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Camera trap as a non-invasive tool in research on rare and elusive mammals

Ph.D. Thesis

Mgr. Tomáš Jůnek

Supervisor

prof. RNDr. Pavla Hejcmanová, Ph.D.

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Declaration

I hereby declare that solely I, under supervision of prof. RNDr. Pavla Hejcmanová, Ph.D., created this thesis and that I cited all relevant references. I also agree with public access to this thesis on a website of the FES CULS.

In Prague, August 13, 2017

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1. Introduction

Knowledge of the richness of species that inhabit a particular area is an essential metric for both conservationists and practitioners (O'Connell, Nichols & Karanth 2010; Rondinini *et al.* 2011). Changes and trends in biodiversity and population sizes in time, for example under human disturbance or habitat loss, are subjects studied worldwide for decades and serve as important indications for future strategies (Henschel *et al.* 2010; Visconti *et al.* 2011). Usual high costs, organizational difficulties, invasiveness and questionable reliability of survey methods, as direct observation, aerial counting surveys or line transects sampling, make their outputs often incompatible (Jachmann 2002; Redfern *et al.* 2002). Also, many taxa or individuals remained undetected because of their nocturnal or crepuscular activity pattern or secretive habits, some species can be confused with others of similar size, shape or colour.

Presence and performance of an observer during his data collecting process, especially in case of recording natural and unaffected animal behaviour, was deeply analysed (Altmann 1974; Marsh & Hanlon 2007). Considering results the negative *seeing what we want to see* effect is known in literature for a long time and bias naturally increases with the number of observers. The majority of animal species cannot be sampled directly by human's eye because of their habitat requirements (e.g. aquatic species), but a variety of remote detectors were invented and offers new possibilities (Austin *et al.* 2007; Owen-Smith, Fryxell & Merrill 2010; Rovero *et al.* 2013; Dumond, Boulanger & Paetkau 2015).

Relatively cost-efficient and easily standardized solution has occurred in last the decades with the digitalization of photography and massive production of the device known as the camera trap (Rovero *et al.* 2013). Such an independent detector is bias-free in the probability of recording objects passing by and in most cases does not disturb animals. Recent discoveries of new mammal species are proof of this (Surridge *et al.* 1999; Robichaud & Timmins 2004; Cheyne, Husson & Macdonald 2010). Moreover, camera traps allow for insight into the otherwise hidden behaviour of even the most timid animals and this feature fulfils curiosity and datasheets of a wide range of scientists.

Camera traps (also photo traps or trail cameras) have gone hand in hand with wildlife photography as a discipline of a new imaginary technique from the end of the 19th century (Carey 1926). A pioneer of the method was George Shiras 3rd (1859-1942). His innovations include a particular system of pedals and wires, which enabled white-tailed deer to take pictures of themselves by stepping on a switch placed on their trail. During the decades prior to WWII self-operated cameras were used in Africa to depict its spectacular game and carnivores.

Worldwide expansion of 35mm film photography had enabled zoologists to use automatized devices in the field and the first methodology, mainly for species inventory or estimating of abundance and density, was postulated (Griffiths & Van Schaik 1993). Digitalization and price reduction in the photographic industry, have led to massive application of camera traps. The potential of a novel monitoring method is described in detail by O'Connell, Nichols & Karanth (2010). Recent digital devices, set into a weather-proof case, are usually activated by motion PIR or thermal sensor when a desired object passes by in front of the lens. Once triggered the camera takes a single photo, sequence of photos or a video sequence of length set by the user. White flash, or more recently lamps producing light in the infrared spectrum, which does not disturb animals ensures photographs at night. Camera traps also register Moon phases, actual outside temperature, barometric pressure, or sound. In addition, large capacity of recording medium (usually SD card) and low energy demand make camera traps a reliable and in many cases only conceivable tool which is able to operate up to several months in the field. The skyrocketing number of published field studies based on camera trapping speaks for itself (Rovero *et al.* 2013).

My own interest in photography, endangered animal species and nature conservation worldwide has led me to the decision to apply a novel camera trapping method in practice. Thanks to personal experiences and contacts from World's biodiversity hotspots and conservation sites I was able to successfully employ an approach and carry out field studies on endangered species. I sincerely hope that results of our team's work will contribute to the development of effective conservation strategies and the methodology itself.

2. Objectives

The goal of my Ph.D. Thesis is to apply the method of camera trapping on a variety of different topical occasions to investigate previously unexplored endangered areas and species, and to evaluate the potential of the approach. I strived to enlarge the pool of knowledge both for conservational and methodological purposes.

2.1. Species inventory

The objectives of our camera-trapping study in the Niokolo-Koba National Park (NKNP), Senegal, were to (1) produce the general mammalian species inventory of the core area of the park, (2) evaluate sampling effort and estimate species' richness, (3) estimate species' occupancy (Ψ), and (4) determine the best ecological and environmental predictors (body mass, trophic guild, distance from rivers, distance from park's border) of Ψ and detection probability (p) as a species' response patterns to these predictors.

2.2. Temporal activity pattern

We conducted a camera-trap field survey on Bohol Island, Philippines, in an attempt to uncover the tempo-spatial co-occurrences of terrestrial vertebrate species on regularly used trails with the confirmed presence of cats in the protected primary rainforest (Zone I), a transition zone along the border of the primary rainforest with the agricultural landscape (Zone II), and inside the rural landscape in the proximity of human settlements (Zone III). Our objectives were to (1) create a general inventory of camera-trapped taxa, (2) model the species accumulation curve using previous knowledge of the possible number of mammalian, avian and reptile species detectable by camera-traps, and (3) compare the diel activity levels of cats with those of potential prey and competitors.

2.3. Density and abundance estimates

Our survey in the Fathala Reserve, Senegal, was designed to empirically determine the most appropriate model, which will enable reliable estimates of the abundance of the Western Derby eland based on the proposed detector array, duration of sampling and density of cameras. For the first time we applied a nonspatial and spatial capture-recapture models on a closed population of marked antelope. We estimated the Derby eland's abundance using the programs CAPTURE (models M_h and M_0) and R, package secr (basic *Null* and *Finite mixture* models), in two different densities of camera traps in the line and grid placement derived from the x-matrix covering the entire reserve of Fathala. The results, which change with the variable duration of the trapping period, were compared with the known real abundance. We also tested the pooling of trapping occasions and its impact on results and compliance with the closed model assumptions.

3. Review

3.1. Species inventory

Making a list of wild animals occurring in certain areas commonly requires an enormous endeavour by researchers. In the case of elusive species such as those inhabiting tropical rain forests some animals remain unknown until the camera traps have captured them in the wild (Surridge *et al.* 1999). Camera traps are usually used for monitoring terrestrial vertebrate medium- to large-bodied fauna (Brugière *et al.* 2005; Lyra-Jorge *et al.* 2008; O'Brien 2008). Improving the quality of images nowadays allow for the successful determination of species and size of rat, also ground-dwelling birds can be sampled with a noticeably broader range of desired taxa (Jayasilan & Davison 2006; Lazenby & Dickman 2013).

The most important parameters emerging from inventory studies include the following:

- List of recorded species;
- *n* of independent events of capture that accounts only the initial picture taken during one encounter of species with a camera; to ensure independence, a 10min to 1hour gap is required between two consecutive bouts of triggering a camera trap;
- The species accumulation curve models number of captured species is based on the cumulative number of camera trapping days;
- Relative abundance index (RAI) is the number of independent events per 100 trapping days;
- Naïve occupancy is the number of trapping sites positive to the presence of the species divided by the total number of sites sampled;
- Occupancy (Ψ) is a function of abundance and the dynamic parameters of how animals are distributed in the environment; defined as the probability that a site is occupied by a target species;
- Detection probability (p) is the probability of detection of target species at an occupied site.

Leading pan-tropical system monitoring long-term trends in biodiversity and land cover was recently conducted by the TEAM (Tropical Ecology Assessment and Monitoring Network). Until May 2016 hundreds of cameras placed in 17 sites on three continents had collected more than 3.4 million pictures of animals (TEAM 2016). Such a pool of data enabled the postulation of standardized and compatible methods for designing, conducting and reporting inventory surveys (Rovero *et al.* 2014). Also, among their outputs Ahumada *et al.* (2011) confirmed that mammal communities from highly fragmented sites have lower species richness, species diversity, functional diversity and higher dominance in comparison with the continuous forest. Omnivores and insectivores especially showed a larger reduction in richness of species and occupancy compared with carnivores and herbivores in more fragmented areas.

The World Wildlife Fund as a major conservation organisation has run number of camera trap studies all around the world (WWF 2016a). Among others the tiger was monitored in the protected areas of Nepal, Sumatra and Malaysia. Inventory surveys were also conducted in the Amazonian Yasuní National Park. The leopard cat and the giant panda were surveyed in China, leopard in Russia, bush dog and jaguar in Brazil and Sumatran rhino in Kalimantan. Temperate ecosystems and its elusive fauna have been also commonly surveyed (Moen & Lindquist 2006).

Camera traps often serve as an indication to confirm the presence of the last surviving individuals of animals in remote but disturbed areas. Scientists in Luando Natural Integral Reserve in Angola proved the existence of the last sable antelopes after the civil war in 2005 (Estes 2011). The critically endangered greater bamboo lemur in Madagascar was documented from two sites in Madagascar and confirmed in one new (Olson *et al.* 2012). In the Niokolo-Koba National Park in Senegal one of the last African elephants was camera-trapped in the middle of 2013 (Ndiaye, personal communication 2013), The critically endangered Western Derby eland and African wild dog were recorded in 2015 (Jůnek *et al*, in prep.).

Camera traps also can uncover the composition of a group of animals. A family of the rarest gorilla subspecies, Cross river gorilla, was for the first time filmed at Kagwene Gorilla Sanctuary in Cameroon (WCS 2012). A group of nine endangered Nigeria-Cameroon chimpanzees was similarly recorded at the proposed Tofala Hill Sanctuary in Cameroon in December 2010 (Jůnek & Jůnková Vymyslická, unpublished data).

The efficiency of the inventory survey by camera traps was measured in the primary lowland Amazonian moist forest in south-eastern Peru during two 60-day periods (Tobler *et al.* 2008). A grid of 39 cameras recorded 86 % of 28 medium- to large-sized terrestrial mammal species known to occur in the site. Capture frequencies for different species highly correlated between the surveys, and the capture probability for animals passing in front of the cameras increased with the increasing size of the species. A similar study conducted in the deciduous Atlantic-Forest Park in southern Brazil captured within a 336 trap-day period 85 % of the known local species (Melo, Sponchiado & Cáceres 2012).

3.2. Temporal activity pattern

Almost every zoologist desires observing the authentic behaviour of an animal in its natural habitat. Despite the sophisticated methodology of data collection the observer's presence may influence the behaviour of studied animals (Altmann 1974, Marsh and Hanlon 2007). Avoidance of humans for example because of hunting pressure may increase vigilance or change biorhythms and make direct observation hardly possible (Ario 2007). The non-invasiveness of camera traps overcomes these obstacles. Results can be now be applied in such unusual areas far of zoology as the building industry.

An animal's activity pattern is one of a logically discovered issue because cameras usually record the hour and date of a trap event. Gómez *et al.* (2005) conducted a camera trap research of the activity periods of Amazonian mammals during the dry season period. In four camera-trapping campaigns, containing in total 3161 trap-nights, the activity pattern of 15 mostly large mammal species was registered. Photographic events were distinguished as diurnal, nocturnal and crepuscular while animal taxa were classified as (also mostly) diurnal, nocturnal and cathemeral. The study supported the previous natural history knowledge of these species in a humid forest.

Van Schaik & Griffiths (1996) used camera traps at two sites of rain forest one in Sumatra and the other in Java. Exploratory analysis finds out that body size and substrate are the major correlates of the activity period despite travel mode and diet. They explain the effect of substrate that vision-related constraints force diurnal animals in the forest to stay diurnal, while nocturnal ones are kept from becoming diurnal by the predation risk of visually hunting diurnal predators. Researchers suggest that the largest animals are cathemeral because they need longer time to forage than is provided by the 12-hour diurnal or nocturnal period.

Summer and autumnal activity patterns of forest dormouse were studied by Duma & Giurgiu (2011) in Romania. Eight cameras monitored wooden nest-boxes in territory of one adult female with a litter of five pups. The study revealed that the forest dormouse is mainly crepuscular and nocturnal.

A monitored area also offers data on the home range use of selected species. Vanderhoff *et al.* (2011) studied a population of margays at Wildsumaco Wildlife Sanctuary in Ecuador. During 3220 trap-night and 85 capture events ten animals, mostly nocturnal, were recognized. At least two females permanently occupy a matrix, which includes agricultural land. Others use it as a corridor. A relatively high noticed abundance of margays makes the sanctuary an important area for conservation efforts.

The direct civil application of data collected from camera traps can be used from studies of wildlife crossings on roads. The four-lane highway 64 in North Carolina was a place of common road accidents between black bears and vehicles (Van Manen *et al.* 2001). A combination of 243 photographs from infrared camera traps, 337 DNA samples of bears' hair and 6,000 track counts of bear population finally led into the creation of three underpasses in a 19.3-km section of the highway. Camera traps placed at seven underpass sites in Virginia recorded during a year more than 2,700 photographs of animals crossing the road (Donaldson 2007). The study resulted in the knowledge that an underpass with a minimum height of 12 ft fits the requirements of the White-tailed deer the most common visitor. Study of radio-tracked Florida panthers and black bears along the State road 29 corridors in Florida revealed that location plays a more important role than design probably because of animals' habits (Land & Lotz 1996). Scientists collected over 28,000 bear and panther sampling locations during a decade. In total 12,519 crossings were recorded by scientists via tunnels and bridge along a 70km portion of the motorway from Zagreb to Rijeka in a wildlife core area called Gorski kotar in Croatia (Kusak *et al.* 2008). Study revealed animals' preference of the use of a wildlife bridge as equal to its availability.

Even human behaviour has been surveyed with the use of camera traps. McKenzie & Katic (2002) conducted a field study on the spatial and temporal distribution of recreational users at Banff National Park and its closest vicinity in an attempt to ease the distribution of visitors.

Recent scientific techniques such as telemetry and camera-trapping allow for an almost non-invasive insight into the intimate aspects of life history such as diel and seasonal activity patterns, regardless of the rarity of the taxon (O'Connell, Nichols & Karanth 2010). The temporal co-occurrence of two species at one site can be analysed with an application of kernel density estimation on circular data (time of the day in format from 0 to1) following Ridout and Linkie (2009). The R statistical environment (R Core Team 2014) package 'overlap' (Meredith & Ridout 2014) allows for the calculation of overlap (Δ) of two areas lying under a 24-hour activity curves of a given species with standard parameters as standard error and confidence intervals. Diel activity overlaps were used for example to quantify the temporal avoidance of competing five species as felids in Sumatran rain forest (Sunarto *et al.* 2015). Cats from marbled cat to Sumatran tiger had lower overlap, hence bigger avoidance, when cats' size or size of their mutual prey was similar. Predator-prey temporal avoidance can be also expected particularly in the case of introduced species such as feral cats (Lazenby & Dickman 2013). (Wang & Fisher 2012) found out that the activity of dingoes in wet periods affects the timing of the activity of feral cats, which resulted in the reduction of overlap between feral cat and its prey bridled nailtail wallaby. Bogdan, Jůnek & Jůnková Vymyslická (2016) reported an increase of daytime activity of Philippine rodents and shifts of activity peaks of ground-dwelling birds across sites where feral cats were absent.

