Estimating leopard (*Panthera pardus*) densities when populations comprise polymorphic phenotypes: an application of spatial mark-resight models

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Abstract

Melanism is a form of pigmentation polymorphism where individuals have darker coloration than what is considered the "wild" phenotype. In the case of leopards, *Panthera pardus*, melanism occurs at higher frequencies amongst populations in tropical and subtropical moist forests of south and southeast Asia, presenting a unique challenge in estimating and monitoring these populations. Unlike the wild phenotype that are readily recognizable by their rosette patterns, melanism results in individuals being unidentifiable or 'unmarked' through photographic captures obtained using white flash cameras. Spatial mark-resight (SMR) models that require only a subset of the population to be 'marked' offer the opportunity to estimate population density. In this study, we present an application of SMR models to estimate leopard densities using camera trap survey data from three sampling sessions at Manas National Park (MNP), India. By using an SMR model that allowed us to include captures of unidentified sightings of marked individuals, we were also able to incorporate captures where identity was either not confirmed or only known from a single flank. Following 18,674 trap-days of sampling across three sessions, we obtained 728 leopard photo-captures, of which 22.6% (165) were melanistic. We estimated leopard densities of 4.33, 2.61and 3.37 individuals/100km^2 across the three sessions. To our best knowledge, these represent the first known estimates of leopard densities from such populations. Finally, we highlight that SMR models present an opportunity to revisit past camera trap survey data for leopards and other species that exhibit phenotypic polymorphism towards generating valuable information on populations.

1. Introduction

Melanism is an observed form of pigmentation polymorphism that occurs in several organisms (Majerus, 1998). Melanistic individuals have darker coloration than what is considered the natural or "wild" phenotype. Amongst Felids, melanism is believed to have evolved independently several times, being documented in 14 of 40 species, and is likely associated with several ecological, physiological and behavioral factors (Eizirik et al., 2003; Graipel et al., 2019; Schneider et al., 2015, 2012). In the case of leopards, *Panthera pardus*, melanism is induced by a recessively inherited mutation in the ASIP (agouti signaling protein) gene and occurs at range-wide frequency of ~11%(da Silva et al., 2017; Schneider et al., 2012). Although melanistic individuals most often occur as a polymorphic phenotype, some populations exhibit near fixation of this recessive allele (Kawanishi et al., 2010). As tropical and subtropical moist forests of south and southeast Asia harbour higher frequencies of melanism (da Silva et al., 2017), this presents a unique challenge in estimating and monitoring populations in these regions.

As the "wild" phenotype is individually identifiable by rosette patterns, photographic capture-recapture sampling is regarded as the most robust and cost-effective method of estimating population size and density (Balme et al., 2009; Farhadinia et al., 2019). However, the masking of rosettes, caused by melanism (Schneider et al., 2012), results in a proportion of individuals remaining 'unmarked'. Hedges et al., (2015) discovered that by forcing infrared flash camera traps (IR cam-traps) into night mode, the rosettes of melanistic leopards were revealed allowing for individuals to be identified and population density estimated using spatial capture-recapture (SECR) analysis. Using IR cam-traps to monitor leopard populations that comprise both wild and melanistic phenotypes allows for "all" individuals to be identified. Given that IR cam-traps are at least 1.5-2 times more expensive than white flash units (Trailcampro, 2020), this leads to increased survey costs. The use of IR cam-traps may be

inevitable at sites where a near fixation of melanism has been observed (Kawanishi et al., 2010). But at most other sites where both phenotypes occur, mark-resight models that require only a subset of the population to be 'marked' offer an alternative to estimating population size and density (Royle et al., 2014).

