

ESTIMATION OF TIGER DENSITIES IN INDIA USING PHOTOGRAPHIC CAPTURES AND RECAPTURES

K. ULLAS KARANTH^{1,3} AND JAMES D. NICHOLS²

¹ *Wildlife Conservation Society (International Programs), Bronx, New York 10460-1099 USA*

² *U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland 20708-4017 USA*

Abstract. The tiger (*Panthera tigris*) is an endangered, large felid whose demographic status is poorly known across its distributional range in Asia. Previously applied methods for estimating tiger abundance, using total counts based on tracks, have proved unreliable. Lack of reliable data on tiger densities not only has constrained our ability to understand the ecological factors shaping communities of large, solitary felids, but also has undermined the effective conservation of these animals. In this paper, we describe the use of a field method proposed by Karanth (1995), which combines camera-trap photography, to identify individual tigers, with theoretically well-founded capture–recapture models. We developed a sampling design for camera-trapping and used the approach to estimate tiger population size and density in four representative tiger habitats in different parts of India. The field method worked well and provided data suitable for analysis using closed capture–recapture models. The results suggest the potential for applying this methodology to rigorously estimate abundances, survival rates, and other population parameters for tigers and other low-density, secretive animal species in which individuals can be identified based on natural markings.

Estimated probabilities of photo-capturing tigers present in the study sites ranged from 0.75 to 1.00. Estimated densities of tigers >1 yr old ranged from 4.1 ± 1.31 to 16.8 ± 2.96 tigers/100 km² (mean \pm 1 SE). Simultaneously, we used line-transect sampling to determine that mean densities of principal tiger prey at these sites ranged from 56.1 to 63.8 ungulates/km². Tiger densities appear to be positively associated with prey densities, except at one site influenced by tiger poaching. Our results generally support the prediction that relative abundances of large felid species may be governed primarily by the abundance and structure of their prey communities.

Key words: abundance estimation; camera traps; capture–recapture models; density estimation; felids; India; leopards; *Panthera tigris*; tigers.

INTRODUCTION

The tiger (*Panthera tigris*) is an endangered big cat whose demographic status is uncertain across its entire distributional range, spanning 13 Asian countries. Because of their large body size and carnivorous diet (Eisenberg 1981), tigers naturally occur at low population densities. Further, wild tiger populations are now being affected by adverse factors such as prey depletion due to overhunting (Karanth and Stith, 1998), tiger poaching (Kenny et al. 1995, WCS 1995), and habitat shrinkage and fragmentation (Wikramanayake et al., 1998). Although recent field surveys, combined with forest cover maps, have generated more accurate distribution maps for tigers (Wikramanayake et al., 1998), their utility for assessing the status and viability of tiger populations is limited by the absence of reliable data on population densities.

Tigers are adapted to a wide range of environments

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³ Present address: 403, Seebo Apts., 26-2, Aga Abbas Ali Road, Bangalore-560 042, India.

(Schaller 1967, Sunquist 1981, Seidensticker and McDougal 1993) through a social organization that permits considerable behavioral plasticity (Sunquist 1981, Smith et al. 1987, Smith 1993). Based on their studies of prey selection in Nagarhole Park, India, Karanth and Sunquist (1995) suggested that ecological densities of tigers and other syntopic predators may be governed primarily by how their prey community is structured, in terms of abundances of different size classes. According to their predictions, where tigers and leopards occur syntopically, if both large and medium-sized prey are abundant, tigers would select large prey, enabling the coexistence of leopards at high densities. Where large prey are scarce, tigers would switch to medium-sized prey and reduce leopard densities through competition, as hypothesized for Chitwan Park, Nepal (Seidensticker et al. 1990). On the other hand, if both large and medium-sized prey are scarce, leopards would be relatively more abundant because of their ability to survive on smaller prey, as recorded in Huai Kha Khaeng, Thailand (Rabinowitz 1989). In the absence of reliable data on tiger and prey densities, however, it is difficult to test these predictions. Therefore, es-

establishing theoretically sound and practically feasible population sampling methods to estimate densities of wild tiger populations is critically important for both scientific and management reasons.

Most prevailing methods of counting wild tigers appear to fail, because they are unable to deal with three important ecological characteristics of the species: scarcity, extensive range, and secretiveness. Because of their secretive behavior, tigers cannot be visually counted under usual field conditions. Consequently, most methods depend on counting tiger tracks. In India, the official "censuses" of tiger populations are based on the assumptions that each individual tiger can be identified by its unique track shape, and that track prints of every tiger can be simultaneously found and recorded (Panwar 1979). Because both of these fundamental assumptions are demonstrably erroneous (Karanth 1987, 1988, 1995), the results are neither total counts nor valid sample statistics. Although methodologically better, the snow-track counts used by Russian scientists also have problems that may result in undercounts (E. N. Smirnov and D. G. Miquelle, *unpublished manuscript*). In Chitwan Park, Nepal, counts of long-term resident tigers are made by experienced naturalists from individual identification of tracks, based primarily on injury-related differences (McDougal 1977; C. McDougal, *personal communication*). This site-specific technique still does not solve the general problem of density estimation at other sites or of counting tigers including transients and juveniles. The application of radiotelemetry to estimate tiger densities (Sunquist 1981, Smith 1993) is constrained by the small number of animals that can be tagged simultaneously, uncertainty about numbers of untagged tigers, and the high costs and effort involved.

