Population density and feeding ecology of the striped hyena (*Hyaena hyaena*) in relation to land use patterns in an arid region of Rajasthan

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EXECUTIVE SUMMARY

Population size (or abundance) and density, are parameters of critical importance to studies that aim to understand how animal species adapt to their environments as well as to studies that try to address conservation issues affecting these species. Large carnivores are generally considered to be among animals that are threatened most by human impacts. The striped hyena (*Hyaena hyaena*) is one such large carnivore species whose range spans the tropical and subtropical regions from western Africa to central and southern Asia. Densities of striped hyenas appear to vary greatly across their range and factors driving this variation are poorly understood because of paucity of rigorous studies. Measuring densities of hyenas under ecologically different conditions would thus help assess the factors that determine hyena distribution and abundance as well as their ability to survive in human dominated landscapes under severe anthropogenic pressures.

This comparative study was conducted across two landscapes in an arid region of India that varied in terms of basic ecology, human impacts as well as management status. The first study site covered an area of 307 km² of the Kumbhalgarh Wildlife Sanctuary in southern Rajasthan while the second site covered 218 km² of a rural human-dominated-landscape around the Esrana Forest Range in south-western Rajasthan. My a priori hypotheses were: Hyena densities were likely to be (1) positively correlated to livestock densities because of their value as a food source; (2) positively correlated to the proportion of steeper terrain that provided hiding and breeding refugia and (3) positively correlated to land use regimes that regulated excessive human pressures under protected area status. These hypotheses were tested by estimating hyena densities at the two sites,
rigorously, and comparing these estimates in the light of specific predictions based on the above-stated hypotheses.

Photographic capture-recapture sampling methodology was applied to estimate abundances and densities of hyenas in the two study areas, based on the ability to distinguish individual hyenas from their unique stripe patterns from camera trap images. Secondary data on livestock numbers and the presence of livestock in hyena diet derived from scat studies was used to elucidate the impact of livestock on hyena abundance. A digital elevation model (DEM) based slope map was created for both areas and comparisons were made between them to determine proportion of topography suitable as hyena refugia in these two areas. Hyena densities were also compared across the protected and non-protected areas.

Because of resource constraints, under the trapping intensity I could achieve, the sample sizes of hyena captures and recaptures obtained were relatively small, thus constraining choice of capture-recapture models and estimators I could use to derive hyena densities. The lack of any recaptures at Esrana also required borrowing of some information from Kumbhalgarh while estimating the sampled area. Despite these problems, I was able to photo capture at least 15 individual hyenas in Kumbhalgarh based on an effort of 538 trap nights and 8 individuals in Esrana with a trapping effort of 548 trap nights, thus being able to complete closed model capture-recapture photographic surveys of short durations of 36 days at each site.
The estimated effectively sampled area was 307 km$^2$ at Kumbhalgarh based on a buffer width of 1.95 km that I computed from distances between recaptures of hyenas using the MMDM methodology. However, because there were no recaptures of any hyenas in Esrana, I could not derive site-specific buffer width estimates. I borrowed the buffer width estimate from Kumbhalgarh to compute the Esrana sampled area at 218 km$^2$. Hyena densities were thereafter derived by dividing the estimated population size by the sampled area size.

I used the software program CAPTURE 2.1 to analyze capture histories obtained from the surveys to derive estimates of hyena abundance. The hyena abundances were estimated at $\hat{D}(\hat{S}\hat{E}(\hat{D})) = 10.4 \pm 2.9$ hyenas/100 km$^2$ at Kumbhalgarh and $10.09 \pm 5.5$ hyenas/100 km$^2$ at Esrana using the jackknife estimator under model M (h) that incorporates individual heterogeneity in capture probabilities. However, under the removal model that accounts for hyena behavioral response to trapping, the abundance estimates $\hat{D}(\hat{S}\hat{E}(\hat{D}))$ for Kumbhalgarh and Esrana, were respectively $6.5 \pm 2.5$ hyenas/100 km$^2$ and $3.67 \pm 0.3$ hyenas/100 km$^2$.

Based on the overall assessments, hyena densities were higher in Kumbhalgarh, supporting the hypotheses that these densities were higher in this area because of greater availability of hilly terrain and a greater degree of protection offered by the protected area status that prevailed at Kumbhalgarh. The hypothesis that hyena densities were determined by livestock densities was not supported by my results because of lower hyena densities at Esrana despite livestock densities being over 3 times higher than those at Kumbhalgarh. From a wildlife management perspective, this study proved that striped
hyena numbers and densities could be rigorously monitored for conservation purposes using photographic capture recapture sampling. Based on the weaknesses observed in my study some specific suggestions are made for improving this methodology in future for monitoring of striped hyena populations across their range.
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INTRODUCTION

Background

The arid zone ecosystems in India (Figure 1) are of great conservation interest because of their unique faunal assemblages, which are under serious threat from degradation of habitat due to a variety of anthropogenic pressures (Kumar & Shahabuddin, 2005; Hocking & Mattick, 1993; Khan & Frost, 2004). However, such ecosystems occupy 11.8% of the Indian subcontinent (Shankarnarayan et al., 1987) and extend into west Asia. Despite tremendous anthropogenic pressures, these regions still support a rich and varied large mammalian fauna. The large predatory carnivores of this region – lions, tigers, dholes, wolves and bears - are particularly threatened by the fact that effectively protected nature reserves essential for their survival form a very small proportion of the landscape. However, contrary to intuition, the status of large sized carnivores like the striped hyenas (and to some extent leopards) appear to be better here because of their ability to adapt to human settlements and even to exploit livestock and other food resources that are generated by human settlements.

