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Estimation of Population and Survivorship of Leopard *Panthera pardus* (Carnivora: Felidae) Through Photographic Capture-Recapture Sampling in Western India

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Abstract: Understanding population ecology is fundamental to effectively managing large, wide-ranging carnivores such as the leopard, *Panthera pardus*. Being elusive and inhabitant of both forested and human dominated landscape, leopard is always in conservation priority. But the information of population dynamics of leopard is scarce because of methodological and logistical problems of sampling populations at the required spatial and temporal scales. In the present study, the population dynamics of leopard was studied based on capture histories of 40 individuals during five years from 2007 to 2011 in Sariska Tiger Reserve, Western India. The data was modeled under a likelihood-based, "robust design" capture-recapture analytic framework and ecological parameters such as time-specific population, density, survival, recruitment, emigration and growth rate was estimated explicitly. The estimated population size (N_t) of leopard varied from 9.0 ± 1.5 to 22.2 ± 3.6 and geometric mean rate of annual population change estimated as $\lambda = 1.04 \pm 0.29$. The estimated density of leopard varied from 3.1 ± 0.4 to 10.7 ± 1.8 in the effective trapping area with half MMDM model. The overall survival rate of leopard was estimated to be 0.71 ± 0.06. The "robust design" framework estimated a random temporary emigration parameter of y" = y' = 0.23 ± 0.11. The estimated recruitment of new animals, B_t, varied from 0 ± 1.9 to 11.7 ± 3.4. Despite some annual losses and temporal variation in annual recruitment, the leopard population in the study area was comparatively high with other study sites in Asia and Africa. In the present study, the photographic capture recapture technique gave the ability to model mean annual population change and survival rates of leopard, which were sufficiently precise and be useful for management purposes. This non-invasive method can be used for long term investigation of population dynamics of leopard in similar study sites.

Key words: Camera trapping · Growth rate · Leopard · Population estimation · Recruitment · Robust design · Survivorship

INTRODUCTION

Population estimation of carnivores is extremely difficult owing to an extensive spatio-temporal distribution, secretive life, wide ranging behavior, low detectability and low densities [1]. With time, several technologically sophisticated methods were evolved to estimate carnivore population. In Indian context, for carnivore density estimation, capture-recapture framework through camera trap has been found useful [2]. Camera traps have also enabled more accurate estimates of species abundance, species distribution, spatial variation and population size of cryptic carnivores like leopard and tiger. With long-term use, camera traps enable monitoring of changes in populations over time. The camera trap based on capture-recapture framework to estimate population of large carnivores has proven to be amongst the most successful non-invasive method, such as studies on tiger *Panthera tigris* [3, 4], leopard *P. pardus* [5, 6], jaguar *P. onca* [7], Geoffrey's cat *Leopardus geoffroyi* [8], snow leopard *Uncia uncia* [9] and striped hyena *Hyaena hyaena* [10, 11].

The problems of animal population sampling are the inability to survey the entire area of interest and the inability to detect all individuals even within the surveyed area [12, 13]. These problems have proven to be particularly intractable when estimating abundances and vital rates of rare or elusive species [14]. Such problems are exemplified by the leopard, which has an extensive range spanning a 40 million km^2 area across Asia and Africa, within which surviving populations occur patchily and at low densities. Thus far only two studies, in Phinda

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Private Game Reserve, South Africa [15] and Mkhuze Game Reserve, South Africa [16], both involving radio tracking of leopard, have generated estimates of leopard survival rates. However, high costs and logistical difficulties severely limit the potential use of radio-telemetry for estimating demographic parameters in leopard populations.

In this study, camera-trap sampling was followed to obtain capture history data for individual leopards over multiple seasons at a single location using the "robust design" capture-recapture approach [13, 17]. This capture-recapture design includes several secondary sampling occasions within each primary period (each year). This approach explicitly models the effect of capture probabilities on capture history data and is more efficient in terms of costs and effort than any other proven method of sampling tiger (*P. tigris*) and leopard populations in Indian sub-continent [18-20].

The present study was conducted in the National Park area of Sariska Tiger Reserve from 2007 to 2011. This 274 km^2 Sariska National Park supports high densities of wild prey 155 ungulates/ km^2) and leopards [21]. Before 2004, the tiger got exterminated from Sariska Tiger Reserve due to poaching, but the leopard and associated prey populations within the National Park area were reasonably well protected during study period. A number of six tigers were reintroduced in the study area during 2008-2011 to re-establish the tiger population. The surrounding Aravalli landscape, consisting of other protected areas, multiple-use forests, agricultural land and competition with tiger provided some possibilities for leopards to move in and out of the study area.