Based on the fact that tigers are individually identifiable from their stripe patterns (Schaller 1967, McDougal 1977), Karanth (1995) has demonstrated the potential for estimating their population size using photographic "captures," within the theoretical framework of formal capture-recapture theory (reviewed by Nichols 1992). However, his pilot study (Karanth 1995) was constrained by the small size of the population sampled and the arbitrariness associated with the sampling design. In this paper, we report results of a detailed study in which we overcame these problems and estimated tiger densities using photographic capture-recapture sample surveys at four ecologically representative sites in India. Our study had the following objectives:

1) To develop field methods and sampling designs appropriate for camera-trapping tigers, and to evaluate the suitability of different capture-recapture models (see Otis et al. 1978, White et al. 1982, Pollock et al. 1990, Nichols 1992) for estimating tiger population size and density under field conditions.

2) To estimate densities of wild tiger populations using photographic capture-recapture models in four ecologically distinct study sites.

3) To estimate densities of principal ungulate prey species at these four sites using line-transect sampling (Burnham et al. 1980, Buckland et al. 1993), in order to evaluate the role of prey abundance and community structure in shaping predator communities.

STUDY AREAS

Because tiger densities appear to be influenced primarily by the characteristics of their ungulate prey assemblages (Seidensticker and McDougal 1993, Karanth and Sunquist 1995), we selected four sites representing important tiger-prey communities in India. These consisted of the best preserved, representative sites within the National Parks of Pench (290 km²), Kanha (900 km²), Kaziranga (488 km²), and Nagarahole (644 km²). Ecological features of these areas, described elsewhere (Puri et al. 1983, Kothari et al. 1989), are briefly summarized.

The Pench site, located in central India (21°38'–21°51' N, 79°09'–79°22' E), receives an average annual rainfall of 1400 mm and supports a tropical deciduous teak (*Tectona grandis*) forest type, classified as *Tectona-Terminalia* series by Puri et al. (1983) and as a tropical moist deciduous forest (TMD) tiger habitat by Wikramanayake et al. (1998). Common ungulate prey species of tigers in Pench are chital (*Axis axis*), sambar (*Cervus unicolor*), nilgai (*Boselephas tragocamelus*), gaur (*Bos gaurus*), wild pig (*Sus scrofa*), muntjac (*Muntiacus muntjac*), and four-horned antelope (*Tetracerus quadricornis*).

The Kanha site is also located in central India (22°07'–22°27' N, 80°26'–81°03' E), with an annual rainfall of 1500 mm. Kanha has tropical deciduous forests dominated by sal (*Shorea robusta*), classified as *Shorea-Terminalia-Adina* series by Puri et al. (1983) and classed under the tiger habitat category tropical moist deciduous forest (TMD) by Wikramanayake et al. (1998). Grassy meadows of anthropogenic origin are interspersed within the forested area. The common tiger prey species are chital, sambar, gaur, barasingha (*Cervus duvacei*), wild pig, and muntjac.

The Nagarahole site in southwestern India (11°50'–12°15' N, 76°00'–76°15' E) gets an annual rainfall ranging from 1100 mm in the east to 1600 mm in the west. It supports tropical deciduous forests classified as *Terminalia-Anogeissus-Tectona* series in low-rainfall zones, and *Tectona-Dillenia-Lagerstremia* series in the higher rainfall zones (Puri et al. 1983). The site is included under the tropical moist forest (TMF) tiger habitat category by Wikramanayake et al. (1998). The common ungulate prey species are chital, gaur, sambar, wild pig, and muntjac.

The Kaziranga site in northeastern India (26°33'–26°45' N, 93°08'–93°40' E) gets an annual rainfall of 3000 mm. Although placed under the TMD tiger habitat category by Wikramanayake et al. (1998), our specific study site was an alluvial floodplain grassland (AGD) interspersed with patches of tropical moist forest. The



FIG. 1. Differences in stripe patterns between two tigers in Nagarahole noted from photographic captures using camera traps.



FIG. 2. Repeated photographic captures of the same tiger in Nagarahole.

common ungulate prey species are wild buffalo (*Bubalus bubalis*), barasingha, hog deer (*Axis porcinus*), muntjac, wild pig, and gaur.

Earlier studies (Schaller 1967, Sunquist 1981, Seidensticker and McDougal 1993, Karanth and Sunquist 1995) show that numerically abundant ungulate species are the principal prey of tigers. Tiger predation on Asian elephants (*Elephas maximus*) and one-horned rhinos (*Rhinoceros unicornis*) is rare and restricted to small calves. Therefore, we ignored these two species in our analysis of data from Kaziranga, where both occur, and from Nagarahole, where elephants are present. We carried out the fieldwork during February–June 1995 at Pench, October–December 1995 at Kanha, and February–April 1996 at Kaziranga and Nagarahole.

