griffon, indicating its potential inclination towards human-supplemented prey.

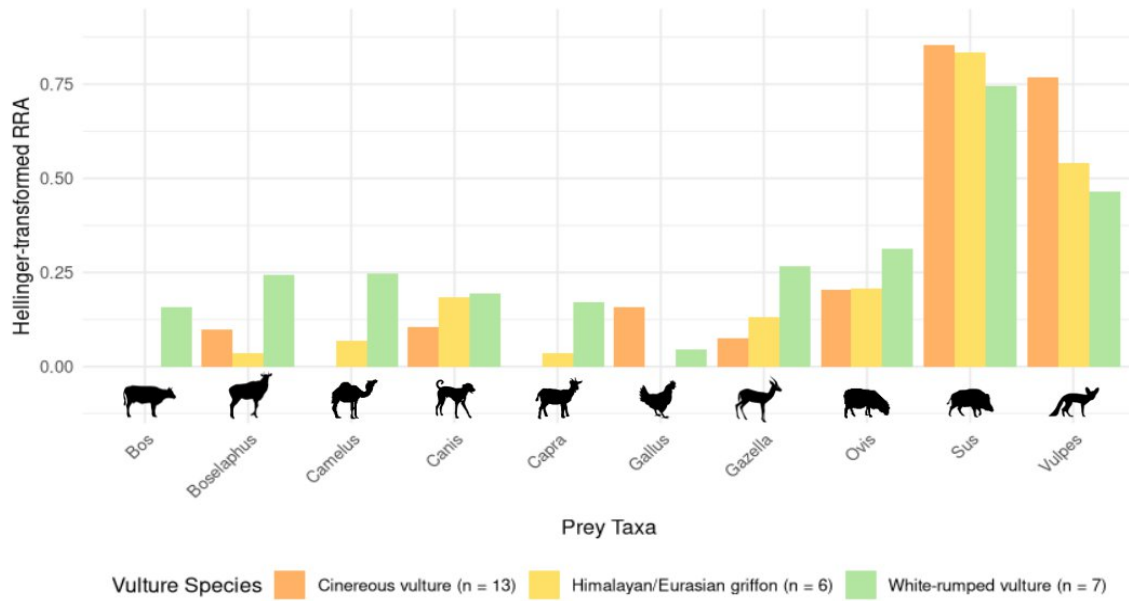


Figure 2: Diet composition of vultures as observed from Hellinger-transformed Relative Read Abundance (RRA)

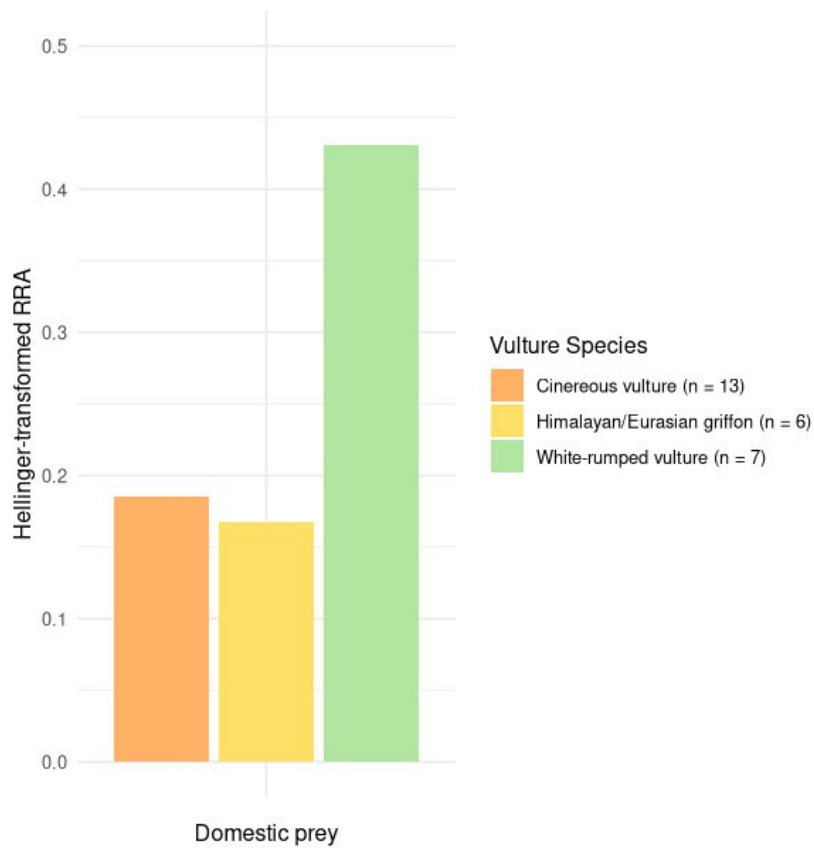


Figure 3: Hellinger-transformed RRA of livestock prey (summed RRA of Bos, Camelus, Capra and Ovis from Fig. 2)

Evaluation of Pianka's niche overlap index revealed a high overlap (>0.85) for all three vultures (Fig. 4), with the maximum overlap of 0.98 between Cinereous vulture and griffon. This high overlap of dietary niche creates ground for resource competition between these three species, and possible risk of the less dominant and resource inefficient species getting outcompeted.

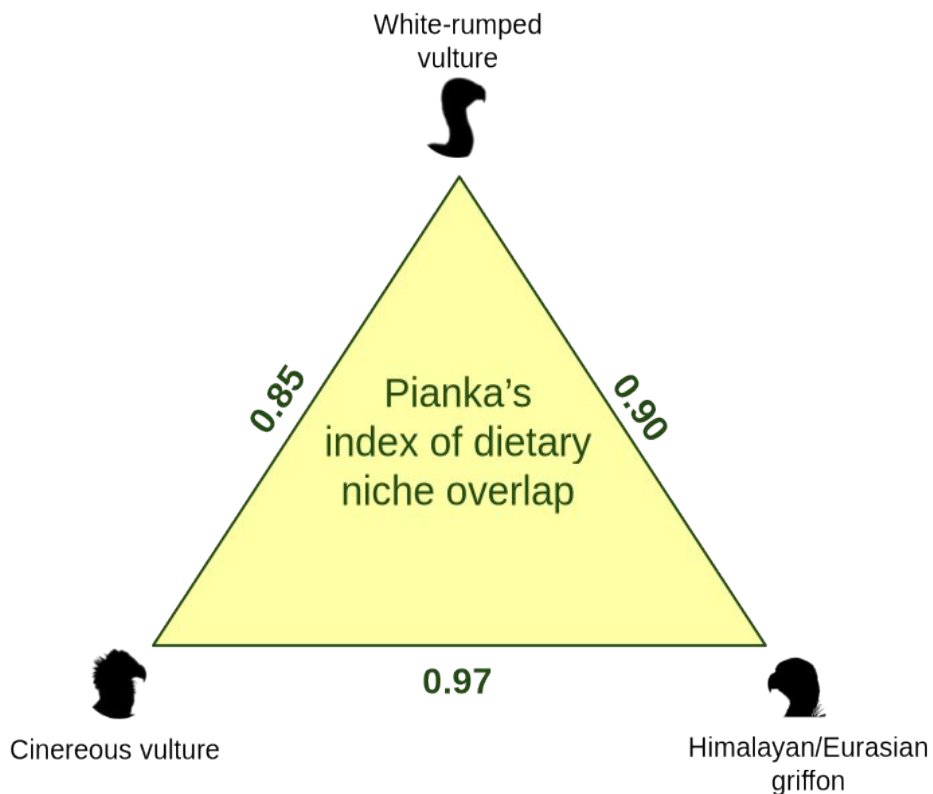


Figure 4: Pianka's index of niche overlap as reflected by Hellinger-transformed RRA

4.4 DISCUSSION

While findings of dietary analysis could not suggest a strong dependency of White-rumped vulture (*G. bengalensis*) on domestic prey due to limited sample size, a reliable pipeline was consequently created which can be useful in pursuing future research. No other strong quantitative inferences were drawn from DNA sequence read data due to the number of biases that follow: different degradation of prey species, unequal digestion of soft tissue, bone or skin, environmental contamination, DNA extraction efficiency, primer bias in PCR amplification, sequencing biases, etc. However, several biases were tackled in the study, such as by standardising sample collection, storage, DNA extraction and PCR amplification protocols, using positive and negative controls during extraction and amplification, filtering sequences to remove noise, and by collecting samples from different nest and roost sites to ensure adequate representation. At the very least, RRA, when used as means of conducting relative measurements, is capable of providing insights on dietary ecology.

Aligning with their nesting ecology, the nest sites of White-rumped vulture discovered in the study area were usually present in agricultural and fallow lands, often in close proximity to village peripheries and isolated homesteads of livestock herders (Dhanis). Dhanis have relatively less disturbance than villages, and the domestic carcass availability is more predictable than the rest of the landscape. In contrast, the roosting sites of migrant vultures were typically found in areas where disturbance is lower than villages, such as enclosures or arid zones.

A high dietary niche overlap (>0.9) between the migratory and breeding vultures, compared using Pianka's metric, gives a clear indication of high interspecific competition for shared resources, as per Gause's competitive exclusion principle (Gause GF, 1934), especially in the

resource scarce landscape of the Thar desert. When there is an overlap to such a degree, the species which fails to be efficient or dominant in feeding naturally tends to be outcompeted.

To build a spectra of prey species for these three vultures, results of DNA metabarcoding, camera trap observations and other ancillary observations were pooled together, and is visualised in the following plot:

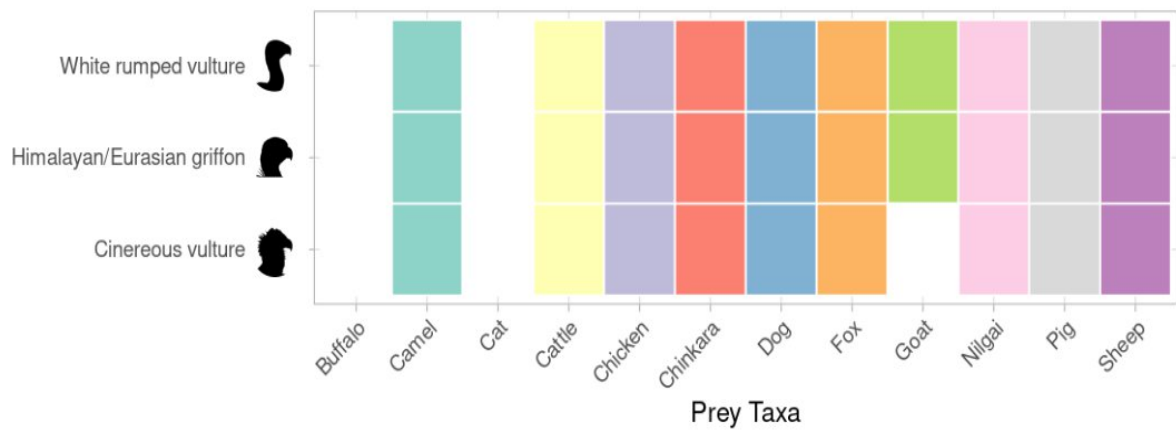


Figure 5: Resource spectrum of breeding and migratory vultures, based on information from DNA metabarcoding, camera traps and other field observations (coloured tiles signify presence)

CHAPTER II

**NSAID USAGE PATTERN OF
LIVESTOCK HERDERS AND
PASTORALISTS**

5.1 INTRODUCTION

With a multitude of studies directly linking the massive declines in vulture populations to the veterinary use of some toxic NSAIDs, such as diclofenac, aceclofenac, ketoprofen, and nimesulide (Oaks et al., 2004, Galligan et al., 2014, Naidoo et al., 2010, Bohra et al., 2023) bans have been consequently enforced by the Indian government to regulate their use. However, the use of some NSAIDs which were banned in recent years still prevails (Galligan et al., 2020), especially in remote villages where the enforcement of the ban is not as strict as compared to relatively developed districts. This study aimed to understand the usage pattern of harmful NSAIDs by the livestock herders and pastoralists residing in the study area through interviews, alongside covert surveys of major pharmacies to assess the over-the-counter availability of these banned drugs.

