

Factors influencing densities of striped hyenas (*Hyaena hyaena*) in arid regions of India

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The striped hyena (*Hyaena hyaena*), despite being a threatened species, frequently occurs in human-dominated landscapes of India's Rajasthan State. We estimated hyena densities using photographic capture–recapture sampling to identify key ecological factors influencing hyena abundances in such areas. Our 2 study sites (307 km² in Kumbhalgarh Wildlife Sanctuary and 218 km² in Esrana Forest Range) had different topographies and levels of human disturbances. We proposed explicit hypotheses regarding effects of livestock densities and topographic features on hyena abundances. We tested these hypotheses by examining the correspondence of estimated hyena densities to food availability in the form of livestock carcasses and potential refugia offered by hilly terrain. Sampling efforts of 548 and 538 camera-trap nights were invested in Kumbhalgarh and Esrana, respectively. Density estimates (hyenas/100 km²) based on capture–recapture sampling were higher ($6.5 \pm 2.6 SE$) for Kumbhalgarh than Esrana ($3.67 \pm 0.3 SE$). Our results supported the prediction that denning refugia in hilly terrain sustain higher hyena densities, but the prediction that higher livestock densities maintain higher hyena densities was not supported. Because the striped hyena is a threatened species for which few data exist, our findings have major potential utility for range-wide conservation of the species. DOI: 10.1644/09-MAMM-A-159.1.

Key words: abundance estimation, capture–recapture, denning refugia, land use, livestock, semiarid zones

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The striped hyena (*Hyaena hyaena*) is a large carnivore that prefers rocky and open landscapes (Hofer 1998; Reiger 1981) within semiarid and arid ecosystems in the tropics (Leakey et al. 1999; Mendelsohn and Yom-Tov 1999; Wagner 2006). In India, arid regions in Rajasthan State are important habitats for hyena persistence (Karanth et al. 2009, 2010). Rajasthan is among the most densely populated arid regions of the world for both humans (Baqri and Kankane 2001) and livestock (Rahmani and Soni 1997), with only 4.3% of land area held in legally protected nature reserves (Kankane 2009). Consequently, conservation efforts urgently require knowledge of hyena ecology in dry zones.

Population size is a key ecological parameter for understanding the biology and conservation status of a species (Williams et al. 2002). However, traditional methods such as

pugmark censuses used by wildlife managers in India to count large carnivores are seriously flawed (Karanth et al. 2003) relative to modern approaches to sampling animal populations (Williams et al. 2002). Robust estimates of striped hyena densities in India have not been published from dry zones, although some studies are currently in progress (Y. V. Jhala, Wildlife Institute of India, pers. comm.). Data on environmental factors influencing hyena densities also are limited.

Because of the complex nature of ecological processes, interactions between several biotic and abiotic factors (Williams et al. 2002) potentially can influence animal



densities. However, measuring all such factors to identify those that significantly influence hyena densities using classical experiment-based hypothesis testing is impractical for field studies of large carnivores. Therefore, we could not use classical hypothesis-testing paradigms that often must satisfy assumptions such as normally distributed point estimates and equal variances in linear regression or analysis of variance approaches. Instead, we chose an evidence-based approach more practical (Burnham and Anderson 2002) for our observational study. We used a probabilistic modeling framework for explicitly comparing a priori ecological predictions to observed data (Bolker 2008; Burnham and Anderson 2002; Hilborn and Mangel 1997; Royle and Dorazio 2008; Williams et al. 2002).

Based on prior knowledge of striped hyena biology (Hofer 1998; Kruuk 1976; Leakey et al. 1999; Mendelsohn and Yom-Tov 1999; Reiger 1981; Wagner 2006) and nature of human impacts, we identified 2 ecological factors that appeared to be important in influencing hyena densities in our 2 study areas that differed in ecology and levels of human impacts. We observed that striped hyenas are predominantly scavengers on domestic ungulate carcasses in the region (see Appendices I and II). Most livestock in Rajasthan consists of cattle, goats, and sheep that exist at very high densities ranging from 42 animals/km² to 226 animals/km² (Rahmani and Soni 1997) reared under conditions of semistarvation by uncontrolled free-grazing on overloaded ranges (Robbins 1998; Sharma and Mehra 2009). In combination with inadequate veterinary care, this leads to high livestock mortality rates. A religiously rooted avoidance of meat in general, and beef specifically, by a large proportion of the population (Chhan-gani 2009; Karanth et al. 2009) increases availability of unexploited carcasses for hyenas. Therefore, we hypothesized that a facultative scavenger like the striped hyena might benefit more in this circumstance than obligate predators that need to hunt prey in such a setting (Bagchi et al. 2003; Carbone and Gittleman 2002; Karanth et al. 2004).

Despite abundant food availability, hyenas with cubs or at rest are vulnerable to harassment by humans and predation by feral dogs in daytime. Therefore, we additionally hypothesized that availability of secure den sites (Prater 1948) also could be critical to hyena survival. Steep and rocky terrain, unsuitable for agriculture or pasturage and hence unattractive to humans or guard dogs, offers such refugia in the study areas. Thus, our specific objectives were to test whether, comparatively, higher livestock densities would support higher hyena densities, and whether a site with higher proportion of hilly terrain would support higher hyena densities.