METHODS

Field methods

We used commercially made TRAILMASTER TR-1500 (Goodson and Associates, Lenexa, Kansas, USA) tripping devices attached to two cameras positioned to photograph simultaneously both flanks of an animal that broke the infrared beam. We mounted the camera

traps on wooden posts 350 cm away on either side of a trail, with the infrared beam set at a height of 45 cm. To eliminate mutual flash interference, the two cameras were not positioned directly facing each other. Tigers regularly travel along forest roads and trails, communicating with conspecifics through scent marking (Sunquist 1981, Smith et al. 1987). In order to obtain adequate numbers of tiger captures, we found it critical to place camera traps on such travel routes. Camera trap points were selected based on cues such as presence of earlier tiger sign (scats, scrapes, scent deposits, tracks) and intersections of trails. All points were marked on maps using a GPS unit. Date, time, and location of each photographic “capture” of a tiger were noted. Photographs with distorted perspectives, or which lacked clarity, were not used for identifications. Tigers were identified from photographs by comparing stripe patterns (Schaller 1967, McDougal 1977, Karanth 1995). We compared shapes of specific individual stripes and positions of several such stripes relative to each other on the animal’s body. Examples of such identifications are presented in Figs. 1 and 2.

In each study area, we selected 4–6 forest roads or trails (each 10–20 km long) as our “triplines” tra-

TABLE 1. Summary statistics for camera-trap, capture-recapture data on tigers sampled at four locations in India.

Location	Sampling period	No. occasions	Effort (trap-nights)	Total no. individuals caught, M_{t+1}	Total no. captures, n
Kanha	10/95–12/95	10	803	26	59
Kaziranga	2/96–4/96	9	552	22	47
Nagarahole	2/96–4/96	18	936	25	60
Pench	3/95–6/95	16	788	5	21

versing the sampled area. On each trapline, we established 12–15 camera trap points 0.8–2.0 km apart from each other. An important consideration was to ensure coverage of the entire area, without leaving holes or gaps that were sufficiently large to contain a tiger's movements during the sampling period and within which any tiger had a zero capture probability. Because tigers are mostly crepuscular and nocturnal (Sunquist 1981), and to minimize tripping by other animals and risk of theft and damage, we deployed the units only from dusk to dawn. Therefore, each sampling occasion was defined by the 4–6 successive trap nights during which all of the traplines were sampled once. Details of the sampling effort and tiger capture records at each site are presented in Table 1. In addition to tigers, we were able to photographically capture leopards (*Panthera pardus*), using the same camera-trapping system.

To estimate prey densities, we employed line-transect sampling (Burnham et al. 1980, Buckland et al. 1993), using field methods described in detail elsewhere (Karanth and Sunquist 1992). Our transect lines sampled the same areas in which we set our camera traps. The data collected for each prey species included the line length traversed and the number of clusters of animals detected. For each detection, we recorded the cluster size, sighting distance (measured with a rangefinder), and sighting angle (measured with a compass), as described in the line-transect literature (Burnham et al. 1980, Buckland et al. 1993).

Statistical methods

Capture histories were developed for each adult tiger identified in the camera-trapping. The capture history for animal i consisted of a row vector of t entries, where t denoted the number of trapping occasions for the particular study site. Each entry, denoted as X_{ij} for individual i on occasion j , assumed a value of either "0," if the animal was not photographed on that particular occasion, or "1," if the animal was photographed on that occasion. The matrix of such t -dimensional row vectors for all M_{t+1} individuals caught during the sampling is often referred to as the X matrix (Otis et al. 1978), and these matrices were the data from which tiger abundance was estimated.

The capture history data were analyzed using program CAPTURE (Otis et al. 1978, White et al. 1982,

Rexstad and Burnham 1991), software developed to implement closed-population capture-recapture models. Program CAPTURE computes estimates of abundance under seven models that differ in their assumed sources of variation in capture probability. We define p_{ij} as the probability that individual i is captured on occasion j . Sources of variation in capture probability that are considered in the models of CAPTURE are individual heterogeneity, behavioral response, and time. Individual heterogeneity refers to variation in capture probability among individuals, such that each tiger is thought of as having its own capture probability, which may differ from the capture probabilities of all other animals. Behavioral response refers to changes in capture probability that occur after an individual is caught for the first time. Thus, at any sampling occasion j , unmarked animals have one capture probability and previously marked animals have a different capture probability. Time variation simply refers to variation in capture probability from one sampling occasion to another.

Model M_0 assumes no variation in capture probability associated with individuals or occasions, and models capture probability with a single parameter, $p_{ij} = p$. Model M_h permits a different capture probability for each individual, but this probability remains the same over all sampling occasions and regardless of previous capture history. Model M_b permits a different capture probability for unmarked and previously marked animals, but otherwise includes no temporal or individual variation in capture probability. Model M_t assumes variation in capture probability from one sampling occasion to the next but permits no variation among individuals within an occasion. In addition to M_0 and the three models permitting single sources of variation in capture probability, program CAPTURE also computes estimates under models that include two sources of variation in capture probability parameters, M_{bh} , M_{th} , and M_{tb} . Program CAPTURE does not compute estimates under the most complicated model permitting all three sources of variation in capture probability, M_{tbh} , although an estimator is now available for this model (Lee and Chao 1994).