5.2 METHODOLOGY

5.2.1 FIELD METHODS

A semi-structured interview was conducted across multiple village clusters and isolated pastoral homesteads (locally referred to as “Dhani”) within the study area. The interview was aimed to document the types of NSAIDs used, their sources of purchase, livestock ownership details, frequency of NSAID administration, and carcass disposal practices. To avoid potential response bias, herders were asked about all of their general livestock treatment practices, without hinting that NSAID usage was the target information. Additionally, the local pharmacies were surveyed in a covert manner where the surveyor posed as a pastoralist and requested medication for their cattle experiencing pain. Along with the type of NSAID offered, data on the requirement of a prescription and suggestion of alternative medications was also recorded.

5.2.2 ANALYTICAL METHODS

Data analysis was done using R (version 4.5.0) and QGIS (version 3.22). In order to explore patterns in the use of harmful NSAIDs among livestock herders, a combination of descriptive statistics and cross-tabulations was used. The proportion of sales by major pharmacies were graphically analysed to illustrate the distribution of NSAID types sold, as reported by livestock herders, and was compared using chi-square tests to determine if usage patterns differed significantly across pharmacies respectively. Pharmacy-level data was cleaned to handle multiple entries per respondent and cross-tabulated to calculate the proportion of harmful versus safe NSAIDs sold at each outlet. Cases labeled “No NSAID used” were categorized as safe, while “Unknown” entries were treated as a separate group. A binomial logistic regression was also conducted (using the `glm()` function) to examine the relationship between distance from the main city (Jaisalmer) and the predicted probability of harmful NSAIDs being used was calculated by using the `predict_response()` function in `ggeffects()` package. Additionally, to examine spatial variation in usage of harmful NSAIDs, a kernel density heatmap was created in QGIS using GPS coordinates of reported harmful NSAID use to identify potential geographic hotspots where vultures might be at a relatively higher risk of secondary/accidental poisoning. These analyses helped to evaluate the availability, preference, and geographic distribution of harmful NSAIDs in the landscape.

5.3 RESULTS

A total of 128 livestock herders and pastoralists were surveyed in and around the study area in Jaisalmer district across 41 villages and dhanis to understand NSAID usage patterns. The only harmful NSAID used was reported to be nimesulide, which was used by 32.56% of the respondents (Fig. 6), while meloxicam was used by 10.85% of the respondents. Unknown or unclear usage and no NSAID usage were reported to be 7% and 49.6% respectively.

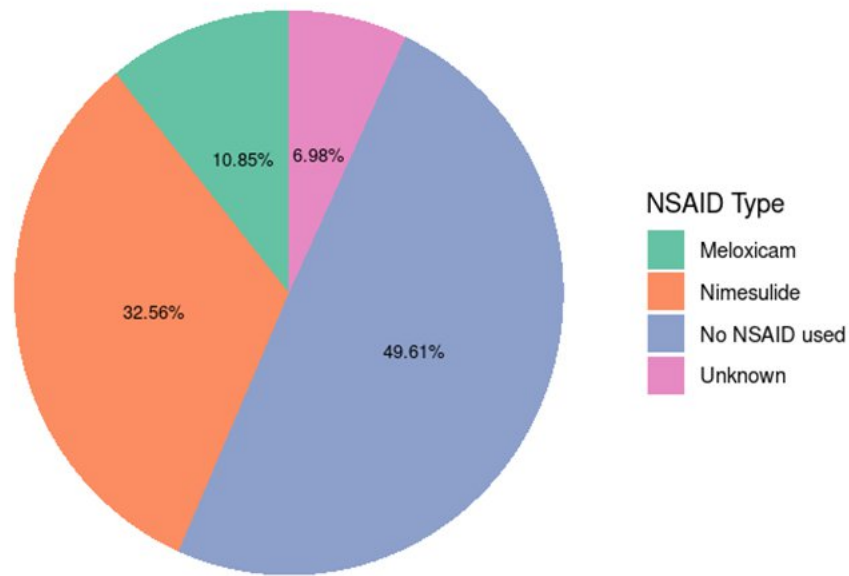


Figure 1: Proportion of respondents with the NSAID type used

A chi-square test showed a statistically significant difference in the proportions of NSAIDs being sold across surveyed pharmacies ($\chi^2 = 23.58$, $df = 5$, $p = <0.01$), indicating that the availability of harmful and safe NSAIDs varies across different pharmacies in the region. A significant difference was also observed in the use of harmful NSAIDs across the surveyed villages ($\chi^2 = 60.96$, $df = 40$, $p = 0.018$). These proportions are illustrated graphically in Figure 6.

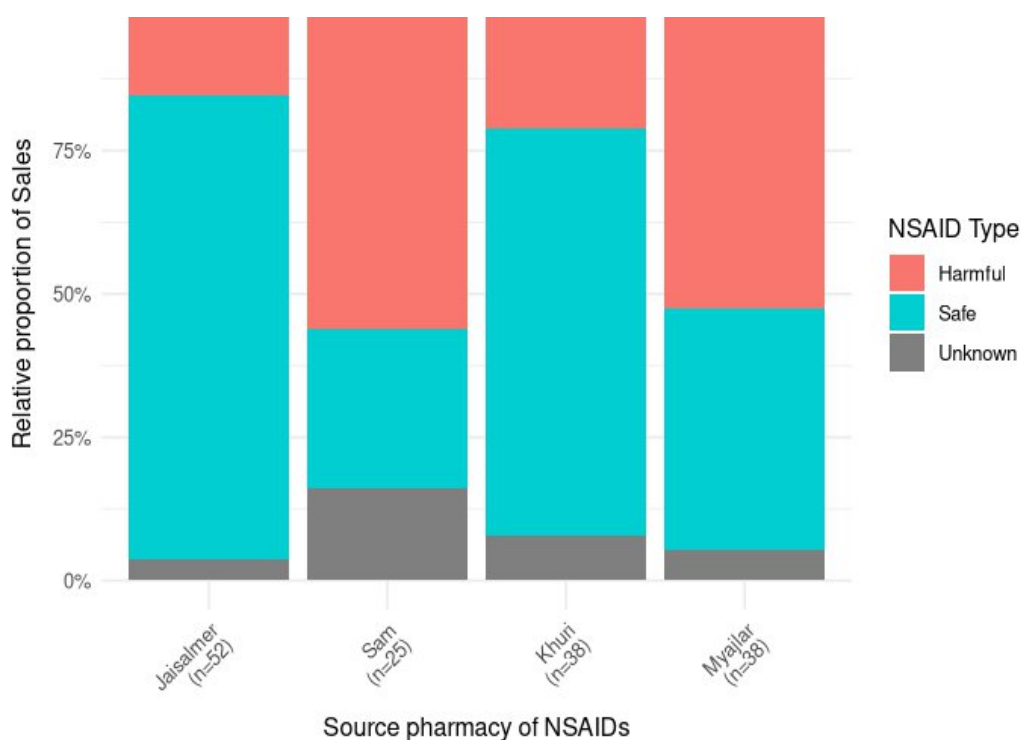


Figure 6: Source of NSAIDs used by surveyed pastoralists, categorised by their toxicity to vultures

During covert pharmacy surveys, 4 major pharmacies were sampled from Jaisalmer, Sam, Khuri and Myajlar respectively. While the pharmacy in Jaisalmer offered only Meloxicam and Paracetamol injections for pain relief, Sam and Myajlar offered Nimesulide tablets alongside Meloxicam. The pharmacy in Khuri, however, offered neither of these NSAIDs and could offer only antibiotics like Oxytetracycline and Enrofloxacin.

Table 2: Coefficients of predictor Distance of household from Jaisalmer (*Distance_jsm*) for the binomial response variable of presence of harmful NSAIDs for $n = 128$ pastoralists interviewed

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-2.050	0.560	-3.620	<0.001 ***
Distance_jsm	2.643e-05	1.033e-05	2.56	0.01 *

Table 2 shows the model coefficients of distance from Jaisalmer against the presence of harmful NSAIDs. A line graph (Fig. 7) plotting the prevalence of harmful NSAID use in the form of predicted probabilities of the aforementioned model against distance from the main city (Jaisalmer) showed an increasing likelihood of presence away from the main city, complementing the prediction that remote locations may be associated with a higher use of vulture-toxic drugs.

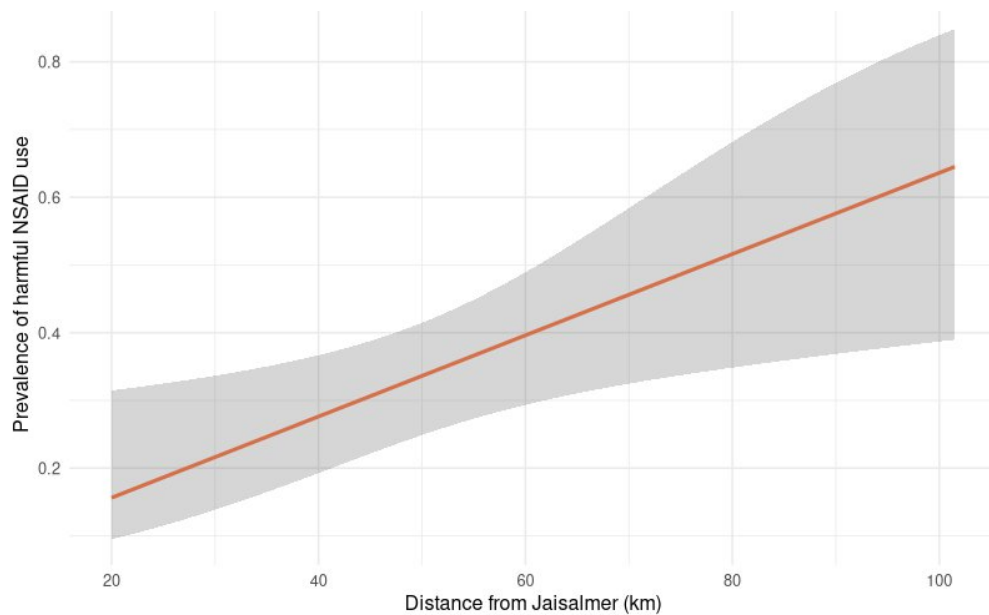


Figure 7: Prevalence of harmful NSAID usage by pastoralists (n = 50)

A kernel density heatmap (Fig. 8) generated from the survey data shows spatial clustering in the usage of harmful NSAIDs across the landscape, indicating that these areas have a higher potential of carcass contamination from vulture-toxic NSAIDs. The nest locations of White-rumped vulture and pharmacy locations are also overlaid to visualise the potential threat to their breeding populations.