MATERIALS AND METHODS

Study Area: The study was carried out in Sariska Tiger Reserve from January 2007 to June 2011. Sariska Tiger Reserve lies in the State of Rajasthan, Western India (N27°05' to N27°45' and E76°15' to E76°35') (Fig. 1). The total area of the Tiger Reserve is 881 km^2, of which 273.8 km^2 is a notified National Park. The vegetation of this region is tropical dry deciduous forest and tropical thorn forest [22]. The climate is subtropical, characterized by a distinct winter (November-February), summer (March-June), monsoon (July-August) and post-monsoon (September-October). The average annual rainfall is 700 mm, occurring mostly during July-September.

The wild ungulates found in Sariska are chital (*Axis axis*), sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelus)* and wild pig (*Sus scorfa)*. Apart from leopards, other carnivores present are tiger, striped hyaena *(Hyaena hyaena)*. Small carnivores found are jackal *(Canis aureus)*, jungle cat (*Felis chaus*), common mongoose *(Herpestes edwardse*), small Indian mongoose (*H. auropunctatus*), palm civet (*Paradoxurus hermaphroditus*), small Indian civet (*Viverricula indica*) and Ratel (*Mellivora capensis*). In 2009, desert cat (*Felis silvestris*) was reported from Sariska [23]. Rhesus monkey (*Macaca mulatta*) and common langur (*Seminopithecus entellus*) are the two primates found. Porcupine (*Hystrix indica*), Rufous tailed hare (*Lepus nigricollis ruficaudatus*) also occur in Sariska [20].

There are 32 villages within the Tiger Reserve boundary and out of them ten are in Sariska National Park. The human population is over 1700 in the villages of National Park along with a population 10,000 livestock including buffalo, cow, goat and sheep. In the entire Sariska Tiger Reserve, the human population is around 6000 and the livestock population is more than 20,000 [20].

Estimation of Population of Leopard: Camera trapping data was collected from January 2007 to June 2011 in the study area to estimate the population of leopard. A preliminary survey was carried out during November to December 2006 in the intensive study area of 160 km^2 in the Sariska National Park by surveying available trails. Indirect signs such as pugmarks and scats of leopard were identified and marked using a handheld Global Positioning System. The entire study area was divided into two 80 km^2 blocks and each block was subdivided into 20 grids of 2x2 km^2. One pair of cameras was placed in each 2x2 km^2 grid. Camera traps were placed on the basis of leopard evidence (pugmark, scats) on the trails (Fig. 2).

Forty units of analog cameras were used which worked on passive infrared motion/ heat sensors. The camera traps were equipped with 35 mm lens and recorded the date and time of each photograph. The camera delay was kept at minimum (15 seconds) and sensor sensitivity was set at high. A total of 40 locations were selected for the placement of camera traps in the study area. Every five nights were considered as a single occasion, resulting in 18 occasions and effort of 3520 trap nights in 2007, 22 occasions and effort of 4720 trap nights in 2008, 26 occasions and effort of 5200 trap nights in 2009, 18 occasions and effort of 3440 trap nights in 2010 and 21 occasions and effort of 4080 trap nights in 2011. Individual leopard obtained from camera trap photographs were identified by combination of distinguishing character such as position and shape of rosettes on flanks, limbs and forequarter [2, 24].

Capture history of each individual was generated in an X matrix format [25]. Occasion-wise capture matrix was prepared for the analysis of population estimation. Estimation of population size using closed capture models requires the population under investigation to be both demographically and geographically closed. Population closure test was performed using software CloseTest [26]. The density (D) of leopard in the study area was