Program CAPTURE computes several goodness-of-fit and between-model test statistics providing information about the appropriateness of the different cap-

ture–recapture models. We computed and examined these individual tests for all data sets. CAPTURE also includes a model selection algorithm that uses a discriminant function to provide an objective criterion for selecting the most appropriate model (Otis et al. 1978, Rexstad and Burnham 1991). Our a priori expectation was that model M_h would provide a reasonable model for tiger capture probability. We expected variation among individuals in capture probability, and we hoped that the field sampling methods would reduce the likelihood of temporal variation and behavioral response to “capture.” We computed the M_0 vs. M_h , M_0 vs. M_b , and M_0 vs. M_t test statistics to test for heterogeneity, behavioral response, and temporal variation, respectively. In addition to expecting heterogeneity of capture probabilities, we also favored M_h because the jackknife estimator (Burnham and Overton 1978) for this model is robust to deviations from underlying model assumptions and has performed well in simulation studies (Otis et al. 1978, Burnham and Overton 1979).

These models were developed for closed populations and assume that the sampled population does not change during the course of the study. The camera-trap sampling was restricted to periods of time that were sufficiently short that mortality and permanent movement in and out of the study areas were not anticipated. CAPTURE computes a closure test statistic from the capture history data, and we used this statistic to test the closure assumption for each data set. A specific kind of closure violation that we considered was the existence of animals briefly passing through the study area en route to locations outside the study area (e.g., see Pradel et al. 1997). These animals would not have an opportunity to be caught on multiple occasions, and their capture histories would lend the appearance of a trap-shy response. In addition to the closure test, the M_0 vs. M_b test provides information about the existence of this type of capture history.

We report the estimates computed by CAPTURE for capture probability, abundance (\hat{N}), and estimated standard error of abundance ($\widehat{SE}[\hat{N}]$) for appropriate models. The capture probability estimates correspond to individual sampling occasions. It is also of interest to consider the probability that a tiger present in the sampled area is captured at least once during the sampling. This quantity can be estimated as M_{t+1}/\hat{N} , where M_{t+1} is the total number of individual tigers caught during all sampling occasions.

Finally, we were interested in using these abundance estimates to estimate tiger density in the different study areas. Density is defined as $D = N/A$, where N is animal abundance and A is the area on which the animals are found. In trapping-grid studies, trap spacing is usually established such that all animals moving in the grid interior are exposed to traps, and we believe that this was the case with camera-trapping (see *Field methods*). However, in trapping-grid studies, it is also recognized that the area from which animals are trapped is not

equal to the area defined by assuming that the perimeter traps represent the outer boundary of the area (Dice 1938, Otis et al. 1978, White et al. 1982). Instead, it is typical to add a boundary strip to the area defined by the perimeter traps in order to account for the additional area from which trapped animals are taken (Dice 1938, Otis et al. 1978, White et al. 1982). Several approaches have been suggested for estimating the boundary strip width, and we used an ad hoc approach that has performed well in simulation studies (Wilson and Anderson 1985).

Our approach to computing a boundary strip width was to use “mean maximum distance moved” for tigers that were camera-trapped on more than one occasion. This mean distance and its associated variance were computed using all animals caught more than once in each study area. Let d_i denote the maximum distance moved between recaptures for animal i , and let m denote the number of animals on the area that were caught at least twice. Then we can estimate the mean, \hat{d} , and its variance, $\widehat{\text{var}}(\hat{d})$, using

$$\hat{d} = \left(\sum_{i=1}^m d_i \right) / m$$

$$\widehat{\text{var}}(\hat{d}) = \frac{\sum_{i=1}^m (d_i - \hat{d})^2}{m(m - 1)}. \tag{1}$$

Boundary strip width, W , and its variance, were then estimated as

$$\hat{W} = \hat{d}/2$$

$$\widehat{\text{var}}(\hat{W}) = 0.25 \times \widehat{\text{var}}(\hat{d}). \tag{2}$$

Let $\hat{A}(W)$ denote the estimated area sampled by the camera-trapping (sometimes termed the “effective area”; e.g., Wilson and Anderson 1985). This area was computed directly from maps of the study sites. First, the actual trapline locations were plotted, and the traps on the edges of the sampled area were connected to form the perimeter of the area covered by camera traps. Then a boundary strip of width \hat{W} was added around the perimeter to obtain the sampled area. In cases where landscapes containing habitat types not used by tigers intruded into the boundary strip, the area of such habitat was deducted when computing the sampled area. Tiger density and its associated variance are then estimated as

$$\hat{D} = \hat{N}/\hat{A}(W)$$

$$\widehat{\text{var}}(\hat{D}) = \hat{D}^2 \left[\frac{\widehat{\text{var}}(\hat{A}(W))}{[\hat{A}(W)]^2} + \frac{\widehat{\text{var}}(\hat{N})}{\hat{N}^2} \right] \tag{3}$$

where $\widehat{\text{var}}(\hat{N})$ is computed for the selected estimator by program CAPTURE and $\text{var}(\hat{A}(W))$ is estimated as described in the appendix.