Therefore, a study comparing how such adaptable large carnivores fare under different land management regimes is a matter of both scientific and conservation interest.
Figure 1. Semi-arid and arid regions of India (adapted from Shankarnarayan et al., 1987)
The striped hyena: in the context of large carnivore conservation

The Order *Carnivora* has attracted scientific attention due to its unique inter-specific diversity with respect to variations in behavioral and ecological adaptations. Because of their tendency to come into conflict with humans, large home range requirements and a diet of meat which often includes livestock, larger carnivore species are also very threatened. Several studies of large predatory carnivores in the Indian subcontinent, such as *Panthera tigris* (Schaller, 1967; Sunquist, 1981; Karanth *et al.*, 2004), *Panthera leo* (Chellam & Johnsingh, 1993), *Panthera pardus* (Karanth & Sunquist, 1995; Chellam & Johnsingh, 1993), *Canis lupus* (Jhala & Giles, 1991), *Cuon alpinus* (Johnsingh, 1982; Karanth & Sunquist, 2000) and *Melursus ursinus* (Laurie & Seidensticker, 1977; Yoganand T.R.K, 2006), show that these species require large, relatively undisturbed habitats and/or a substantial wild prey base to survive. Most of these studies also highlight the vulnerability of such carnivores to the escalating human modifications of landscapes and consequently impacts on their natural habitats.

However, another large predatory carnivore of the subcontinent, the striped hyena has received comparatively little research attention, although other species of hyenas in Africa have been better studied (Kruuk, 1972; Frank, 1986; Holekamp *et al.*, 1997(a); Holekamp *et al.*, 1997(b); East & Hofer, 2001). The ecology of the more elusive, nocturnal *Hyaena hyaena* remains poorly understood and its ability to survive in rapidly changing habitats has remained un-assessed. However, it is likely that because of its large body size and a predominant diet of meat (Prater, 1971; Mendelssohn & Tom-Yov, 1999), hyenas are also under severe threat. *Prima facie*, the semi-arid landscapes of Northwestern India as mentioned above appear to be the stronghold of the striped hyena because populations are reported from several locations, albeit *anecdotally* (Prater, 1971).
The importance and need for studying striped hyenas

The striped hyena is the most important large scavenger found in tropical forest and grassland ecosystems. Its role in clearing off carrion in tropical ecosystems and in recycling mineral compounds from dead organic matter enhances its biological importance (Jhala, in press). The species is known to inhabit a diversity of landscapes ranging from semi-arid, rocky country interspersed with scrub type vegetation to agro-pastoral landscapes dominated by high livestock and human presence. It is often found within close proximity of urban centers and can survive on human organic waste generated at these sites (Mendelssohn & Yom Tov, 1999). In India, hyenas occur in arid and semi arid ecosystems, as well as in the extremely wet regions of south-western coast of India (Karanth, 1986).

This ability of striped hyenas to survive in human-dominated landscapes is often assumed to indicate that the species is abundant and its conservation status secure. This assumption requires to be tested through field studies urgently. It is fundamentally important for scientific and conservation studies of striped hyenas to assess their population size and densities, if we are to understand how the species is faring in the face of rapid human-induced changes in its environment.

However, the evasive, nocturnal behavior exhibited by the *H. hyaena* makes it difficult to apply traditional population estimation methods to determine its abundance or obtain other relevant demographic data. Prior studies on the home range size and densities of the striped hyena in Africa have usually involved small numbers of study animals (Kruuk, 1976) and insufficient sampling effort to assess population parameters rigorously.
Despite the striped hyena being a generalist species capable of surviving in sympatry with dense human and livestock populations, factors that drive variations in hyena abundance across different landscape types still need to be assessed. In view of the fact that substantial populations of hyenas survive successfully in some human-dominated-landscapes in north-western India, studies in this region can shed light on factors that enable such survival in the context of extinction of hyenas in several other parts of their range in Asia and Africa (Mills & Hofer, 1998; Kasparek et al., 2004).

The importance of abundance and density in shaping the ecology and conservation of larger mammals

Population size or abundance, which is usually reported as density (number of animals/unit area) is a key ecological parameter of interest to scientists interested in understanding species biology as well as its conservation status. From a systems ecology perspective, density (or abundance) is referred to as a ‘state variable’ (Williams et al., 2002). Similarly, another state variable of interest is often habitat occupancy or simply occupancy which is the proportion of the total potential habitat within which a species is actually present (Williams et al., 2002; Mackenzie et al., 2006). Such key state variables are important parameters that determine the basic demography of animal populations and are often measured directly. However, in case of large carnivores such as hyenas, their diet and feeding ecology are likely to be the basic drivers of their abundance and habitat occupancy, thus requiring careful study to understand how hyena populations function across time and space. The inter-relationship between carnivore diet and abundance has been studied through coarse-scale literature surveys (McDonald, 1987; Carbone & Gittleman, 2002; Bagchi et al., 2003) as well as detailed macro-ecological field studies (Karanth et al., 2004). Other than dietary specialization, carnivores such has hyenas are
also likely to have certain habitat requirements. The present study attempts to relate hyena ecology to habitat and prey biomass characteristics at two landscapes that are under differing management and land use regimes, in order to answer some of the above questions.

**Objectives of the study**

In this study, I tried to test the following hypotheses with respect to hyena ecology through comparisons across two different study locations in Rajasthan state of India.

**Hypothesis 1: Hyena densities are dependent upon livestock densities.**

Because a large majority of human inhabitants of the arid areas of Rajasthan are averse to killing or consuming livestock (Rangarajan, 2001), the region supports large numbers of domestic livestock. Most of this livestock belongs to indigenous breeds and is starved for adequate foraging resources. These factors along with inadequate veterinary facilities result in high numbers of livestock mortalities, which in turn provide high rates of scavenging opportunities thus supporting high densities of striped hyenas. Therefore, I hypothesize hyena density in an area to be strongly dependent on livestock abundance in general.

**Hypothesis 2: Because hilly terrain provides resting and breeding refugia, hyena densities will be dependent on the proportion of such habitat in a region.**

Hyenas are vulnerable to disturbance and harassment by humans as well as domestic dogs during the day when they are resting. They also require secure dens to successfully raise young. The presence of steep hilly terrain, which does not attract humans and domesticated animals are thus critical resources for their survival and reproduction.
Therefore, I hypothesize that hyena abundance is likely to be higher where proportion of hilly terrain (and thus availability of resting and breeding refugia) is higher in the overall landscape.