Usage of vulture-toxic NSAIDs in and around DNP, Jaisalmer

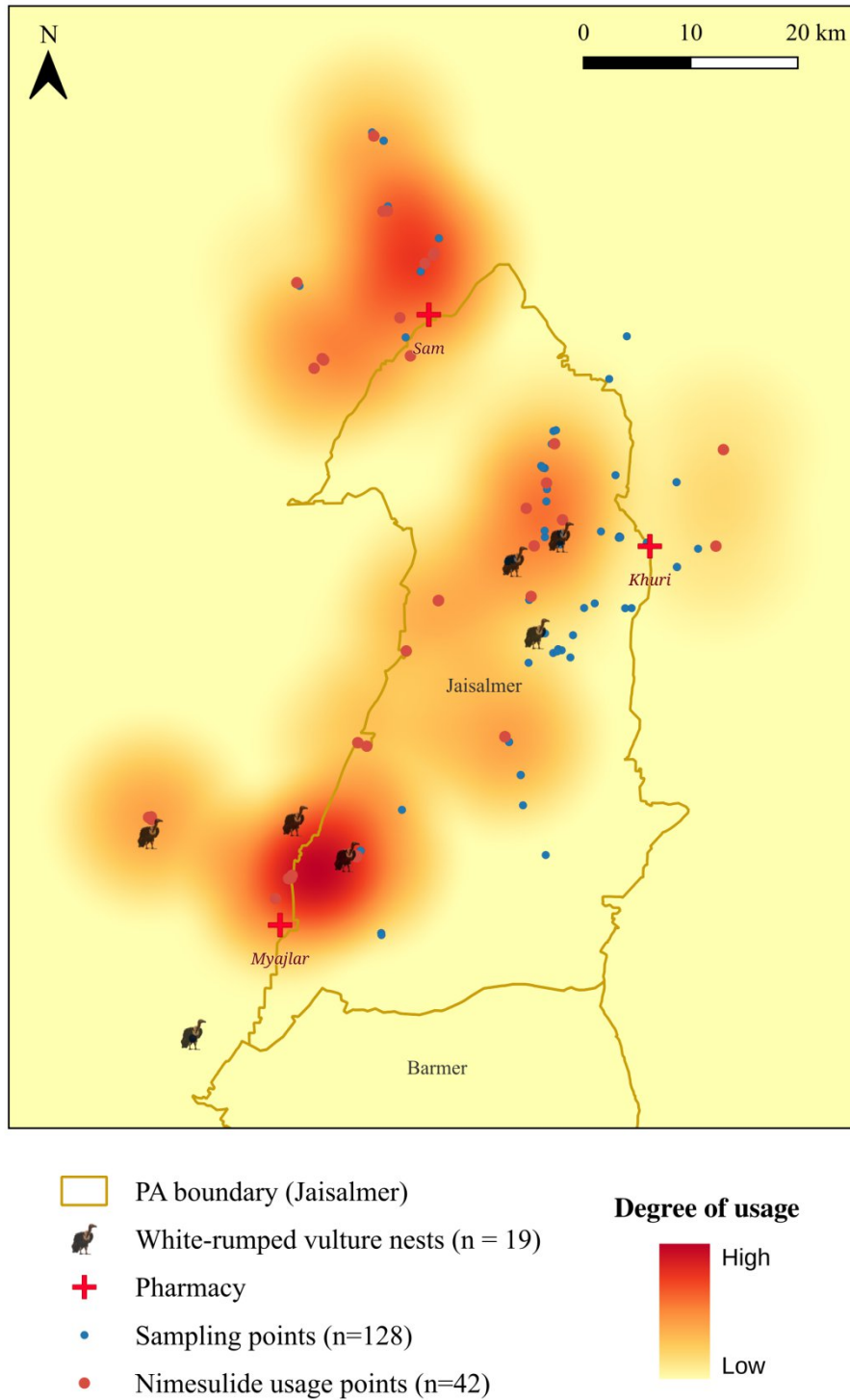


Figure 8: Usage of vulture toxic drugs in the study area

5.4 DISCUSSION

Interviewing livestock herders and assessing their pattern of NSAID usage assisted in building a better picture of the threat of harmful NSAID exposure to vultures. With isolated villages distant from the main city, having higher usage frequency of Nimesulide and with the vulture nests also being in close proximity to usage hotspots, there is a high likelihood of poisoning. However, this does not translate to every available domestic carcass being infected with harmful NSAIDs in those regions. There is no coherent pattern in drug usage, and it is loosely based on the random occurrence of inflammation or any symptoms of pain in livestock. Though this is not the case in certain villages, where people tend to use NSAIDs more frequently due to the presence of diseases such as foot-and-mouth disease (FMD), Peste des Petits Ruminants (PPR), lumpy skin disease (LSD), cerebral coenurosis, etc. Some households which were distant from any local pharmacy would contact Mobile Veterinary Units (MVUs). These four-wheeler MVUs, launched by the Rajasthan government under the Mukhyamantri Bhramyamana Prani Chikitsa Seva scheme, are well equipped to diagnose, treat and monitor diseases especially in remote areas. The respondents reported that Meloxicam was the only NSAID used by these units to treat their livestock, and the treatment charges are subsidized under the scheme. Despite this convenience, the most of respondents had to resort to local pharmacies instead of MVUs for drugs, especially if the former was more cost effective and accessible.

The most commonly used harmful NSAID tablets were a formulation of Nimesulide, paracetamol, and serratiopeptidase which were present in 400 mg, 1500 mg, and 60 mg weights per bolus respectively. The quantity of dose used at a time varied with the animal being treated. Where cattle or a camel would be given an entire tablet when in pain, smaller livestock like goats and sheep would be given half a tablet in one go. The usage was reportedly more common for cattle and camels, and in most cases of pain in sheep and goats, formula-

tions of enrofloxacin and ivermectin were given. Though there are limited studies on long term impact of veterinary pharmaceuticals on wildlife, accumulation of enrofloxacin in *Gyps* vultures can potentially lead to gastrointestinal issues, cartilage disorders, hypersensitivity reactions, etc. (Blanco et al., 2016). Recalling the higher visitation of Red-headed and griffon vultures on smaller-sized prey from the camera trap data, a higher use of fluoroquinolones like enrofloxacin in sheep/goat could be causing accumulation of these chemicals in vultures.

Covert surveys in pharmacies away from the main city showed Nimesulide tablets were readily available, and also significantly cheaper than Meloxicam injection bottles. The latter also came with the additional costs of syringes, making it a relatively costlier option for the pastoralists. However, only one major pharmacy was sampled per village, making the covert survey data useful only when used as a supplement to the questionnaire data, where there already is an adequate representation of pharmacies of a village/town from respondents. The respondents living in Dhanis and villages distant from main city were buying the most readily available drugs at the pharmacy, regardless of whether it is legal or not. There is a general lack of awareness about the impact of veterinary drugs on wildlife, and especially about the ecosystem services provided by vultures. Many pastoralists reported that they associate vultures with a negative connotation, particularly White-rumped vultures and Egyptian vultures as they occupy the *Prosopis cineraria* trees in farmlands for nesting, putting them in direct conflict with a pastoralists depending on those trees for fuelwood and fodder. Some even admitted to pelt stones on individuals trying to build a nest in early winters, becoming yet another addition to the multitude of threats these endangered raptor populations already face. The nesting ecology traits of these vultures, which were naturally selected in evolution to maximise chances of resource availability, now seem to be acting against the interests of their survival in more than one way.

CHAPTER III

COMPETITIVE
INTERACTIONS OF
SCAVENGING RAPTORS

6.1 INTRODUCTION

The absence of large mammalian predators in the Thar desert landscape has enabled the scavenging community to completely take over a high abundance of animal carcasses, which has mostly led to an unregulated growth in the populations of free ranging dogs (Markandya et al., 2008) and pigs. Moreover, due to the arrival of migratory raptors in high numbers, including large bodied obligate scavengers like the Cinereous vultures (*Aegypius monachus*) and Griffons (*Gyps fulvus* and *G. himalayensis*), the food availability to resident vultures like the Red-headed vulture (*Sarcogyps calvus*) and *G. bengalensis* plummets further. This begs the question of whether other scavengers in the landscape, including mammals and migratory raptors, are outcompeting the resident vultures in terms of feeding efficiency (by exploitative competition) and/or by asserting dominance and aggressively displacing them from carcasses (by interference competition). By looking into carcass utilisation dynamics through this part of the study, another major aspect of scavenging that can be understood is the influence of several feeding site factors on the visitation of scavengers. When planning species-centric conservation measures, such as designing carcass dumps/enclosures for vultures, such information will prove to be key for long-term effective species conservation and upkeeping the integrity of desert ecosystems.

6.2 METHODOLOGY

6.2.1 FIELD METHODS

Carcasses were located using a combination of vehicular surveys and local information networks. Vehicular surveys were conducted in a both on-road and off-road manner and carcasses of wild and domestic animals were located opportunistically, and a camera trap was placed on any carcass which was not completely consumed. Livestock herders were also

routinely contacted to gather information on recent livestock mortalities, ensuring timely deployment of camera traps. A Cuddeback C2 camera was installed upon carcass detection, and was configured to record 30-second time-lapse images, motion captures and a short 10-second video clip. Biological covariates including carcass species, size class, decomposition and presence of other scavengers at the installation time were recorded at each carcass site. Furthermore, disturbance indicating variables such as distance from the nearest road, village and GIB enclosures were calculated post-fieldwork using the tools available in QGIS. These approaches facilitated a comprehensive documentation of scavenger behaviour and resource utilisation dynamics across a gradient of ecological and anthropogenic factors.

6.2.2 ANALYTICAL METHODS

Analysis was conducted using R (version 4.5.0) and QGIS (version 3.22). To summarise field effort, descriptive statistics was used to calculate the proportion of carcass species sampled. Generalised Linear Models (GLMs) were used to examine the effect of carcass covariates (e.g., carcass type, size, and disturbance variables) on the presence of each scavenger species. The best fitting model (with the lowest AIC) was taken to predict the probability of visitation for scavengers under their model conditions using the `ggeffects::predict_response()` function.