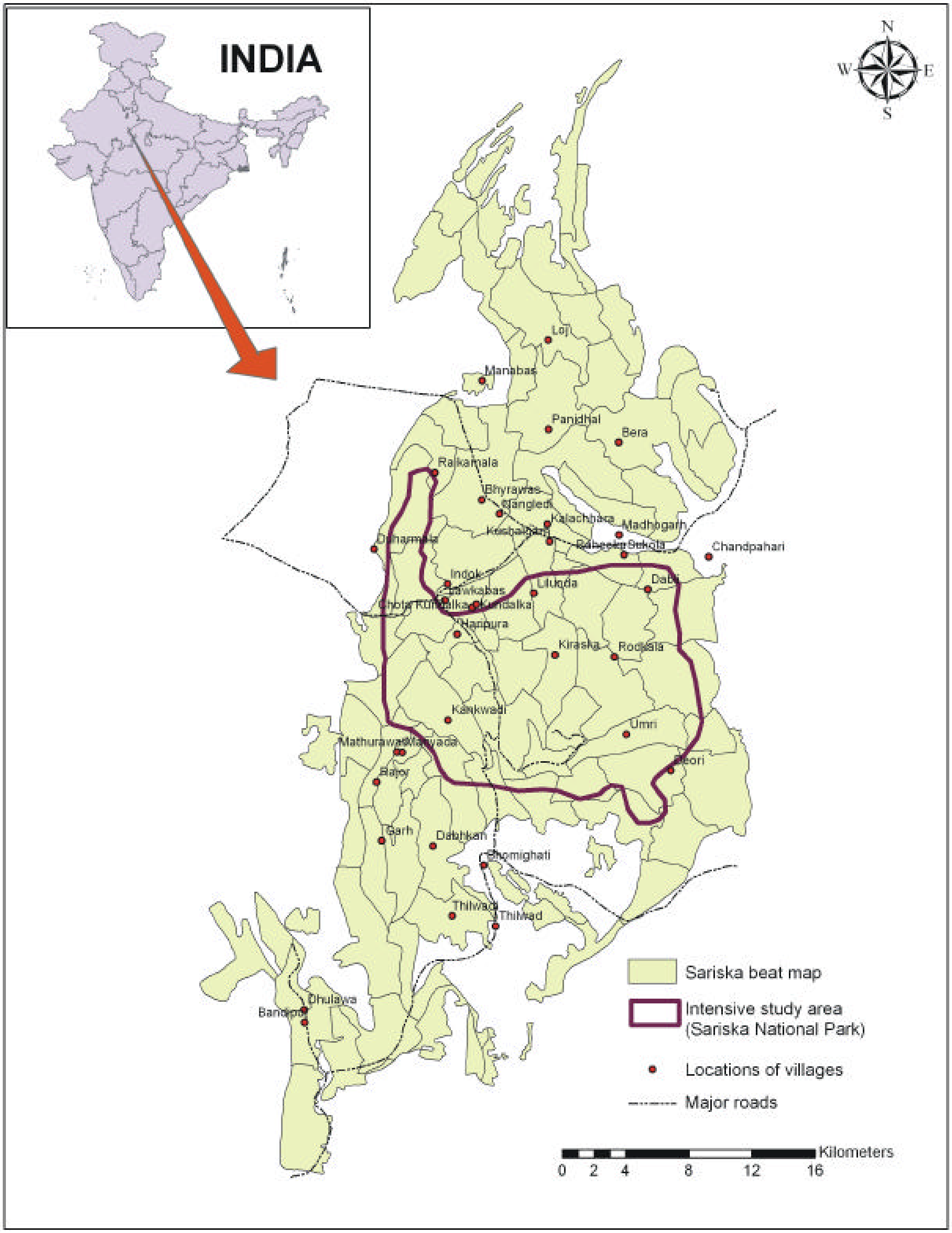

Fig. 1: Location of Sariska Tiger Reserve and the intensive study area

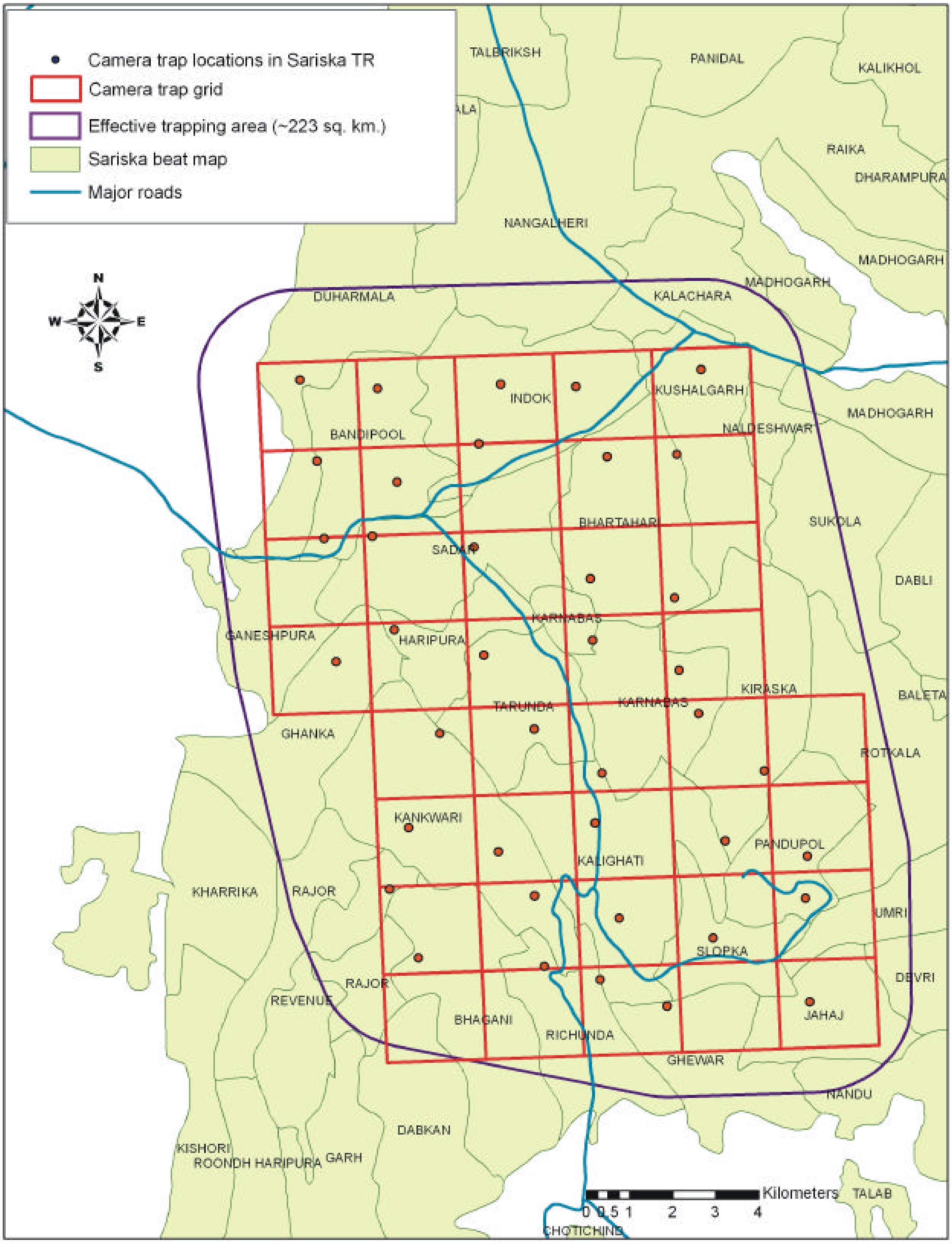

Fig. 2: Camera trap locations and effective trapping area in Sariska Tiger Reserve

estimated using different methods such as MMDM/2 model, spatial maximum likelihood model [27] and Bayesian model [28] using program DENSITY 4.1 [27] and SPACECAP [28].

Estimation of Survival Rates of Leopard: To estimate the survival rates of leopard in the study area, the X matrix [25] was used following 'Robust Design' [12, 17, 29, 30] model with full closed capture with heterogeneity option in program MARK [31]. The study consisted of five "primary periods" sampling covering five years. The leopard population was expected to be open to gains and losses between these primary periods. There were multiple "secondary sampling periods" within each primary period. Each occasion in the primary sampling period was considered as one secondary sampling period and the population was assumed to be closed to gains and losses among these secondary periods [13].

The analytic methods dealt with possible effects of individual heterogeneity, trap-response behavior and time-related variations on capture probabilities [12, 13, 25], as well considered temporary emigration (the probability of an individual leopard not being available for trapping during one or more primary sampling period); transience (the probability that a newly captured individual leopard was just passing through the study area, with a near-zero chance of returning to be recaptured during the study); and losses (the probability of death or permanent emigration) [13].