**Hypothesis 3: Legally protected wildlife reserves will support higher hyena densities than unprotected areas.**

Although hyenas are capable of surviving in human-dominated-landscapes, factors such as lower levels of human disturbance, denser vegetation cover for escaping from harassment and the presence of other large predatory carnivores that provide additional scavenging opportunities, are likely to further facilitate hyena survival and reproduction. Therefore, I hypothesize that legally protected wildlife reserves will support higher hyena abundance compared to land-uses that are devoid of such wildlife reserve status.

By choosing two study sites where all three factors identified above are clearly distinct and measurable the above hypotheses can be tested. The present study attempts to do so by comparing two highly ecologically contrasting study sites.

**Study area**

This study was conducted between December and May 2008 in the state of Rajasthan in north-western India (Figure 2). This study was conducted at two locations with differing land-uses, proportion of hilly terrain and management regimes/status. The first study area comprised of 165 km² designated as a part of the Kumbhalgarh Wildlife Sanctuary in central-south Rajasthan and the second site comprised of 110 km² of non-protected area around the Esrana Forest Range and its surroundings in Jalore district of south-western
Rajasthan. These two sites will henceforth be briefly referred to as Kumbhalgarh and Esrana in this report.

The selection of these two study areas for comparing hyena ecology was based on the following three features that characterized them:

a. The differing proportion of steep hilly terrain between the two areas
b. Differing management regimes and protected status of the two areas
c. The practical feasibility of conducting camera trap studies to estimate hyena abundance rigorously

**Figure 2.** Rajasthan state map showing the two study locations
Kumbhalgarh

The selected study area of 165 km$^2$ was located within the Kumbhalgarh Wildlife Sanctuary which covers a total area of 610 km$^2$ extending from 73º 15' E on the west, to 73º 45' E on the east. It is bounded by 25º 00' N and 25º 30' N latitudes in the north and south. The average annual rainfall received by the region is 73 cm mainly from the Southwest monsoon. Annual temperatures can vary from 2º C in January to 46º C in June. The diverse topography of the area and the Precambrian remnant in the form of the Aravalli hill range harbor a dry deciduous forest dominated by *Anogeissus pendula*, *Anoigeissus latifolia*, *Boswellia serratta*, *Butea monosperma* and *Acacia senegal*. The area hosts two felid species namely *Panthera pardus* and *Felis chaus*; two canid species comprising of *Canis aureus* and *Canis lupus*; one primate species viz. *Semnopithecus entellus*; four ungulate species namely, *Boselaphus tragocamelus*, *Gazella bennetti*, *Tetracerus quadricornis* and *Cervus unicolor* (Chhangani, 2004). *Melursus ursinus* is also found in the region (Chhangani, 2004).

Legally Kumbhalgarh is a wildlife sanctuary, where theoretically the habitat is protected from human pressures except for regulated and managed grazing. It is administered by the Rajasthan Forest Department as a wildlife reserve for conservation and wildlife tourism purposes. The wildlife sanctuary is surrounded by several human settlements, highly dependent upon the forest for grazing livestock and to collect forest products like fodder, firewood, honey and *Diospyros melonoxylon* and *Madhuca longifolia* fruits. Quite often such multiple use of the reserve exceeds legal limits or restrictions.
Esrana

The second study area of 110 km² in Jalore district is dominated by hills composed of granite, rhyolite, sandstone and sand dunes. This area lies between 73° 15' E and 73° 45' E. It is bounded on the north by 25° 00' N and 25° 30' N. The annual average rainfall is 30 cm (IMD, 2007) less than that received by Kumbhalgarh. The January isotherm could be as low as 1° C while summer temperatures can be as high as 46° C with the region facing acute water crisis. The granite hills harbor large cavities, which act as den sites for the two main large carnivores in the area, *Panthera pardus* and *Hyaena hyaena*. The other carnivores in the area include *Canis lupus*, *Felis chaus*, *Felis silvestris ornata* and *Vulpes vulpes pusilla*. *Gazella bennetti* and *Boselaphus tragocamelus* are the only wild ungulate species while the region has several small mammals and one primate species, *Semnopithecus entellus* (*unpublished data*). *Sus scrofa* is common and often known to cause crop damage (*pers. comm.*).

The desert like topography of the region with very low vegetation cover comprising chiefly of xerophytes and shrubs like *Cassia aungustifolia* (Bhandari, 1978), makes it imperative for the wild fauna to share space with the local inhabitants.

In terms of legal status, the Esrana Forest range is managed by the Forest department and its land use is officially for multiple uses. The surrounding hyena habitat comprises of privately owned farmland and some public lands administered by the revenue department (*pers. comm.*).
Study species

Taxonomy, distribution and general biology of striped hyenas

The striped hyena belongs to the Order *Carnivora* and sub-order *Feliformia*. It has a wide distribution that spans across northern and eastern Africa, central Asia and south central Asia and the Indian subcontinent except the north eastern part. This wide distribution and local adaptations have resulted in several variations in hyena morphology. Such morphological variations resulted in the striped hyena having been classified into 28 subspecies until 1934. However, Pocock (1934) definitively reclassified them into five subspecies based on pelage characteristics and cranial structure (Wagner, 2006). These include *H. h. barbara*, *H. h. dubbah*, *H. h. syriaca*, *H. h. sultana* and *H. h. hyaena*, the last sub-species being found in the Indian subcontinent and the subject of this study.

The nocturnal nature of the striped hyena could, possibly be an adaptation to conserve water and reduce competition for food with sympatric diurnal scavenging species (Gittleman, 1986).

The anthropocentric perception of the “ungainly” appearance and non-charismatic nature of the striped hyena often results in the species being associated with superstition and witchcraft in culture, unfortunately even rendering it unworthy of scientific attention!

Previous scientific studies on striped hyenas: A brief literature review

The only published scientific literature available on the ecological attributes of the striped hyena is an outcome of studies conducted on the *H. h. dubbah* in Africa (Kruuk, 1976; Leakey *et al.*, 1999; Wagner, 2006) and *H. h. syriaca* in Israel (Mendelssohn & Yom-Tov, 1988). Mills and Hofer (1998) attempted to map the distribution of the species
across Africa and Asia using data from literature available and responses to the ‘Hyena Status Survey’ and conservation action plan questionnaires. While these data are important to map the current distribution of the hyena, they may not be sufficient for conservation planning and management at the site or landscape level. Two short studies were conducted recently to determine the presence of *H. h. syriaca* in Jordan (Qarqaz, *et al.*, 2004) and Turkey (Kasparek *et al.*, 2004). Other than these studies, no study focusing on the distribution or population dynamics of the hyena has been conducted in Asia.