The activity level (or proportion of time that animals are active) recorded by camera traps can be also be quantified by itself. The non-invasive technique of Rowcliffe *et al.* (2014) relies on the key assumption that each member of the sampled population is active at the peak of the daily activity cycle. Camera trap placement should be random according to the diel patterns of target species movement. The approach in R statistical environment (R Core Team 2014) package *activity* (Rowcliffe 2014) estimates the activity level (i.e. the proportion of time active) from the diel distribution of the activity records of animals, using a circular probability density function fitted to the radian time of such records. For calculating standard errors and confidence intervals bootstrapping with 1,000 iterations is usually used. Incorporated Wald test enables testing the significance of pair-wise comparisons of the activity level estimates between for examples of seasons and times of day within a season etc.

3.3. Density and abundance estimates

Identification of individual animals from camera trap recordings is an ideal predisposition for further modelling of its population estimates (density, abundance) based on the capture-mark-recapture method (Griffiths & Van Schaik 1993; Karanth 1995; O'Connell, Nichols & Karanth 2010). A considerably larger portion of animal species feature none, or poorly visible marks but there are some taxa metaphorically predestined for such a purpose - dotted, striped and clouded felids, antlered cervids, and stripped, dotted or reticulated ungulates.

Studies of population parameters employing the closed capture-mark-recapture model should satisfy several conditions to fulfil an ambition to reach plausible estimates: a) studied populations are closed, b) the population is constant during the sampling period, c) every individual in the population has a capture probability greater than zero, d) sampling is random, and e) all individuals are identifiable (Royle & Nichols 2003; Harmsen, Foster & Doncaster 2010; O'Brien 2011). Ignorance especially of heterogeneity in capture probabilities of animals can cause inaccuracy. Models assuming the equal capture probabilities, while there is real individual heterogeneity will underestimate abundance. Heterogeneity in capture probability is presumed because individual activity varies with sex, age or social status. If the point c) is violated then the population estimate refer only to the „catchable“ population. It can also be expected that studied populations are not geographically and demographically closed. So condition a) is violated mainly in that case when the camera trap sampling grid is smaller than the average home range of the studied species and most of the recorded animals live outside the grid.

Harmsen, Foster & Doncaster (2010) tested the reliability of the recommended and commonly used jack-knife model estimator, M_h, (Karanth & Nichols 1998) for estimating abundance allowing capture probabilities to vary between individuals. As the threshold for reliable abundance estimates is considered overall, capture probability of sampled individuals equals or is greater than 0.1. Harmsen *et al.* (2010)

validated that estimates with lower capture probabilities are inaccurate for a small population (n = 50) and the reliability is further reduced if there is a high level of heterogeneity in capture probabilities in the population when using the jack-knife M_h estimator. Therefore, published results of abundance estimates from low-density populations should be accompanied by the capture frequencies of individuals.

A similar formal prerequisite of density estimation, as sample size and capture probabilities, ad hoc density estimation from the calculation of an effective trapping area or spatially explicit capture-recapture model (SERC) were discussed (Foster & Harmsen 2012). Greater transparency in study designs was also recommended.

After postulation of the potential of camera traps for population estimates (Griffiths & Van Schaik 1993), two years later the global application of the method started by pioneering study of tiger density from Nagarahole National Park in India (Karanth 1995). Karanth used 15 different camera trap sites on trails throughout the area to maximize trap access to all transferring tigers. Cameras were periodically moved among the sites and the total trapping period was at last divided into nine sampling occasions. During 387 trap-nights Karanth collected in total 31 photographic captures of individual tigers in 15 km^2 of the studied area. Individuals were recognized from the pattern of stripes on flanks. For 10 individuals their capture histories were obtained. Using the CAPTURE software, Karanth estimated with 95% confidence interval the mean tiger numbers at 11 (10 – 22), respectively 10 (10 – 15), with the M_h (jack-knife), and M_h (Chao) estimators. Based on prey biomass in the area, the mean tiger density of 13.3 – 14.7 subadult or adult tigers pet 100 km^2 could be reasonable in the light of calculated abundance. Tigers' density estimates were widely described during following surveys at four sites in India with data from 3079 trap-nights (Karanth & Nichols 1998).

Studies of tigers (Karanth 1995; Karanth & Nichols 1998; Karanth *et al.* 2004) encouraged other authors focused on felids in camera traps usage. Trolle & Kéry (2003, 2005) used camera traps to estimate the density of ocelots Brazilian Pantanal. Silver *et al.* (2004) the monitored abundance and density of jaguars of rain forests in Belize and Bolivia and in the Bolivian dry forest. Yasuda (2004) monitored the diversity and abundance of domestic cats, masked palm civet and other mammals on Mount Tsukuba in Japan. Soisalo & Cavalcanti (2006) uncovered the density of the jaguar population in Pantanal, Brazil. Heilbrun *et al.* (2006) estimated the abundance of bobcats in Texas. Ario (2007) surveyed the population of the Javan leopard in human altered habitats. Kelly *et al.* (2008) studied the densities of puma across three sites in Bolivia. Marnewick (2008) estimated the abundance of cheetah in ranching areas of South Africa. Vanderhoff *et al.* (2011) investigated the abundance of margay in Andes of Ecuador. Weingarth *et al.* (2012) estimated the abundance and density of the Eurasian lynx in Germany.

New insight and progress into the technique allowing estimation of density was made by Rowcliffe & Field (2008). The new method minimalized the need for individual recognition based on contacts between animals and cameras, which originate from a more than 150 years old mechanistic model describing rates of collisions between gas molecules. Animals are equal to particles moving in space. The expected contact between particles in a given period is the ratio of the area contained. The key assumption is that animals behave like ideal gas particles, moving in random patterns and independently of one another. For stationary object with a circular detection zone (camera trap) in which contact occurs, the area covered by moving animals is defined as the product of animal speed (v), time (t), twice the radius of the detection zone (r), and the number of present particles, given by the product of density and area (DA). Dividing this covered area by A the number of contacts y is independent of the area notionally sampled: $y = 2rtvD$. The method was used for estimations of the densities of cryptic antelopes, duikers, for example in Tanzania (Rovero & Marshall 2009).

A recent approach which incorporates the location-specific capture histories of marked individuals is the spatially explicit capture-recapture, SECR (Borchers & Efford 2008). The basic assumption is that the source of variability in the detection of individuals is the proximity of a detector to the centre of activity. SECR deals with accidental visits along the edges of the trapping array, and the estimated density of animals refers to the study area. Likelihood-based SECR modelling allows multiple detections of individuals per trapping occasion, even from polygons or linear transects (Efford 2011). Despite widespread use of the method among a scientific audience (Dawson & Efford 2009; Marques *et al.* 2012; Tobler & Powell 2013), empirical evaluations of its outputs are rare (Sharma *et al.* 2010; Gerber & Parmenter 2014; Dumond, Boulanger & Paetkau 2015; Jůnek *et al.* 2015).

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5. Results

Species inventory

Jůnek, T., Jůnková Vymyslická, P., Kane, M. D., Barták, V., Pivrnec, O., & Hejcmanová, P. (2017) Under review. Keeping a lens on African savannah in peril: Species inventory and occupancy modelling in the Niokolo-Koba National Park. *Scientific Reports.*

Temporal activity pattern

Bogdan, V., Jůnek, T., & Jůnková Vymyslická, P. (2016). Temporal overlaps of feral cats with prey and competitors in primary and human-altered habitats on Bohol Island, Philippines. *PeerJ*, *4*, e2288.

Density and abundance estimates

Jůnek, T., Jůnková Vymyslická, P., Hozdecká, K., & Hejcmanová, P. (2015). Application of Spatial and Closed Capture-Recapture Models on Known Population of the Western Derby Eland (Taurotragus derbianus derbianus) in Senegal. *PloS one*, *10*(9), e0136525.

5.1. Species inventory

Jůnek, T., Jůnková Vymyslická, P., Kane, M. D., Barták, V., Pivrnec, O., & Hejcmanová, P.

Keeping a lens on African savannah in peril: Species inventory and occupancy modelling in the Niokolo-Koba National Park.

Under review

Keeping a lens on African savannah in peril: Species inventory and occupancy modelling in the Niokolo-Koba National Park

LIST OF AUTHORS:

Tomáš Jůnek[1], Pavla Jůnková Vymyslická[1], Mamadou Daha Kane[2], Vojtěch Barták[3], Ondřej Pivrnec[1] and Pavla Hejcmanová[4]

[1]Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 1176, 165 00 Prague 6–Suchdol, Czech Republic,

[2]Direction des Parcs Nationaux (DPN), Siège du Ministère de l'Environnement et du Développement Durable, Parc Forestier de Hann, Route des Pères Maristes, BP 5135 Dakar-Fann, Sénégal,

[3]Department of Applied Geoinformatics and Spatial Planning, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 1176, 165 00 Prague 6–Suchdol, Czech Republic,

[4]Department of Animal Science and Food Processing, Faculty of Tropical AgriSciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 00 Prague 6–Suchdol, Czech Republic,

Abstract

Wildlife of the West African savannah is struggling with an unprecedented existential distress. Populations of large-bodied mammals have declined by significant percentages over the last decades, affecting the whole trophic system. Potentially profitable destinations, such as UNESCO-listed national parks, are suffering from defaunation and neglect, which adds to the socioeconomic insecurity. Relatively cost-effective camera-trap monitoring provides reliable insights into the richness and trends of biodiversity. We applied this method to assess the basic inventory measures in a core area of the Niokolo-Koba National Park, Senegal. We registered 35 mammals, including critically endangered West African wild dogs and Derby elands, whereas no elephants or lions were detected. The trapping success rate in 1,000 trap days was 87.6%. We analysed the data using a Bayesian hierarchical modelling framework. The mean detectability and occupancy was 0.058 and 0.364, respectively, with highest occupancy values for the common warthog, Western bushbuck, and crowned duiker. Only six species showed significant response in occupancy to environmental covariates such as distance to the nearest river, road, and park border. The urgent need for solid biodiversity data from African savannahs for conservation strategies is indisputable. We have endeavoured to lay down a transparent methodological cornerstone for future comparative studies.

Key-words

Bayesian, biodiversity, camera trap, detectability, occupancy, remote sensor, savannah, species richness, Senegal, West Africa

Introduction

The region of West Africa faces a dramatic decline in its fauna. Destruction of habitat, overhunting, diseases, and linear barriers such as fences and roads represent the most important drivers of the isolation of protected areas and biodiversity loss[1,2]. Populations of large-bodied mammals dropped within African protected areas by 59% on average between 1970 and 2005[3], and an alarming situation is also reported in birds[4]. Projected net biodiversity loss for the majority of the West African region will exceed 25% by 2095[5]. Megafauna and large carnivores are considered the most vulnerable to defaunation driven by humans, with consequences for the trophic cascade[6–8]. The largest terrestrial animal, the African elephant (*Loxodonta africana*), has lost 33% of its West African and 76% of its Central African population since 1980, leaving less than 8,000 individuals in the whole region[2]. The Western black rhino (*Diceros bicornis longipes*) has gone extinct[9], the endangered West African giraffe (*Giraffa camelopardalis peralta*) survives in the only refuge in Niger, lions (*Panthera leo*) and African wild dogs (*Lycaon pictus*) isolated in several reserves have been listed as critically endangered, and the Central African populations of topi (*Damaliscus lunatus*) have declined by 90%[10–12].

One of the largest and most western conservation areas in West Africa is the Niokolo-Koba National Park (NKNP) in Senegal, recognized as a UNESCO World Heritage Site and Biosphere Reserve since 1981[13]. The park is considered one of the last refuges for the Western Derby eland (*Taurotragus derbianus derbianus*) and a stronghold for other iconic fauna including lions, African wild dogs, leopards (*Panthera pardus*), chimpanzees (*Pan troglodytes verus*) and Temminck's red colobus (*Piliocolobus temminckii*). Consistently with other reserves in the region, the community of large mammals in the NKNP has vanished in recent decades, with local extinctions of giraffe, korrigum (*Damaliscus lunatus korrigum*) and effectively also elephants, still believed to be surviving in one last individual since the 2010s[2,14–16]. Large carnivores reflect the decrease in prey. The entire population size of lions in the NKNP was estimated at only 16 individuals, with less than 50 African wild dogs in three packs[10,17,18].

Thanks to its long-term safe and stable socio-economic situation, Senegal is predestined to become a major regional hub for tourism, with the NKNP as its crucial eco-touristic destination. The importance of large mammals for ecotourism is significant in the decision-making process[19,20], hence the relatively easily accessible NKNP has viable economic potential. However, illegal pasture, poaching, bush fires, and a succession of invasive plants, in combination with insufficient management funds, have resulted in a continual decline in biodiversity as well as infrastructure damage. The park has therefore been listed as UNESCO World Heritage in Danger since 2007. The last systematic inventories of wildlife took place in 1990/91 with a ground survey[16], and in 2006 using both a ground and aerial survey[14]. These studies suggested the importance of a core area bounded by the rivers of Gambia and Niokolo and the summit of Mt. Assirik. Despite the existence of a reporting system, a lack of knowledge persists regarding medium- to small-bodied elusive species in the NKNP, along with drivers in distribution.

Systematic long-term monitoring of biodiversity with camera traps exists only for communities of terrestrial vertebrates in tropical forests[21–23]. The associated analyses of occupancy allow for indications, however nonlinear, of abundance or the likelihood of the extinction of a species within the surveyed area. Bayesian models[24], when measured accordingly, allow for long-term refining of the estimates and the incorporation of newly emerging variables. The approach has brought new and nearly real-time insights into population dynamics, replenishing the pool of knowledge together with parameters such as the Living Planet Index (LPI)[25].

In savannah, including the NKNP[18,26], researchers using remote detectors such as camera traps have focused mostly on carnivores[18,27–31] or on the impact of land use on species richness[32–34]. Large-scale studies introducing potentially comparative measures remain rare[35,36]. The scarcity of monitoring data sources for West, Central, and North African species constrains regional LPI reliability, with a direct impact on Strategic Goal C of the Convention on Biological Diversity and its Aichi Biodiversity Targets[25,37]. To fill this gap, we decided to shed some light on the Sudano-Guinean savannah and lay a methodological foundation for future comparative surveys of this relatively overlooked ecosystem.