To quantify aggressive interspecific interactions, an Elo rating system (Elo et al., 1978) was used to assign scores to scavenger species by categorising winners and losers based on individual interspecific interactions. Any interaction involving a scavenging raptor was taken into account, and a species was listed as a “winner” when it successfully displaced another off of a carcass. This rating system has shown to be advantageous than other methods (like interaction matrices) in building animal dominance hierarchies with reliable ranks, especially when relative dominance is to be inferred from a sparse dataset (Neumann et al., 2011). The Elo ratings were calculated as follows:

- Expected probability that the winner would win:

$$E_w = \frac{1}{1 + 10^{\left(\frac{R_l - R_w}{400}\right)}}$$

- Expected probability that a loser would win:

$$E_l = \frac{1}{1 + 10^{\left(\frac{R_w - R_l}{400}\right)}}$$

- Updated Elo score for the winner

$$R'_w = R_w + K \cdot (1 - E_w)$$

- Updated Elo score for the loser

$$R'_l = R_l + K \cdot (1 - E_l)$$

Where,

- R_w = Current Elo score of the winner
- R_l = Current Elo score of the loser
- K = Constant of the maximum possible rating change per interaction

A dominance index was developed which was calculated a scaled value of the Elo ratings, ensuring that the values are centered around 0 with standard deviation as 1. This makes relative interspecific dominance easier to interpret than the raw Elo scores. The interaction data was cleaned pre-analysis by discarding the scavenger species which had the total number of interactions less than 5.

$$\text{Dominance index (DI)} = \frac{\text{Elo score of a given scavenger} - \text{Mean Elo score}}{\text{Standard deviation}}$$

Exploitative competition was assessed using time-lapse images since it provided a standardised 30-second interval data. A feeding efficiency index was developed which was calculated using the following formula:

$$\text{Efficiency index (EI)} = \frac{\text{Time spent feeding on a carcass}}{\text{Total time spent on a carcass}}$$

To get these values of time, the number of time-lapse frames for time feeding and total time were multiplied by 30. This index was analysed by implementing Generalised Linear Models (GLMs) using the `betareg()` package in R, wherein each species' efficiency was tested against the covariates and modelled separately.

6.3 RESULTS

A total of 34 carcasses (32 from vehicle surveys, 2 from local information networks) of various species were sampled (Fig. 9). At least one scavenger was present on every carcass, indicating the limited resource availability in the landscape. Cattle emerged to be the most commonly available carcass, with 20 encounters in the sample. In terms of size class, about 50.8% of the carcasses sampled were small sized (<25 kg), whereas large carcasses (>50 kg) made up 28.8% of the sample (Fig. 10).

The total camera trapping effort is listed as follows:

1. **Time-lapse images:** 1,72,505
2. **Motion captures:** 72,314
3. **Video duration:** 968.5 minutes

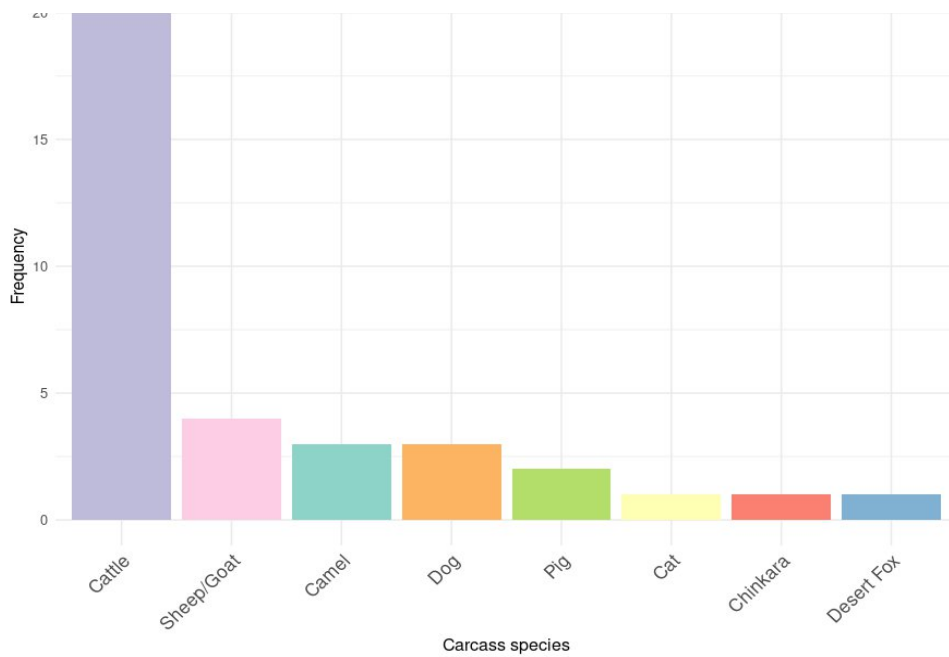


Figure 9: Number of sampled carcasses per species

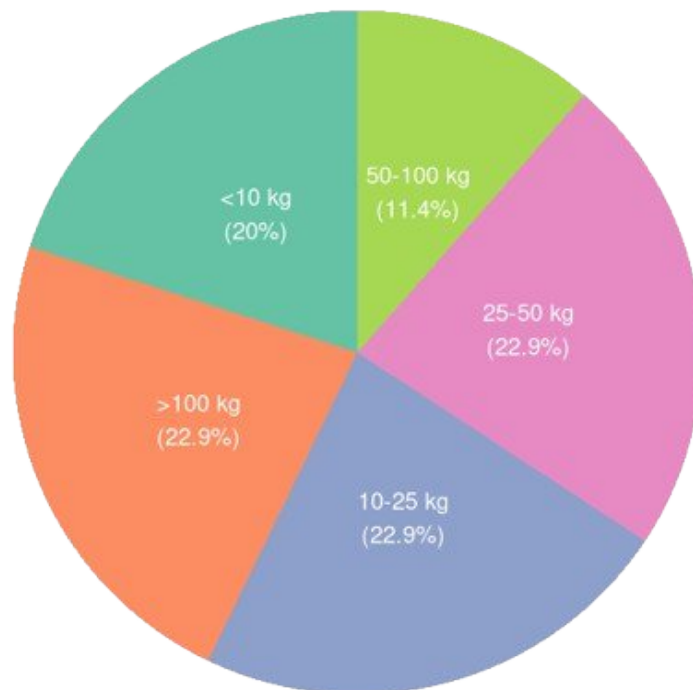


Figure 10: Proportion of sampled size classes of carcasses

The influence of carcass site covariates (including carcass species, size class, type (domestic or wild), decomposition stage, and distances from the nearest enclosure and village) on the visitation (presence) of scavengers on carcasses were examined using GLMs for each scavenger species individually, wherein the model with the lowest AIC was assumed to be the best. White-rumped vulture and Imperial eagle were exempted from this analysis due their extremely low sample sizes ($n < 5$). Five scavenger species showed significant predictors for presence based on their best fitting model. On the contrary, testing covariates for the presence of other scavengers did not reveal any significant predictors. Broadly, disturbance and size class of prey were the only prominent predictors of scavenger presence.

Table 3: Effect size of significant predictors of scavenger visitation.

Scavenger	Predictor	Std. Coefficient (Effect Size)	Lower CI	Upper CI
Red-headed vulture	Size_class	-2.39	-5.35	-0.51
	Dist_village	1.92	0.54	4.05
Himalayan/Eurasian Griffon	Size_class	-1.1	-2.57	-0.04
	Dist_village	1.21	0.32	2.33
Tawny eagle	Size_class	-1.11	-2.18	-0.28
Dog	Dist_village	-0.78	-1.62	-0.07
Fox	Dist_village	0.86	0.09	1.82

The degree of influence of each significant predictor on scavenger visitation was also quantified using effect sizes from the `standardized_parameters()` function in the `effect-size()` package. The standardised effect sizes and their 95% confidence intervals are listed

in Table 3. The predictors whose upper and lower confidence intervals do not cross zero indicate strong directionality in the data.

Visitation probabilities were predicted for the scavengers in Table 3 based on the high and low values of their predictors, taken from their 75% quantile and 25% quantile respectively. Thus, small and large prey size would be 10-25 kg and 50-100 kg respectively, whereas near and far distance would be ~650 m and ~4890 m respectively.