The modeling of capture probabilities were investigated by assessing the discriminant function model selection statistics for the four likely models in program MARK [31] following M(o) (constant capture probability), M(h) (capture probability heterogeneous among individuals), M(bh) (behavioral response in capture probability with heterogeneity among individuals) and M(tbh) (capture probability affected by secondary sampling period, trap response and heterogeneity) models. Accordingly, the overall X matrix was analyzed to estimate the survival rates for the entire study period and also for each primary sampling period in the study area [13].

The set of models for the analysis of leopard survivorship following robust-design included a number of parameters. The abundance of leopard {N(t)} was considered time dependent for all five primary periods. The annual survival rate of leopard was modeled as time variant {S(t)} or constant {S(.)} for all five primary periods to get the information at both annual and overall scale. The rate of emigration (γ") and immigration (γ') was modeled as time variant {γ"(t), γ'(t)} or constant {γ"(.), γ'(.)} and also whether they are different within each primary periods or equal { γ"(t)=γ'(t) or γ"(.)=γ'(.)}. In heterogeneity model, the probability of mixture between two groups was modeled time variant {π(t)} (different mixing parameter for each primary sampling period) or constant {π(.)} (same mixing parameter to all five primary periods). The probability of capture (p) and recapture (c) were modeled time variant {p(t), c(t)} or constant {p(.), c(.)}. In heterogeneity model, both of these parameters were grouped {p(g), c(g)} (two group heterogeneity). It was also investigated that, the probability of capture (p) and recapture (c) were different or equal {p(g)=c(g)} in heterogeneity model.