Although additional habitat-related covariates, such as targeted hunting by humans or presence of other large predators, could influence hyena densities in other ecological contexts, we did not consider these as critical because wildlife legislation in India strictly prohibits hunting of hyenas throughout the country, and social tolerance of hyenas is typical of the region (Karanth et al. 2009, 2010). Although leopards were present at both sites, the specialized scavenging

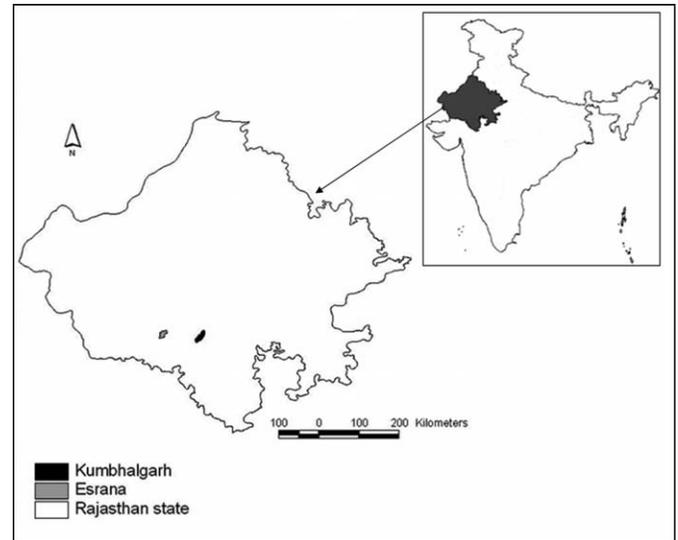


FIG. 1.—Rajasthan state map showing the 2 study locations, Kumbhalgarh and Esrana, with a map of India in the inset.

niche occupied by hyenas did not appear to overlap substantially with the leopard niche as obligate hunters of wild and domestic prey animals. Furthermore, both study areas had lower numbers of leopards camera-trapped compared to hyenas, suggesting that leopard numbers could be much lower (P. Singh, pers. obs.). Because striped hyenas could be individually identified from differences in stripe patterns and other natural marks, we used a photographic capture–recapture sampling method (Karanth and Nichols 1998, 2002b) to estimate their densities to test our predictions.

MATERIALS AND METHODS

Study areas.—This study was conducted between December 2007 and May 2008 at Kumbhalgarh and Esrana sites in the state of Rajasthan in northwestern India (Fig. 1). The selection of these 2 sites was based predominantly on the differences in proportion of hilly terrain, land-use regimes, and logistical feasibility of conducting camera-trap surveys. Unlike Kumbhalgarh, which is a legally designated wildlife reserve, the Esrana Forest Range is managed for multiple land uses. The State Forestry Department managed the entire Kumbhalgarh area but had authority only on a part of Esrana, with remaining hyena habitat being under other public authority or in private holdings.

Kumbhalgarh.—A study area of 307 km² was selected within Kumbhalgarh Wildlife Sanctuary (25°00′–25°30′N, 73°15′–73°45′E), which covers a total area of 610 km², in the Aravalli hill range of northwestern India. The region receives an average annual rainfall of 730 mm, and temperatures can be as low as 2°C in December–January to as high as 46°C in May–June. The altitudinal gradient is from 288 to 1,215 m. Such dry-deciduous forest tree species as *Anogeissus pendula*, *Anogeissus latifolia*, *Boswellia serrata*, *Butea monosperma*, and *Acacia senegal* are common. The area supports several other carnivores, including leopard (*Panthera pardus*), jungle cat (*Felis chaus*), wolf (*Canis lupus*), jackal (*Canis aureus*),