Mark-resight methods have been in use for some time (McClintock and White, 2012), and more recently spatial mark-resight (SMR) models have also been developed (Chandler and Royle, 2013; Efford and Hunter, 2018; Sollmann et al., 2013). These models estimate population density under the assumption that both marked and unmarked individuals have the same probability of being encountered in the re-sighting occasions. A rare circumstance when this assumption is satisfied is when some individuals carry natural marks and others do not (Rich et al., 2014). However, unlike in studies where the number of individuals that are physically marked and released prior to the resighting session is known, in cases where individuals are identified by natural markings (as with leopards), the number of marked individuals is unknown and needs to be estimated from resighting data (Efford and Hunter, 2018; Royle et al., 2014). Another assumption is that marked individuals are always correctly identified. Often during camera trap surveys, partial identities are obtained (i.e. right-only and left-only captures) and/or marks are unreadable (owing to motion blur obscuring marks or marks being hidden from view; Figure A1). Although the inclusion of this information is believed to have negligible effects on the estimate of density, recent developments in SMR models allow for the incorporation of such data in the estimation process (e.g. Efford and Hunter, (2018)), ensuring no loss of capture data.

In this study we present an application of SMR models to estimate leopard densities at Manas National Park (MNP), India, where the population comprises of both wild and melanistic phenotypes (Figure 1). Furthermore, as we use data from three camera trapping

sessions, we explore the effects of pooling parameter values that could be common across sessions towards improving the precision of our density estimates.

Figure 1

2. Materials and Methods

2.1 Study area

MNP is a 850 km^2 protected area along the Indo-Bhutan international border (see Lahkar et al., (2020) & (2018) for further details). It lies within the Tropical and Subtropical Moist Broadleaf Forest biome (Olson et al., 2001), where the observed frequency of melanism is five-fold higher than the expected number based on the overall average (da Silva et al., 2017). Since the end of ethno-political conflict in the region in 2003, MNP has received much biodiversity research and conservation attention (Borah et al., 2014; Lahkar et al., 2020, 2018). Nevertheless, the population status of leopards is poorly understood. Borah et al., (2014) estimated a density of 3.40±SE 0.82 leopards per 100 km^2; however, this was based on an SECR analysis of only rosetted individuals.

2.2 Field methods

Leopard photo-capture data for this study were obtained from systematic camera trapping surveys conducted across three successive cool dry seasons (December to April) of 2016-17, 2018 and 2018-19 across MNP (Table 1; Figure A1). We used 4 km^2 (in 2016-17 & 2018-19) and 2 km^2 (in 2018) grids to guide the placement of digital white flash passive camera traps (Panthera, New York, USA, Models V_4, V_5 and V_6) that were operational for 24 hours a day. Within each grid we placed a pair of cameras, facing each other, at a single trap-location that was selected to maximize the capture of large carnivores. Trap locations were selected following reconnaissance surveys conducted along forest paths, roads, ridges, dry river beds and animal trails prior to each session's camera-trapping. Sampling was restricted to a period of 60 days to ensure temporal closure. We downloaded the photographs from all trap stations

and catalogued them using Camera Trap File Manager software (Olliff et al., 2014), at regular intervals (usually twice a week). Finally, we created session-specific databases of leopard captures that specified the date, time and location of capture for further analyses.

Table 1

2.3 Spatial Mark-Resight analysis

To estimate density, SMR models require two key datasets: the spatial detection histories of 'marked' and occasion-specific spatial counts of 'unmarked' individuals. To generate detection histories of marked individuals, we first linked left and right flank images based on time and location and identified leopards based on their unique rosette patterns by visual comparisons, confirmed by at least 2 authors. We constructed session-specific spatial detection histories that indexed the capture location and daily sampling occasion of each individual capture. Non-independent captures (i.e. the same individual at the same location on a single sampling occasion and observations of non-independent individuals, e.g. cubs) were discarded. Given that we obtained several captures of individuals whose identity was only known from a single flank (either left or right), we created two spatial detection history datasets for each session (Both+Left and Both+Right datasets). Session-specific spatial counts of 'unmarked' (melanistic) individuals (*Tu*) were constructed as matrices where detectors represented rows and sampling occasions columns.

As we also wished to include capture data of unidentified sightings of marked individuals (*Tm*), we constructed session-specific spatial count datasets that incorporated captures of rosettted individuals where marks were unreadable (Figure A1) and captures where identity was only known from a single flank (either right or left). Prior to analyses, 'capthist' objects were constructed using package 'secr' in program R (Efford, 2020; R Development Core Team, 2014). Flank- and session-specific 'capthist' objects were compiled that included spatial detection history dataset (e.g. Both+Right), spatial counts of 'unmarked' individuals

(Tu), the complementary spatial count dataset of unidentified sightings of marked individuals (Tm_{Left}) and a session-specific matrix that specified individual trap layout (X and Y location in UTMs) and functionality across sampling occasions.