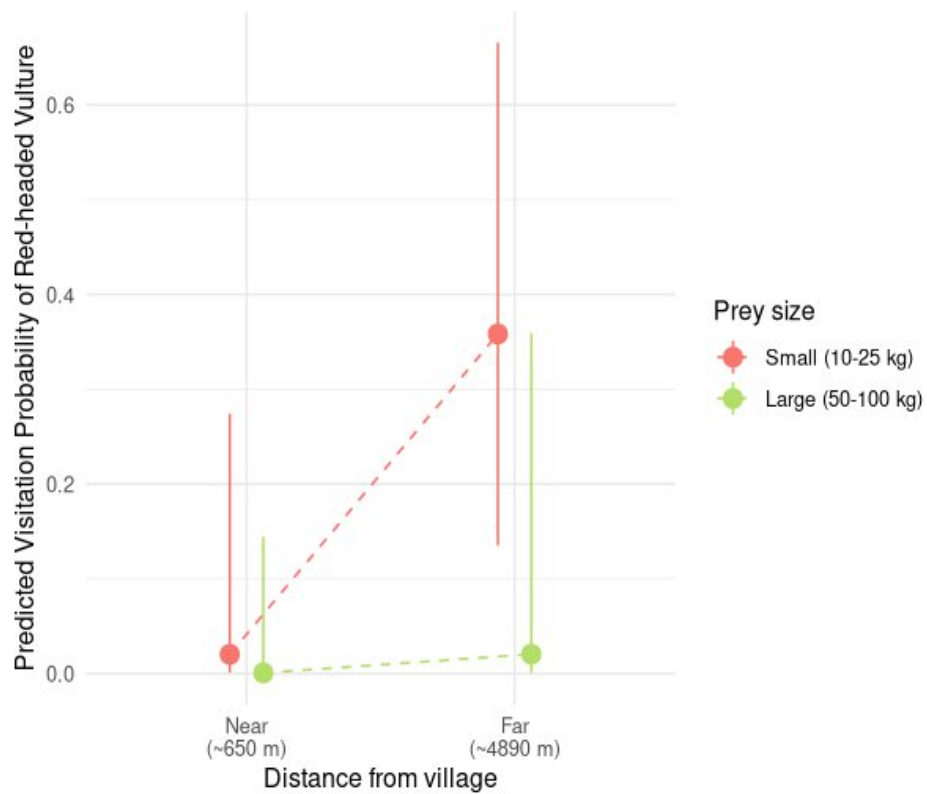


Figure 11: Predicted visitation probability of Red-headed vulture

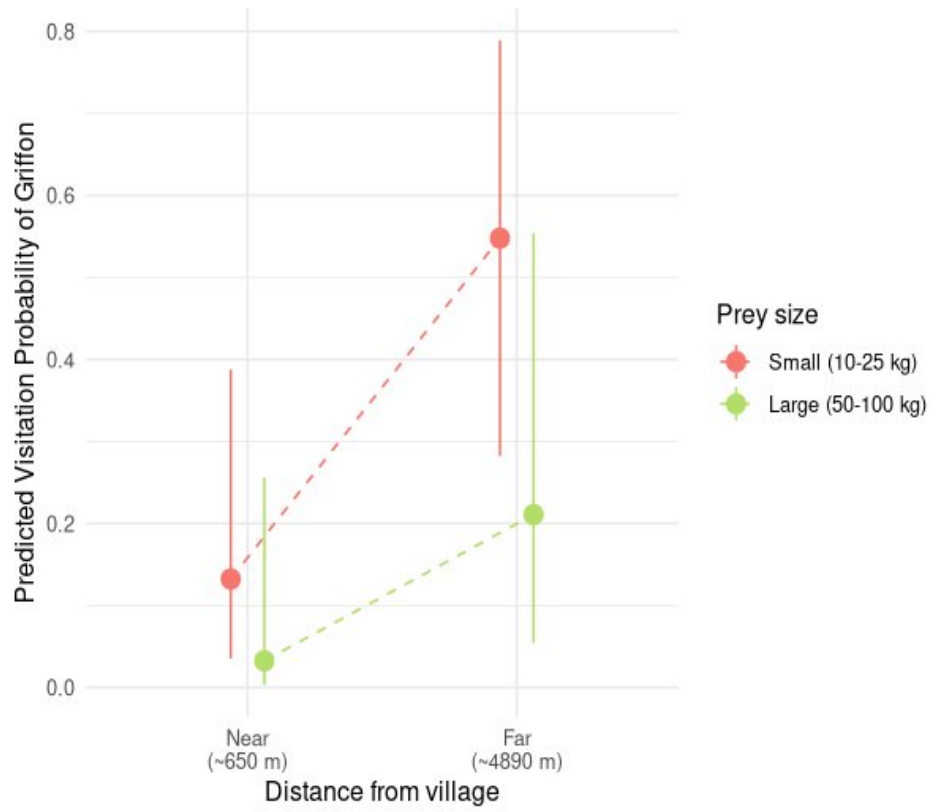


Figure 12: Predicted visitation probability of Griffon

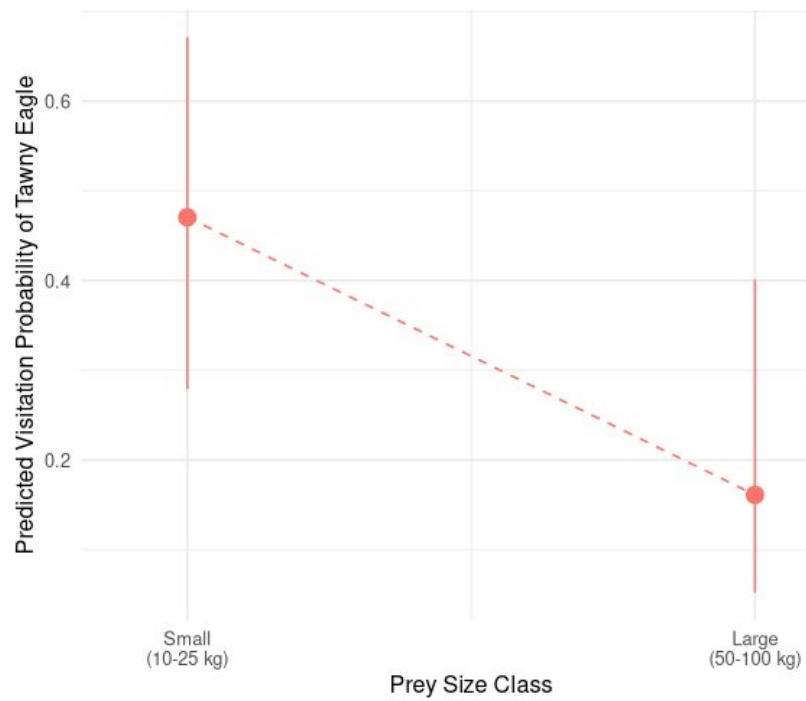


Figure 13: Predicted visitation probability of Tawny eagle

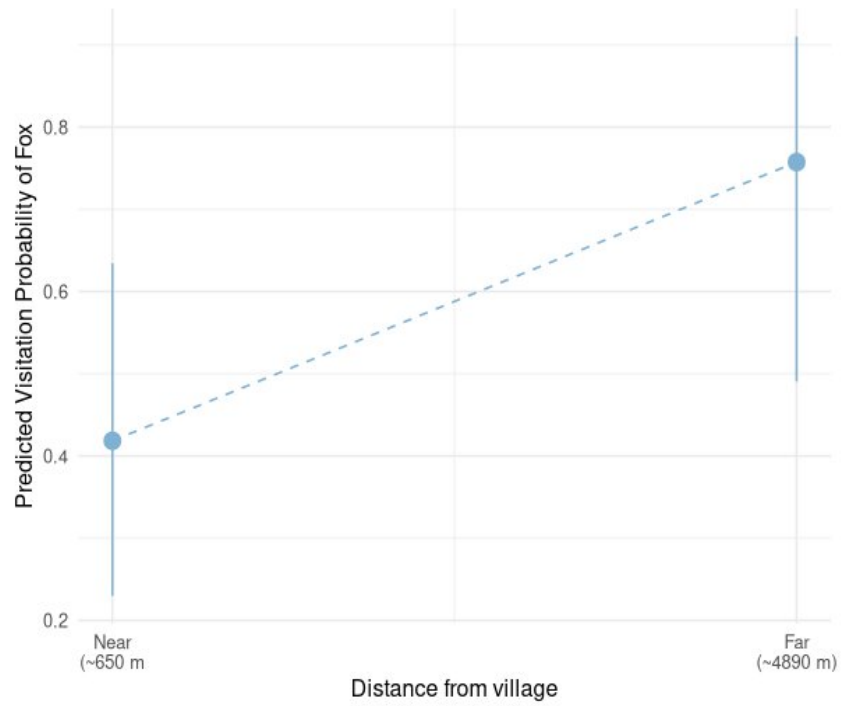


Figure 14: Predicted visitation probability of Fox

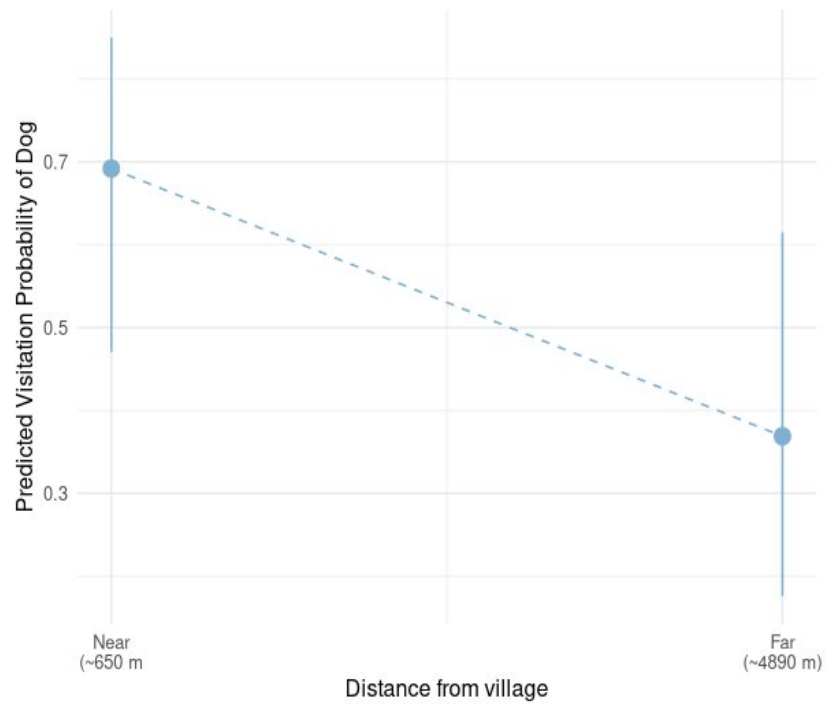


Figure 15: Predicted visitation probability of Dog

Due to a larger effect size, the predicted probability of Red-headed vulture (Fig. 11) showed a higher net increase with smaller prey than with larger prey, going away from the village.

For Griffon, however, the effect sizes of the predictors were comparable (Fig. 12). This suggests their selection of smaller prey in remote locations, possibly to avoid human disturbance or competition. Tawny eagle showed a steep decline in visitation probability when the prey size is low (Fig. 13). While the visitation probability of fox was observed to be higher away from the village (Fig. 14), the case was flipped with Dog with the latter having an increase in visitation probability closer to the village, reflecting their association with human settlements (Fig. 15).

Overall, different scavenger species showed varying responses to either carcass size or distance from the nearest village. The influence of human disturbance on scavenger presence highlights the role of human settlements in shaping scavenger assemblages in the landscape. Though the spatial partitioning observed in this data may indicate functional complementarity in carcass utilisation, the higher presence of scavenging dogs near human areas could be constraining scavenger coexistence, especially for subordinate species which are easier to outcompete.

To assess interference competition, 225 aggressive encounters involving scavenging raptors were recorded in motion captures and videos, and a dominance index was computed for each scavenger species using Elo scores. The dominance index for a species drops below zero if the species loses more interactions than it wins. These values are listed in Table 4 and visualised in Fig. 16.

Table 4: Raw Elo scores and dominance index (DI) of scavengers, based on n = 225 interactions involving scavenging raptors

Species	Interaction count	Elo score	Dominance Index (DI)	Std. Error
Cinereous vulture	153	1302.05	1.39	0.11
Dog	26	1300.39	1.38	0.27
Imperial eagle	8	1046.26	0.21	0.08
Pig	6	1045.66	0.21	0.09
Fox	6	1039.49	0.18	0.07
Steppe eagle	18	984.37	-0.07	-0.02
Tawny eagle	14	940.19	-0.28	-0.07
Griffon	138	906.21	-0.43	-0.04
Red headed vulture	12	897.55	-0.47	-0.14
Egyptian vulture	68	537.83	-2.13	-0.26