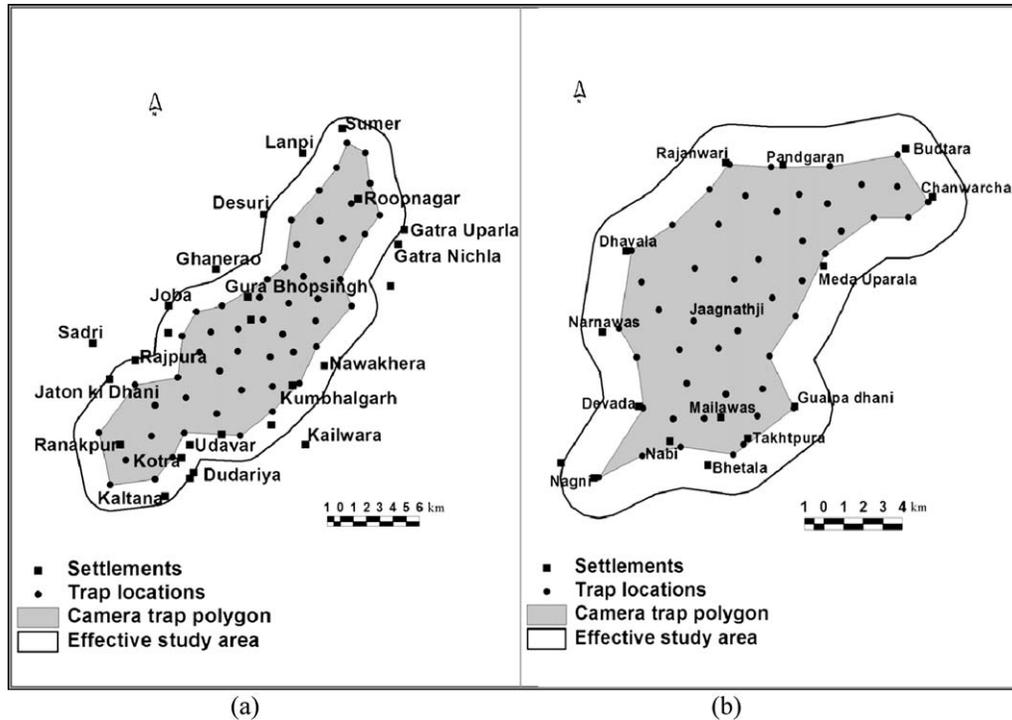


FIG. 2.—Map of a) Kumbhalgarh study area and b) Esrana study area in western Rajasthan, India. Camera-trap locations are indicated by dots within the camera trap polygon area (gray). Human settlements are indicated within the camera-trap polygon area and outer strip (white), which represents the effective sampling area.

and sloth bear (*Melursus ursinus*), and the wild ungulate species nilgai (*Boselaphus tragocamelus*), chinkara (*Gazella bennettii*), four-horned antelope (*Tetracerus quadricornis*), and sambar (*Rusa unicolor*—Robbins et al. 2007). Although Kumbhalgarh is legally protected, to some extent human settlements on its peripheries do illegally impact the habitat by grazing livestock, lopping fodder or firewood, and collecting fruits of *Diospyros melanoxylon* and *Madhuca longifolia*.

Esrana.—The 2nd study area of 218 km² was located in Jalore District of southwestern Rajasthan around the Esrana Forest Range (25°′–25°30′N, 73°15′–73°45′E). The region receives an annual average rainfall of 300 mm and has an altitudinal gradient of 160–835 m. Temperature can be as low as 1°C in January to as high as 46°C in June. The Esrana site supports low vegetation cover composed chiefly of such xeromorphic species as *Euphorbia* sp., *Salvadora* sp., *Senna alexandrina*, *Zizyphus nummularia*, *Calligonum polygonoides*, and *Aristida* sp. (Bhandari 1990). With the exception of *M. ursinus*, all carnivore species found in Kumbhalgarh also are found in this region, together with the desert cat (*Felis silvestris ornata*) and desert fox (*Vulpes vulpes pusilla*). Among wild ungulates only *G. bennettii* and *B. tragocamelus* are present. Wild pig (*Sus scrofa*) also is common.

Field-survey design.—We conducted an initial field survey covering more than 500 km² at each of the sites, based on responses to a preliminary questionnaire survey of expert opinions ($n = 30$) on hyena status across the region. Using observed encounter rate of hyena tracks, scats, and dens, we identified 52 camera-trap locations in Kumbhalgarh and 48 in Esrana (Fig. 2).

Camera traps were spaced ~2.2 km apart in an irregular configuration to effect saturation sampling and maximize the probability of encountering all individuals (Karanth and Nichols 1998, 2002b). This trapping design was based on striped hyena movement and home-range data reported from sites in East Africa (Kruuk 1976; Wagner 2006). To increase photo-capture rates and keep hyenas in position to get clear photos we baited trap sites with putrid meat.

A total of 36 passive infrared camera traps (MC2-GV STEALTHCAM, Good Sportsman Marketing, LLC, Grand Prairie, Texas) were used. Each trap consisted of 2 cameras positioned 6–7 m apart to photograph both flanks of passing hyenas (Karanth and Nichols 1998). The study areas were divided into 3 trapping blocks that were successively trapped under “survey design 4” (Karanth and Nichols 2002b). The traps were stationed at each location for 12 successive nights before being moved to the next block, thus enabling the allocation of each photo-capture event to 1 of the 12 sampling periods (Karanth and Nichols 2002b). The total survey efforts were 548 trap nights in Kumbhalgarh and 538 trap nights in Esrana, respectively. All hyena photographs were assigned to specific trap locations and sampling occasions, based on date and time of capture.

We used pelage markings on hind limbs and forelimbs to identify individual hyenas from camera-trap photos (Fig. 3). Stripe patterns on hind limbs were most variable and useful, followed by patterns on the forelimb. In some cases we made additional use of such other conspicuous features as notches on the ear pinnae.