The goal of our camera-trapping study was to (1) inventory all mammalian species of the core area of the NKNP, (2) evaluate sampling efforts and estimate species richness, (3) estimate species occupancy (Ψ), and (4) determine the best ecological and environmental predictors (distance from the nearest rivers, a passable road, and the park's border) of Ψ and detection probability (p) as species response patterns to these predictors.

Methods

Study area

The Niokolo-Koba National Park, located in south-eastern Senegal, covers 9,130 km^2 of Sudano-Guinean savannah on both banks of the Gambia River and shares part of its southern border with Guinea. It was declared the first Senegalese national park in 1954.

Climatic data recorded for the year 2015 for the main park's camp of Simenti (GPS coordinates 13.026300, -13.293843) shows an average annual temperature of 32.8°C and precipitation of 733.9 mm, with a 275.5-mm peak in August [38]. The dry season, with rare rainfall and mean high temperatures reaching up to 43°C, runs from November to May; the wet season begins in June and lasts till October (Fig. 1).

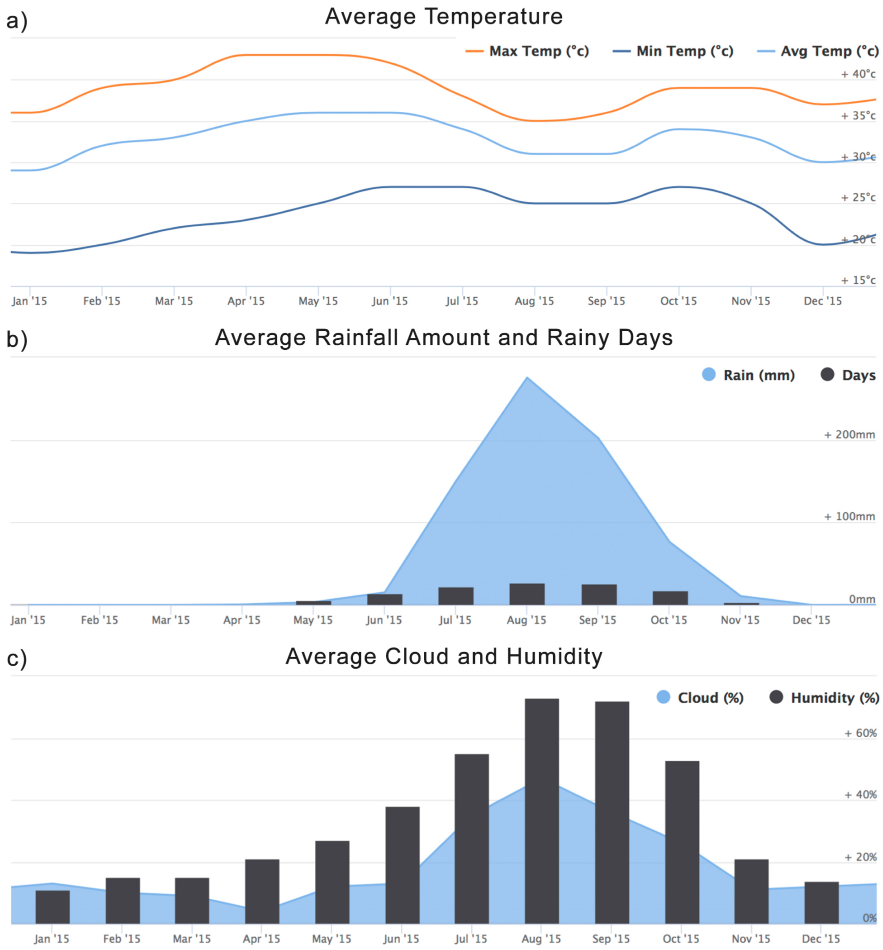

Figure 1. Mean (a) temperatures, (b) rainfall amount, number of rainy days, and (c) cloud and humidity for the Simenti Camp, Niokolo-Koba National Park, Senegal, recorded in the year of 2015[38].

Most of the park's area is topographically flat, with altitudes between 16 and 100 m above sea level and a hilly eastern section where the highest peak (Mt. Assirik, 311 m) is located. Ridges above the level of 200 m occur in this area, and valleys with dense bush subsidize few springs. The Gambia, Niokolo, and Koulountou rivers are the only persistent water sources in the park and cause floods in rainy seasons. Shallow temporary lakes periodically emerge in the vicinity of rivers and attract a variety of animal species. Gallery forest lines the riverbanks; the woodland savannah covers the majority of the landscape, with patches of bamboo growth and sterile plinthitic hardpans called '*bowal*'.

Data collection

Our study in the core area of the park took place from January to October 2015. We used weatherproof digital camera traps Ltl Acorn 5310MC (Shenzhen Ltl Acorn Electronics Co., Ltd., China). We designed a regular grid of 41 camera trap locations with a 5-km span (density of one camera per 25 km^2) covering an area of 1,025 km^2. Three teams led by one researcher, each accompanied by three anti-poaching brigade members, deployed cameras (Fig. 2) in two periods: (1) 20 units were set up between January 11th and April 28th 2015, and, after removal, (2) 17 units were deployed and operated between April 28th and October 27th 2015. Four locations had to be omitted due to logistical constraints during the second period.

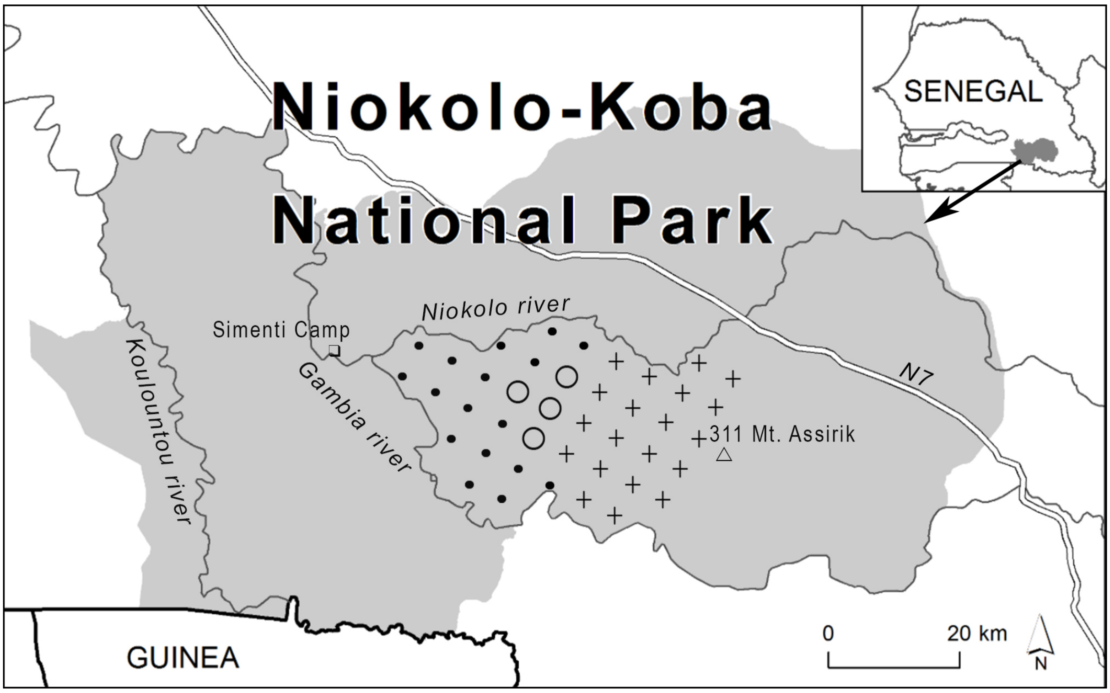

Figure 2. Schematized map shows camera trap placement at core area of the Niokolo-Koba National Park, Senegal. Circles highlight omitted locations, '+' denotes first set of camera traps deployed in January, '**.**' denotes cameras placed in May 2015. The figure was produced by Tomáš Jůnek and Vojtěch Barták with use of ArcGIS 10.5 (Esri Inc., Redlands, USA, http://www.esri.com/arcgis).

Every final camera location varied within a 50-m radius from the preliminary defined point, in order to ensure that the camera was aimed at the most-used animal trail. Units were tightened to tree trunks or large bushes of average height 1 m. A passive infrared motion sensor and 52-degree-wide camera lens faced as perpendicularly as possible to the animal trail, at a distance of between 3 and 15 m from a focal point where the animal was expected to occur. Cameras with a built-in infrared flash were set up to work in a single photo mode (5-megapixel resolution) with a 1-second interval between two consecutive triggering events. Units operated 24 hours a day and no form of bait was used. The sensitivity of the motion sensor was set at ‘normal’. A flat metal sheet covered each camera as a protection against rain and direct sun.

Data analysis

According to the average durability of the whole camera array, a dataset from two 70-day-long sampling periods was analysed: January 12th - April 22th and May 1st - July 9th, 2015.

All taxa recorded were identified and independently crosschecked by all authors on the basis of visible features. We specified the nomenclature, body mass, and home range size of animals using the Handbook of the Mammals of the World[39–42]. Body mass was calculated as a mean between the averaged weights of males and females. If data was lacking, we used the known weight of the closest related taxon of a similar size.

We filtered all photographs of animals in an attempt to avoid multiple detection of the same individual by including only the first photograph in a sequence, with a 1-hour gap between possible consecutive encounters of an animal with a camera trap[43]. We considered such record to be an independent event (hereinafter “an event”). As standard descriptors of the animal community, the relative abundance index (RAI), namely the number of events divided by the sampling effort (total number of trap days) and multiplied by 100, was computed. Naïve occupancy was calculated as the number of sites positive for the presence of a given species divided by the total number of sampled sites[44]. To ensure the compatibility of our study with others, we calculated the species accumulation curve to find out if our study lasted sufficient long to capture the maximum possible number of species in a given area[45].

A calculation based on the cumulative number of camera-trapping days was processed in EstimateS Version 9.1.0[46], with 1,000 random iterations of samples to gain 95% confidence intervals (CI).

To estimate species richness, occupancy, and detectability, we fitted several Bayesian hierarchical models[24]. First, we fitted two kinds of multiple-species (i.e. community) single-season models, one based on direct occupancy and a species-level detectability estimation, and the second being a multiple-species generalization of the Royle-Nichols model based on abundance and an individual-level detectability estimation[47]. In both cases, we fitted models with/without occupancy covariates, and with/without data augmentation, which resulted in eight different models (see Table 3). Data augmentation[48] enables estimation of the number of present species from a large virtual super-community. In our case, we augmented the data to form a super-community of 150 species, and then we checked for the proportion of species present (whether the parameter Ω[48] is sufficiently below its upper limit (i.e. one)). We considered distance to the nearest river ("river"), distance to the nearest passable road ("road"), and distance to the NKNP border ("border") as possible occupancy covariates for each species. We didn't consider any covariate of detectability, as we believe the constant (species-specific) detectability between sites corresponds well with the camera-trapping design. All covariates were standardized to zero mean and unit variance.

We encountered severe difficulties when trying to fit the community models with the environmental covariates. The models either did not converge or were not able to initiate the simulations at all (see Table 3). This was probably because for many species we had recorded only a few occurrences, or only a few sites with at least one occurrence, and such sparse data simply did not allow for drawing inferences about the environmentally-driven spatial variation in occupancy. For this reason, we fitted a separate single-species model for each species. We tried both occupancy-detectability and abundance-detectability (i.e. Royle-Nichols) models, but the latter ones didn’t initiate the simulations for some species, obviously for the same reason as the corresponding community models, as described above. Therefore, we based our covariate-related conclusions on the single-species occupancy-detectability models. For species with at least one significant covariate effect, we drew predicted occupancy maps based on predictor values computed in 500-m grids covering the central part of the national park.

All our models were single-season and thus assumed closed populations, for which we excluded from the analysis any species with an expected home-range size larger than approx. 25 km^2 (corresponding to the 5-km distance between traps). Therefore, our analysis focused on sedentary mammals with small- to medium-sized home ranges.

We fitted all the models using the MCMC algorithm, with five independent chains, each chain consisting of 100,000 simulations, of which the first 50,000 were used as burn-in, and we applied a thinning rate of 50. Thus, each posterior histogram and summaries were computed based on 5,000 simulated values. All prior distributions were chosen to be uninformative. We checked the convergence of all our models using the Gelman-Rubin $\hat{R}$ statistic[49] and multiple $\hat{R}$ statistic[50]. We also checked the goodness of fit of the models using Pearson χ^2 residuals, evaluated both on the original data (χ^2_{obs}) and on the data simulated from the model (χ^2_{sim}). We calculated the Bayesian p-value, defined here as $P(\chi^2_{sim} > \chi^2_{obs})$[51,52], with a value close to 0.5 indicating perfect fit and values below 0.025 or above 0.975 indicating lack of fit, leading to rejection of the model at the 0.05 significance level.

For all data manipulation and computation, we used R statistical software[53]. For fitting the models, we used the OpenBUGS program[54] via the R2OpenBUGS package[55]. For model diagnostics and summaries, we used the coda package[56] together with our own functions written in R. All statistical plots were created using the ggplot2 package[57]. We used ArcGIS 10.5 for computation of environmental covariates as well as creation of predicted occupancy maps.

Results

We registered altogether 1,876 trap days out of 2,590 possible (72.4%). From a total of 33,909 photographs taken, 3,734 (11%) contained animals or parts thereof, and four pictures showed alleged poachers. One camera captured on average 10.1 species (ranging from 1-18 species). One camera trap malfunctioned and three cameras were lost from bushfire, but we managed to extract data from two of them and include records into the analysis. Hence 35 cameras functioned on average for 52.1 days.

We recorded and identified 35 species of mammals altogether (Table 1), which is noticeably more than the coincident 22 species listed during both the ground survey in the years 1990/1991, and the ground and aerial combined survey in 2006.

A list of the recorded mammal species is shown in Table 2. Only one species, Guinea baboon (*Papio papio*), was captured in >200 events. Crowned duiker (*Sylvicapra coronata*) and common warthog (*Phacochoerus africanus*) were captured in >100 and <199 events, respectively. Western bushbuck (*Tragelaphus scriptus*) and roan antelope (*Hippotragus equinus*) had >50 and <99 events, respectively. We recorded from 20 to 49 events for ten mammals, in this order: (1) Western oribi (*Ourebia quadriscopa*), (2) patas monkey (*Erythrocebus patas*), (3) aardvark (*Orycteropus afer*), (4) African savannah hare (*Lepus microtis*), (5) Egyptian mongoose (*Herpestes ichneumon*), (6) common crested porcupine (*Hystrix cristata*), (7) white-tailed mongoose (*Ichneumia albicauda*), (8) side-striped jackal (*Canis adustus*), (9) green monkey (*Chlorocebus sabaeus*), and (10) red-flanked duiker (*Cephalophus rufilatus*). Five species had >5 and <19 events; for the remaining 16 species we reported less than five events.