While research on the ecology of the hyena has been in progress in India (Jhala, *in press*), published scientific literature is greatly lacking. The only literature available on the species from the Indian sub-continent is in the form of popular articles or short notes in journals (e.g. Davidar, 1985; Karanth, 1986; Davidar, 1990; Jhala, 2002; Sankar & Jethwa, 2002).

With the exception of the above mentioned studies, most literature available on the striped hyena deals with studies on individuals in captivity (Reiger & Weihe, 1975; Spoor & Badoux, 1986; Spoor & Badoux, 1988; Abi-Said, 2004). This paucity of scientific studies on ecology of the *H. hyaena* has been recognized as a major conservation impediment globally (IUCN/SSC, 1998; Ray *et al.*, 2005) and the species has been recognized as being most in need of conservation attention by the IUCN hyaenidae species specialist group (Mills & Hofer, 1998). The present study reported here attempts to address some of these gaps in our knowledge of hyena ecology.
Conservation context of the present study

Thus far meager attention has been directed towards rigorously estimating abundance for the striped hyena. In Indian wildlife reserves, the traditional managerial approach of hyena abundance estimation has relied on methods like ‘total counts’ at water holes or through ‘pug mark censuses’ (individual track recognition based total counts: pers. comm.). The pug mark census method involves obtaining pug mark tracings, creating plaster casts and measuring gait for comparisons. These censuses attempts to count all individuals in the area, irrespective of the variations associated with gait of an animal, the substrate from which the tracks have been collected and variations in the observer skills. Similarly, the water hole count method does not have much statistical or biological logic associated with it.

Both these methods make 3 important assumptions:

1. The probability of detecting and counting all hyenas present is perfect (p=1) in all surveyed areas.
2. That entire area of interest is covered effectively by the survey.
3. There are no multiple counts of the same individual animal.

Because these basic assumptions of traditional wildlife censuses are regarded as unrealistic and unattainable in the modern wildlife science literature (Williams et al., 2002) such methods have been virtually abandoned by the scientific community in favor of rigorous modern methods based on the concept of sampling (rather than censusing) animal populations. The present study incorporates these more current approaches to counting of hyenas to estimate their abundance.
Photographic capture-recapture using camera traps has been proven to be amongst the most successful non-invasive method to estimate abundance of nocturnal, elusive species that can be individually identified from natural markings on their bodies (Karanth et al., 2004), such as the tiger (Karanth & Nichols, 1998), ocelot (Trolle & Kery, 2002) and jaguars (Silver et al., 2004). An important prerequisite for successfully using capture recapture models to estimate abundance is the need for the study species to be individually identifiable based on photographs obtained from automated camera traps (Karanth & Nichols, 1998; Wallace et al., 2003; Karanth et al., 2004).

In this study, closed model capture-recapture method (Otis et al., 1978; Williams et al., 2002) was used for estimation of hyena abundance. This method assumes that the study population does not have any recruitment or losses during the survey, a requirement taken care of by short duration of the field study. The method involves capturing of a proportion of the population being estimated, and assigning unique identity numbers to each captured animal. In case of previously marked individuals, identity codes are recorded and the individuals released back. Over a period of several sampling occasions or periods a ‘capture history’ is created for each individual that is captured, indicated by 1s (sampling occasion when an individual was captured) and 0s (when the individual was not captured). A typical capture history of an animal in a five sample study would look like: 10010, indicating that it was caught only in the first and fourth sampling periods. Based on probabilistic models, the capture probability parameter \( p \) giving rise to the observed capture history matrix is estimated (Otis et al., 1978; William et al., 2002; Karanth & Nichols, 2002). Based on these capture probabilities the total abundance \( N \) of all animals (including uncaught ones) in the sampled population is estimated.
The striped hyena has unique stripe patterns which can potentially be used for individual identification. Thus I wanted to test the application of photographic capture recapture sampling to estimate hyena densities and abundance in the present study. Apart from some work in preparation (K. U. Karanth *unpublished data* from India); this is the first ever such study of striped hyenas.

**METHODS**

**Hyena density estimation: Field methods**

**Reconnaissance survey of hyena spoor**

A preliminary regional reconnaissance survey based on questionnaires and interviews was conducted to first identify locations with sizeable populations of hyenas. This survey was followed by an intensive field reconnaissance survey in three areas of southern and western Rajasthan, each covering an area of about 200 km$^2$. The objectives of the intensive survey were to:

a) Assess the feasibility of conducting camera trapping to estimate abundance of hyenas in these areas

b) Record locations of trails and paths which were being frequented by hyenas to ensure optimal placement of camera traps

c) Collect an adequate sample of hyena scats to assess hyena diet in the three study areas.

Based on this intensive survey, I selected Kumbhalgarh and Esrana study areas (described earlier) for further detailed camera trap studies.
Although striped hyena may not exhibit absolute territoriality, group members have been found to operate within exclusive zones (Wagner, 2006). Additionally, the limited number of demographic studies conducted on the species, appear to suggest low densities for the species: less than 2 animals/100 km² in the Serengeti National Park (Kruuk, 1976); a minimum regional density of 3 hyenas/100 km² in the Laikipia district of Kenya (Wagner, 2006); and 10 to 5 hyena/100 km² in Kutch (Jhala, in press).

In order to successfully estimate hyena densities using camera traps, it is essential to maximize the probability of capturing most of the individuals within the study area. The reconnaissance surveys helped determine the most frequently used trails and consequently the most appropriate camera trap sites as prescribed by Karanth and Nichols (2002). Hyena track locations were recorded using a Garmin 12X Global Positioning System (GPS) unit. Any intact hyena scat detected was collected in zip lock bags with a record of location, time, day and description of the habitat characteristics of the collection site. Thereafter, Survey of India (R.F.1:50,000) topographic maps were used to map all hyena track locations and scat locations encountered to determine appropriate camera trap locations.