Capture-recapture analyses.—Because of high camera failure rates most photographs were obtained from only 1 of



FIG. 3.—Camera-trap photographs showing variability in hind-limb and forelimb stripe patterns of hyenas.

the 2 paired cameras, thereby yielding several single-flank photo-captures and leading to loss of some data. Therefore, capture-history matrices for individual hyenas could be constructed only by using photos from a flank that provided higher number of captures.

The survey duration was 36 days at each site, and thus kept short in relation to expected demographic turnover rates to provide reasonable assurance that the assumption of “demographic closure” was met. We used the closure test (Z) to test the null hypothesis of population closure (Karanth and Nichols 2002b; Otis et al. 1978; Williams et al. 2002).

A buffer width estimated at half the home-range diameter was added to the polygon formed by traps (Fig. 2) to estimate the effective area sampled by camera traps, after considering geographic closure (Karanth and Nichols 1998; Wilson and Anderson 1985). The mean maximum distance moved by hyenas photo-captured more than once (Wilson and Anderson 1985) was used as a surrogate for average home-range diameter.

Closed capture–recapture analytic models implemented in standard software CAPTURE 2.1 (Rexstad and Burnham 1991) were used to analyze capture history data. We assessed the goodness-of-fit tests (χ^2) and the overall discriminant function test to compare models $M(o)$, $M(h)$, and $M(b)$ implemented in CAPTURE 2.1 (Otis et al. 1978) and selected the appropriate model to derive abundance estimates for hyenas in the 2 study areas. Model $M(o)$ assumes an equal capture probability for all individuals. Model $M(h)$ assumes a differing capture probability for each individual. Model $M(b)$ allows for variations in capture probabilities due to behavioral responses (Karanth and Nichols 2002b; Otis et al. 1978; Williams et al. 2002).

Identification of hyena refugia from topographic features.—Availability of striped hyena refugia in the form of den sites was observed to be closely associated with hilly terrain, which is unattractive to grazing livestock and human uses. Thus, a slope-based landform classification map used to identify steep terrain was created. We used the extension Topographical Position Index in geographic information system program ArcView (Jenness 2006; Fig. 4) using elevation grids from an SRTM 3 hole-filled Digital Elevation Model (Jarvis et al.

2006) for the 2 study areas. The number of pixels in each topographic gradient category was used to calculate the areas under flat or hilly terrain.

Estimates of livestock abundance.—We obtained livestock census data for the year 2007–2008 from official local government records in Jalore, Ahore, Kailwara, and Desuri Tehsils to obtain numbers of bovinds for each village within the effectively sampled areas at both study sites (Appendixes I and II).

RESULTS

Abundance of hyenas at Kumbhalgarh and Esrana.—We obtained a total of 33 hyena photographic captures at Kumbhalgarh and 16 captures at Esrana, from which we identified 15 and 8 individual hyenas (M_{t+1}), respectively, and constructed standard capture–recapture matrices (Otis et al. 1978; Williams et al. 2002). The demographic closure test ($Z = -1.289$, $P = 0.10$) in program CAPTURE 2.1 supported the assumption that the Kumbhalgarh hyena population was closed during the survey duration. The goodness-of-fit test showed that the null model $M(o)$ provided a better fit to data relative to $M(b)$ ($\chi^2_1 = 0.91$, $P = 0.34$). The goodness-of-fit test supported model $M(h)$ versus any alternate model ($\chi^2_{11} = 4.81$, $P = 0.94$). Similarly, model $M(b)$ was supported versus any alternate model ($\chi^2_{18} = 15.72$, $P = 0.61$). Thus, $M(o)$, $M(b)$, and $M(h)$ emerged as 3 candidate models that fit these capture data well. Because of small sample sizes model $M(o)$ versus model $M(h)$ could not be tested.

During field surveys, on several occasions hyena track patterns indicated some degree of trap-avoidance behavior. Thus, field observations, together with model selection test results, showed that the null hypothesis of the trap response model, $M(b)$, could not be rejected. Also the assumption of demographic closure was not violated ($Z = -1.289$, $P = 0.10$), which provided support for the $M(b)$ model (Otis et al. 1978). Furthermore, considering that hyenas are carnivores with a well-defined territorial spatial organization (Wagner 2006) and with some behavioral responses to camera trapping, we did not consider the $M(o)$ model because of its lack of robustness to violations of underlying assumptions (Karanth