Apart from mammals, we also recorded during the entire monitoring period three ground-dwelling, large-sized birds: Northern ground hornbill (*Bucorvus abyssinicus*) in 30 events, helmeted Guineafowl (*Numida meleagris*) in 14 events, and black-bellied bustard (*Lissotis melanogaster*) in one event.

The species accumulation curve (Fig. 3) showed a steep increase in the number of species detected in the first 200 trap days (59.4%, e.g. 20.8 species); 1,000 trap days resulted in 87.6%, or 30.7 recorded species with an on-going slow progression of the curve. Furthermore, we did not record any new mammal species in the full dataset of our survey effort of 2,670 trap days.

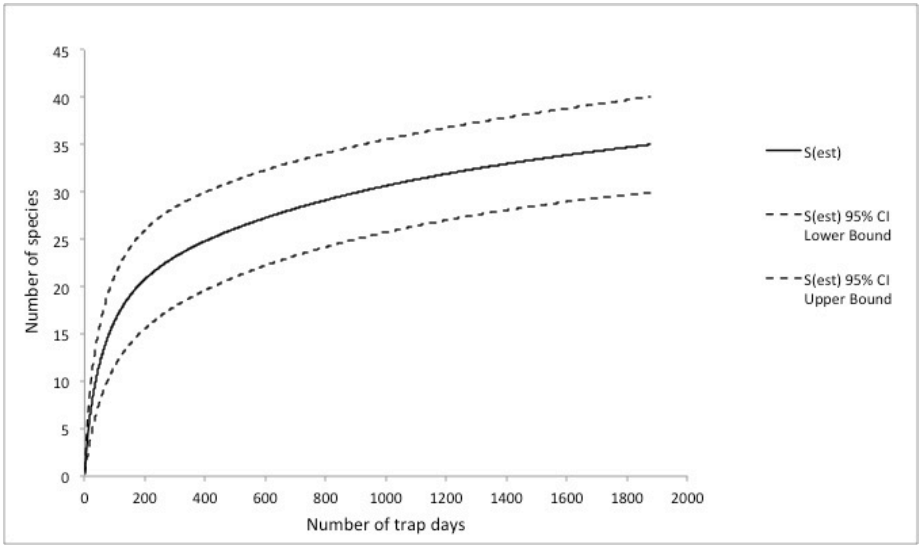

Figure 3. Species accumulation curve for mammals detected by camera traps in the Niokolo-Koba National Park in 2015. Detection of species was randomized 1,000 times and we used results to derive the 95% CI.

Model performance

For fitting the models, we decided to exclude seven species whose reported or expected home range was considerably larger than 25 km^2, which indicated violation of the closure assumption (see Table 2). This was the case for roan antelope, West African buffalo (*Syncerus brachyceros*), Western Derby eland[40], honey badger (*Mellivora capensis*), West African wild dog[39], patas monkey, and Guinea baboon[41].

The convergence and goodness of fit of all eight multi-species models is shown in Table 3. Neither abundance-detectability model with environmental covariates (i.e. models MSA_{covs} and $MSA\text{-}N_{covs}$) even initiated the simulation process, which was obviously caused by insufficient data (i.e. too few occurrences of the number of species) for estimation of all the model parameters. Two models, MSO_{covs} and MSA, didn't converge, having the value of their $\hat{R}$ statistic close to 9. From the remaining four models with a satisfactory convergence, only the model MSA-N, i.e. the abundance-detectability model with a known number of species, fitted the data well (Bayesian p value being 0.6). This model has thus been used for occupancy and individual-based detectability estimation.

Occupancy and detectability

The species-specific occupancies and (individual-level) detectabilities derived from the MSA-N model are shown in Fig. 4. The mean detectability and occupancy were 0.058 (0.0279, 0.0877) and 0.364 (0.2093, 0.5637), respectively (95% CI are shown in parentheses).

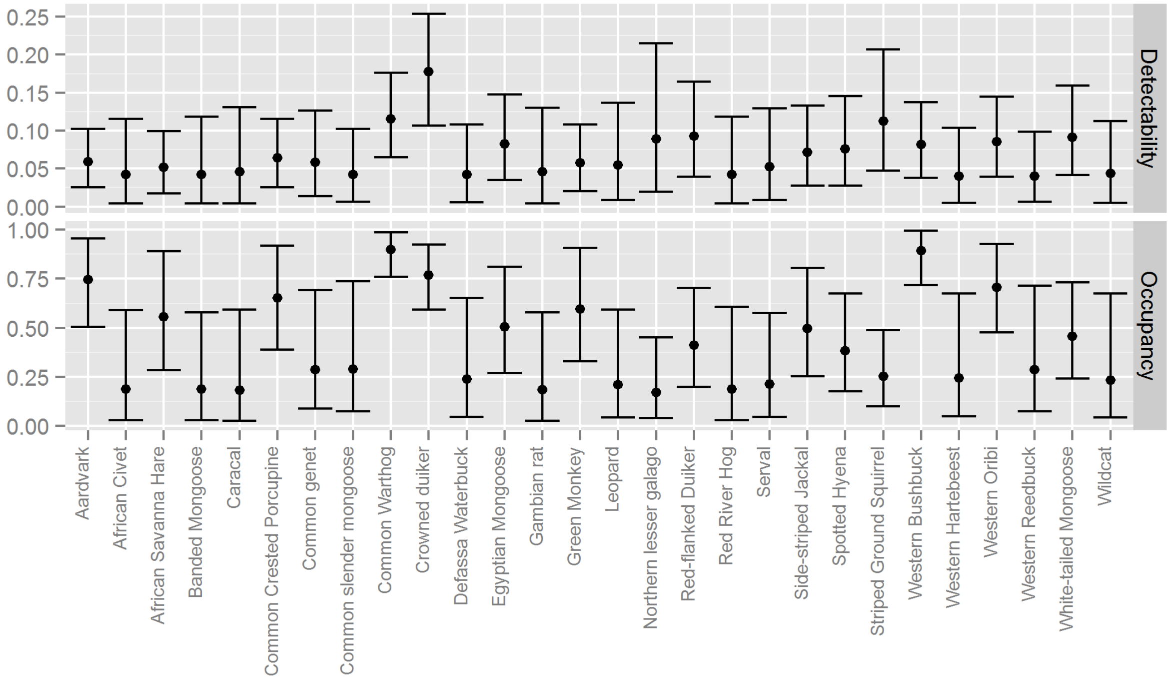

Figure 4. Posterior species-specific detectabilities (upper panel) and occupancies (lower panel), together with their 95% CI, based on MSA-N model. Note different y-axis scales in the panels.

Environmental covariates

The convergence of single-species occupancy-detectability models used for evaluation of the effect of environmental covariates was good, with all multiple $\hat{R}$ values being less than 1.1 for all species except one, with $\hat{R}$ 1.12. Most of the Bayesian *p* values indicated a satisfactory fit. For crowned duiker, common warthog, and Western bushbuck, the models exhibited a significant lack of fit, having *p* values of <0.0001, <0.0001, and 0.0111, respectively. Hence, we are not reporting the covariate effects for these species. Three other species, Western oribi, aardvark, and white-tailed mongoose, had a *p* value less than 0.05, namely 0.0444, 0.0389, and 0.0278, respectively. The covariate effects for the species with a *p* value greater than 0.025 and less than 0.975 are shown in Fig. 5, with the "significant" effects (i.e. those whose 95% CI didn't include zero) highlighted in red. Most of the effects are "non-significant" or weak, and have large confidence intervals. Our data supported significant covariate effects in only six out of 25 species, namely: common crested porcupine exhibited an increasing probability of occurrence with increasing distance from the nearest road and river; Egyptian mongoose was found to have higher occupancy probability closer to the NKNP border as well as farther from the nearest road; Northern lesser galago (*Galago senegalensis*) tended to occupy sites more distant from rivers; by contrast, spotted hyena (*Crocuta crocuta*) occupied sites closer to rivers, but farther from roads; Western oribi had higher occupation probability closer to the roads, but farther from the NKNP border (although, as mentioned, it had a relatively poor fit); and finally, Western reedbuck (*Redunca redunca*) preferred sites more distant from roads. The predicted occupancy maps are shown in Fig. 6.

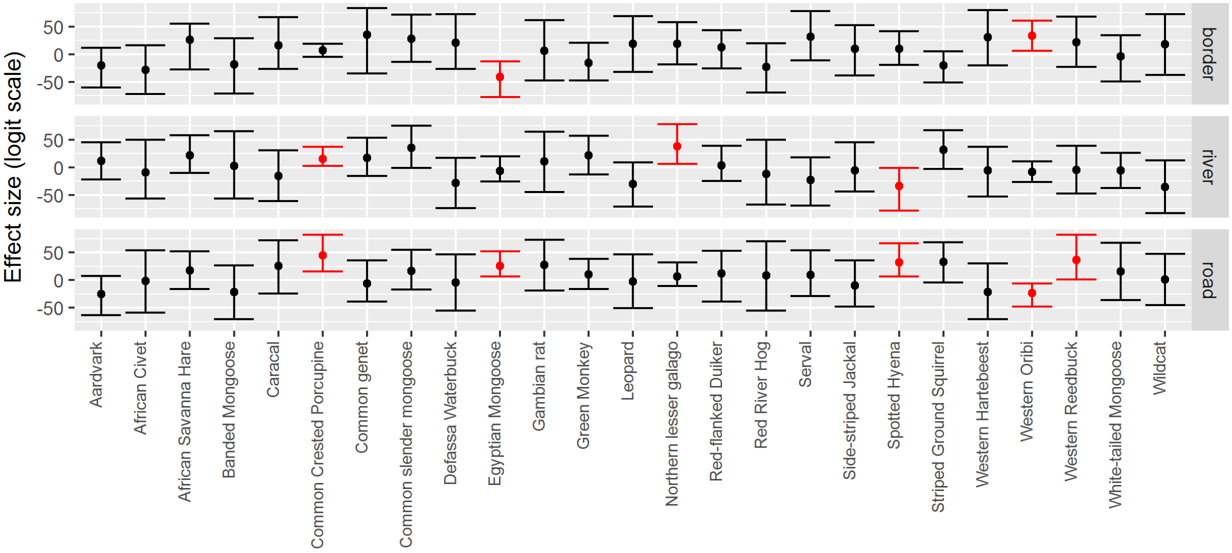

Figure 5. Occupancy covariate effects based on fitting separate hierarchical single-season occupancy-detectability model for each species. The points and whiskers represent posterior means and 95% CI, respectively, all based on 5,000 MCMC samples. The "significant" effects, i.e. those whose 95% CI don't include zero, are highlighted red.

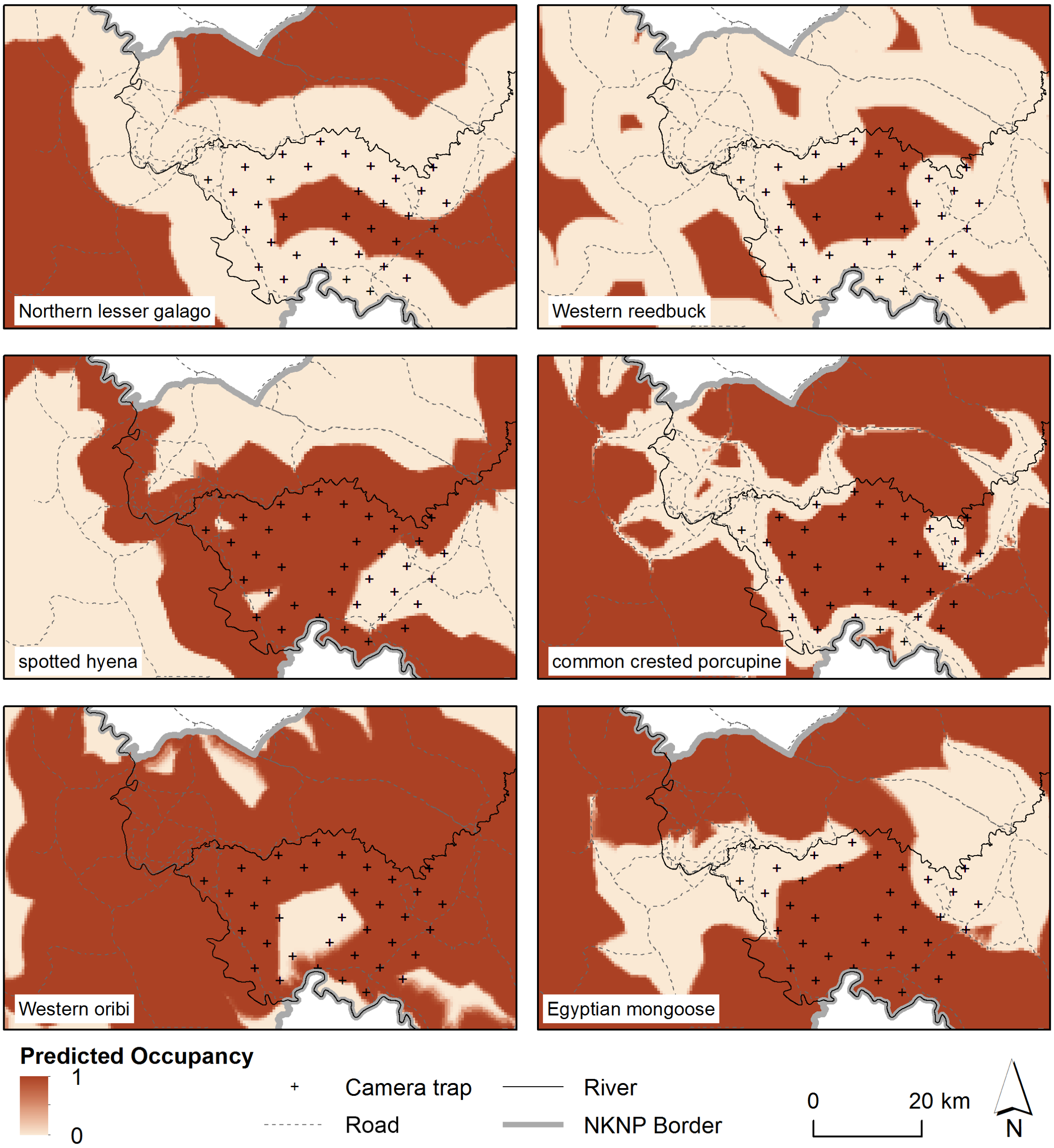

Figure 6. Predicted occupancy of six species with significant covariate effects in the core area of the Niokolo-Koba National Park. The figure was produced by Vojtěch Barták with use of ArcGIS 10.5 (Esri Inc., Redlands, USA, http://www.esri.com/arcgis).