Population densities ($\widehat{D}$) were estimated using a maximum likelihood-based SMR model implemented in package 'secr' within the R environment (Efford, 2020; Efford and Hunter, 2018; R Development Core Team, 2014). We fit 'sighting-only' models where the number of marked individuals was unknown and no marking occasions were specified. As we incorporated data on unidentified sightings of marked individuals, we allowed for the estimation of a parameter for incomplete identification of marked animals when they were resighted (pID). As the sampling frames across sessions were consistent, we created a single state-space file by applying a 15 km buffer around the trap area and generating a fine grid of equally spaced points, each representing 0.25 km^2. We used forest cover to represent suitable and non-suitable habitat. Flank- and session-specific population densities ($\widehat{D}$), were obtained using a half-normal detection function where an intercept (g0) and scale parameter (sigma) were estimated.

To assess the effects of pooling parameter values that could be common across sessions, we also implemented multi-session analyses of the data. We first merged the session-specific data for each of the flanks and created two multi-session datasets (Both+Left and Both+Right). We constructed a candidate set of eight models where g0, sigma and pID were modelled in all parameter combinations of constant (.) and session (s) variant effects. We ranked models using Akaike's Information Criterion adjusted for sample size (AICc; Burnham and Anderson, (2002)). All parameter inferences were based on model-averaged estimates. Finally, we also estimated the population densities of rosetted leopards using a maximum likelihood-based SECR analysis implemented in package 'secr' within the R environment to compare against estimates obtained from the SMR analysis.

3. Results

From a trap effort of 18,674 trap-days across three sampling sessions at MNP, we obtained 728 leopard photo-captures, of which 22.6% (165) were melanistic. While individuals were identified from both flank images in 445 (61.2%) captures, we obtained 70 (9.6%) captures of individuals identified from a single flank and 445 (61.2%) and 48 (6.6%) captures of unidentified rosetted individuals. The number of individuals uniquely identified from rosette patterns (Mt+1), detections (*ndet*) used in spatial detection histories, detections of unidentified marked individuals (*Tm*) and detections of melanistic individuals (*Tu*) varied between flank and session-specific datasets (Table 1).

Leopard population density point estimates ranged from 2.61 to 4.33 individuals/100km^2, with strong congruence between both single session and multi-session analyses (Table 2 and Figure A3). The 'best-flank' datasets (i.e. datasets with higher number of individuals identified) varied between sessions resulting in point estimates of 4.33±SE 0.18, 2.61±0.15 and 3.37±0.14 individuals/100km^2 for session 1, 2 and 3, respectively (Table 2). Estimate precision was relatively higher for multi-session analyses (CI width (D); Table 2 and Figure 2). The best fit multi-session model for both flank datasets was one that incorporated constant proportion identified (*pID*) and session-specific intercept (g0) and scale parameters (σ) (Table A1). Finally, we show that point estimates of rosetted leopards obtained from an SECR analysis were lower than estimates derived from the SMR analysis (Table A2).

Table 2

Figure 2

4. Discussion

In this study, we present an application of SMR models to estimate leopard densities when the population comprises of both melanistic and wild phenotypes. The point estimates of 4.33±SE 0.18, 2.61±0.15 and 3.37±0.14 individuals/100 km^2 across three sampling sessions

likely represent (to our best knowledge) the first robust estimates of leopard densities from such mixed populations. In addition, we show that by sharing parameters across sessions, our estimate precision was improved.

Leopards are the most wide-ranging of large felids, yet their populations have been reduced, isolated, and even extirpated from large portions of their historic range owing to a host of threats (Jacobson et al., 2016; Rostro-García et al., 2016; Stein et al., 2020). Although the species receives research and conservation attention, there is a spatial bias in these efforts with studies estimating population size using camera-trap surveys being concentrated in Africa (*P. p. pardus*) and south Asia (*P. p. fusca*) (Farhadinia et al., 2019; Jacobson et al., 2016). Amongst populations that comprise both phenotypes (e.g. the Western Ghats of India; da Silva et al., (2017)), camera-trap surveys have either not estimated leopard densities (e.g. Karanth et al., (2017)), or have excluded captures of melanistic individuals (e.g. Jhala et al., (2015)). Given excluding melanistic captures misrepresents the population, SMR models provide an opportunity to revisit photographic capture data from past surveys towards generating estimates of leopard densities at these sites.