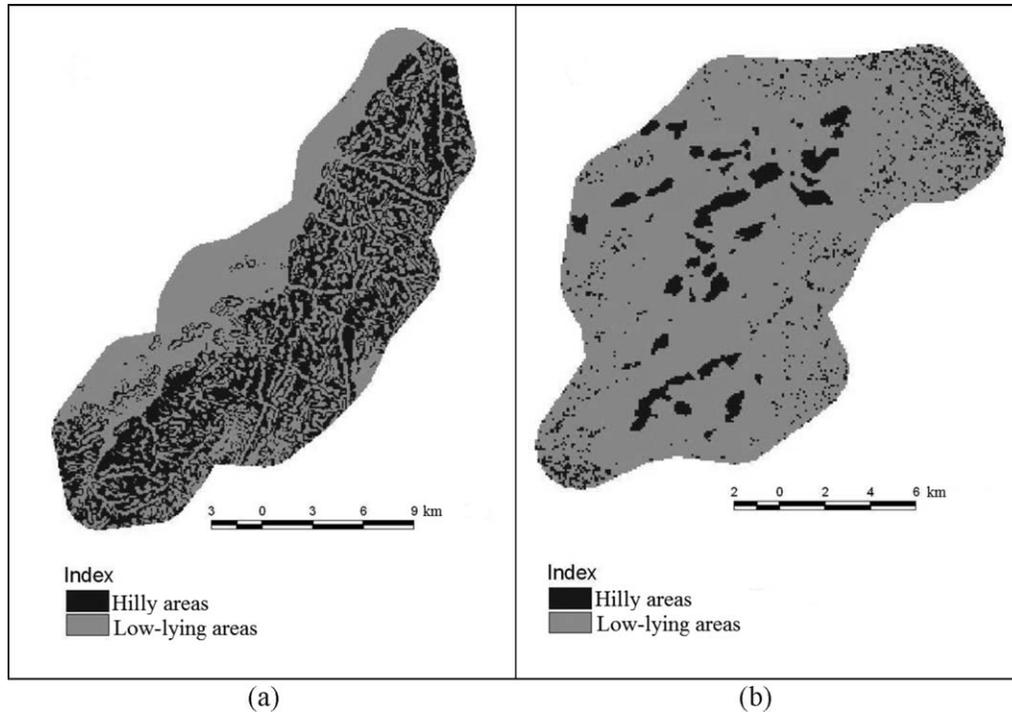


FIG. 4.—Slope-based landform classification map showing hilly areas and low-lying areas (flat land) at a) Kumbhalgarh and b) Esrana sites in India.

and Nichols 1998; Williams et al. 2002). Overall, based on ecological considerations, field observations, and model selection test scores above, the trap-response model M (b) was selected as a plausible model for estimating capture probabilities and abundance. Using the M (b) model, the estimated per sample capture probability (\hat{p}) was 0.10 with an estimated recapture probability (\hat{c}) of 0.03, leading to an estimated abundance (\hat{N}) of 20 hyenas ($SE = 7.85$) for this site.

The closure test in program CAPTURE 2.1 for Esrana ($Z = 6.00$, $P = 1.00$) could not converge in the absence of any recaptures (based on single-flank comparisons). Because of our sparse data set, with no recaptures, model selection tests based on the discriminant functional analysis scores generated by CAPTURE 2.1 could not be used. Instead, we could select the model based only on ecological and statistical considerations. Thus, the removal model M (b) was selected for estimation of capture probabilities and abundance (Karanth and Nichols 2002b). The M (b) model is a maximum-likelihood estimator that is valid even when no individuals are recaptured (Flickinger and Nichols 1990; Karanth and Nichols 2002a) because the estimation of the parameters N and p is independent of the estimation of c (Otis et al. 1978). Using the M (b) removal model, the estimate of per sample capture probability (\hat{p}) was 0.27, resulting in an estimate of abundance (\hat{N}) of 8 hyenas ($SE = 0.55$) for the Esrana site. The higher estimate of \hat{p} in Esrana relative to Kumbhalgarh resulted in reducing the variance for parameter N .

Sampled area and hyena density estimation.—In Kumbhalgarh the buffer width was set at half the mean-maximum distance between 2 captures observed for each individual

hyena. Because no recaptures were obtained in Esrana, we used the same buffer width as at Kumbhalgarh. We assumed that differences in average home-range sizes between the 2 areas were unlikely to result in major differences in estimated buffer width using the mean-maximum distance moved approach. The trap polygon measured 165 km² in Kumbhalgarh and 110 km² in Esrana. A buffer strip width (\hat{W}) of 1.95 km with an SE of 0.15 km was estimated for Kumbhalgarh using the half mean-maximum distance moved approach described in Karanth and Nichols (1998, 2002b). This area was added to the trap polygons for both study sites, deriving an effective sampled area (\hat{A}) of 307 km² for Kumbhalgarh and 218 km² for Esrana. The estimated population size (\hat{N}) was divided by the effective sampled area (\hat{A}) to derive hyena density estimates (\hat{D}). The estimated density for Kumbhalgarh was estimated at 6.5 hyenas/100 km² $\pm 2.6 SE$, and that for Esrana 3.67 ± 0.3 hyenas/100 km².

Assessment of potential hyena refugia.—Kumbhalgarh had 85% of its area (261 km²) in the hilly area category, and Esrana had only 35% such area (76 km²), with the remainder being flat land based on the number of pixels in either of the topographic categories (Fig. 4). Thus, Kumbhalgarh offered more potential refugia for supporting hyenas.

Availability of livestock.—The total livestock population size in the Kumbhalgarh study site was 22,304 animals, with an estimated density of 73 animals/km² for the total sampled area of 307 km². The livestock numbers in Esrana were much higher at 67,842 animals, resulting in a density of 311 animals/km².