Species richness

The only model that could be used for estimation of the number of species present in the study area was the multi-species occupancy-detectability (MSO) model. We present here the species richness estimate based on this model, despite its poor fit (Table 3; see Discussion for further justification). The posterior density of the number of present species is shown in Fig. 7; the posterior mean was 42.6 and 95% CI was (29, 73). The distribution of the proportion of present species (parameter Ω) was concentrated around 0.25 (see Fig. 8), which indicates the data augmentation up to the total number of 150 species in the virtual super-community was sufficient for an unbiased estimate of species richness.

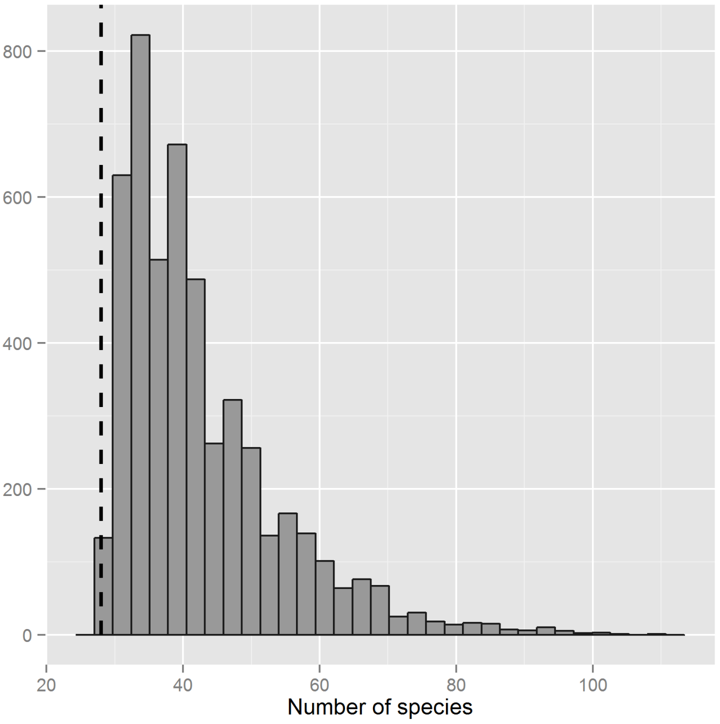

Figure 7. Posterior histogram for the proportion of present species based on 5,000 MCMC samples. The dashed line represents the observed value of 28.

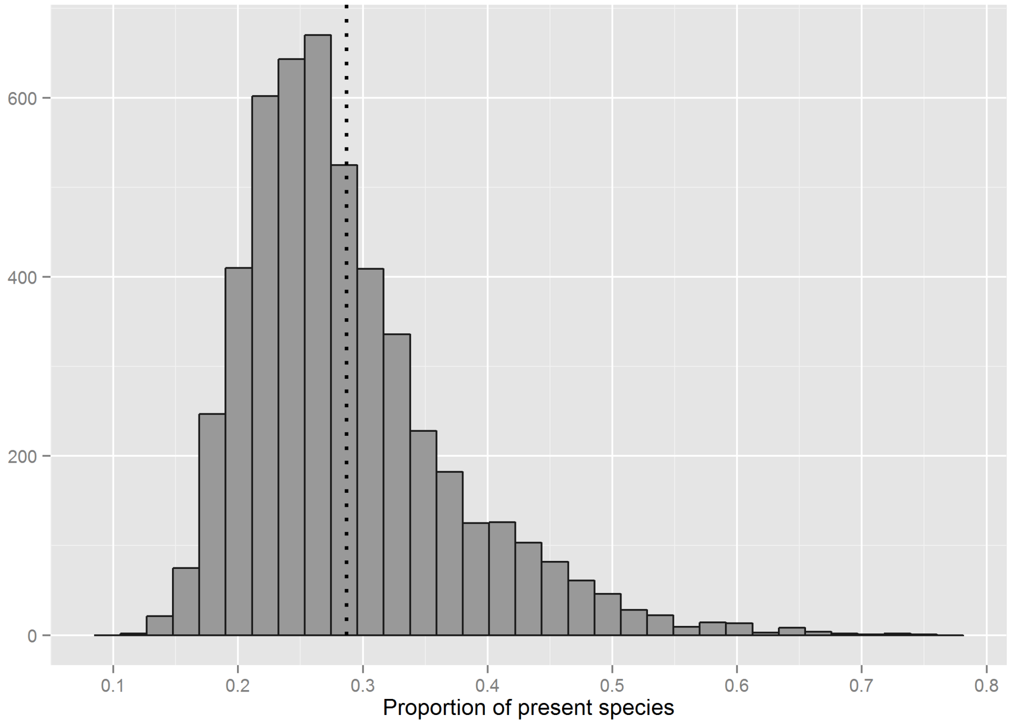

Figure 8. Posterior histogram for the proportion of present species based on 5,000 MCMC samples. The dotted line indicates mean value.

Discussion

Species inventory

The list of mammal species is a basic measure for any protected area[58,59]. As is commonly known, camera traps allow for successful recording of cryptic animals, and our results are coherent. The main breakthrough of our study was the capability of listing and analyzing small-bodied vigilant species (e.g. mongoose, wildcat *Felis silvestris*, rodents) as well as medium-sized mammals with significant ecological and eco-tourism importance, such as aardvark, honey badger, West African wild dog, serval (*Leptailurus serval*), caracal (*Caracal caracal*), African civet (*Civettictis civetta*), and common crested porcupine. These species were unreported in ground and aerial surveys in the past due to the chosen methodology at the time[14,16]. However, despite the former effort, red river hog (*Potamochoerus porcus*), Western reedbuck, and spotted hyena were also poorly documented. In contrast to these inventories, and supporting our approach, an opportunistic camera-trapping survey targeting large felids along rivers produced an analogous list of 35 species, but lacking caracal, Derby eland, red-flanked duiker, and Gambian rat (*Cricetomys gambianus*) in exchange for lion, marsh mongoose (*Atilax paludinosus*), common hippopotamus (*Hippopotamus amphibious*), and Buffon's kob (*Kobus kob*)[18].

We confirmed the proposed reliability of 1,000 trap days for the detection of rare species[60], and our 87.6% of recorded species is similar to those from tropical forests differing in detector arrays[45,61–63]. To our knowledge, no comparative data are available for the ecosystem of the savannah. However, we are aware that we missed at least three medium- to large-sized species (hippopotamus, Buffon's kob, and lion) and many others seemed extremely rare (e.g. Western Derby eland and red river hog). In the case of hippopotamus and marsh mongoose, our camera traps were not close enough to rivers to enable encounters. Despite cameras being placed in sites occupied by lions, which we confirmed through observations of fresh tracks, none were detected. This implies that the sampling effort should be considerably intensified (i.e. a denser array of detectors) in areas with a low density of lions, such as are found in West African reserves and national parks[10,31]. The same treatment should also lead to improvement in the case of hartebeests, Derby elands, red river hogs, and wild dogs, known to occur in herds, groups, and packs, respectively[39,40]. On the other hand, we cannot explain the absence of Buffon's kob, considered a relatively common antelope in the NKNP[18]. Seasonal changes in habitat preferences or the species-specific pressure of poachers targeting the surveyed area might be taken into account. Interestingly, four out of six signs of elephant were found during a 2006 inventory in the area equivalent to our surveyed zone[14]. We did not record any signs of the presence of elephant but, regardless of the eminent risk of its extinction, this species could occur close to remaining water sources in the dry period, and thus an opportunistic sampling design should be employed.

Models

Because of their ability to account for multiple sources of uncertainty, hierarchical models are increasingly popular among ecologists[64,65]; occupancy-detectability estimation and modelling represents one of the classical fields of their application[24]. Recently, this modelling framework was naturally extended to include the analysis of camera-trap data[62,66–68]. Although these models can be analysed in both a frequentist and Bayesian way, ecological studies tend to prefer the latter. Such a preference is probably mostly due to practical rather than conceptual reasons[65], which is sometimes criticized[69]. We consider the use of the Bayesian approach in the type of studies we are presenting here, however, to really be conceptually appropriate. Our study is descriptive rather than theoretical, and is aimed at setting up a sound long-term survey methodology for the national park, with the possibility of repeatedly updating the knowledge base concerning the status of species in the area. This perfectly suits the ability of Bayesian methods to use such updates via specification of informative prior distributions for model parameters in future analyses.

Despite a sound literature about how to properly analyse data using Bayesian methods[51,52,65], there is still a certain lack of consensus on how to report the model fit results in the camera trap studies. Most notably, some studies[62,68] do report the important convergence as well as goodness-of-fit measures, but some do not[67], which makes their results questionable. Here we included a check of both convergence (the $\hat{R}$ and multiple $\hat{R}$ statistics) and goodness of fit (the Bayesian *p*-value based on the Pearson χ^2 statistic).

To date, the development of occupancy modelling has offered a number of models for different situations. The two most typical formulations include the occupancy-detectability model and Royle-Nichols abundance-detectability model. Whereas the former is appropriate whenever the functional independence between abundance and species-level detectability can be assumed, i.e. most typically when the abundance can be assumed more or less constant among sites, the latter is much more realistic in situations with spatially varying abundance, which directly induces variation of species-level detectability (see[24], Chap. 4). In our case, our species pool included fully territorial species (e.g. white-tailed mongoose, banded mongoose, side-striped jackal, and wildcat), non-territorial species (e.g. red river hog, Western bushbuck, and common warthog), and those with only territorial males (e.g. crowned duiker, Western oribi, and Western reedbuck), as well as those for which this information is not available (e.g. red-flanked duiker and African civet). Hence, it is not surprising that when fitting the multiple-species models, the Royle-Nichols type MSA-N model was the only one with both satisfactory convergence and reasonable fit. This is also in agreement with other similar studies[62,68]. However, the MSO model was the only one that could be used for species richness estimation, and since we decided to report it despite its poor fit, we provide here a justification. The species richness estimate from the MSO model seems reasonable given the observed number of species and generally low detectabilities. Moreover, the MSO occupancy estimates were nearly identical and the pattern of detectability estimates very similar to those from the MSA-N model. The MSO detectabilities are generally lower than the MSA-N ones, which is expected given that the first are species-level whereas the latter are individual-level. In summary, we believe the MSO model is not completely wrong and reasonably accounted for imperfect detection when estimating species richness. One should not forget, however, that the model in general did not fit well, and the estimates based on it should be taken cautiously.

For fitting a separate model with environmental covariates for each species, it seems natural to use different models (i.e. occupancy-detectability or abundance-detectability) according to the nature of the species (i.e. territorial or not). As the convergence and goodness of fit, as well as the estimates, were almost identical for both model types, however, we decided to use only the occupancy-detectability ones, as we were able to fit them for all species. We realize that conclusions from the predicted occupancy need to be drawn carefully. As we can see in Fig. 6, the gradient between 0 and 1 is very sharp, resulting in an apparent and abrupt divide between the occupied and unoccupied areas. This is a consequence of the relatively large mean effect sizes displayed in Fig. 5. The prediction maps, however, ignore the extremely large confidence intervals of the effect sizes (see Fig. 5), which gives rise to a false impression of having highly precise knowledge about the species response. In fact, the large confidence intervals indicate high uncertainty related to the effect of environmental covariates on the species occupancy, with the lower bounds corresponding mostly with almost no effect. More precise estimates would require more data, ensured by either a denser camera trap network or longer observation period. With the data collected in this study, the effect of environmental covariates remains rather unclear, despite the good-looking prediction maps that display only the mean effects and ignore the uncertainty related to them.

Camera-trapping in the savannah

The urgency of having a source of solid biodiversity data for conservation strategies and actions in the socio-economically languished region of West Africa is indisputable[25,37,70]. The cost-effectiveness of camera-trapping is considered to be one of the main advantages of this method[66]. However, we encourage researchers to be aware that large-scale camera trap placement, even in protected areas in the potentially unsafe regions of West or Central Africa, should comply with a strict security policy. In the NKNP, this means involvement of an anti-poaching brigade. Deployment and collection of three cameras was therefore equal to four person-days (one researcher and three guards). The dry season, ideal for its limitation of foliage (i.e. false triggering of cameras), is associated with extreme daylight temperatures exceeding 45°C, a shortage of water for researchers, and a high risk of damage to detectors due to bushfires or battery leakage. These additional costs must be taken into account while the project is being planned.

We strived to examine and offer both a user-friendly methodology and the first reliable outputs, as a basic building block for future comparative studies. The situation in West Africa[10,71] is far from the premature optimism reported from the surprisingly stable animal populations camera-trapped in tropical rainforests[23]. The issue is of paramount importance because these results showed a grave asymmetry, with alarming LPI reports[25,72]. We hope that our call for further systematic investigation of trends in biodiversity will also be heard throughout the iconic African savannah landscape.

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Author contributions

T.J., P.J.V., M.D.K. and P.H. designed the study; T.J., P.J.V., M.D.K., O.P. conducted the fieldwork; T.J. and V.B. performed the data analysis and drafted the manuscript. All authors discussed presented results and commented on the manuscript.

Competing Financial Interests

The authors have declared that no competing interests exist.

Table 1. List of mammal taxa recorded in the Niokolo-Koba National Park during inventory surveys in 1990/91, 2006 and 2015. Values represent numbers of direct encounters with species or events in 2015; 'NA' is unavailable number of encounters, and '-' denotes absent species.

Taxonomic group	**Common name**	**Latin name**	**camtrap 2015**	**ground 1990/91**	**ground 2006**	**aerial 2006**
Ungulates	Crowned duiker	*Sylvicapra coronata*	129	96	25	103
	Common warthog	*Phacochoerus africanus*	126	265	171	232
	Western bushbuck	*Tragelaphus scriptus*	77	399	60	57
	Roan antelope	*Hippotragus equinus*	56	43	14	100
	Western oribi	*Ourebia quadriscopa*	46	165	43	19
	Red-flanked duiker	*Cephalophus rufilatus*	21	271	16	32
	West African buffalo	*Syncerus brachyceros*	13	44	8	20
	Western reedbuck	*Redunca redunca*	4	NA	-	1
	Western hartebeest	*Alcelaphus major*	2	50	6	18
	Defassa waterbuck	*Kobus defassa*	2	55	1	8
	Red river hog	*Potamochoerus porcus*	1	NA	1	-
	Western Derby eland	*Taurotragus d. derbianus*	1	-	1	1
	Buffon's kob	*Kobus kob*	-	443	8	16
	Common hippopotamus	*Hippopotamus amphibius*	-	-	-	8
Carnivores	Egyptian mongoose	*Herpestes ichneumon*	27	-	-	-
	White-tailed mongoose	*Ichneumia albicauda*	25	-	-	-
	Side-striped jackal	*Canis adustus*	23	18	13	-
	Spotted hyena	*Crocuta crocuta*	14	NA	-	1
	Common genet	*Genetta genetta*	8	-	-	-
	Leopard	*Panthera pardus*	4	-	2	-
	Common slender mongoose	*Galerella sanguinea*	3	NA	-	-
	Serval	*Leptailurus serval*	3	-	-	-
	Honey badger	*Mellivora capensis*	3	-	-	-
	Wildcat	*Felis silvestris*	2	-	-	-
	West African wild dog	*Lycaon pictus manguensis*	1	NA	-	-
	Banded mongoose	*Mungos mungo*	1	-	-	-
	Caracal	*Caracal caracal*	1	NA	-	-

	African civet	*Civettictis civetta*	1	-	-	-
	Lion	*Panthera leo*	-	NA	1	1
Primates	Guinea baboon	*Papio papio*	245	191	73	91
	Patas monkey	*Erythrocebus patas*	40	56	6	5
	Green monkey	*Chlorocebus sabaeus*	22	116	11	5
	Northern lesser galago	*Galago senegalensis*	5	-	-	-
	Western chimpanzee	*Pan troglodytes verus*	-	-	-	1
Afrotheria	Aardvark	*Orycteropus afer*	35	-	-	-
	African savanna elephant	*Loxodonta africana*	-	NA	-	-
Rodents	Common crested porcupine	*Hystrix cristata*	27	-	-	-
	Striped ground squirrel	*Xerus erythropus*	18	-	-	-
	Gambian rat	*Cricetomys gambianus*	1	-	-	-
Lagomorpha	African savanna hare	*Lepus microtis*	28	-	-	-
SUM species			**35**	**22**	**18**	**19**

Table 2. Basic inventory parameters of mammalian community recorded during camera-trapping survey in the Niokolo-Koba National Park in 2015. Relative abundance index (RAI) is a number of events divided by total number of trap days and multiplied by 100. Naïve occupancy is number of sites positive to species' presence divided by total number of sites.