These different parameters and corresponding sources of variation led to set of 32 models of which 17 models were considered being most reasonable following Mh estimator. The AICc (Akaike Information Criterion) and AICc weight were used to select the most appropriate model for the data [32]. The population growth rate and recruitment were estimated from parameters by the modeling. The recruitment (B_t) was estimated by subtracting the expected number of survivors from the previous period (*t*) from the present (*t+1*) population size [12, 17]. The finite rate of increase (λ_t) or growth rate in abundance between sampling periods *t* and *t + 1* was calculated dividing the abundance in present period (*t+1*) by the abundance of previous period (*t*).

RESULT

Estimation of Population of Leopard: The camera trapping resulted in a total of 71 photographs of 19 individual leopards in 2007, 64 photographs of 17 individuals in 2008, 61 photographs of 14 individuals was recorded in 2009, 38 photographs of 10 individuals in 2010 and 42 photographs of 14 individuals in 2011. The 40 trapping locations covered minimum convex polygon area of 118 km^2 and an effective trapping area (ETA) of 206.1 km^2, 223.8 km^2, 223.1 km^2, 250.5 km^2 and 231.5 km^2 with a buffer of half mean maximum distance moved model (1/2 MMDM) in 2007, 2008, 2009, 2010 and 2011 respectively (Table 1).

The statistical test in program CloseTest [26] was consistent with the assumption that the population was closed ($p>0.05$) in each primary period (Table 2). The model selection algorithm of program MARK [31] identified M(h) as most appropriate model which was highest in the model selection criteria in each primary period (Table 2). Although M(o) scored high in 2008 and 2010, this model is not robust to any deviations from the model assumption of homogeneous capture probabilities among individuals [13]. M(h) estimator scored highest (1.00) for all the primary periods, hence, M(h) jackknife and half normal detection function for spatially explicit density was used for all the five years to estimate the leopard population in the study area. The overall model selection test based on discriminant functions comparatively scored over various models between 2007 and 2011 is given in Table 2.

Table 1: Primary and secondary sampling periods, sampled areas, camera-trapping effort and number of individual leopards photo-captured at Sariska from 2007 to 2011

Primary Period	No. of secondary period	No. of days	Effective trapping area	Effort trap nights	No. of leopards caught	Cumulative no. of leopards caught
1 (2007)	18	88	206.6	3520	19	19
2 (2008)	22	108	223.8	4720	17	25
3 (2009)	26	130	223.1	5200	14	32
4 (2010)	18	86	250.5	3440	10	36
5 (2011)	21	102	231.5	4080	14	40

Table 2: Tests for population closure and model selection statistics based on leopard photographic capture history data in Sariska from 2007 to 2011.

			Model score			
Primary Period	Test for additions (p-value)	Test for losses (p-value)	M^0	M^h	M^{bh}	M^{tbh}
1 (2007)	p>0.05	p>0.05	0.98	1.00	0.63	0.68
2 (2008)	p>0.05	p>0.05	1.00	1.00	0.48	0.59
3 (2009)	p>0.05	p>0.05	0.94	1.00	0.64	0.64
4 (2010)	p>0.05	p>0.05	1.00	1.00	0.53	0.61
5 (2011)	p>0.05	p>0.05	0.95	1.00	0.85	0.76

Table 3: Population and Density estimation of leopard in the study area of Sariska Tiger Reserve between 2007 and 2011.

	Estimated population in the study area		Estimated density / 100 km^2		
Primary Period	Mo	Mh (Jackknife)	MMDM/2	MLDens	Bayesian
1 (2007)	19.0 (0.9)	22.2 (3.6)	10.7 (1.8)	9.3 (2.2)	8.4 (1.4)
2 (2008)	17.0 (0.6)	17.9 (3.0)	7.6 (0.6)	7.7 (1.9)	7.4 (1.3)
3 (2009)	14.0 (0.6)	16.3 (3.3)	6.2 (0.8)	5.3 (1.4)	5.2 (0.8)
4 (2010)	8.0 (0.3)	9.0 (1.5)	3.1 (0.4)	3.3 (1.2)	2.3 (0.5)
5 (2011)	14.0 (0.9)	16.9 (3.4)	6.0 (0.5)	7.1 (2.0)	5.8 (1.1)

Note: The number in the parentheses is the standard error of that estimator

Population estimates were calculated using model M(h) in the same study area between 2007 and 2011. Since the probability of additions and losses in each primary sampling period was greater than 0.05 [26], it was confirmed that the leopard population was geographically and demographically closed for each year. The population and density of leopard in the study area was estimated in the program DENSITY 4.1 [27]. The estimated population (*N*) of leopard in the study area with M(h) Jacknife estimator was 22.2 ± 3.6 in 2007, 17.9 ± 3.0 in 2008, 16.3 ± 3.3 in 2009, 9.0 ± 1.5 in 2010 and 16.9 ± 3.4 in 2011 (Table 3). The population of leopard was also estimated with M(o) model (Table 3).