We further examined additional ecological factors that could influence carcass availability temporally across seasons. Most livestock in Esrana were owned by a pastoral community

known as Raika. This community and other nonspecialized livestock herders in Rajasthan migrate annually out of the area (Agarwal 1991; Robbins 1998) for 6–8 months of the year starting in October–November (Agarwal 1991). During this period only livestock holders with <25–30 animals remain (Agarwal 1991). Therefore, it is likely that the number of livestock carcasses available to hyenas in Esrana for a major part of the year decreases dramatically. Approximately 50% of cattle and almost the entire sheep population of Esrana had migrated by December 2007 when the study was conducted (P. Siana, Siana Safari and Camps, pers. comm.), but <4,000 sheep migrate out of the Kumbhalgarh study site annually (H. Singh, Lokhit Pashu-Palak Sansthan, pers. comm.). After accounting for this migratory trend, we find that Esrana still continues to have much higher livestock density (140 animals/km²) when compared to Kumbhalgarh (60 animals/km²).

DISCUSSION

We attempted to identify the key ecological determinants of striped hyena densities in an arid landscape of India. Unexpectedly, this large carnivore appears to survive at high densities even in these human-dominated landscapes compared to elsewhere across its range (Kruuk 1976; Wagner 2006). We expected hyena densities to vary positively with food availability in the form of livestock carcasses and with increased availability of refugia in the form of hilly, steep terrain. Hence, we hypothesized that hyena densities would be higher at the site with greater availability of livestock and having a greater proportion of area with hyena denning refugia.

Livestock densities from the 2 study sites differed remarkably, with Esrana having more than 3 times the total livestock density at Kumbhalgarh. Contrary to our prediction, hyena densities were higher at Kumbhalgarh. However, absolute livestock numbers were very high in both sites. Based on dietary studies on the spotted hyena that indicate that the species requires approximately 946 g of dry meat/day (Nagy et al. 1999), the striped hyena likely requires access to a similar quantity of dietary resources, which are easily met by the high rate of livestock mortality and, consequently, carcasses in this region. Therefore, it is likely that availability of carcasses exceeded requirements of hyenas at both sites, with differences in livestock densities not being a critical determinant of differences in hyena densities at the 2 sites. Thus, we focused on testing the importance of the other predicted limiting resource, the extent of hyena refugia available at each study site. Kumbhalgarh offered a substantially larger area of potential refugia from humans or feral dogs. This finding was consistent with our prediction.

Overall, persistence of hyenas in this arid region appears to be a function of availability of disturbance-free denning refugia in hilly terrain and abundant availability of livestock carcasses. Our study also supports the general speculation (Karanth et al. 2009, 2010) that social attitudes such as no consumption of meat from livestock carcasses and relatively

higher tolerance for wildlife presence characteristic of this region contributes substantially to persistence of hyenas in these human-dominated landscapes compared to elsewhere across the range of this species.

Our findings above should be viewed cautiously as preliminary because of some limitations of our study. One constraint was the poor performance of inexpensive cameras, leading to many single-flank pictures and slow camera response time leading to loss of some pictures; these limitations resulted in sparse data sets with low recapture rates. Nonetheless, we provided evidence that hyena abundances and densities differed between the 2 sites, with both greater at Kumbhalgarh.

Another important methodological issue (Soisalo and Cavalcanti 2006) is our determination of the effective sampled area using the half mean–maximum distance moved buffer width (Karanth and Nichols 2002b). Further, our use of buffer width estimated from Kumbhalgarh hyenas with potentially smaller home ranges for the Esrana population could have caused an underestimate of the effective sampled area in Esrana, resulting in an overestimate of hyena densities. However, this possibility does not negate the main finding that hyena densities were relatively higher at Kumbhalgarh. In addition, because of our sparse data sets, we could not use recent advances in capture–recapture models that incorporate spatial data on capture locations to estimate densities directly, avoiding the buffer width approach altogether (Borchers and Efford 2008; Royle et al. 2009a, 2009b). We hope to address both these practical and analytical constraints in our future studies.

We concede that the strength of inference from our study is relatively low when viewed in the framework of classical experimental design because of its observational nature (as most field studies of large carnivores tend to be). However, we believe our results have provided increased evidence for factors important to the ecology of striped hyenas because our study was based on a priori, alternative hypotheses and explicit predictions that were tested with carefully gathered survey data on hyena densities from rigorous capture–recapture sampling. We argue that our work is better viewed in the context of evidence under the likelihood-based approach (Bolker 2008; Burnham and Anderson 2002; Hilborn and Mangel 1997; Royle and Dorazio 2008). Overall, despite limitations mentioned earlier, our study contributed to the understanding of the population status of striped hyenas in human-dominated landscapes of India and of ecological and management factors that determine it. The photographic capture–recapture method we used generated more precise estimates of hyena densities than earlier surveys. Methodological refinements we suggest above can help in rigorous assessments of ecology and conservation needs of striped hyenas across their entire range.