Because the pattern recognition protocols for iden-

TABLE 2. Statistics relevant to selection of appropriate capture–recapture models for the camera-trapping data on tigers sampled at four locations in India.

Location	Model selection criteria†		M ₀ vs. M _h			M ₀ vs. M _t			M ₀ vs. M _b			M _h goodness-of-fit			Closure test	
	M ₀	M _h	χ ²	df	P	χ ²	df	P	χ ²	df	P	χ ²	df	P	z	P
Kanha	1.00	0.89	1.95	2	0.38	10.47	9	0.31	0.66	1	0.42	12.90	9	0.17	0.57	0.72
Kaziranga	1.00	0.84	1.67	2	0.43	11.70	8	0.17	2.64	1	0.10	12.21	8	0.14	1.31	0.90
Nagarahole	1.00	0.70	0.27	2	0.87	9.45	17	0.92	0.19	1	0.67	10.93	17	0.86	-0.35	0.36
Pench	1.00	0.89	4.35	15	>0.99	0.66	1	0.42	14.46	15	0.49	0.92	0.82

† M_h had the second-highest model selection criterion in all locations except Kaziranga, where M_{bh} had a criterion score of 0.91 and M_{bh} had a score of 0.85.

tifying individual leopards from photographs are still under development, we did not estimate capture probabilities and absolute abundances for leopards. Instead, we used an index of relative leopard abundance based on number of leopard captures per 100 trap-nights of sampling effort.

We analyzed the count and distance data on ungulate prey generated from our line-transect surveys using program DISTANCE (Buckland et al. 1993, Laake et al. 1993). We considered as principal prey the numerically abundant ungulates for which we had a reasonable number of detections on our transects. We generated density estimates using ungrouped distance and cluster-size data, opting for both the Half-Normal and the Uniform Cosine estimators available in DISTANCE. Both models usually generated similar estimates. In each case, we selected the estimates with the lower Akaike Information Criterion value generated by the model selection process in DISTANCE (Laake et al. 1993).

RESULTS

Camera-trapping was successful in all four study areas, yielding a minimum number of five individuals caught 21 times at Pench and a maximum of 26 tigers caught 59 times at Kanha (Table 1). The relatively long sampling sessions (2–3 mo; Table 1) for each study area and the large number of sampling occasions (9–18; Table 1) led to a concern about violation of the closure assumption. However, results of the closure test provided no evidence of violation of this assumption on any of the four areas (Table 2). We were also concerned about the possibility of tigers traveling through the study area en route to locations outside the area (a specific kind of violation of the closure assumption) and the influence of such animals on abundance estimates. As previously noted, capture histories of such animals would lend the appearance of a trap-shy response to our data. However, test and model selection results from CAPTURE provided no evidence of a behavioral response in capture probability, so we have no reason to suspect the existence of animals traveling through the study area.

The model selection algorithm of CAPTURE iden-

tified M₀ as the most appropriate model for each of the four study areas (Table 2). Our a priori expectation was that tiger capture probabilities would be heterogeneous over individuals. Model M_h had the second highest model selection criterion for all areas except Kaziranga, where M_h again received a high model selection criterion score. Model M_h fit the data well in all four study areas. However, the test (M₀ vs. M_h) for heterogeneity provided no evidence of this effect on any of the three areas for which it was tested (Table 2). We also tested for temporal variation in capture probability (M₀ vs. M_t), but found no evidence (Table 2). Although model M₀ was the apparent model of choice for all four areas, the estimator of population size associated with this model is known to be sensitive to violations of the underlying model assumption of homogeneous capture probabilities (e.g., Otis et al. 1978). The population size estimator of model M_h, in contrast, is known to be robust to violation of underlying model assumptions (Otis et al. 1978, Burnham and Overton 1979). We thus report population size estimates computed under both of these models, although we have more confidence in the M_h estimates, because of estimator robustness.

Estimated capture probabilities per occasion (the probability that a tiger in the sampled area is photographed on a single sampling occasion) were consistent across the four areas, ranging from 0.12 to 0.26 under model M₀. The estimated average capture probabilities under model M_h were slightly lower, as expected, ranging from 0.11 to 0.22 (Table 3). The estimated probability that a tiger was photographed on at least one occasion (estimated by M_{t+1}/\hat{N}) ranged from 0.92 to 1.00 under model M₀ estimates, and from 0.79 to 1.00 under model M_h estimates (Table 3). At Pench, we estimated only five adult tigers, and the estimates for the other three areas ranged from 24 to 33 adult tigers, depending on the estimation model used and the location (Table 3).

The mean maximum distances moved by tigers caught at least twice ranged from nearly 3 km to >5 km, yielding estimated boundary strip widths ranging from 1.38 km to 2.67 km (Table 4). The estimated effective areas sampled by the traplines ranged from just >120 km² to >280 km². Because of the robustness

TABLE 3. Estimated abundance and capture probabilities of tigers sampled at four locations in India. Estimates are based on capture–recapture analysis of camera-trapping data.