The estimated densities with Mh jackknife estimator and half mean maximum distance moved model (MMDM/2) were 10.7 ± 1.8 individuals/ 100 km^2 in 2007, 7.6 ± 0.6 individuals/ 100 km^2 in 2008, 6.2 ± 0.8 individuals/ 100 km^2 in 2009, 3.1 ± 0.4 individuals/ 100 km^2 in 2010 and 6.0 ± 0.5 individuals/ 100 km^2 in 2011 (Table 3). Half normal detection function fitted the best and the densities arrived using multiple likelihood model (MLDens) were 9.3 ± 2.2 individuals/ 100 km^2 in 2007, 7.7 ± 1.9 individuals/ 100 km^2 in 2008, 5.3 ± 1.4 individuals/ 100 km^2 in 2009, 3.3 ± 1.2 individuals/ 100 km^2 in 2010 and 7.1 ± 2.0 individuals/ 100 km^2 in 2011 (Table 3). The estimated densities using Bayseian model is given in Table 3.

Estimation of Survival Rates of Leopard: To estimate the survival rate of leopard following "robust design", combinations of different parameters were determined following M(h) estimator, because M(h) estimator was selected as the best estimator according to model selection test based on discriminant functions, These various combinations of parameters led to the development of a set of 32 models for the entire robust design data set, of which 17 models were found appropriate following M(h) estimator. Model selection statistics for the full robust-design likelihoods (Table 4) provided inferences about variation in the parameters. The model with the lowest AICc was judged to be substantially better than the others in the set of 32 models (AICc weight = 0.34; the AICc weight of the nearest competitor is 0.11). Thus, inferences were based on this model and it was decided not to use model averaging for parameter estimates.

Model {S(.), γ'(.)=γ''(.), π(.), P(g)=C(g), N(t)} was selected based on lowest AICc. Estimates for leopard population survival rates generated by the selected model are reported in Table 4. Under this model, heterogeneous capture probabilities were modeled using constant group-specific capture (p = 0.37 ± 0.05; p = 0.10 ± 0.01) and same recapture probabilities (c = 0.37 ± 0.05; c = 0.10 ± 0.01) (means ± SE), but the probability of mixture of animals in each group π(.) was not changed over time (0.14 ± 0.05). This model and associated estimates suggest no trap response behavior, where probability of capture of unmarked leopard was equal of the recapture of marked leopard. The overall survival rate of leopard in the entire sampling period was estimated to be 0.71 ± 0.06. The annual survival rate of leopard in the study area varied

Table 4: Model selection statistics for robust design analysis of leopard capture data in Sariska from 2007 to 2011.

Model	AICc	Delta AICc	AICc weight	Model Likelihood	No. of parameters	Deviance
{S(.), y'(.)=y"(.), pi(.), P(g)= C(g), N(t)}	1188.7835	0.0000	0.33511	1.0000	10	1168.8048
{S(.), y'(.), y"(.), pi(.), P(g)=C(g), N(t)}	1190.9177	2.1342	0.11528	0.3440	11	1168.7479
{S(t), y'(t), y"(t), pi(.), P(g)=C(g), N(t)}	1191.4681	2.6846	0.08755	0.2613	17	1155.7491
{S(.), y'(t)=y"(t), pi(.), P(g), C(g), N(t)}	1191.5888	2.8053	0.08242	0.2460	13	1164.9801
{S(t), y'(t)=y"(t), pi(.), P(g), C(g), N(t)}	1191.6745	2.8910	0.07896	0.2356	16	1158.2629
{S(.), y'(t)=y"(t), pi(t), P(t,g)=C(t,g), N(t)}	1191.8584	3.0749	0.07202	0.2149	23	1141.8613
{S(.), y'(t), y"(t), pi(.), P(g), C(g), N(t)}	1192.2239	3.4404	0.05999	0.1790	16	1158.8122
{S(t), y'(.)=y"(.), pi(.), P(g), C(g), N(t)}	1192.7600	3.9765	0.04589	0.1369	13	1166.1514
{S(t), y'(t)= y"(t), pi(t), P(t,g)=C(t,g), N(t)}	1193.1901	4.4066	0.03701	0.1104	26	1135.7619
{S(.), y'(.)=y"(.), pi(t), P(g)=C(g), N(t)}	1193.9127	5.1292	0.02579	0.0770	14	1165.0560
{S(.), y'(t), y"(t), pi(t), P(t,g)=C(t,g), N(t)}	1194.2942	5.5107	0.02131	0.0636	26	1136.8660
{S(t), y'(.), y"(.), pi(.), P(g), C(g), N(t)}	1194.9965	6.2130	0.01500	0.0448	14	1166.1397
{S(.), y'(.), y"(.), pi(t), P(t,g)=C(t,g), N(t)}	1195.1315	6.3480	0.01402	0.0418	21	1149.9784
{S(t), y'(t), y"(t), pi(t), P(t,g)=C(t,g), N(t)}	1197.3541	8.5706	0.00461	0.0138	28	1134.8581
{S(t), y'(.)= y"(.), pi(t), P(t,g)=C(t,g), N(t)}	1198.6824	9.8989	0.00238	0.0071	23	1148.6852
{S(.), y'(.)=y"(.), pi(t), P(t,g)=C(t,g), N(t)}	1199.1223	10.3388	0.00191	0.0057	21	1153.9691
{S(t), y'(.), y"(.), pi(t), P(t,g)=C(t,g), N(t)}	1200.9480	12.1645	0.00077	0.0023	24	1148.4962