Our results suggest that striped hyenas, despite the ability to adapt to human-modified landscapes, require natural habitats free of anthropogenic disturbances to serve as refugia for source populations. The strikingly higher densities of hyenas in the protected reserve of Kumbhalgarh, with some degree of

regulation of human uses, support this conclusion. Thus, creation of more such protected refugia for hyenas across arid regions is a key conservation need identified from this study.

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LITERATURE CITED

- AGARWAL, A. 1991. The grass is greener on the other side. Report submitted to the International Institute for Environment and Development, London, United Kingdom.
- BAGCHI, S., S. P. GOYAL, AND K. SANKAR. 2003. Prey abundance and prey selection by tigers (*Panthera tigris*) in a semi-arid, dry deciduous forest in western India. *Journal of Zoology (London)* 260:285–290.
- BAQRI, Q. H., AND P. L. KANKANE. 2001. Desert: Thar. Pp. 94–109 in *Ecosystems of India* (J. R. B. Alfred, A. K. Das, and A. K. Sanyal, eds.). ENVIS–Zoological Survey of India, Kolkata, India.
- BHANDARI, M. M. 1990. *Flora of the Indian Desert*. Revised ed. MPS Repros, Jodhpur, India.
- BOLKER, B. M. 2008. *Ecological models and data* in R. Princeton University Press, Princeton, New Jersey.
- BORCHERS, D. L., AND M. G. EFFORD. 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* 64:377–385.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model selection and multimodel inference: a practical information theoretic approach*. 2nd ed. Springer-Verlag, New York.
- CARBONE, C., AND J. L. GITTLEMAN. 2002. A common rule for the scaling of carnivore density. *Science* 295:2273–2276.
- CHHANGANI, A. K. 2009. Present status of vultures in the Great Indian Thar Desert. Pp. 65–82 in *Faunal ecology and conservation of the Great Indian Desert* (C. Sivaperuman, Q. H. Baqri, G. Ramaswamy, and M. Naseema, eds.). Springer-Verlag, Berlin, Germany.
- FLICKINGER, E. L., AND J. D. NICHOLS. 1990. Small mammal populations at hazardous waste disposal sites near Houston, Texas, USA. *Environmental Pollution* 65:169–180.
- HILBORN, R., AND M. MANGEL. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, New Jersey.
- HOFER, H. 1998. Species accounts: striped hyena *Hyaena* (*Hyaena hyaena* (Linnaeus, 1758)). Pp. 21–26 in *Hyaenas: status survey and conservation action plan* (G. Mills and H. Hofer, comps.). IUCN/SSC Hyaena Specialist Group, IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- JARVIS, A., H. I. REUTER, A. NELSON, AND E. GUEVARA. 2006. Hole-filled seamless SRTM data v3. International Centre for Tropical Agriculture (CIAT), Cali, Colombia.
- JENNESS, J. 2006. Topographic position index (tpi_jen.avx) (ArcView 3.x, v.1.2. extension). Jenness Enterprises, Flagstaff, Arizona.
- KANKANE, P. L. 2009. Revival prospects of larger mammals in the Thar Desert of Rajasthan. Pp. 209–219 in *Faunal ecology and conservation of the Great Indian Desert* (C. Sivaperuman, Q. H. Baqri, G. Ramaswamy, and M. Naseema, eds.). Springer-Verlag, Berlin, Germany.
- KARANTH, K. K., J. D. NICHOLS, J. E. HINES, K. U. KARANTH, AND N. L. CHRISTENSEN. 2009. Patterns and determinants of mammal species occurrence in India. *Journal of Applied Ecology* 46:1189–1200.
- KARANTH, K. K., J. D. NICHOLS, K. U. KARANTH, J. E. HINES, AND N. L. CHRISTENSEN. 2010. The shrinking ark: patterns of large mammal extinctions in India. *Proceedings of the Royal Society of London, B. Biological Sciences* 277:1971–1979.
- KARANTH, K. U., AND J. D. NICHOLS. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- KARANTH, K. U., AND J. D. NICHOLS. 2002a. Ecological status and conservation of tigers in India. Final Technical Report to the Division of International Conservation, United States Fish and Wildlife Service, Washington, D.C., and Wildlife Conservation Society, New York. Centre for Wildlife Studies, Bangalore, India.
- KARANTH, K. U., AND J. D. NICHOLS (EDS.). 2002b. *Monitoring tigers and their prey: a manual for researchers, managers and conservationists in tropical Asia*. Centre for Wildlife Studies, Bangalore, India.
- KARANTH, K. U., J. D. NICHOLS, N. S. KUMAR, W. A. LINK, AND J. E. HINES. 2004. Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences* 101:4854–4858.
- KARANTH, K. U., ET AL. 2003. Science deficiency in conservation practice: the monitoring of tiger populations in India. *Animal Conservation* 6:141–146.
- KRUUK, H. 1976. Feeding and social behaviour of the striped hyaena (*Hyaena vulgaris* Desmarest). *African Journal of Ecology* 14:91–111.
- LEAKEY, L. N., ET AL. 1999. Diet of striped hyaena in northern Kenya. *African Journal of Ecology* 37:314–326.
- MENDELSSOHN, H., AND Y. YOM-TOV. 1999. *Fauna Palaestina: Mammalia of Israel*. Israel Academy of Sciences and Humanities, Keterpress Enterprises, Jerusalem, Israel.
- NAGY, K. A., I. A. GIRARD, AND T. K. BROWN. 1999. Energetics of free ranging mammals, reptiles and birds. *Annual Review of Nutrition* 19:247–277.
- OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1–135.
- PRATER, S. H. 1948. *The book of Indian animals*. 1st ed. Oxford University Press, New Delhi, India.
- RAHMANI, A. R., AND R. G. SONI. 1997. Avifaunal changes in the Indian Thar Desert. *Journal of Arid Environments* 36:687–703.
- REIGER, I. 1981. *Hyaena hyaena*. *Mammalian Species* 150:1–5.
- REXSTAD, E., AND K. BURNHAM. 1991. *User's guide for interactive program CAPTURE*. Abundance estimation of closed animal populations. Colorado State University, Fort Collins.
- ROBBINS, P. 1998. Nomadization in Rajasthan, India: migration, institutions, and economy. *Human Ecology* 26:87–112.
- ROBBINS, P. F., A. K. CHHANGANI, J. RICE, E. TRIGOSA, AND S. M. MOHNOT. 2007. Enforcement authority and vegetation change at Kumbhalgarh Wildlife Sanctuary, Rajasthan, India. *Environmental Management* 40:365–378.