Common name	Body mass (kg)	Home range (km2)	*n* of events	RAI	Naïve occupancy
Crowned duiker	17.4	0.27	129	6.88	0.62
Common warthog	83.8	1.7	126	6.72	0.73
Western bushbuck	51.0	0.2	77	4.10	0.68
Roan antelope	257.5	40-120	56	2.99	0.57
Western oribi	13.1	0.25-1	46	2.45	0.49
Red-flanked duiker	10.5	<1	21	1.12	0.24
West African buffalo	387.5	61	13	0.69	0.27
Western reedbuck	44.8	0.15-0.6	4	0.21	0.08
Western hartebeest	182.0	3.7-5.5	2	0.11	0.05
Defassa waterbuck	208.8	6	2	0.11	0.05
Red river hog	80.0	0.2-10	1	0.05	0.03
Western Derby eland	567.5	174-422	1	0.05	0.03
Egyptian mongoose	3.3	0.3-3.1	27	1.44	0.30
White-tailed mongoose	4.1	0.39-4.27	25	1.33	0.27
Side-striped jackal	9.2	0.2-4	23	1.23	0.30
Spotted hyena	65.0	20-1500	14	0.75	0.19
Common genet	2.0	0.25-1.7	8	0.43	0.11
Leopard	46.0	6-63	4	0.21	0.05
Common slender mongoose	0.5	0.25-1	3	0.16	0.08
Serval	10.3	9.5-31.5	3	0.16	0.05
Honey badger	9.5	126-541	3	0.16	0.08
Wildcat	4.5	1.6	2	0.11	0.05
West African wild dog	25.0	400-600	1	0.05	0.03

Banded mongoose	1.4	0.9	1	0.05	0.03
Caracal	12.5	5.5-65	1	0.05	0.03
African civet	13.5	11.1	1	0.05	0.03
Guinea baboon	16.8	4-40	245	13.06	0.89
Patas monkey	7.8	51.8	40	2.13	0.43
Green monkey	4.0	0.4	22	1.17	0.32
Northern lesser galago	0.2	0.1	5	0.27	0.05
Aardvark	61.0	2-5	35	1.87	0.46
Common crested porcupine	20.0	0.34-0.5	27	1.44	0.38
Striped ground squirrel	0.6	0.01-0.4	18	0.96	0.14
Gambian rat	1.2	0.1	1	0.05	0.03
African savanna hare	2.3	0.05-0.1	28	1.49	0.27

Table 3. Performance of community models. $\hat{R}$ refers to multiple Gelman-Rubin statistic with $\hat{R}$ close to 1 indicating good model convergence, *p* is a Bayesian *p* value calculated as $P(\chi^2_{\text{sim}} > \chi^2_{\text{obs}})$, with values greater than 0.975 or less than 0.025 indicating significant lack of fit.

Model	**Model description**	$\hat{R}$	***p***
MSO	Multi-species occupancy-detectability	1.251	0.0116
MSO_{covs}	Multi-species occupancy-detectability with covariates	8.729	0.4270
MSO-N	Multi-species occupancy-detectability with known N	1.012	0.0048
$\text{MSO-N}_{\text{covs}}$	Multi-species occupancy-detectability with known N and covariates	1.057	0.0056
MSA	Multi-species abundance-detectability	9.256	0.4016
MSA_{covs}	Multi-species abundance-detectability with covariates	NA	NA
MSA-N	Multi-species abundance-detectability with known N	1.029	0.5892
$\text{MSA-N}_{\text{covs}}$	Multi-species abundance-detectability with known N and covariates	NA	NA

5.2. Temporal activity pattern

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Temporal overlaps of feral cats with prey and competitors in primary and human-altered habitats on Bohol Island, Philippines.

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Temporal overlaps of feral cats with prey and competitors in primary and human-altered habitats on Bohol Island, Philippines

Vlastimil Bogdan, Tomáš Jůnek and Pavla Jůnková Vymyslická

Department of Ecology/Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

ABSTRACT

The vertebrate fauna of the Philippines, known for its diversity and high proportion of endemic species, comprises mainly small- to medium-sized forms with a few large exceptions. As with other tropical ecosystems, the major threats to wildlife are habitat loss, hunting and invasive species, of which the feral cat (*Felis catus*) is considered the most damaging. Our camera-trapping study focused on a terrestrial vertebrate species inventory on Bohol Island and tempo-spatial co-occurrences of feral cats with their prey and competitors. The survey took place in the Rajah Sikatuna Protected Landscape, and we examined the primary rainforest, its border with agricultural land, and rural areas in the vicinity of villages. Altogether, over 2,885 trap days we captured 30 species of vertebrates–10 mammals (including *Sus philippensis*), 19 birds and one reptile, *Varanus cumingi*. We trapped 81.8% of expected vertebrates. Based on the number of events, the most frequent native species was the barred rail (*Gallirallus torquatus*). The highest overlap in diel activity between cats and potential prey was recorded with rodents in rural areas ($\Delta = 0.62$); the lowest was in the same habitat with ground-dwelling birds ($\Delta = 0.40$). Cat activity was not recorded inside the rainforest; in other habitats their diel activity pattern differed. The cats' activity declined in daylight in the proximity of humans, while it peaked at the transition zone between rainforest and fields. Both rodents and ground-dwelling birds exhibited a shift in activity levels between sites where cats were present or absent. Rodents tend to become active by day in cat-free habitats. No cats' temporal response to co-occurrences of civets (*Paradoxurus hermaphroditus* and *Viverra tangalunga*) was found but cats in diel activity avoided domestic dogs (*Canis lupus familiaris*). Our first insight into the ecology of this invasive predator in the Philippines revealed an avoidance of homogeneous primary rainforest and a tendency to forage close to human settlements in heterogeneous habitats. A detailed further investigation of the composition of the cat's diet, as well as ranging pattern, is still needed.

Subjects Biodiversity, Conservation Biology, Ecology

Keywords Biodiversity, Camera trap, *Felis catus*, Invasive species, Overlap, Philippines, Relative abundance index, Species accumulation curve, *Canis lupus familiaris*

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Corresponding author
Tomáš Jůnek, tom_junek@yahoo.com

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INTRODUCTION

The Philippine Archipelago is considered a global biodiversity hotspot, known for its high proportion of endemic species (*Ambal et al., 2012*). The terrestrial vertebrate taxa, which primarily encompass small to medium sized species, inhabit more than 7,100 islands. These species include at least 213 mammals (*Heaney et al., 2010*), 674 birds (*Lapage, 2015*), 270 reptiles and 111 amphibians (*BREO, 2015*).

Similar to other oceanic islands, the predominantly small fauna of the Philippines suffers from the presence of competing invasive species, such as *Rattus* spp., and the feral cat (*Felis catus*). The cat is listed as the most widespread and probably most damaging of the four carnivores included on the list of the 100 worst invasive species (*Lowe et al., 2000*). At least 175 vertebrates are threatened or have been driven to extinction by feral cats on at least 120 islands (*Medina et al., 2011*). Meta-analysis has revealed that the negative impact of feral cats is largest for insular endemic mammals, and is exacerbated by the presence of invasive cat prey species such as mice (*Mus musculus*) or rabbits (*Oryctolagus cunuculus*) (*Nogales et al., 2013*). The cat is widely kept as a pet by people throughout the Philippines and can be found foraging in every habitat (*Duffy & Capece, 2012*). Despite the general prevalence of cats in the Philippine landscape, there is a noticeable lack of knowledge regarding the cat's impact on the biodiversity of this archipelago.

Cats feed on a wide range of animals, from arthropods, reptiles and birds to mammals the size of a rabbit (*Pearre, Maass & Maass, 1998*). In Australia alone, with a variety of animals of similar size such as those found in the Philippines, 400 prey species consumed by cats have been recorded (*Doherty et al., 2015*). In the Philippines, members of the orders Chiroptera and Rodentia are the most numerous mammalian species (*Heaney et al., 2010*). A wide range of terrestrial and arboreal rodents with body mass ranging from the 15-g *Musseromys* spp. to the 2.6-kg *Phloeomys* spp. risk predation by cats. Only adult individuals of *Phloeomys* and *Hystrix pumila* (*Heaney et al., 2010*) exceed the potential prey dimensions. According to size and niche, members of the Tupaiidea (treeshrews), Erinaceidae (moonrats) and Soricidae family (shrews) should be listed as mammalian prey for cats. Similarly, the smallest Philippine primate, *Tarsius syrichta*, which inhabits Bohol and other islands of the Mindanao faunal region, can be included (*MacKinnon & MacKinnon, 1980*).

On Bohol Island (3,269 km^2), as on the other Philippine islands, bats and rodents dominate among local mammals. The small mammalian fauna consists of one insectivorous species and nine species of rodents, including the introduced *Mus musculus, Rattus rattus, Rattus norvegicus, Rattus tanezumi* and *Rattus exulans* (*Heaney et al., 2010*). The avifauna of Bohol numbers 235 species, with Passeriformes forming the largest sub-group at 83 species. Bohol is also home to 14 ground-dwelling bird species inhabiting the woody or bushy inland habitats potentially affected by cats (*Kennedy, 2000*).

Along with dogs (*Canis lupus familiaris*), possible competitors of cats on Bohol include two mammalian carnivores, Asian palm civet (*Paradoxurus hermaphroditus*) and Malayan civet (*Viverra tangalunga*) (*Heaney et al., 2010*) and two reptile species: yellow-headed water monitor (*Varanus cumingi*) and reticulated python (*Python reticulatus*) (*BREO, 2015*). To our knowledge, no predation between cat and civets has been published.

The timing of activity of mammalian predators is a well discussed topic (e.g., *Palomares & Caro, 1999*; *Tambling et al., 2015*). Time-stamped records from camera traps allow for detailed insights into the time budget and temporal coexistence of animals across trophic guilds, seasons, etc. (*Rowcliffe et al., 2014*), and recent camera trapping studies have successfully examined overlaps in diel activity patterns (*Ridout & Linkie, 2009*), confirming significant activity overlap between carnivores and their preferred prey (*Harmsen et al., 2009*; *Lucherini et al., 2009*; *Sweitzer & Furnas, 2016*) and suggesting predator behavior to reduce foraging energy expenditure (*Foster et al., 2013*). In their role as mesopredators cats must optimize their use of time not only to encounter prey but also to cope with a sympatric superior predator (*Brook, Johnson & Ritchie, 2012*). The combination of partitioning of habitat, prey size and a 24-h daily cycle is thought to be a complex mechanism allowing competing felids to coexist in different animal communities (*Di Bitetti et al., 2010*; *Foster et al., 2013*; *Silmi, Anggara & Dahlen, 2013*; *Sunarto et al., 2015*). For example, low overlap in activities has been found between marbled cat (*Pardofelis marmorata*) and clouded leopard (*Neofelis nebulosa*) in Thailand (*Lynam et al., 2013*). *Wang & Fisher (2012)* also confirmed higher segregation of diel activities of cats with respect to dingoes during wet months. The particularly suppressive effect of an apex carnivore on invasive populations of cats is considered an important conservation issue (*Brook, Johnson & Ritchie, 2012*; *Lazenby & Dickman, 2013*; *Doherty, Bengsen & Davis, 2015*).

We conducted a camera-trap survey on Bohol Island in an attempt to uncover tempo-spatial co-occurrences of terrestrial vertebrate species on regularly used trails and to confirm the presence of cats in the protected primary rainforest (Zone I), a transition zone along the border of the primary rainforest with the agricultural landscape (Zone II), and inside the rural landscape in the proximity of human settlements (Zone III). Our objectives were to: (1) create a general inventory of camera-trapped taxa; (2) model the species accumulation curve using previous knowledge of the possible number of mammalian, avian and reptile species detectable by camera-traps; and (3) compare the diel activity levels of cats with those of potential prey and competitors.

MATERIALS & METHODS

Study site

Our study was conducted under research permit No. 2014-04, issued by DENR, Region VII, Philippines, between July 2nd and December 4th, 2014 in the surroundings of the town of Bilar, Bohol Island, Philippines. The landscape consists of a mixture of distinctive flat rural areas near human settlements, used as rice fields and plantations for various crops, steep karst hills covered by brush and secondary forest, and primary rainforest in protected areas. The town of Bilar lies between two conservation areas, the Rajah Sikatuna Protected Landscape (RSPL) and the Loboc River Watershed Forest Reserve. RSPL is the second largest protected sanctuary on Bohol, covering 11,034 ha of a mostly hilly limestone environment rich in characteristic landforms such as ravines, sinkholes and caves. The altitude in RSPL varies between 300 and 826 m above sea level. The forest canopy is multi-layered, with trees reaching up to 20 m in height. Members of the families Dipterocarpaceae, Moraceae

Table 1 **Summary of the camera trap deployment in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines.**

Zone	Site	Date	*n* camera traps	*n* trap-days	Range of distances between traps (m)
I	SP	12.7.–30.7.2014	12	204	60–514
I	SF	30.7.–14.8.2014	12	173	38–307
I	WS	1.8.–15.8.2014	9	125	37–265
II	BI	2.8.–4.12.2014	10	850	28–395
II	LS	12.7.–4.12.2014	7	536	48–174
II	BU	2.8.–4.12.2014	4	383	38–44
III	HB	5.7.–31.7.2014	10	224	25–236
III	SU	2.7.–31.7.2014	16	390	23–139

and Melicacea dominate the canopy. Certain regions of RSPL have been reforested with white teak (*Gmelina arborea*) and Honduras mahogany (*Swietenia macrophylla*) (*Barcelona et al., 2006*). The average annual precipitation reaches 1,600 mm; the rainy season typically lasts from June to December, with an increase in precipitation to 200 mm per month. The driest month is April when approximately 40 mm of rain falls.