SMR models have been developed and implemented for a range of sampling scenarios (Efford and Hunter, 2018; Sollmann et al., 2013; Whittington et al., 2018). In particular, the use of camera-trap surveys are appealing as they are cost-effective and allow for sampling carnivores that are wide-ranging, nocturnal, secretive and occur at low population densities (Alonso et al., 2015; Jimenez et al., 2019; Kane et al., 2015; Murphy et al., 2019; Whittington et al., 2018). When individuals are identified by natural markings (as in the case of leopards), it is appropriate to assume that marked individuals are a random subset of the entire population, thereby allowing for the robust estimation of population density (Efford and Hunter, 2018; Royle et al., 2014). Additionally, when a greater proportion of captures are of marked individuals as opposed to unmarked animals, it is expected that the accuracy and precision of

the estimates is enhanced (Chandler and Royle, 2013). In our study, we assigned individual identity to ~70% of photo-captures, likely resulting in the high precision of our estimates. This is in contrast to studies where individuals have been identified either by artificial markings (e.g. tags, radio-collars) and/or semi-permanent natural markings (e.g. nicks, scars, physical deformities) that typically result in a greater proportion of detections of unmarked animals (Kane et al., 2015; Whittington et al., 2018).

Estimating the abundance and density of species is vital to understanding population ecology and informing species conservation. Camera-trapping in combination with spatially-explicit capture-recapture (SECR) or SMR models provides the means to obtain such information. While IR cam-traps forced into night mode in combination with SECR models could help estimate leopard densities when both wild and melanistic phenotypes exist, SMR models allow for the estimation of density with photo capture data obtained from camera trap surveys conducted using only white-flash units. Additionally, SMR models allow researchers to revisit historic camera trap survey data, thereby generating valuable information on populations. Finally, these models can also be applied to estimate the population densities of other cryptic carnivores that exhibit similar phenotypic polymorphism such as Jaguars *Panthera onca* and Oncilla *Leopardus tigrinus (Mooring et al., 2020; Silveira et al., 2010).*

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Tables

Table 1. Summary of photographic capture-recapture sampling conducted over three sessions in Manas National Park, India. Presented are the sampling start and end dates for the three sessions, the number of trap locations deployed, the number of sampling occasions, the trap effort in trap days, total number of independent leopard captures obtained and the number of individuals (Mt+1), number of detections (ndet), number of captures of unidentified marked individuals (Tm) and number of detections of melanistic individuals (Tu) summarized for Both + Left and Both + Right datasets.

Session	Sampling start and end dates	No. of trap locations	No. of sampling occasions	Trap effort (trap days)	No. of independent captures	Flank dataset	No. of individuals identified (Mt+1)	No. of detections of identified individuals (ndet)	No. of detections of unidentified marked individuals (Tm)	No. of detections of melanistic individuals (Tu)
Session 1	24/12/16 - 21/02/17	118	60	6238	316	Both + Left	33	218	17	81
						Both + Right	29	212	23	
Session 2	15/02/18 - 15/04/18	236	60	6372	170	Both + Left	18	113	16	41
						Both + Right	20	116	13	
Session 3	30/12/18 - 27/02/19	121	60	6064	242	Both + Left	24	173	26	43
						Both + Right	27	176	23	

Table 2. Parameter estimates from single session and multi-session analyses of leopard data from Manas National Park, India. Presented are the intercept parameter ($\widehat{g0}$), scale parameter in meters ($\hat{\sigma}$), proportion identified ($\widehat{pID}$), estimated density ($\widehat{D}$; individuals/100km2), with associated standard errors (SE) and the width of the confidence interval of the estimated density (CI width (D)).