Table 5: Estimation of survival rates of leopard in the study area between 2007 and 2011

Primary Period	No. of leopards caught	Abundance (N)	Survival rate with Robust Design (S)	Population growth rate (λ)	Recruitment (*B*)
1 (2007)	19	22.2 (3.6)	0.72 (0.14)	0.81 (0.15)	1.92 (0.58)
2 (2008)	17	17.9 (3.0)	0.59 (0.13)	0.91 (0.21)	5.74 (1.96)
3 (2009)	14	16.3 (3.3)	0.94 (0.16)	0.55 (0.08)	0 (1.97)
4 (2010)	10	9.0 (1.5)	0.58 (0.08)	1.87 (0.91)	11.68 (3.45)
5 (2011)	14	16.9 (3.4)			
Overall			0.71 (0.06)	1.04 (0.29)	

Notes: Values in parentheses are estimated standard errors. Blank cells (for 2007) indicate value that was not estimated because the study was beginning.

from 0.72 ± 0.14 between 2007 and 2008 to 0.59 ± 0.13 between 2008 and 2009, 0.94 ± 0.16 between 2009 and 2010 and 0.58 ± 0.18 between 2010 and 2011. The equality of the two temporary emigration parameters indicated random temporary emigration, with an estimate of y" = y' = 0.24 ± 0.11 (~24% temporary emigrants in each primary period ± SE). Theoretically, the probability of temporary emigration (γ") of one individual from the sample between sampling occasions was estimated to be 0.24, eventually the probability of remaining in the sample (1-γ") between sampling occasions was 0.76. Similarly, the probability of remaining outside the sample (γ') (not emigration) was estimated to be 0.24 and the probability that an individual which was out of the sample (1?γ') in one sampling period but enters the sample in next sampling period (i.e., return rate of temporary emigrants) was 0.76. Recruitment estimates (B_i) for these sample periods varied between 0 and 11.7 (Table 5), but these estimates were relatively imprecise, because the reasons behind temporary emigration between primary sampling periods were unknown. The population growth rate varied between 0.55 and 1.87 (Table 5). Overall, the geometric mean rate of population change was estimated as λ_t = 1.04 ± 0.29 (estimated mean ± SE), representing an approximate 4% increase in population in the entire study period.

DISCUSSION

The population and density of leopard in the study area was estimated using Mh model and jackknife estimator as the capture and recapture probabilities were different in different primary periods depending upon the movement pattern of leopard individuals. Poor recapture rates of some individuals in the five yearlong study, can affect population estimation and it was understandable that larger number of recaptures will result in more accurate and precise population estimates. Effort required in terms of sampling occasions suggested that a minimum of 80-90 days are required in an area of 250 km^2 to get reliable density estimates for leopard in the study area while for tigers in Corbett Tiger Reserve it varies from 30 to 40 days to get reliable density estimates [33].

Although photographic capture-recapture sampling methodology has been used to estimate the density of tigers in many protected areas throughout India [3, 4], similar density estimates of leopards are only available from Rajaji National Park [5, 6], Pench Tiger Reserve (WII, ongoing study) and Mudumalai Tiger Reserve [34]. The leopard population estimate in the present study based on the capture-recapture framework is lower than the density estimated from the moist deciduous forests of Rajaji National Park and Mudumalai Tiger Reserve (Table 6). A comparison of camera trapping results in the present study with similar studies conducted at other sites on leopard showed that the density estimate in 2007 (10.7/ 100 km^2) was comparatively similar to estimates obtained from other studies (Table 6). The density estimate in 2010 (3.1/100 km^2) in the study area was found comparatively lower than the other studies (Table 6). However, in the absence of comparable density estimates

Table 6: Estimated leopard densities in different protected areas.