**Camera-trap survey design considerations**

Approximately 100 potential camera trap locations were identified during the intensive reconnaissance survey. Among these locations the most optimal 48 and 52 locations were selected at Esrana and Kumbhalgarh study sites respectively, following recommendations of Karanth & Nichols (2002) on survey designs (Figures 3 & 4).
Total of 18 paired passive infra-red MC2-GV STEALTHCAM® were available for the study. Each camera trap consisted of 2 cameras positioned to photograph both flanks of the hyenas to assist in unambiguous individual identification (Karanth & Nichols, 1998; 2002), these camera units have an option of selecting either date or time imprints on the photographs obtained. The option of obtaining prints with date imprinted on it was chosen to obtain records of date and capture location for each hyena photograph obtained in the survey.

Since there were not enough camera traps to cover the entire study area in each sampling period the study areas were divided into three trapping blocks that were successively trapped using survey design 4 recommended in Karanth and Nichols (2002). The cameras were stationed at each trap site for 12 successive nights before being moved to the next block, thus enabling the allocation of all photo captures to one of the 12 sampling periods constructed as per the survey design above (Karanth & Nichols 2002).

**Baiting of Traps**

In order to maximize capture probabilities for each individual, putrid raw meat bait was used. The aim of the bait was to:

a) Position the hyenas and detain them between the cameras for sufficient duration to obtain clear and useful photographs

b) Try to attract passing hyenas to camera points
Figure 3 Camera trap locations and settlements at Kumbhalgarh study site

Figure 4 Camera trap locations and settlement at Ekrana study site
**Trap spacing**

The home range sizes for a male and female striped hyena in the Serengeti, Tanzania were reported to be 44 km$^2$ and 72 km$^2$, respectively (Kruuk, 1976). At Laikipia, Kenya, 4 males and 6 females covered an average area of 68.9 km$^2$ (Wagner, 2006). However, the latter study found groups of up to three males and a female exhibiting a complete overlap in home ranges. For want of radio telemetry data from India on the striped hyena, the data from the above African studies guided me to set the trap spacing in my two study areas. Assuming that the arid region of India, with a high livestock mortality rate could support smaller home ranges than Kenya, camera traps were conservatively set 2.2 km apart in order to cover the study area without leaving any holes in the trap array where an individual could have zero capture probability.

**Distinguishing individual hyenas based on stripe patterns.**

The following three distinct anatomical features were used to identify individual hyenas from camera trap photographs (Appendix 4).

*Stripe pattern on hind limbs*: The most prominent stripe patterns observed for hyenas were on the upper hind limbs. Also, the maximum variability between individuals was observed to be within this region.

*Stripe pattern on forelimbs*: The second stage of identifying an individual was to compare stripe patterns on the forelimbs.

*Notches in ears*: The last stage was to look for prominent notches in the ears.
Construction of capture histories of individual hyenas

For analysis of capture-recapture data, a capture history matrix (Tables 1 & 2) needs to be created for each individual. To do so, based on the date of capture each photographic capture of an individual hyena is allocated into one of the 12 sampling occasions constructed as earlier mentioned. Using this scheme, capture histories were created for all individuals photographed. These followed the standard X matrix format (Otis et al., 1978) wherein a 1 indicates the capture of a particular individual in a particular sampling occasion and a 0 indicates absence of capture during that particular occasion. Such capture histories were created separately for each flank since most photographs were obtained from only one unit of the paired camera traps because of frequent camera failures. Capture histories were created separately for the two study sites (Tables 1 & 2).

Analytic methods

Closed capture-recapture models for estimation of abundance

The study was designed to estimate abundance of the hyena in a closed capture-recapture modeling framework. Thus, measures were taken to ensure demographic and geographic closure.

Demographic closure: The study was conducted within a sampling period of 36 days in each study area. This short duration relative to demographic changes with reference to hyenas was aimed at observing closure.

Geographic closure: During analysis a buffer width estimated at half the home range length was added to the polygon formed by traps in an attempt to ensure geographic closure (Wilson & Anderson, 1985; Karanth & Nichols, 1998).
Analytic software

Capture-recapture analytic models implemented in standard software CAPTURE 2.1 (Rexstad & Burnham, 1993) and MARK 4.3 (Cooch & White, 2007) were used to analyze the hyena capture history data. These are free software available from www.mbr-pwrc.usgs.gov/software.html. A combination of these two software was required to take advantage of some models and analytic features unique to each software code. The CAPTURE 2.1 software has M (h) jackknife estimator, which is not available in MARK 4.3. Similarly, while CAPTURE 2.1 uses a discriminant function analysis test for model selection, MARK 4.3 additionally provides information theoretic methods of model selection. Furthermore MARK 4.3 also offers closed models based on methods of finite mixtures (Pledger, 2000) which are not implemented in CAPTURE 2.1.

Diet analysis: Field methods

Collection and analysis of hyena scats

Hyena scats were opportunistically collected throughout the study period from all areas surveyed. Scat samples were put in zip lock bags with details of collection time, GPS location and characteristics of the substrate from which the scat was collected. Precaution was taken to ensure that there was no cross sample contamination, in order to enable the possibility of using the samples for DNA analysis subsequently. During the study period, a total of 106 putative hyena scats were collected from Kumbhalgarh and 90 scats from Esrana.

Identification of scat in field

Hyena scat was identified in field primarily using visual characteristics like shape, color, size and location of scat. Most scat identified as hyena scat was composed of round, oval,
ball like masses, white or off-white in color because of ingested bones, and were located around dens, on regular trails used by hyenas or in dry stream-beds. Other hyena signs, like tracks were also used to confirm species identity.

**Analytical methods**

**Identification of fecal remains**

In order to identify components of the scat, the following methodology was used:

*Processing scats:* A small portion of each scat was kept aside for DNA analysis and the remaining part was weighed. Thereafter, each individual scat was soaked in water separately for a period of 4-6 hours in order to soften the scat and enable the process of washing it. Scats were separately washed under running water over a sieve.

Once all fecal material was washed off, the components contained in the scat were sun-dried following which they were stored in zip lock bags. Precaution was taken to ensure that no moist scat was stored.