Location	Estimates based on M_0			Estimates based on M_h		
	\hat{p}	M_{t+1}/\hat{N}	$\hat{N}(\widehat{SE}[\hat{N}])$	\hat{p}	M_{t+1}/\hat{N}	$\hat{N}(\widehat{SE}[\hat{N}])$
Kanha	0.21	0.93	28 (2.04)	0.18	0.79	33 (4.69)
Kaziranga	0.22	0.92	24 (2.13)	0.19	0.79	28 (4.51)
Nagarahole	0.12	0.93	27 (1.95)	0.11	0.89	28 (3.77)
Pench	0.26	1.00	5 (0.20)	0.22	1.00	5 (1.41)

Notes: \hat{p} denotes the estimated capture probability per sampling occasion under model M_0 ; \hat{p} denotes the average capture probability per sampling occasion under model M_h ; M_{t+1}/\hat{N} estimates the capture probability over all sampling occasions.

of the model M_h estimates of population size, we used these estimates in conjunction with Eq. 3 to estimate tiger density. The estimated density at Pench was only 4.1 tigers/100 km², but the estimates for the other three areas ranged from 11.5 to 16.8 tigers/100 km² (Table 4).

The values of the relative abundance indices for leopards calculated from camera trap data were: 5.44 captures/100 trap-nights of sampling effort for Nagarahole, 2.28 for Pench, 0.50 for Kanha, and 0.18 for Kaziranga. The estimated densities of principal prey species from our line-transect surveys are reported in Table 5. Based on the natural size differences prevailing among these species, following Karanth and Sunquist (1995), we categorized them by mass as large prey (>176 kg), medium-sized prey (21–175 kg), and small prey (<20 kg).

DISCUSSION

Applicability of the photographic capture–recapture method

In our short-duration surveys, camera traps were mounted in the open and suffered some damage from occasional attacks by elephants and rhinos, and, on three occasions, by tigers. At places where animal damage or theft by humans is a significant factor, it may be necessary to provide robust protective structures for the camera traps.

Our study showed that photographic capture–recapture studies offer a practical and reasonable approach to estimating the abundance of tiger populations. The estimated average capture probabilities (0.11–0.22 per occasion) were fairly good, and certainly much higher

than capture or detection probabilities resulting from any other tiger sampling methods of which we are aware. The estimated probabilities of missing an animal ($1 - M_{t+1}/\hat{N}$) were <0.25, and overall capture probabilities were very high. Despite the reasonable capture probabilities, however, the total numbers of animals caught were low (<30). These low numbers are expected to limit our ability to investigate sources of variation in capture probability and, thus, to select the most appropriate model for estimating abundance (e.g., Otis et al. 1978, White et al. 1982). We dealt with this limitation by basing our density estimates on the M_h estimator, which is the most robust of the estimators considered by Otis et al. (1978). Of course, we would still like to base our estimates on larger numbers of animals, but our small samples were a natural consequence of studying animals at such low densities. Despite the limitations of our approach imposed by low tiger densities, we believe that camera-trapping is superior to every other method that we have considered for estimating tiger abundance and density.

As noted by Karanth (1995), we found that tiger cubs (age <1 yr) had low capture probabilities, with no animals in this age class being captured at Kaziranga, and only one capture each in Kanha and Nagarahole. The only exception was at Pench, where one particular litter was caught four times. Moreover, although we knew from direct observations that several cubs existed at Nagarahole, none of them was camera-trapped. Deliberate avoidance of traps and other behavioral differences between young and adults usually appear to result in cubs having extremely low capture probabilities. Therefore, estimating population size for tiger cubs

TABLE 4. Mean maximum distance moved by tigers (\hat{d}), effective area sampled by camera-trapping ($\hat{A}(W)$), and estimated tiger density (\hat{D}) at four sampled locations in India.

Location	Area with camera-traps	Maximum distance moved (km ²)		Strip width (km)		Effective area (km ²)		Tiger density (no./100 km ²)	
		\hat{d}	$\widehat{SE}(\hat{d})$	\hat{W}	$\widehat{SE}(\hat{W})$	$\hat{A}(W)$	$\widehat{SE}(\hat{A}(W))$	\hat{D}	$\widehat{SE}(\hat{D})$
Kanha	142.37	4.31	0.793	2.16	0.396	282.02	23.59	11.7	1.93
Kaziranga	92.90	2.75	0.530	1.38	0.265	167.02	12.13	16.8	2.96
Nagarahole	138.66	3.74	0.536	1.87	0.268	243.38	14.82	11.5	1.70
Pench	48.66	5.33	0.905	2.67	0.453	121.57	17.69	4.1	1.31

TABLE 5. Estimated densities (\hat{D}) and their standard deviations for principal prey species (no. animals/km²), derived from line transect sample surveys at four locations in India. The numbers of detections (n) from which the estimates are derived are also shown.