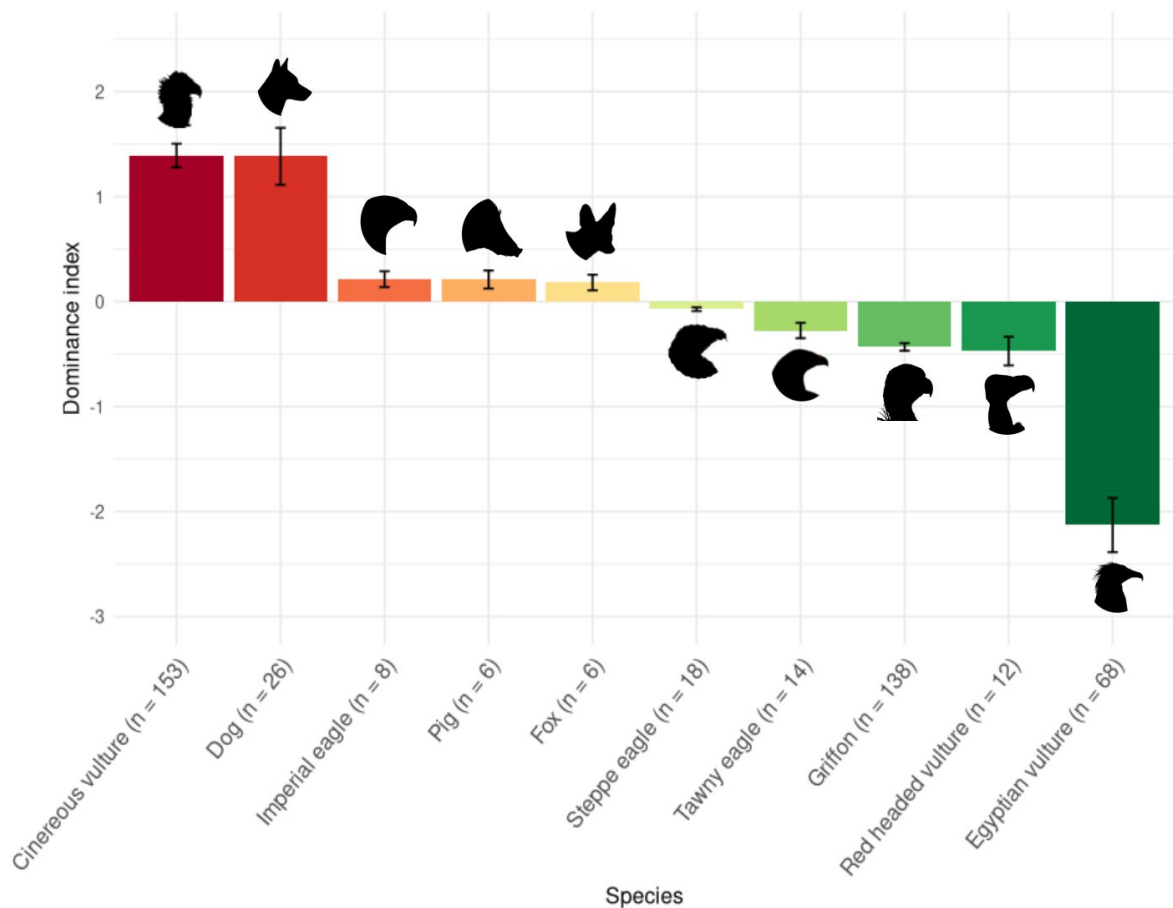


Figure 16: Dominance hierarchy of scavengers based on $n = 225$ aggressive encounters involving scavenging raptors. Species with DI above zero are winning more interactions than they are losing, and vice versa.

The species with the most number of interactions and highest dominance index turned out to be the Cinereous vulture (DI = 1.39), followed by free-ranging dog (DI = 0.27). Egyptian vulture, however, had the maximum proportionate losses and displacements by other dominant species (DI = -2.13), followed by the Red-headed vulture (DI = -0.47) and Griffon (DI = -0.43).

For assessing exploitative competition in the scavenger community, the predictor covariates were tested against Efficiency Index (EI) as the response variable, and the model with the lowest AIC value was chosen for each question. To understand whether EI varies across

scavenger species, a model with scavenger as a predictor was built which produced the following coefficients:

*Table 5: Untransformed coefficients of the best fitting model for efficiency index (EI), having scavenger species as the only significant predictor (Significance codes: * : 0.05, ** : 0.01)*

Fixed effects	Estimate	Std. Error	f value	Pr(> z)
Cinereous vulture (Intercept)	0.73	0.36	2.06	0.04 *
Dog	-0.23	0.49	-0.47	0.64
Egyptian vulture	-0.89	0.45	-1.95	0.05 ' ,
Fox	-0.34	0.47	-0.72	0.47
Griffon	0.41	0.56	0.73	0.47
Pig	0.7	0.49	1.42	0.16
Red headed vulture	-1.68	0.64	-2.64	< 0.01 **
Steppe eagle	-0.4	0.63	-0.63	0.53
Tawny eagle	-0.11	0.53	-0.2	0.84

Since 'Scavenger' is a categorical variable, the first level i.e. Cinereous vulture was taken as the intercept. While Red-headed vulture and Egyptian vulture had consistently low efficiency indices, Cinereous vulture had relatively higher efficiency throughout the dataset, as indicated by the positive estimate of the intercept.

The EI for each scavenger species were averaged out and arranged in a descending order to rank the scavengers as per their feeding efficiency (Fig. 17).

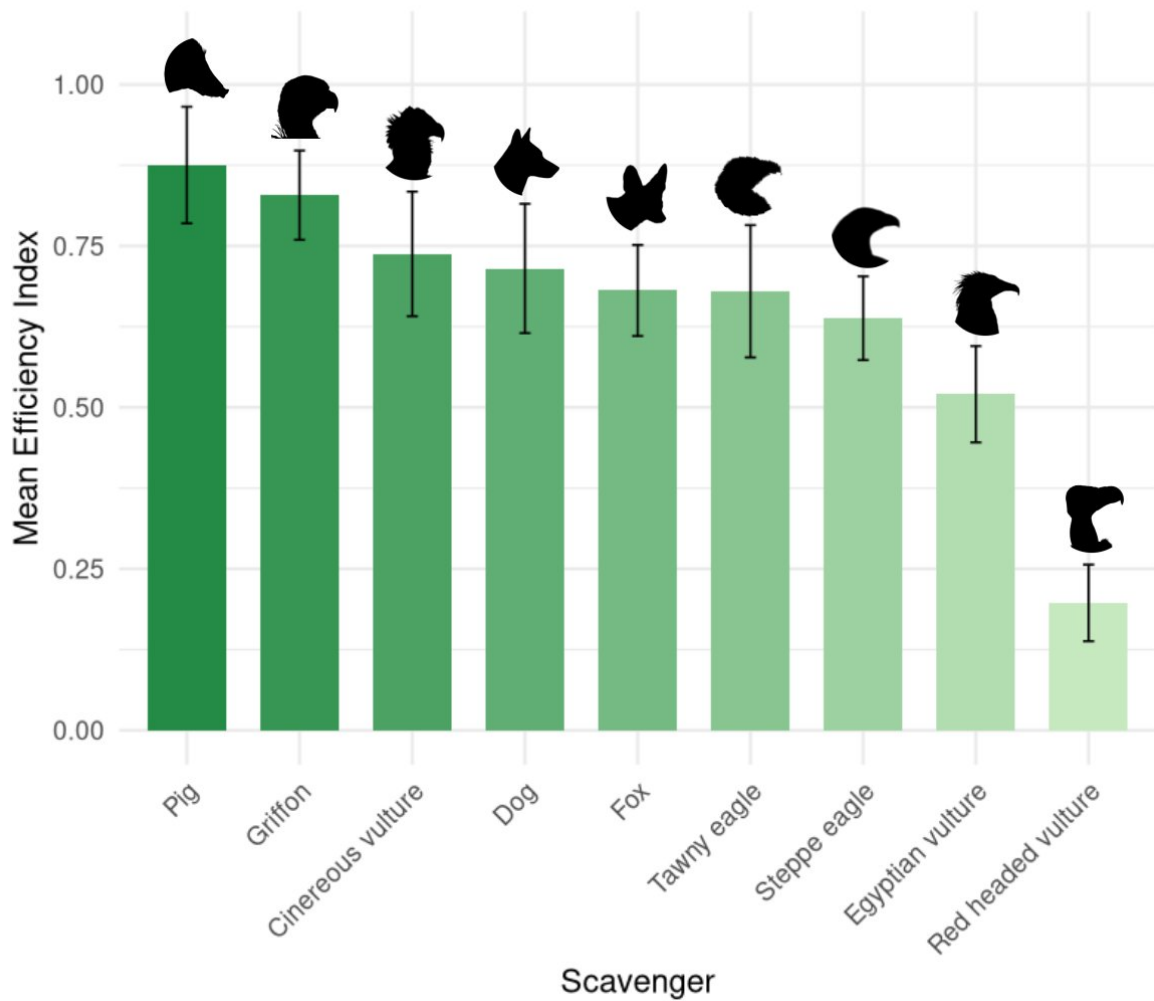


Figure 17: Hierarchy of feeding efficiency in scavengers

Mammalian scavengers and migratory vultures had higher mean EI values than other scavengers, with the Red-headed vulture having the lowest.

In order to assess how the covariates influence the relative feeding duration of scavengers, proportionate feeding duration was modelled as the response variable in GLMs and the lowest AIC model was chosen. The coefficients of the best model are listed as follows:

Table 6: Untransformed coefficients of the best fitting model for proportionate feeding duration of scavengers at a carcass site (Significance codes: ** : 0.01, *** : 0.0001)

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.75	0.37	-4.74	< 0.001 ***
Efficiency	1.29	0.36	3.61	< 0.001 ***
group_feeder	0.52	0.24	2.21	0.026 **

Efficiency and group_feeder turned out to be significant predictors in the best model, implying that scavengers with higher efficiency or social feeding strategies fed for relatively longer duration than other scavengers.

6.4 DISCUSSION

The camera trap data attests to the higher proportion of domestic prey available in the landscape, representing a variety of size classes and disturbance gradients. However, the quantum of available resource does not assure its accessibility to vultures. Scavenger visitation models showed a higher probability of feral dogs being present on a carcass closer to the village, which primarily constitutes of livestock. Comparison of feeding efficiencies, dominance indices, and a number of dissatisfying field observations have all pointed to the fact that dogs are actively displacing the resident raptors off of available livestock carcasses, all year round. In cases of large-bodied prey, like cattle, it was observed that dogs would consume as much soft tissue as they could from the fresh carcass, and then wait for other scavengers to open up the tough hide, like vultures do with their sharp beaks, making the rest of the soft tissue accessible to dogs which would be followed by them displacing the vultures and finishing up the meal. The monopoly of dogs over livestock carcasses could likely be the reason for low

presence of vultures on carcasses near the villages, given the fact their presence used to be much higher before the population crash, even in areas with high human disturbance. Ever since the decline of vulture populations in India, the numbers of feral dogs have shot up tremendously which has increased the prevalence of many fatal pathogens, especially *Lyssavirus*. Their populations in the study area have become self-sustaining, without requiring deliberate food provisioning from humans. Given their numbers, even the idea of mass sterilisation is far from efficient, making this one of the biggest barriers in restoring ecosystem health and food availability to scavenging raptors.

While pigs and foxes also have higher efficiencies and contribute to lower food availability to raptors, they were observed to usually partition their activities temporally to avoid direct interaction and maximise their duration of feeding. Although, there were observations of foxes displacing smaller raptors like Egyptian vultures from carcasses in a few cases.

It was also noted that migrant vultures were present in relatively larger numbers than the residents, and were also bigger in size, especially Cinereous vulture and Himalayan griffon. Resultantly, their sample sizes in terms of fecal matter for diet estimation, carcass visits, and interspecific interactions were higher than resident vultures. While the dominance indices may show that griffons are losing more interactions than winning, this does not mean that they are not aggressive at carcass sites. The low DI of griffons was majorly due to the number of interactions individual griffons have lost against Cinereous vultures, but at the level of the species, they do manage to acquire resources and feed more efficiently than many other scavengers, largely owing to their fission-fusion group feeding strategy where it often becomes a challenge to spot a carcass, or even count the number of individual griffons which are feeding on it. With group feeders having consistently higher proportionate durations of feeding, it is clear how successful of a feeding strategy this is. It is a characteristic feeding ecology trait of many *Gyps* vultures, even White-rumped vultures, but this foraging success is far fetched

when their numbers are too low to dominate a carcass. Red-headed vultures, on the other hand, often arrive either solitary or in pairs on carcasses. Though they were observed feeding in later stages of carcass decomposition as well, they would generally be an early visitor on fresh carcasses. Their detections in the study area were even lower than White-rumped vulture, indicating that their population might be at a higher risk of local extinction.