*Weighing components of the scat:* Components from each washed scat were assigned to the five categories: hair, bone, vegetative material, insects and others. These segregated components were reweighed and measurements recorded. The process of identification of prey species using hair obtained from scat by comparing with a reference collection of potential prey animal hair samples is currently in progress.
RESULTS

Estimation of hyena abundance and density

The trapping was conducted for 36 days during February-March and April-May 2008 in Esrana and Kumbhalgarh study areas respectively. The survey duration for both these areas was divided into 3 blocks of effort, and each block was portioned into 12 sampling occasions. The total sampling effort was 548 trap nights for Esrana and 538 trap nights for Kumbhalgarh. During this period, 33 photographs (15 right flanks of individuals, 12 left flanks of individuals) were obtained from Kumbhalgarh while 16 photographs (8 right flank individuals, 7 left flank individuals) were obtained from Esrana study area.

The unique stripe pattern of hyenas was used to identify individuals and build separate capture histories created for both the study sites (Table 1 & Table 2). Due to slow reaction time of the cameras used, in many cases only single flank captures were made. Unclear photographs or those which could not be compared to other individual flanks were not considered in the analysis.

Kumbhalgarh study area

a) Test for population closure

The statistical test in CAPTURE 2.1 was used to test for closure. The test (z-value = -1.289, \( P = 0.10 \)) supported the assumption that the population was closed during the survey duration. The null hypothesis of population closure could not be rejected.
Model selection (Goodness of fit tests)

Analysis of Data using software CAPTURE 2.1

The goodness of fit test for M (h) versus any alternate model showed ($\chi^2 = 4.813$; d.f = 11; $P = 0.939$) while M (b) versus any alternate model showed ($\chi^2 = 15.717$, d.f = 18; $P = 0.6122$), thus supporting models M (h) and M (b) in the two cases. While M (o) versus M (t) showed ($\chi^2 = 2.687$, d.f = 11; $P = 0.994$), M (o) versus M (b) ($\chi^2 = 0.911$, d.f = 1, $P = 0.339$), supporting M (o) in both cases. In the event of a small sample size M (o) versus M (h) could not be tested.

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Table 1. Capture history matrix of hyenas (right flanks) in Kumbhalgarh study area.

The model selection test comparing the null hypothesis of model M (b) versus not model M (b) was also of interest, because of the potential problem of behavioral response to trapping by hyenas. In my study area, in several cases I observed tracks of hyenas passing around the cameras without going between the paired traps, and suspect that hyenas, after experiencing the flash of the cameras once, avoided camera traps subsequently (trap response behavior). Thus, I felt model M (b) might be relevant. The model selection test
showed that the null hypothesis of the true model being M (b) could not be rejected ($\chi^2 = 15.71, \text{d.f.} = 18, P = 0.61$), showing some support for the idea of there being trap response behavior.

The overall model selection test based on discriminant functions comparatively scored the various models as follows: M (o) = 1.00, M (h) = 0.83, M (b) = 0.45, M (bh) = 0.74, M (t) = 0, M (th) = 0.48, M (tb) = 0.35 and M (tbh) = 0.77.

Although M (o) model weighed the highest in the model selection criteria, this model is not robust to any deviations from the model assumption of homogeneous capture probabilities among individuals. Considering hyenas are cryptic mammals with a well defined territorial spatial organization (Wagner, 2006), it might not be reasonable to assume such homogeneity among all individuals. Based on ecological considerations and model selection test scores, I judged model M (h) jackknife and model M (b) as the two strongest candidate models for estimating hyena abundance from this study.

c) Estimate of capture probabilities and population size

I used the M (h) jackknife estimator (Burnham & Overton, 1978; Otis et al., 1978) to estimate capture probabilities and population size for hyenas in the area. Altogether, 15 individuals were captured over the 12 sampling occasions, with three individuals having two recaptures each. Using M (h) jackknife estimator, the estimated average per sample probability of capture ($\hat{p}$) = 0.0469, leading to an estimated abundance (population size) ($\hat{N}$) of 32 with a standard error ($S\hat{E}(\hat{N})$) of 8.78. Alternatively, under the M (b) model, the estimated per sample capture ($\hat{p}$) = 0.10 with an estimated recapture probability ($\hat{c}$)
= 0.03, leading to an estimated abundance (\(\hat{N}\)) of 20 with a standard error (\(SE(\hat{N})\)) of 7.85.

d) Estimation of effective sampled area and density estimation

In an attempt to create the trap polygon, the average mean maximum distance moved (MMDM) by hyenas in the area was taken to join the outermost camera trap locations. Thus, only traps located within a distance of 3.9 kilometers or less were directly joined to form a polygon measuring 165 km\(^2\). A buffer strip width (\(\hat{W}\)) of 1.95 km with \(\text{var}(\hat{W})\) of 0.15 was estimated and an effective sampled area of (\(\hat{A}\)) = 307 km\(^2\) was estimated using the approach described in Karanth and Nichols (2002).

The effective sampled area (\(\hat{A}\)) divided by the estimated population size (\(\hat{N}\)) was used to obtain a hyena density estimate (\(\hat{D}\)). The estimated hyena density \(\hat{D}(SE(\hat{D}))\) for Kumbhalgarh was found to be 10.4 ± 2.9 hyenas/100 km\(^2\) based on hyena abundance derived under M (h) jackknife model. Using the alternate model M (b), the estimated hyena density \(\hat{D}(SE(\hat{D}))\) was found to be 6.5 ± 2.6 hyenas/100 km\(^2\).
Esrana study area

a) Test for population closure: The statistical test for closure in CAPTURE 2.1 was performed to test for closure in this study area ($z = 6.00, P = 1.00$). The results indicate that the test did not perform in the absence of recaptures.