ROYLE, J. A., AND R. M. DORAZIO. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations, and communities. Academic Press, San Diego, California.

ROYLE, J. A., K. U. KARANTH, A. M. GOPALASWAMY, AND N. S. KUMAR. 2009a. Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. *Ecology* 90: 3233–3244.

ROYLE, J. A., J. D. NICHOLS, K. U. KARANTH, AND A. M. GOPALASWAMY. 2009b. A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* 46:118–127.

SHARMA, K. K., AND S. P. MEHRA. 2009. The Thar of Rajasthan (India): ecology and conservation of a desert ecosystem. Pp. 1–10 in *Faunal ecology and conservation of the Great Indian Desert* (C. Sivaperuman, Q. H. Baqri, G. Ramaswamy, and M. Naseema, eds.). Springer-Verlag, Berlin, Germany.

SOISALO, M. K., AND S. M. C. CAVALCANTI. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* 129:487–496.

WAGNER, A. P. 2006. Behavioral ecology of the striped hyaena (*Hyaena hyaena*). Ph.D. dissertation, Montana State University, Bozeman.

WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.

WILSON, K. R., AND D. R. ANDERSON. 1985. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy* 66:13–21.

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APPENDIX I

Livestock figures for the effective study area of Kumbhalgarh, India, 2007–2008 (source: Office of the Tehsildar of Kailwara Tehsil and Desuri Tehsil).

Settlement	Cattle	Buffalo	Sheep and goats
Sumer	324	251	878
Lanpi	90	75	3,475
Desuri	1,736	1056	4,293
Joba	469	118	782
Gura Bhopsingh	418	180	680
Rajpura	203	100	900
Jaton ki Dhani	140	90	800
Ranakpur Temple	0	0	0
Roopnagar	48	15	298
Borda ki Bhagal	65	99	114
Kumbhalgarh	99	103	128
Kotra Pokharia	257	101	274
Boitra ^a	19	5	35
Nadia ^a	5	0	10
Miyawa ^a	2	11	13
Aret ki Bhagal	154	226	100
Mandigarh	183	262	1,111
Garasiya Colony ^a	210	58	461
Udavar	320	142	197
Kharni Tankri ^a	27	16	78
Total	4,769	2,908	14,627

^a Settlements located within Kumbhalgarh Wildlife Sanctuary for which livestock data were collected by Rajasthan Forest Department personnel.

APPENDIX II

Livestock figures for the effective study area of the Esrana site, India, 2007–2008 (source: Office of the tehsildar of Jalore Tehsil and Ahore Tehsil).

Settlement	Cattle	Buffalo	Sheep	Goats
Narnawas	274	602	1,077	1,844
Naya Narnawas	89	340	440	579
Dhavala	204	559	731	1,884
Digaon	129	973	264	684
Nagni	94	451	471	692
Devada	115	279	66	419
Nabi	73	138	2,418	1,018
Bhetala	52	154	1,158	580
Mailawas	154	521	2,959	1,237
Takhatpura	717	803	604	465
Meda Uparla	512	715	18,466	5,786
Meda Nichala	1,519	1,544	1,763	261
Rajanwari	51	63	912	834
Pandgaran	70	295	1,582	1,145
Chanwarcha	318	159	764	1,311
Chipparwara	99	348	696	778
Budtara	160	126	548	706
Total	4,630	8,070	34,919	20,223