Session	Flank dataset	Singe session analysis					Model averaged multisession analysis				
		D (SE)	g0 (SE)	sigma (SE)	pID (SE)	CI width	D (SE)	g0 (SE)	sigma (SE)	pID (SE)	CI width
Session 1	Both + Left	4.31 (0.45)	0.018 (0.002)	3644.3 (165.4)	0.944 (0.02)	40.4	4.33 (0.36)	0.018 (0.002)	3627.07 (150.69)	0.93 (0.02)	20.0
	Both + Right	3.73 (0.43)	0.019 (0.002)	3726.2 (173.7)	0.924 (0.02)	45.1	3.74 (0.27)	0.019 (0.002)	3732.86 (160.93)	0.93 (0.02)	26.0
Session 2	Both + Left	2.34 (0.33)	0.013 (0.002)	4061.4 (282.9)	0.898 (0.03)	55.4	2.35 (0.21)	0.014 (0.002)	3944.75 (239.3)	0.91 (0.02)	36.6
	Both + Right	2.6 (0.35)	0.013 (0.002)	3976.3 (268.4)	0.923 (0.03)	52.9	2.61 (0.22)	0.014 (0.002)	3886.35 (228.33)	0.93 (0.02)	34.8
Session 3	Both + Left	3.09 (0.35)	0.025 (0.003)	3202.6 (159.5)	0.896 (0.03)	43.9	3.05 (0.21)	0.024 (0.003)	3304.63 (146.61)	0.91 (0.02)	24.1
	Both + Right	3.43 (0.35)	0.025 (0.003)	3206.5 (172.3)	0.917 (0.02)	39.3	3.37 (0.22)	0.023 (0.003)	3319.48 (157.45)	0.92 (0.02)	24.6

Figure legends

Figure 1. Photo-capture of melanistic and rosetted/wild phenotype leopards at Manas National Park, India.
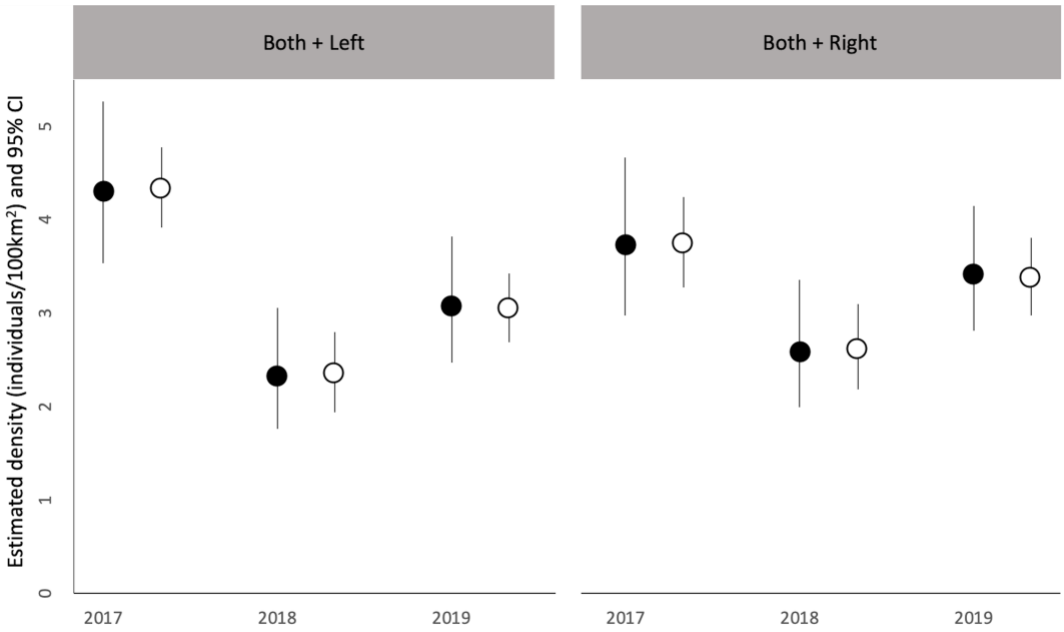
Figure 2. Estimates of leopard density (individuals/100km2) from Manas National Park, India. Closed circles (●) represent estimates from single session analyses and open circles (○) represent estimates from multisession analyses of Both + Left and Both + Right datasets. Error bars indicate 95% confidence intervals around estimates.