Sampling design

We monitored three types of landscape typical of tropical regions and deployed cameras in groups, one camera per location, at eight trapping sites (Fig. 1): Zone I—protected primary rainforest including the Watershed Forest Reserve (site WS), interior of RSPL (site SP) and abandoned farms in the early stages of succession into RSPL (site SF); Zone II—transition zone between the primary rainforest of RSPL and rice fields close to the village of Bulak (site BU), transition zone between RSPL and rice and corn fields close to Logarita Springs (site LS), and transition zone between RSPL and the farms of the village Binantay (site BI); Zone III—mixture of brush and degraded forest and plantations on the edge of the village of Subayon (site SU), and at Bohol Habitat Conservation Center on the edge of the town of Bilar (site HB). Details on camera traps' deployment and duration of sampling are shown in Table 1.

Sampling procedures

We used 41 weatherproof infrared digital camera traps –29 units of Ltl Acorn 5210MC (Shenzhen Ltl Acorn Electronics Co., Ltd.) and 12 units of SPYPOINT IR7 (SPYPOINT^{MD}, G.G. Telecom). Prior to the study, we tested both types of cameras in a week-long trial which was focused on the difference in detection rates for moving objects. No difference larger than 10 % between numbers of independence events was found. Both types of cameras were also used in every habitat to avoid a bias from site-specific detection rates. Cameras were set up to perform the same delay between recordings –SPYPOINT to take two images with a delay of 10 s between consecutive triggering, and Ltl Acorns to take one picture followed by a 5 s video, with a 5 s delay between triggering. Video sequences served as an additional tool for the identification of species.

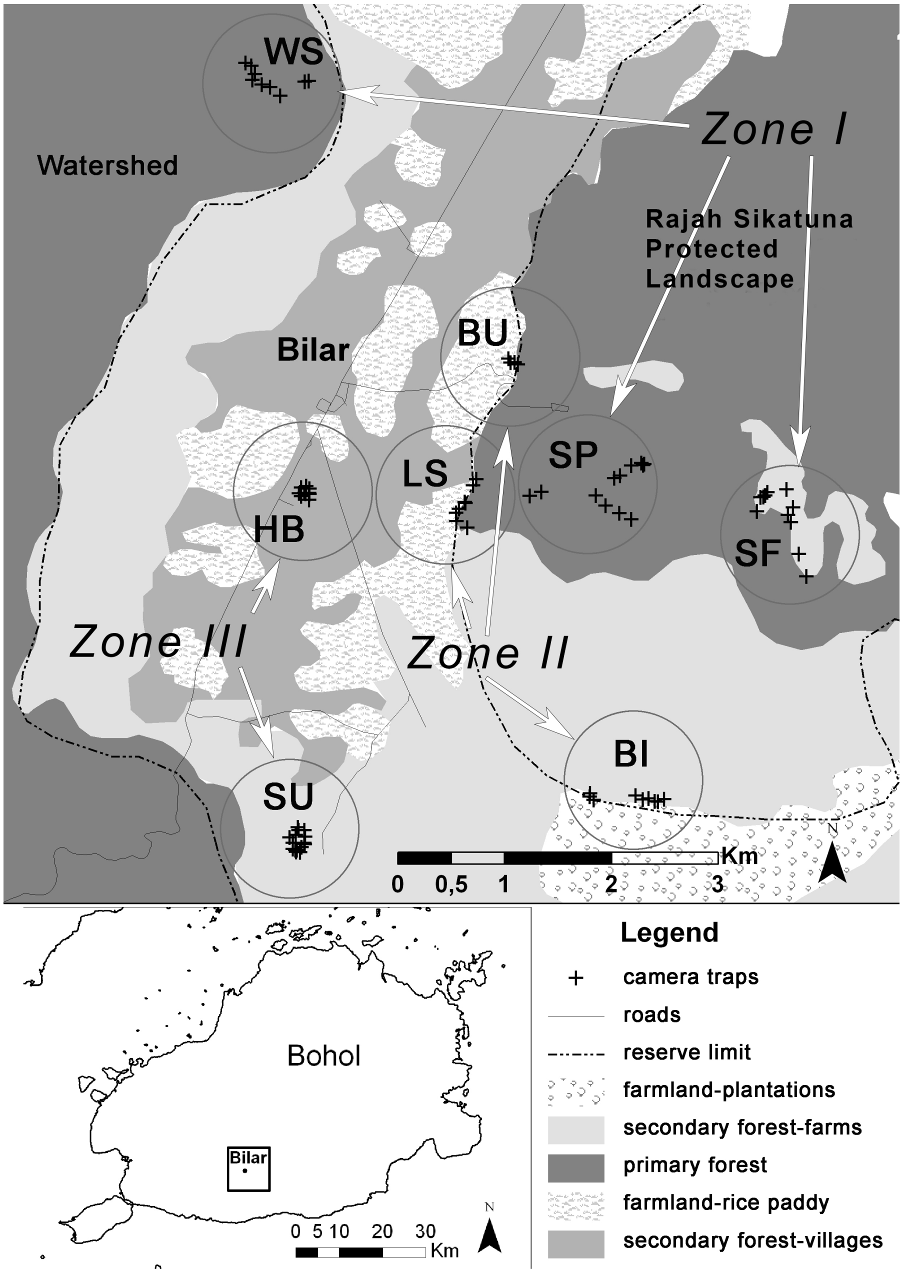

Figure 1 Schematized map of the study area in the municipality of Bilar, Bohol, Philippines. Circles highlight eight sites surveyed from July to December 2014.

We placed all cameras opportunistically on the most frequented trails or their junctions and, according to the expected size of target vertebrates, we fastened cameras with a belt onto the trunks of trees or bushes nearest to the trail, at a height of up to 0.5 m, with a focal point approximately 2 m from the lens. All cameras were active 24 h a day; all records in infrared mode were available only in a black-and-white version. No bait was used.

Identification of taxa

Two observers, VB and TJ, independently identified all species visually from images and videos; the results were mutually crosschecked, and disagreeing or unidentifiable records were excluded from the analysis. Based on available databases (*Heaney et al., 2010*; *BREO, 2015*; *Lapage, 2015*), we made a list of terrestrial mammalian and avian ground-dwelling species known or expected to occur on Bohol (Table 2). From reptiles, we included only the largest four-legged taxon, the yellow-headed water monitor (*Varanus cumingi*). Members of the order Chiroptera and the strictly arboreal Philippine colugo (*Cynocephalus volans*) were *a priori* omitted. The conservation status of each species was assessed following *IUCN (2015)*.

Due to the limited nature of the recordings, for the identification process and the calculation of a species accumulation curve all taxa the size of a mouse (*Mus musculus* and also the insectivorous *Crocidura beatus*) were pooled into the group called 'mice', and all species of rats (*Rattus* spp. and *Bullimus bagobus*) into the group 'rats'. In addition, both known species of squirrels (*Exilisciurus concinnus* and *Sundasciurus philippinensis*) were grouped into one taxon: 'squirrels'. In total, the list consisted of eight taxa of mammals, 13 birds and one reptile. For purposes of *overlap* analyses between cats and their competitors and prey, we pooled both native carnivore species into a group called 'civets' and put mice, rats and squirrels into the group 'rodents'. Ground-dwelling species of birds were the second analyzed group of prey; dogs were accordingly examined as competitors.

Data analysis

Photographs were defined as events (or activity records) when the delay between two consecutive images of an individual exceeded 10 min. The same individual could theoretically trigger more than one camera within 10 min. For each species and Zone, in Table 2 we reported occurrences of species at cameras represented by events (*Lazenby & Dickman, 2013*).

We used a species accumulation curve based on the cumulative number of camera-trapping days, computed in EstimateS Version 9.1.0 (*Colwell, 2013*), to find out if our survey lasted a sufficient number of days to capture the 22 expected terrestrial vertebrate species (including three pooled groups) known from Bohol. We followed *Tobler et al. (2008)* and calculated well-performing estimators of species richness: the non-parametric abundance-based estimator ACE, and the non-parametric incidence-based estimators ICE and Jackknife 1. An abundance-based rarefaction approach with 95% confidence intervals and 1,000 random iterations of sample order was used.

The pair-wise temporal overlap of selected activity patterns was analyzed using the R statistical environment package '*overlap*' (*Meredith & Ridout, 2014*). Following *Ridout & Linkie (2009)*, we applied kernel density estimation on circular data pooled within all study sites. Density of activity (y-axis) uses a von Mises kernel, corresponding to a circular distribution, and is based on recorded time of each event on 24-h x-axis. The coefficient of overlap (Δ) was calculated with a smoothing parameter of 1.0. We used a smoothed bootstrap of 10,000 resamples to determine standard errors and 95% confidence intervals. We only analyzed combinations of pairs of species, which scored at least 30 events in the activity record (MS Ridout, pers. comm., 2015) in a given environment. The number

Table 2 **List of species recorded during a survey in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines.** Values represent number of events of species recorded in each zone.

Common name	Scientific name	Zone I	Zone II	Zone III	Site
Philippine warty pig[a]	*Sus philippensis*	1	0	0	SF
Common palm civet[a]	*Paradoxurus hermaphroditus*	10	43	6	Su,Bi,LS,Bu,SP,SF,Ws
Malay civet[a]	*Viverra tangalunga*	1	8	7	Ha,Bi,LS,SP
Long-tailed macaque[a]	*Macaca fascicularis*	3	4	0	LS,Bu,Ws
Philippine tarsier[a]	*Tarsius syrichta*	0	1	2	Su,LS
Philippine tree squirrel[a]	*Sundasciurus philippinensis*	4	42	1	Su,LS,Bu,SP,SF,Ws
Dog	*Canis lupus familiaris*	14	39	91	Su,Ha,Bi,LS,Bu,SP
Cat	*Felis catus*	0	97	83	Su,Ha,Bi,LS
Rat[a]	*Rattus* spp.	32	242	47	Su,Ha,Bi,LS,Bu,SP,SF,Ws
Mice[a]	*Mus* spp.	5	217	5	Su,Ha,Bi,LS,Bu,SP,SF,Ws
Yellow-headed water monitor[a]	*Varanus cumingi*	1	6	5	Su,LS,SF
Hooded pitta[a]	*Pitta sordida*	0	0	41	Ha
Red-bellied pitta[a]	*Pitta erythrogaster*	0	42	0	Bi,LS
Azure-breasted pitta[a]	Pitta steerii	1	0	0	Ws
Striated wren-babbler[a]	*Ptilocichla mindanensis*	1	9	0	LS,Ws
Red junglefowl[a]	*Gallus gallus*	0	5	14	Su,LS,Bu
Barred rail[a]	*Gallirallus torquatus*	0	4	179	Su,Ha,Bi,LS,Bu
Slaty-legged crake[a]	*Rallina eurizonoides*	0	0	15	Su,Ha
Ruddy-breasted crake[a]	*Zapornia fusca*	0	2	1	Su,Bu
Plain bush-hen[a]	*Amaurornis olivacea*	0	0	10	Su
Black-faced coucal	*Centropus melanops*	2	4	2	Su,Bi,LS,Bu,SF,Ws
Philippine coucal	*Centropus viridis*	0	2	3	Su,Bu
Emerald dove	*Chalcophaps indica*	7	7	16	Su,Ha,Bi,LS,Bu,SF,Ws
Philippine magpie-robin	*Copsychus mindanensis*	0	3	1	Ha,Bi
Mindanao bleeding-heart	*Gallicolumba crinigera*	1	2	0	LS,SP
Hair-crested drongo	*Dicrurus hottentottus*	1	0	0	SF
Besra	*Accipiter virgatus*	0	1	1	Su,Bi
Philippine hawk-owl	*Ninox philippensis*	0	0	1	Ha
Yellow-breasted tailorbird	*Orthotomus samarensis*	0	1	0	Bi
Domestic chicken	*Gallus gallus domeaticus*	10	254	9	Su,Bi,LS,Bu,SP,SF

Notes.

[a] Species those expected for the species accumulation curve.

of events used for calculation of the activity pattern overlap for each analyzed group of animals and each location is shown in Table 3.

RESULTS

Species inventory

During the whole survey period, lasting 155 days, we accumulated 2,885 trap days and 2,034 events. The combined capture rate across all sites was 73.1 events per 100 trap days. The list of all 30 animal taxa recorded is shown in Table 2.

Table 3 Number of events used for calculation of activity pattern overlap for each analyzed group of animals and each location in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines. Values in parentheses show the zone-specific relative abundance index (events/total trap days in zone*100). Dashes denote unprocessed entries.

	Zone I	Zone II	Zone III	All sites	No cats	With cats
Cats	0 (0)	67 (4.57)	83 (13.52)	150 (5.81)	–	–
Dogs	14 (2.79)	37 (2.53)	90 (14.66)	141 (5.46)	–	–
Rodents	41 (8.17)	480 (32.76)	47 (7.65)	568 (22.00)	41 (8.18)	527 (25.35)
Ground-dwelling birds	12 (2.39)	242 (16.52)	263 (42.83)	517 (20.03)	12 (2.39)	505 (24.29)
Civets	11 (2.19)	16 (1.09)	13 (2.12)	40 (1.39)	–	–

The most frequent native species was the barred rail (*Gallirallus torquatus*), captured in 183 independence events. We did not record four expected bird species: *Megapodius cumingii, Coturnix chinensis, Turnix sylvaticus* and *Gallinago megala.* On the other hand, we confirmed the survival of the Philippine warty pig (*Sus philippensis*). Given its size, it was probably a male individual that was captured, only once, on three images on August 9th (6:35 pm) in a mud wallow in the interior of RSPL.

We found that feral cats most often occurred in the Zone II and III, and were absent inside the primary forest. A similar trend was found for ground-dwelling birds. Most rats and other small mammals were recorded in the transition Zone II between the RSPL forest and agricultural land. Along with feral cats and domestic dogs, we also recorded all three medium-sized mammals occurring on Bohol—the common palm civet (59 events), Malay civet (16 events) and long-tailed macaque (*Macaca fascicularis*) (7 events). Humans were also captured but excluded from the analysis.

Within all eight sampling sites, we captured 18 of 22 expected target taxa, which corresponds to a success rate of 81.8% of the species inventory (100% of mammals and reptiles, 69.2% of birds). We used these 18 taxa for calculating the species accumulation curve (Fig. 2). The mean estimated species richness computed in EstimateS was 19.7 species (ACE = 19.6, ICE = 19.5 and Jackknife 1 = 20.0). We recorded 15.89 species (72.2% of expected species) in 1,000 trap days. The eight target species of mammals were captured in 1,723 trap days; similarly, nine ground-dwelling birds were recorded within 1,435 trap days.