7. CONCLUSION

The overarching aim of the study was to investigate the possible reasons for the population of *G. bengalensis* remaining stagnant despite the wide availability of nesting habitat. Being a resource-driven species, the distribution and survival of *Gyps* vultures has been linked to availability of carrion (Mundy, 1992, Ghosh-Harihar et al., 2024). Therefore, given the preliminary knowledge of the Thar desert landscape, the study was designed to look into two major aspects of *G. bengalensis*'s resource utilisation: the persistent risk of poisoning by harmful NSAIDs, and the consequent threat of getting outcompeted through interspecific competition due to low food availability in the landscape. In context of the results of this study, the key to restoration of resident vulture populations in the landscape of Thar desert is an improved carcass disposal mechanism and drug administration practices for livestock. The carcasses which are currently being dumped near the village are usually larger in size, making it logistically difficult for villagers to dump it away from the village which results in the frequent monopoly of feral dogs and pigs on carcasses. Based on the significant predictors of scavenger presence which were evaluated in this study, the establishment of carcass dumps away from human settlements can reduce the dominance of dogs. These sites can also be fenced which would further restrict their access and improve food accessibility to scavenging raptors. This will have importance especially in the winter months when the large numbers of migratory vultures increase the competition for breeding vultures and reduce their resource consumption and food provisioning to the nests. The improved food accessibility during the rest of the year will also benefit summer breeders, like Red-headed vultures. Measures to control dog populations should also be prioritised parallelly to limit disease spread, both in livestock and in humans, and reduce interspecific competition with resident vultures. Conducting additional research on disease ecology of the study area, particularly on the role of feral dogs in transmission of pathogens, and on the accumulation

and impact of veterinary drugs in scavenging raptors, will aid in implementing the aforementioned measures.

It is also of utter importance to curb the use of banned harmful NSAIDs, specifically Nimesulide since the ban was enforced only recently (Gazette notification S.O. 5633(E) dated 30th December, 2024) and the use of the drug still prevails in villages distant from main cities. The supply chain should be thoroughly inspected, particularly in vulture sensitive areas like Myajlar, Sam and Khuri. Conducting awareness campaigns targeting pastoralist communities can help to emphasise the cultural significance of vultures and their role in disease control. Coexistence of humans with *Gyps* vultures is practical and has been there for centuries, and preventing their extinction is a far cheaper approach than recovering from the repercussions of an unstable, disease prone ecosystem without obligate scavengers.

8. REFERENCES

1. Blanco, Guillermo & Junza, Alexandra & Segarra, David & Barbosa, Jose & Barron, Dolores. (2015). Wildlife contamination with fluoroquinolones from livestock: Widespread occurrence of enrofloxacin and marbofloxacin in vultures. *Chemosphere*. 144. 1536-1543. 10.1016/j.chemosphere.2015.10.045.
2. Bohra, D. L. "Veterinary Drugs and Associated Impact on Vulture Health in Asia." *Пернатые хищники и их охрана S2* (2023): 175-177.
3. Booms TL, Fuller MR. Time-lapse video system used to study nesting Gyrfalcons. *J. Field Ornithol.* 2003; 74: 416–422.
4. Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M.V., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J. and Wood, M.D. (2017), A review of camera trapping for conservation behaviour research. *Remote Sens Ecol Conserv*, 3: 109-122.
5. Chandramohan, S., et al. "Metabolism of aceclofenac to diclofenac in the domestic water buffalo *Bubalus bubalis* confirms it as a threat to Critically Endangered *Gyps* vultures in South Asia." *Environmental toxicology and pharmacology* 96 (2022): 103984.
6. Cuthbert, Richard J., et al. "Continuing mortality of vultures in India associated with illegal veterinary use of diclofenac and a potential threat from nimesulide." *Oryx* 50.1 (2016): 104-112.
7. Deagle BE, Thomas AC, McInnes JC, et al. Counting with DNA in metabarcoding studies: How should we convert sequence reads to dietary data?. *Mol Ecol.* 2019; 28: 391–406.
8. Delaney DK, Grubb TG, Garcelon DK. An infrared video camera system for monitoring diurnal and nocturnal raptors. *J. Raptor Res.* 1998; 32: 290–296.
9. Elbrecht V, Leese F (2017) Validation and development of COI metabarcoding primers for freshwater macroinvertebrate bioassessment. *Front Environ Sci.*

10. Elo, Arpad E., and Sam Sloan. "The rating of chessplayers: Past and present." (1978).
11. Ficetola GF, Taberlet P, Coissac E (2016) How to limit false positives in environmental DNA and metabarcoding? *Mol Ecol Resour* 16:604–607.
12. Finkelstein, Myra E., et al. "Lead poisoning and the deceptive recovery of the critically endangered California condor." *Proceedings of the National Academy of Sciences* 109.28 (2012): 11449-11454.
13. Galan M, Pons J-B, Tournayre O et al (2018) Metabarcoding for the parallel identification of several hundred predators and their prey: application to bat species diet analysis. *Mol Ecol Resour* 18:474– 489.
14. Galligan, T. H., et al. "Metabolism of aceclofenac in cattle to vulture-killing diclofenac." *Conservation Biology* 30.5 (2016): 1122-1127.
15. Galligan, T. H., et al. "Trends in the availability of the vulture-toxic drug, diclofenac, and other NSAIDs in South Asia, as revealed by covert pharmacy surveys." *Bird Conservation International* 31.3 (2021): 337-353.
16. Gause, George Francis. *The struggle for existence: a classic of mathematical biology and ecology*. Courier Dover Publications, 2019.
17. Ghosh-Harihar, Mousumi, et al. "Metabarcoding for parallel identification of species, sex and diet of obligate scavengers: An application to globally-threatened *Gyps* vultures." *Conservation Genetics Resources* 13 (2021): 61-77.
18. Gotelli, Nicholas J. "Null Model Analysis of Species Co-Occurrence Patterns." *Ecology* 81, no. 9 (2000): 2606–21.
19. Green, R.E., I. Newton, S. Shultz, A.A. Cunningham, M. Gilbert, D.J. Pain & V. Prakash (2004): Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *J. Appl. Ecol.* 41: 793-800

20. Houston, D.C., 1985. Indian white-backed vulture (*G. bengalensis*). In: Conservation Studies on Raptors. International Council for Bird Preservation Technical Publication No. 5. Cambridge.
21. HOUSTON, DAVID C. "Competition for food between Neotropical vultures in forest." *Ibis* 130.4 (1988): 402-417.
22. Jones, Georgia & Woods, D & Broom, C & Panter, Connor & Sutton, Luke & Drewitt, EJA & Fathers, Jason. (2024). Fine-Scale Spatial Variation in Eurasian Kestrel *Falco tinnunculus* Diet in Southern England Revealed from Indirect Prey Sampling and Direct Stable Usotope Analysis. *Ardea*. 112. 129-141. 10.5253/arde. 2023.a3.
23. K.U. Karanth, J.D. Nichols, N.S. Kumar, W.A. Link, & J.E. Hines, Tigers and their prey: Predicting carnivore densities from prey abundance, *Proc. Natl. Acad. Sci. U.S.A.* 101 (14) 4854-4858, (2004).
24. Katzenberg, M. Anne, and Andrea L. Waters-Rist. "Stable isotope analysis: a tool for studying past diet, demography, and life history." *Biological anthropology of the human skeleton* (2018): 467-504.
25. Kneitel, Jamie M. "Gause' s competitive exclusion principle." *Encyclopedia of ecology*. Elsevier BV, 2019. 110-113.
26. Kumar, A (2006). Subject: diclofenac for veterinary use- regarding. Letter to 'All State Drug Controllers' from the 'Drug Controller General (India).
27. Legendre, P., Gallagher, E.D. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280 (2001). <https://doi.org/10.1007/s004420100716>
28. Liu, G., Shafer, A.B., Hu, X., Li, L., Ning, Y., Gong, M., Cui, L., Li, H., Hu, D., Qi, L., Tian, H., 2018. Meta-barcoding insights into the spatial and temporal dietary patterns of the threatened Asian Great Bustard (*Otis tarda dybowskii*) with potential implications for. *Wiley Online Libr.* 8, 1736–1745. <https://doi.org/10.1002/ece3.3791>.

29. Madhusudan, M.D. and Vanak, A.T., 2023. Mapping the distribution and extent of India's semi-arid open natural ecosystems. *Journal of Biogeography*, 50(8), pp.1377-1387.
30. Manigandan, S., et al. "How Availability NSAIDs and Public Perception matters in Vulture Conservation in the Nilgiri Biosphere Reserve, South India: An Overt and Covert Survey Approach." *Ecology, Environment & Conservation* 29.3 (2023): 368-377.
31. Margalida A, Bertrán J, Boudet J. Assessing diet of nestling Bearded Vultures: a comparison between direct observation methods. *J. Field Ornithol.* 2005; 76: 40–45.
32. Marti C.D. 1987. Raptor food habits studies. Pages 67–80 in B. A. Giron Pendleton, B. A. Millsap, K.W. Cline, and D. M. Bird, editors. Raptor management techniques manual. National Wildlife Federation, Washington D.C., USA
33. Marti CD, Bechard M, Jaksic FM. Food habits. In: Bird DM, Bildstein KL, editors. Raptor Research and Management Techniques. Blaine, WA, USA: Surrey, BC: Hancock House Publishers; 2007. pp. 129– 151.
34. McClure, C.; Westrip, J.; Johnson, J.; Schulwitz, S.; Virani, M.; Davies, R.; Symes, A.; Wheatley, H.; Thorstrom, R.; Amar, A.; Buij, R.; Jones, V.; Williams, N.; Buechley, E.; Butchart, S. (2018). State of the World's Raptors: Distributions, Threats, and Conservation Recommendations. *Biological Conservation*, 227, 390–402.
35. Morant J, Arrondo E, Sánchez-Zapata JA, Donázar JA, Cortés-Avizanda A, De La Riva M, Blanco G, Martínez F, Oltra J, Carrete M, Margalida A, Oliva-Vidal P, Martínez JM, Serrano D, Pérez-García JM. Large-scale movement patterns in a social vulture are influenced by seasonality, sex, and breeding region. *Ecol Evol.* 2023 Feb 8;13(2):e9817. doi: 10.1002/ece3.9817.
36. Mundy, Peter, et al. *The vultures of Africa*. Vol. 671. London: Academic Press, 1992.
37. Naidoo, Vinny, et al. "Toxicity of non-steroidal anti-inflammatory drugs to *Gyps* vultures: a new threat from ketoprofen." *Biology letters* 6.3 (2010): 339-341.