Species	Kanha		Pench		Nagarahole		Kaziranga	
	n	\hat{D} ($\widehat{SE}[\hat{D}]$)	n	\hat{D} ($\widehat{SE}[\hat{D}]$)	n	\hat{D} ($\widehat{SE}[\hat{D}]$)	n	\hat{D} ($\widehat{SE}[\hat{D}]$)
Gaur ^L	3	...	28	0.7 (0.22)	113	4.5 (0.77)	0	...
Wild buffalo ^L		NP		NP		NP	44	2.7 (0.89)
Nilgai ^L		NP	43	0.7 (0.17)		NP		NP
Sambar ^L	36	1.5 (0.35)	366	9.6 (0.76)	134	4.2 (0.54)	1	...
Barasingha ^L	142	3.0 (0.43)		NP		NP	38	14.2 (5.42)
Chital ^M	688	49.7 (3.97)	880	51.3 (3.02)	443	38.1 (3.72)		NP
Wild pig ^M	27	2.5 (0.68)	40	0.8 (0.17)	82	3.3 (0.57)	62	2.6 (0.54)
Hog deer ^M		NP		NP		NP	363	38.6 (3.45)
F. H. antelope ^{M†}	0	...	33	0.7 (0.16)	1	...		NP
Muntjac ^S	21	0.6 (0.14)	1	...	114	6.0 (0.72)	0	...
All species		57.3		63.8		56.1		58.1

Notes: Ellipses indicate that there were too few detections to derive reasonable estimates. NP indicates that the species is not present in the sampled area. Superscripts L, M, and S indicate large, medium, and small prey species, respectively.

† Four-horned antelope.

may require impractically high trapping effort. However, the numbers of cubs in an area can be estimated empirically from the number of resident females with litters, based on ancillary observations (Schaller 1967, McDougal 1977, Sunquist 1981, Smith 1993) or, theoretically, using demographic models (Kenny et al. 1995, Karanth and Stith, 1998).

Our approach to estimating tiger densities may also be useful for estimating abundance and density of a number of other secretive animal species that are individually recognizable based on natural markings. In many species with no natural markings, it may be possible to use photographic recaptures following an initial physical capture and artificial marking. We note that the approach can be used, with some modification, when only a subset of the population is potentially identifiable. There also appears to be potential for using long-term camera-trapping surveys to estimate additional population parameters such as survival, mortality, recruitment, and dispersal rates for tigers (and other individually recognizable animals), by applying open capture–recapture models that are currently available (Seber 1982, Pollock et al. 1990, Lebreton et al. 1992).

Densities and sizes of wild tiger populations

The estimates of tiger densities we report (Table 4) are the first such data to be generated using a theoretically well-founded population sampling approach. Our results show that tiger densities did not differ significantly among Kaziranga, Kanha, and Nagarahole areas, but were significantly lower at Pench than in these other areas. The estimated mean tiger densities (Table 4) appear to correspond positively with the mean densities of principal prey (Table 5) at the first three sites, but not at Pench. We suspect that tiger densities at Pench were lower than at limits set by prey abundance, as a result of high incidence of tiger poaching in the region (Wildlife Protection Society of India 1996, unpublished report; K. U. Karanth, personal observations).

In comparing our tiger density estimates to tiger density estimates from other studies, we were constrained by the weak methodologies that underlie most of them (Karanth 1987, 1988). Therefore, for comparisons, we selected three studies that depended on either visual identification or radiotagging of the study animals (Schaller 1967, 1972, Sunquist 1981; E. N. Smirnov and D. G. Miquelle, unpublished manuscript). Because even these studies did not use formal population sampling approaches, they lack comparable estimates of variances for making statistical inferences. However, in view of the scarcity of comparative field data on tigers, in particular, and on large solitary felids in general, we believe it is fruitful to use mean values of the estimates to speculate on the ecological factors underlying the observed patterns of tiger densities across the range of the species.

Our density estimates (Table 4) exclude cubs <1 yr old. Earlier workers have reported density estimates that include cubs. Therefore, for comparisons, we recalculated tiger density estimates for our sites to include cubs. From direct sightings at Pench, we knew that there were 7 cubs, adding up to a total population size of 12, yielding a mean density of 9.9 tigers/100 km². However, the rather high percentage of cubs in the Pench population was probably a result of a depressed proportion of juveniles and transients caused by poaching on the park's boundaries (K. U. Karanth, personal observations). Demographic models of typical wild tiger populations (Karanth and Stith, 1998) suggest that cubs may form ~25% of a "normal" tiger population. Because we did not have exact knowledge of the number of cubs at Nagarahole, Kanha, and Kaziranga, we relied on this percentage to estimate total tiger densities from the data in Table 4. The resulting density estimates for Nagarahole, Kanha, and Kaziranga were, respectively, 15.33, 15.60, and 22.40 tigers/100 km². Based on Schaller's (1967) data on visually

identified adult tigers and their cubs in a 318-km² area in Kanha during 1964–1965, tiger density was 6.9 tigers/100 km². Our calculations based on data on home range and social organization from Chitwan, reported by Sunquist (1981) during field work in 1974–1980, yield tiger density estimates of 5.8–8.7 tigers/100 km². Based on snow tracking and radiotelemetry (E. N. Smirnov and D. G. Miquelle, *unpublished manuscript*), tiger densities reported from the temperate forests of the Russian Far East appear to be considerably lower (0.6–1.4 tigers/100 km²). The mean tiger densities estimated by us at all four sites are higher than the densities reported by other researchers.