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Table 2. Capture history matrix of hyenas (right flank) in Esrana study area

c) Model selection: Because of lack of recaptures at this site only single flank photographs could be compared to build capture histories. Because of sparse data, model selection tests based on the discriminant functional analysis scores generated by CAPTURE 2.1 could not be used. Instead the model was selected based on ecological and statistical considerations as the M (h) jackknife estimator (on account of model robustness) as well as the M (b) removal model that is commonly used in kill trapping studies where there are no recaptures. This model can represent trap response behavior also. As in Kumbhalgarh, I considered both M (h) and M (b) models as potential candidates for generating estimates of capture probabilities and population size for hyenas in Esrana.
c) Estimate of capture probabilities and population size

The total count statistic ($M_{t+1}$) for this survey was 8 individuals, using only right flank for identifying individuals, with no recaptures. Using $M (h)$ jackknife estimator, the estimated capture probability was $\hat{p} = 0.03$ resulting in an estimate of abundance ($\hat{N}$) = 22 with $(S\hat{E})\hat{N}$ of 11.94. Based on the $M (b)$ removal model the estimate of capture probability was $\hat{p} = 0.27$, resulting in an estimate of abundance $\hat{N}$ of 8 with $(S\hat{E})\hat{N}$ of 0.55.

d) Estimation of effective sampled area and density estimation

Because of lack of recaptures the buffer width could not be computed using the standard MMDM based approach used for Kumbhalgarh data. Thus, I borrowed the buffer width information computed for Kumbhalgarh for use in Esrana data. Using this approach the effective sampled area $\hat{A}(W)$ for Esrana was found to be 218 km². Thus, the resultant hyena density estimate for the area $\hat{D}(S\hat{E}(\hat{D})) = 10.09 \pm 5.5 /100$ km² using model $M (h)$. Furthermore, hyena density computed from estimated population size derived from the trap-response model $M (b)$, of $\hat{N} = 8$ with $(S\hat{E})\hat{N}$ of 0.55, for Esrana yields a density of $\hat{D}(S\hat{E}(\hat{D})) = 3.67 \pm 0.3$ hyenas/100 km².

Digital elevation model (DEM)

Proportion of hilly terrain and potential hyena refugia in the two study areas

In order to assess the relative topographical differences between the two study areas, a slope based landform classification map was generated (Figures 6 & 7) using the extension ‘Topographical Position Index’ for ArcView (Jenness, 2006). The SRTM 3 hole filled Digital Elevation Model (DEM) (Jarvis et al., 2006) was downloaded and used
for analysis. Further, Topographic Position Index (TPI) was calculated from elevation grids. TPI compares elevation of each cell in a DEM to a mean elevation of a circular neighborhood (in this case with a radius of 10 cells).

The slope based landform classification makes use of standard deviation and slope values (in degrees) that were derived using a circular neighborhood of 10 grid cells. The breakpoints for the landform categorization were as per Weiss 2001 (Appendix 1). The graph produced below derived from calculating the number of pixels in each topographic category indicates the percentage area occupied in each of the study sites with respect to topography (Figure 5).

![Graph showing percentage area under differing slope classes for two study sites.](image)

**Figure 5.** Total percentage area under differing slope classes for the two study sites.

‘Suitable hyena topography’ indicates steep terrain that can serve as refugium for resting and reproduction.
Figure 6 Topographical Index map for Kumbhalgarh
Figure 7. Topographical index map for Esrana
Livestock densities in the effective study area

The data collected for this analysis is generated from livestock census data collected by governmental agencies for each village in the year 2007-08. Data for (*) marked settlements (as shown in Appendix 2 & 3) was collected from within Kumbhalgarh Wildlife Sanctuary by forest department staff during the study period, since these villages are not classified as revenue villages.

Kumbhalgarh

The Total livestock (N) = 22,304 with an approximate estimate of 73 animals/km$^2$ (Appendix 2) for the effective study area of 307 km$^2$.

Esrana

The total livestock (N) = 67,842 with an approximate estimate of 311 animals/km$^2$ (Appendix 3) for the effective study area of 218 km$^2$.

Preliminary analysis of hyena diet

A total of 102 scats from Kumbhalgarh and 86 scats from Esrana were analyzed and different components from the scat separated and weighed.

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<td>Insects</td>
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<td>Others</td>
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Table 3. Percentage of different contents in hyena scats for the study areas.
Table 3 shows percentage of different types of dietary components consumed by hyenas based on scats collected from the two study sites. These show the preponderance of domesticated mammals in hyena diets.

**DISCUSSION**

In this study, I tried to determine important ecological and environmental determinants of the densities of striped hyenas in an arid landscape of India, where contrary to intuition, this large carnivore species survives in human-dominated-landscapes in reasonable numbers. I had proposed three hypotheses to examine this issue by comparing hyena densities at two study sites with strikingly contrasting ecological and environmental features that formed the basis for my predictions. However, before I examine these hypotheses in the light my results, I will discuss and elucidate some methodological issues that strongly influenced my study results.

**Methodological issues influencing estimates of hyena abundance and densities**

Typically, closed model capture-recapture surveys of large mammals require that a large sample of individuals (N>20) be captured (Otis et al., 1978), whereas this study resulted in small sample sizes (M_{t+1}) of only 15 individuals in Kumbhalgarh and 8 individuals in Esrana. This drawback, which is a consequence of lack of adequate number of good quality cameras and resources to conduct a more intensive trapping study, resulted in relatively weak estimates of abundance from capture-recapture models.

The passive detection type camera traps I used and the small number of traps (16 pairs in Esrana and 17 pairs in Kumbhalgarh) I had, resulted in relatively low sampling intensity of 538 trap nights in Kumbhalgarh and 548 in Esrana as well as loss of several flank
pictures, which potentially could have increased sample sizes I got and reduced variances and biases around estimated abundances.

A few practical considerations should guide future studies to deal with the above problems. While this study was designed to capture both flanks of hyenas, in many cases only single flank picture were obtained. It was also observed that camera flash could influence individual hyenas, causing them to react and run without allowing the passive infra-red sensor to detect individuals in time. This is a technical equipment problem with these types of passive detection camera traps. Thus, additional electronic circuits should be built in to ensure simultaneous firing of both cameras, and active detection camera traps which fire simultaneously should be used in future hyena studies of this nature.

Another important methodological issue arises with respect to the determination of the effective trapping area using the buffer width approach I employed (Karanth & Nichols, 2002; Soisalo & Cavalcante, 2005). The buffer distance used makes major difference to derived estimates of densities and comparisons based on them, as in the case of my study. Unfortunately, I could not derive a site-specific buffer width ($\hat{W}$) for the Esrana study area due to lack of recaptures at this site. I dealt with this issue by borrowing buffer width ($\hat{W}$) estimated from the Kumbhalgarh study and using it to estimate the sampled area for Esrana.