38. Neumann, Christof, et al. "Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating." *Animal Behaviour* 82.4 (2011): 911-921.
39. Oaks, J. Lindsay, et al. "Diagnostic investigation of vulture mortality: the anti-inflammatory drug diclofenac is associated with visceral gout." *Raptors worldwide*. Budapest, Hungary: World Working Group on Birds of Prey and Owls (2004): 241-3.
40. Oaks, J.L., M. Gilbert, M.Z. Virani, R.T. Watson, C.U. Meteyer, B. Rideout, H.L. Shivaprasad, S. Ahmed, M.J.I. Chaudhry, M. Arshad, S. Mahmood, A. Ali & A.A. Khan (2004): Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* 427: 630-633.
41. Ogada, D. L., Keesing, F., & Virani, M. Z. (2012). Dropping dead: Causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences*, 1249(1), 57-71.
42. Ogada, D. L., Shaw, P., Beyers, R. L., et al. (2016). Another continental vulture crisis: Africa's vultures collapsing toward extinction. *Conservation Letters*, 9(2), 89-97.
43. Pain, Deborah & Cunningham, Andrew & Donald, PF & Duckworth, JW & Houston, DC & Katzner, Todd & Parry-Jones, J & Poole, C & Prakash, Vibhu & Round, Philip & Timmins, R. (2003). Causes and Effects of Temporospatial Declines of *Gyps* Vultures in Asia. *Conservation Biology*. 17. 10.1046/j.1523-1739.2003.01740.x.
44. Pianka ER. Niche overlap and difuse competition. *Proc Natl Acad Sci USA*. 1974;71:2141-5
45. Pompanon, François & Deagle, Bruce & Symondson, William & Brown, David & Jarman, Simon & Taberlet, Pierre. (2011). Who is eating what: diet assessment using Next Generation Sequencing. *Molecular ecology*. 21. 1931-50. 10.1111/j.1365-294X.2011.05403.x.
46. Prakash, V., Shultz, S., Pain, D.J, Cunningham, A.A., Saravanan, S., Renade, S., and Green, R. (in prep) "Recent population trends of *Gyps bengalensis*, *Gyps indicus* and *Gyps tenuirostris* in India" (2007).

47. Ram, M., Sahu, A., Tikadar, S., Gadhavi, D., Rather, T.A., Jhala, L. and Zala, Y., 2022. Home Ranges and Migration Routes of Four Threatened Raptors in Central Asia: Preliminary Results. *Birds*, 3(3), pp.293-305.
48. Reif V, Tornberg R. Using time-lapse digital video recording for a nesting study of birds of prey. *Eur. J. Wildl. Res.* 2006; 52: 251–258.
49. Resano-Mayor J, Hernández-Matías A, Real J, Parés F, Inger R, Bearhop S. Comparing pellet and stable isotope analyses of nestling Bonelli's Eagle *Aquila fasciata* diet. *Ibis*. 2014; 156: 176–188
50. Rodgers, W.A. and Panwar, H.S., 1988. Planning a wildlife protected area network in India.
51. Rogers AS, DeStefano S, Ingraldi MF. Quantifying Northern Goshawk diets using remote cameras and observations from blinds. *J. Raptor Res.* 2005; 39: 303–309. PMID: 15725429.
52. Selvaraj, Manigandan & Kannan, P & H., Byju & Subbaiah, Bharathidasan & Thambi, Cimi & Ramakrishnan, Balasundaram. (2021). Death of a Himalayan Vulture in South India highlights the potential threat of power infrastructure. *Vulture News*. 8.10.4314/vulnew.v80i1.3.
53. Shultz, S., H.S. Baral, S. Charman, A.A. Cunningham, D. Das, D.R. Ghalsasi, M.S. Goudar, R.E. Green, A. Jones, P. Nighot, D.J. Pain & V. Prakash (2004): Diclofenac poisoning is widespread in declining vulture populations across the Indian subcontinent. *Proceedings of the Royal Society of London B (Supplement)*, 271: S458-S460.
54. Simmons, R. E., D. M. Avery, and G. Avery, 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *J. Raptor. Res.* 25:63–67.
55. Skelton, J., Cauvin, A., & Hunter, M. E. (2023). Environmental DNA metabarcoding read numbers and their variability predict species abundance, but weakly in non-dominant species. *Environmental DNA*, 5, 1092–1104.

56. Stephen M. Redpath, Roger Clarke, Mike Madders, Simon J. Thirgood, Assessing Raptor Diet: Comparing Pellets, Prey Remains, and Observational Data at Hen Harrier Nests, *The Condor*, Volume 103, Issue 1, 1 February 2001, Pages 184–188
57. Swann DE, Kawanishi K, Palmer J. Evaluating types and features of camera traps in ecological studies: A guide for researchers. In: O'Connell A F, et al. editors. *Camera Traps in Animal Ecology: Methods and Analyses*. Springer; 2011. pp. 27–43.
58. Taberlet P, Coissac E, Pompanon F, Brochmann C, Willerslev E. Towards next-generation biodiversity assessment using DNA metabarcoding. *Mol Ecol*. 2012 Apr;21(8):2045-50.
59. Tapia, Luis & Zuberogitia, Iñigo. (2018). *Breeding and Nesting Biology in Raptors*. 10.1007/978-3-319-73745-4_3.
60. Uddin, M., Dutta, S., Kolipakam, V., Sharma, H., Usmani, F., & Jhala, Y. (2021). High bird mortality due to power lines invokes urgent environmental mitigation in a tropical desert. *Biological Conservation*, 261, 109262.

9. APPENDICES

Appendix 1: Best 3 models of scavenger visitation ranked by AICc values. Null model was selected when $\Delta AICc$ values were less than two.

Scavenger	Visitation predictors	AICc	$\Delta AICc$
Red-headed vulture	Dist_village + Size_class	22.9	0
	Dist_village + Size_class + Prey_type	24.7	1.8
	Dist_enclosure + Dist_village + Size_class	25.1	2.2
Cinereous vulture	Dist_village	48	0
	Dist_village + Size_class	48.9	0.9
	NULL	49.2	1.2
Egyptian vulture	Dist_Village + Prey_type	40.4	0
	Prey_type	40.9	0.5
	Dist_Village + Prey_type + Size_class	42.9	2.5
Tawny eagle	Size_class	42.2	0
	Prey_type + Size_class	43.3	1.1
	Dist_enclosure + Size_class	44.1	1.9
Griffon	Dist_village + Size_class	36	0
	Size_class	41	5
	NULL	42	6
Steppe eagle	Dist_village	35.6	0
	NULL	37.1	1.5
	Dist_village + Size_class	37.4	1.8

Dog	Dist_village	48	0
	Dist_village + Size_class	48.4	0.4
	Dist_village + Size_class + Prey_type	49.6	1.6
Pig	NULL	49.9	0
	Size_class	50.2	0.3
	Dist_village	51.6	1.7
Fox	Dist_village	47.3	0
	Dist_Village + Prey_type	49.1	1.8
	Dist_enclosure + Dist_village	49.1	1.8

Appendix 2: Best 3 models of proportionate-time fed on a carcass ranked by AICc values

Model	AIC
Prop_feeding ~ Efficiency + group_feeder	-90.82
Prop_feeding ~ Efficiency	-88.00
Prop_feeding ~ Scavenger	-71.60

Appendix 3 Camera trap points

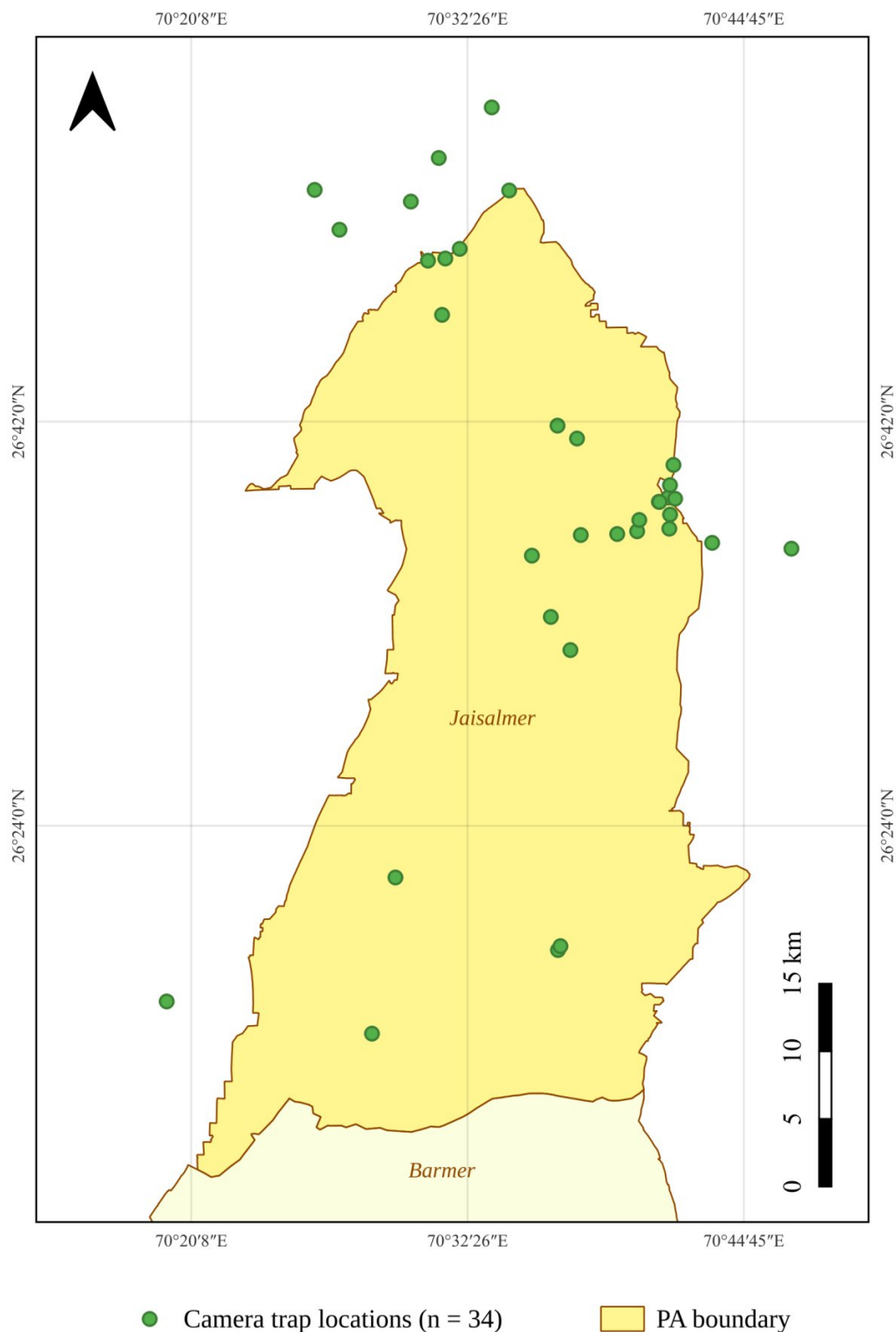


Figure 18: Camera trap locations in the study area

Appendix 4: Fieldwork photographs



Figure 19: A congregation of six vulture species: Cinereous vulture, Himalayan griffon, Eurasian griffon, Red-headed vulture, White-rumped vulture and Egyptian vulture



Figure 20: A White-rumped vulture with its unfluffed chick



Figure 21: Nimesulide (L) and Meloxicam (R): The two major NSAIDs used by surveyed pastoralists



Figure 22: A free-ranging dog displacing a griffon congregation from a sheep carcass



Figure 23: Caught in the chaos: A White-rumped vulture struggles to find food in the midst of a griffon dominated feeding aggregation and an Egyptian vulture escaping with smaller carrion pieces



Figure 24: A pair of Red-headed vultures displaced off of a cattle carcass by Cinereous vulture and griffons