Alluvial grasslands such as Kaziranga provide optimal habitats where tigers probably attain their highest ecological densities. Although Chitwan also is an alluvial grassland, tiger densities appear to be lower there than in Kaziranga, Nagarahole, and Kanha. Recent extirpation of large-sized prey such as wild buffalo and barasingha from Chitwan (Sunquist 1981) may be a contributory factor. Our study site in Nagarahole included both moist deciduous forests, with high prey densities, and dry deciduous forests, with lower prey densities (Karanth and Sunquist 1992). If tiger densities (excluding cubs) in moist deciduous forests of Nagarahole are considered separately, they (14.7 tigers/100 km²; Karanth 1995) seem comparable to the densities in Kaziranga ($\hat{D} = 16.8 \pm 2.96$ tigers/100 km²). Therefore, it appears as though moist deciduous forests and alluvial grasslands of tropical Asia represent the upper limits for ecological densities attained by wild tiger populations, whereas the temperate forests of the Russian Far East may represent the lower limit.

At Kanha, the tiger density estimated by us is considerably higher than the density reported by Schaller (1967) 30 years earlier. Conservation measures implemented during the intervening period, such as effective antipoaching operations, relocation of human settlements, and elimination of forest product exploitation (Panwar 1987), appear to have substantially increased the capacity of the Kanha area to support tiger populations. A similar rebound of tiger populations following comparable conservation interventions was also observed in Nagarahole (Karanth et al., 1998).

Wikramanayake et al. (1998) have synthesized remotely sensed vegetation maps with rapid assessment of tiger distributions to estimate the size of potential habitat blocks called "Tiger Conservation Units" (TCU). The sizes of TCUs containing the specific habitat types in which we sampled tiger densities range from 3600 to 23 900 km². Although these forest blocks are largely composed of suboptimal tiger habitats under multiple uses, they contain better quality habitat patches in wildlife protected areas ranging in size from 488 km² to 7013 km² (Wikramanayake et al., 1998). Assuming a typical, reasonably protected, but insular tiger habitat patch size of 1000 km², and using the lower and upper limits of tiger densities estimated by us in

this study (Table 4), we can estimate the sizes of typical surviving wild tiger populations in such better protected habitat blocks at 41–168 tigers, exclusive of cubs.

Influence of prey community abundance and structure on densities of large felids

Based on our data (Table 5), Kaziranga had the highest densities of large prey (16.9 animals/km²), followed by Pench (11.0 animals/km²), Nagarahole (8.7 animals/km²), and Kanha (4.5 animals/km²). The densities of medium-sized prey at these sites were, respectively, 41.2, 52.8, 41.4, and 52.2 animals/km². According to the predictions of Karanth and Sunquist (1995), Nagarahole, Pench, and Kaziranga, which support abundant prey in both size classes, should have leopards coexisting with tigers at relatively high densities. In Kanha, because of tigers switching to medium-sized prey, leopards should be relatively scarce. Our relative abundance index for leopards (*Results*) shows that this pattern holds true except for Kaziranga, which has a low index of leopard abundance. This exception to the predicted pattern could arise because ecological factors other than prey community structure may also influence leopard abundance in Kaziranga. Seasonal flooding or scarcity of trees that provide escape cover during interspecific interactions with tigers in the grasslands (K. U. Karanth, *personal observations*) could be among the factors constraining coexistence of leopards with tigers in Kaziranga.

Conclusions

We conclude that camera-trapping provides an attractive method for sampling tiger populations. Our estimates of tiger density were reasonable and generally support predictions about the influence of prey abundance and prey community structure on relative abundance of large felids. We are in the process of collecting similar data on tiger and prey abundances at other study locations in India in order to better test these predictions. In addition to estimation of population size and density, camera-trapping data collected at intervals over multiple years can be used to estimate population parameters such as rates of survival, recruitment, and dispersal. We conclude that camera-trapping holds great potential for estimating abundance and density of secretive animals that are individually recognizable, either because of natural markings or artificial marking following initial physical capture.

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APPENDIX

Estimation of $\text{var}(\hat{D})$ (Eq. 3) requires estimates of N and $\text{var}(\hat{N})$, both of which are obtained from program CAPTURE, and estimates of $A(W)$ and its variance. $A(W)$ was estimated as described in *Methods* by drawing the traplines on a map and adding the boundary strip to the perimeter of the defined area. The only other quantity requiring estimation was $\text{var}(\hat{A}(W))$. Our approach to this estimation problem was to

approximate each of the sampled areas as a circle with radius $c + \hat{W}$, where c is a constant computed to satisfy the equality, $\hat{A}(W) = \pi(c + \hat{W})^2$. A delta method approximation of $\text{var}(\hat{A}(W))$ is then given by

$$\widehat{\text{var}}(\hat{A}(W)) = 4\pi^2(c + \hat{W})^2 \widehat{\text{var}}(\hat{W}). \quad (\text{A.1})$$

Values of $\widehat{\text{var}}(\hat{A}(W))$ computed using Eq. A.1 were used in conjunction with Eq. 3 to compute $\widehat{\text{var}}(\hat{D})$.