However, given the relatively lower number of hyena photo capture rates at Esrana (2.9 captures/100 trap nights) compared to Kumbhalgarh (6.8 captures/100 trap nights), if indeed there are lower hyena densities at the former site as hypothesized, the home ranges should be larger and so also the expected buffer width. When hyena density estimates
based on population size estimates computed by the M (h) jackknife estimator, but using identical buffer widths of 1.95 km for both sites are used, there seems to be no strong evidence for higher hyena densities at Kumbhalgarh $\hat{D}(S\hat{E}(\hat{D})) = 10.4 \pm 2.9$ hyenas/100 km$^2$ compared to Esrana with a density of $\hat{D}(S\hat{E}(\hat{D})) = 10.09 \pm 5.5$ hyenas/100 km$^2$.

On the other hand, there is some justification for comparing population size and density estimates derived using the alternative removal model M (b), which can meet the assumption of there being trap response behavior among hyenas. There does seem to be some evidence for use of the M (b) model which deals with trap response: in this case hyenas reacting to the rather slow passive detection camera traps and not getting photographed. This is supported by my anecdotal observations of tracks of hyenas avoiding traps in some cases. Thus, M (b) model was selected as the more appropriate model despite it providing conservative abundance estimates.

Because of lack of any recaptures at Esrana, the buffer width estimate used for computing density was borrowed from Kumbhalgarh in the present study. Considering hyenas in Esrana may have larger home ranges (suggestive by the low trapping rate in this area), extrapolation of the buffer width estimated from Kumbhalgarh could possibly have under estimated the effectively sampled area in Esrana and thus resulted in a positive bias with the density estimates.

Therefore the discussion of the hypotheses presented below has to be viewed in the context of these methodological issues.
Test of hypotheses and predictions

My first hypothesis was that hyena densities are likely to be dependent upon livestock densities. Livestock densities from the two study sites differ remarkably with Esrana having more than three times the total livestock density found in Kumbhalgarh (Appendix 2 and Appendix 3). However, contrary to this prediction, hyena densities appear to be similar in Kumbhalgarh with an estimated density $\hat{D}(SE(\hat{D}))$ of $10.4 \pm 2.9$ hyenas/100 km$^2$ compared to Esrana with a density of $\hat{D}(SE(\hat{D}))$ 10.09 ± 5.5 hyenas/100 km$^2$ derived under the M (h) jackknife estimator. But hyena densities appear to be much higher at Kumbhalgarh $\hat{D}(SE(\hat{D}))$ of 6.5 ± 2.6 hyenas/100km$^2$ when compared to Esrana $\hat{D}(SE(\hat{D}))$ of 3.67 ± 0.3 hyenas/100 km$^2$ under the M (b) estimator of population size.

While these differences in the hyena densities may be small between the two areas, the greater proportion of livestock remains in scats analyzed from Esrana compared to those from Kumbhalgarh (Table 3), does suggest that while livestock prey is an important factor in setting hyena abundance in Esrana, it may not be the most critical determinant of relative hyena densities in the two areas.

My second hypothesis considered the proportion under hilly topography in the two areas to have an influence on hyena abundance because of refugia such terrain provided for hyenas to avoid human harassment and to breed successfully. Kumbhalgarh study site showed 85% of its terrain to be steep and suitable for hyenas in terms of breeding and protection from human disturbance, whereas only 35% of such steep terrain existed in Esrana based on DEM models of habitat (Figure 6 & 7). This hypothesis is supported by the results of the present study, which shows relatively higher hyena densities in Kumbhalgarh.
The third hypothesis was that formal protected area status and greater regulations on land uses and human accesses that resulted from such status in Kumbhalgarh would favor higher hyena densities when compared with non-protected status and more intensively, human dominated area such as Esrana. Of the total effectively camera sampled area for Kumbhalgarh, 85% was under protected area status whereas only 12% of the Esrana sampled area was designated as even multiple-use reserved forest with no part of the area being a protected area as a wildlife sanctuary. The remaining 88% of surveyed area was in totally human dominated, privately owned status. These differences in the administrative protected status of the two areas are reflected by the higher hyena densities in Kumbhalgarh compared to Esrana supporting the hypothesis that formal protected status and restrictions on land use are beneficial to hyenas.

While the difference between the hyena densities for the two areas may not be stark, my results do suggest that striped hyenas, despite being able to adapt their ecology to human modified landscapes while living in a socio-cultural milieu that is rather more tolerant of large carnivores than perhaps anywhere else in their global range, still do require natural habitats free of high levels of anthropogenic disturbances to serve as refugia in which their source populations can survive even if the wider landscapes around is densely populated and intensively used by humans.

Secondly, despite some methodological shortcomings of this study, largely due to time and resource constraints I faced, photographic capture recapture method was successfully applied to assess the conservation status of striped hyenas more rigorously than had been possible earlier. Further refinements to the methodology and its application would make this method even more useful for monitoring the status of this interesting large carnivore
that appears to be losing ground rapidly all over its range. I plan to address these issues in my future studies.
REFERENCES


**APPENDIX 1.** Breakpoint categorization for landform classification (obtained from Weiss, 2001)

<table>
<thead>
<tr>
<th>Class</th>
<th>Description</th>
<th>Breakpoint</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Ridge</td>
<td>&gt; +1 STDEV</td>
</tr>
<tr>
<td>2</td>
<td>Upper slope</td>
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</tr>
<tr>
<td>3</td>
<td>Middle slope</td>
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APPENDIX 2. Livestock figures for the effective study area of Kumbhalgarh study site - 2007-08. (Source: Office of the tehsildar of Kailwara tehsil and Desuri tehsil)

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APPENDIX 3. Livestock figures for the effective study area of Esrana study site- 2007-08 (Source: Office of the tehsildar of Jalore tehsil and Ahore tehsil).

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Identification of individual Hyenas

- Ear Notch
- Hindlimb Stripe Pattern
- Forelimb Stripe Pattern
- Date Imprint