Study Site	Density/ 100 km^2	Author
Present Study (2007)	10.7	
Present Study (2010)	3.1	
Satpura National Park	7-10	Edgaonkar (2007)
Rajaji National Park (West)	9.8	Mondal (2006)
Rajaji National Park (East)	14.9	Harihar *et al.* (2009)
Mudumalai TR	14.9	Kale *et al.* 2011
Pench TR	8.0	WII, ongoing study (2006-11)
Mera Poh, Malayasia	6	Kawanishi and Sunquist (2004)
Phinde Reserve, SA	7.1	Balme *et al.* (2009)
Mkhuze Reserve, SA	10.7	Balme *et al.* (2009)
Ngorongoro NP	7.5	Kruuk (1972)
Hwange, Zimbabwe	2.1	Wilson (1975)
Lake Manyara, Tanzania	11	Schaller (1972)
Serengeti NP, Tanzania	5.6	Schaller (1972)
Nairobi NP, Kenya	8.5	Rudnai (1974)
Kruger NP, South Africa	5.1	Pienaar (1969)

from across representative habitats within India, it is difficult to identify the regulators of relative abundance of leopards.

The present study estimated the overall annual survival rate for leopard in the study area as 71%. The complement of this annual survival estimate was 29%, which includes deaths and permanent or temporary emigration from the study area. Although the bulk of this annual loss of leopards was likely to be from mortalities and emigration, which includes an unknown fraction of animals that permanently emigrate out of the study area as dispersing sub-adults or as evicted residents as observed by Smith [35] in tiger population of Royal Chitwan National Park. Karanth and Stith [36] hypothesized that although tiger populations have high mortality rates from natural and anthropogenic causes, they can be demographically viable if supported by an abundant prey base. This hypothesis can also be implemented on leopard population as both tiger and leopard occupy the top position in food chain [24]. As observed, in the present study the estimated population of leopard in the study area declined from 16.3 ± 3.3 in 2009 to 9.0 ± 1.5 in 2010; which may be attributed to temporary emigration due to tiger re-introduction in the study area. After the extermination of tiger in Sariska, leopard took over the entire tiger habitat, which was the best habitat available in Sariska and became the top predator [20]. The density estimates for leopard in 2007 and 2008 were comparatively higher, when there was no tiger in the study area. Six tigers were re-introduced in the study area between 2008 and 2010 and after that density of leopard declined significantly (from 6.2 ± 0.8 in 2009 to 3.1 ± in 2010) in the study area. But, after tiger established their home ranges in Sariska, the abundance of leopard again went up to 16.9 ± in 2011 and density raised to 6.0 ± 0.5. In regions of high tiger density, for example, tigers are known to out-compete leopards [24, 37]. Radio-tracking studies on tiger and leopard movements indicate that leopards avoid areas frequented by tigers [38]. In Sariska, leopard were found everywhere in the study area before tiger release. But after the tiger release, leopard avoided valley habitats which were frequented by tigers. They largely occupied the peripheral hilly areas close to human population, which are less frequented by tigers in the study area.

After the re-introduction of tigers, the photo-capture rate of leopard and tiger from camera trapping per 100 trap nights in each grid was calculated and projected on Sariska beat map through color gradient. It was found that the grids with maximum tiger photo-captures were largely avoided by leopard and selected those grids where tiger occurrence is less [39]. Site utilization of both the species was estimated with site-wise capture records. Site utilization of leopard was 0.75 before tiger release but after tiger release site utilization of leopard and tiger were 0.55 and 0.53 respectively. The detection probability of leopard was 0.36 in the absence of tiger and it was 0.06 when tiger was present.

The estimated overall survival rate of leopard in the study area was comparable (71%) with other studies [15, 16]. Similar findings were observed by Karanth *et al.* [13] in tiger population in Nagarhole Tiger Reserve. The overall population growth rate of 1.04 ± 0.29 signifies that the leopard population is not declined in the study area. The high wild ungulate prey density in the study area (155 ungulates/ km^2) [21] appears to be critical for sustaining a stable leopard population in the study area as observed by Karanth *et al.* [13] for of tiger population in Nagarahole Tiger Reserve. In total, 11 mortality cases of leopard were recorded in the study area during study period, of which three were due to road accident, one was due to poisoning, one was killed by tiger and six were natural death. In spite of this mortalities, the result from the present study support the general assumptions and predictions of the demographic model as developed for tiger by Karanth and Stith [36], that wild leopard population in Sariska can be demographically viable if supported by an abundant wild prey base. The Tiger Reserve has forest continuity in South with Jamwa Ramgarh Wildlife Sanctuary and in North-East with Alwar Territorial Forest Division, thus encompassing a total area of 2388 km^2, can ensure the long-term survival of leopards in semi-arid landscape of Aravalli Hills.

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