Temporal overlaps

We recorded cats only in transition Zone II and in the rural landscape close to human settlements (Zone III). Diel activity patterns of cats differed among zones (Fig. 3). Cats showed a decrease in late-afternoon activity near villages, whereas activity in the transition area peaked right before noon. Generally, the activity of cats by daylight was higher in transition zones; in Zone III cats were recorded mainly at night.

The highest overlap in activity patterns between cats and rodents (Table 4) was found in the rural landscape of Zone III, and between cats and ground-dwelling birds in transition Zone II (Fig. 4).

Both categories of potential prey showed shifts in temporal occurrence within sites, based on the presence of cat (Fig. 5). As seen, the peaks of rodent activity decreased in the

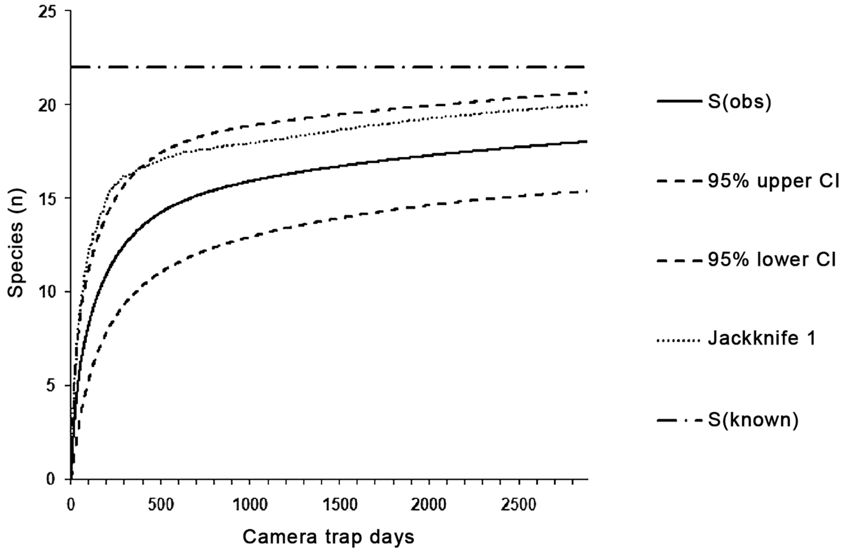

Figure 2 **The species accumulation curves with 95% CIs for species captured in all categories of environment in 2,885 trap days.** The dashed-and-dotted line marks the known number of species, while the dotted lines represent species richness estimated by Jackknife 1 in EstimateS (*Colwell, 2013*).

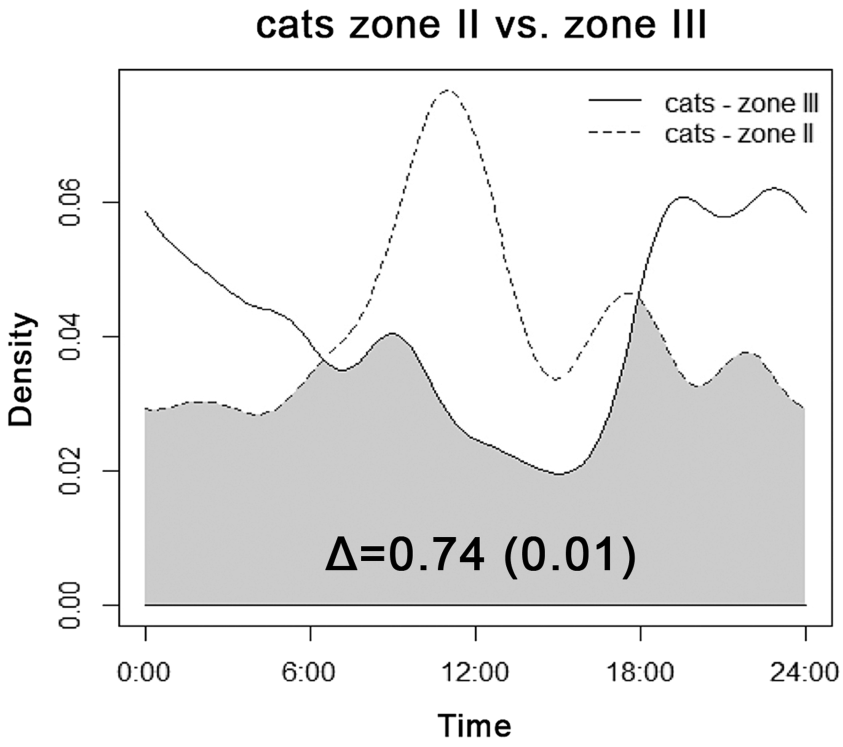

Figure 3 **Overlap between diel activity patterns of cats in transition Zone II (dashed line) and rural Zone III.** The number represents the coefficient of overlap (Δ), with standard error in parentheses.

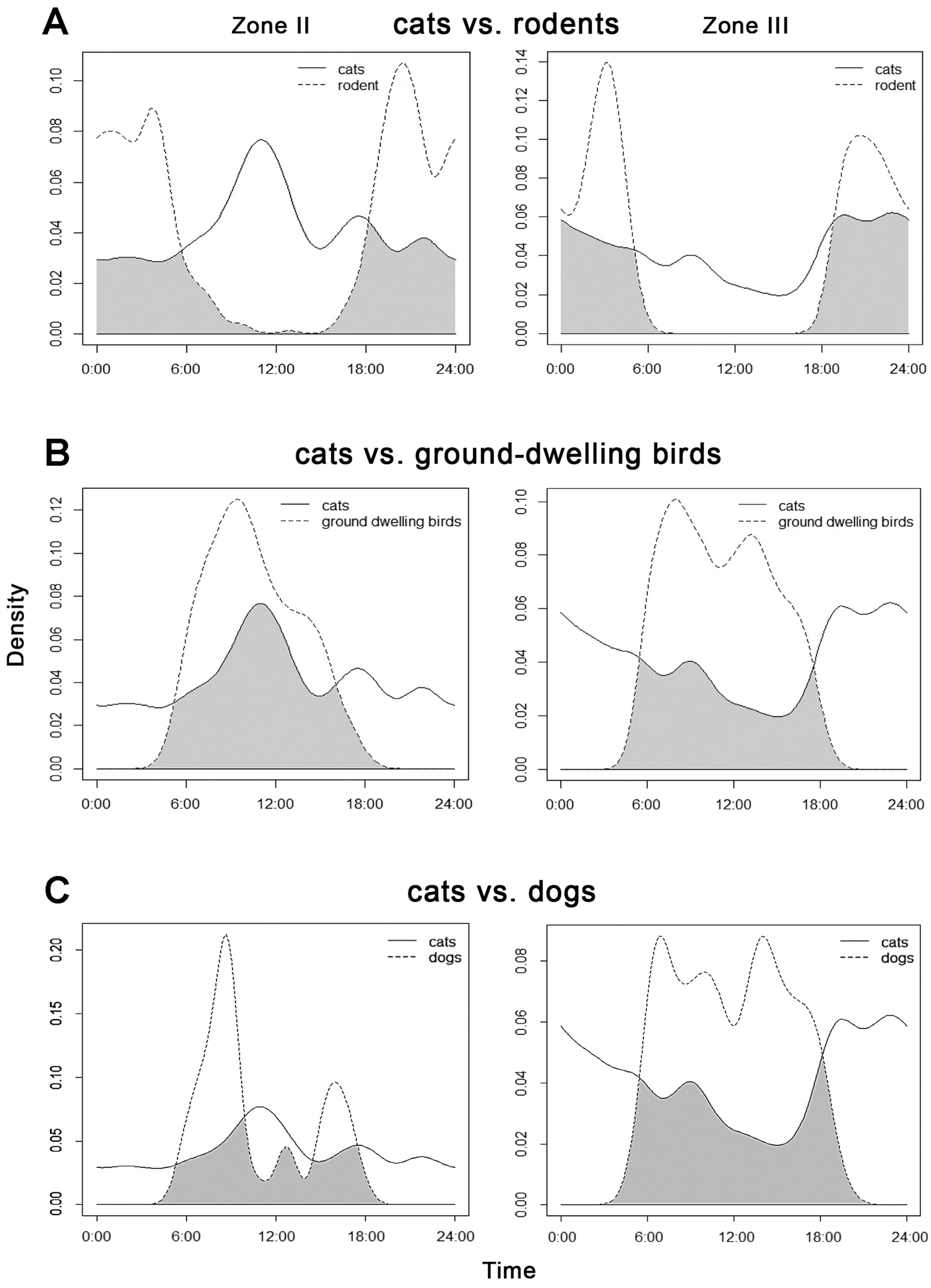

Figure 4 Overlap between the diel activity patterns of cats with (A) rodents, (B) ground-dwelling birds and (C) dogs in transition Zone II and rural Zone III.

Table 4 Activity pattern overlaps between cats, their potential prey (rodents and ground-dwelling birds) and competitors (dogs and civets) in transition Zone II, rural Zone III and among all sites surveyed in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines.

	Site	Overlap Δ	*SE*	95% l*CI*	95% u*CI*
Cats vs. rodents	Zone II	0.48	0.023	0.37	0.58
	Zone III	0.62	0.002	0.52	0.73
Cats vs. ground-dwelling birds	Zone II	0.61	0.019	0.50	0.71
	Zone III	0.40	0.041	0.30	0.50
Cats vs. dogs	Zone II	0.50	0.052	0.36	0.62
	Zone III	0.45	0.041	0.35	0.56
Cats vs. civets	All sites	0.55	0.067	0.45	0.64

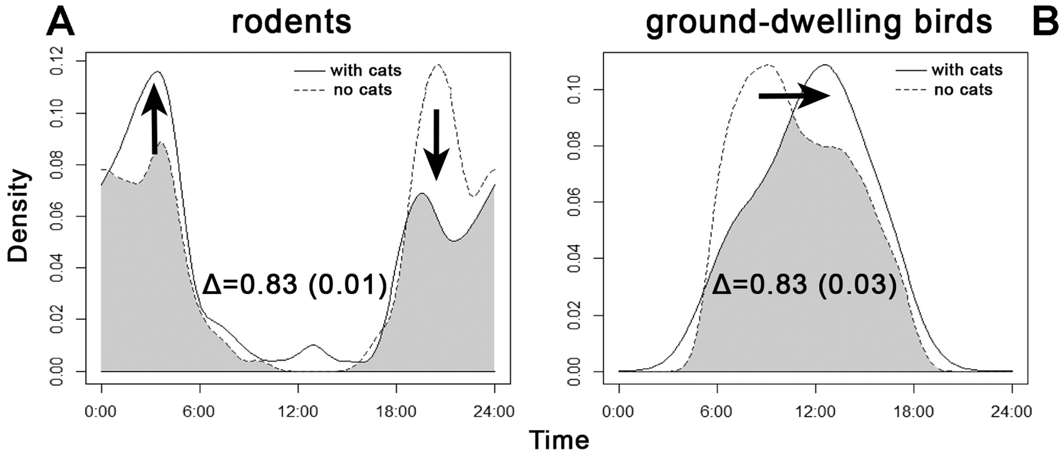

Figure 5 Overlap between the diel activity patterns of (A) rodents and (B) ground-dwelling birds at sites with and without the presence of cats. The numbers represent coefficients of overlap (Δ) with standard errors in parentheses. Arrows indicate shifts in activity levels if cats are present.

hours before sunrise and increased after sunset, whereas the activity of ground-dwelling birds peaked about 4 h sooner at sites where cats were not recorded.

Cats showed the second lowest overlap among all groups with dogs in Zone III (Table 4) where dogs were dominant and active during the day. In Zone II these two animals appeared to peak in their activity at different times: dogs were most active in the morning and late afternoon, whereas cats peaked before noon (Fig. 4).

The overlap between the diel activity patterns of cats and both species of civets is shown in Fig. 6. Cats exhibited roughly consistent activity throughout a 24-h period, with no apparent shift caused by the nocturnal occurrence of sympatric civets.

DISCUSSION

According to our knowledge, to date no study of the behavior and ecology of feral cats has been conducted in the Philippines, nor any camera-trap-based species inventory on Bohol. With the exception of the Philippine pygmy squirrel, *Exilisciurus concinnus*, we were able to capture and identify every non-volant mammalian species recorded as occurring on Bohol larger than a mouse, including an individual of *Sus philippensis*, which is considered to be close to extinction (*Oliver, 1993*), even by local people. Camera traps captured 81.8% of known ground-dwelling mammalian, avian, and reptilian species, similar to the 86 % captured in the Amazon rain forest (*Tobler et al., 2008*) or 89% in the lowland rainforest of Borneo (*Bernard et al., 2013*); both those camera-trapping studies were restricted to mammals. In addition, the initially steep shape of our general species accumulation curve corresponds with studies conducted in tropical ecosystems and confirms the robustness of the approach. Similarly to *Rovero et al. (2014)*, we captured the majority of selected species in 1,000 trap days, considered a reliable threshold enabling the detection of rare species (*O'Brien, 2011*).

The absence of cats in the interior of primary rainforest seems not to be driven by distance from the nearest human settlements, given that all three monitored sites were up to approximately 3 km from houses. We suggest that the absence of preferred features and habitats in the rain forest may have resulted in camera traps failing to capture cats. Cats typically use a mixture of vegetation cover at ground level which provides both cover and open space for observing their prey; such habitat may increase hunting success (*Doherty, Bengsen & Davis, 2015*). The habitat heterogeneity hypothesis by *Tews et al. (2004)* predicts that heterogeneous habitats offer a greater diversity and density of potential prey than homogeneous ones, which could be conceivable for cats. Linear features in space (e.g., tree lines, roads and other corridors) are generally considered to maximize cat's detectability (*Crooks, 2002*; *Bengsen, Butler & Masters, 2012*). We would expect to record cats in primary forest mostly on trails (*Trolle & Kéry, 2005*; *Harmsen et al., 2010*; *Anile et al., 2014*) but they could disperse into the undergrowth on paths that are undetected.

The presence of competing, potentially dangerous predators in primary forest is unlikely to explain the absence of cats. Dogs and both species of civets were equally present in all three zones. The common palm civet and Malay civet are omnivorous with a distinctive nocturnal activity pattern (*Jennings et al., 2009*) but they forage in the habitat of cats, and given their size we consider them to be competitors of cats. Nonetheless, cats do not show any temporal avoidance, indicating no interspecies competition, which has evolved during almost a 500-year co-existence (*Jubair, 1999*). For a more comprehensive view of possible niche partitioning, as found for example between felids on Sumatra (*Sunarto et al., 2015*), a camera-trapping study should be conducted on Negros, where the Visayan leopard cat (*Prionailurus bengalensis* ssp. *rabori*) occurs as a regional direct competitor (*IUCN, 2015*).

Our results (Tables 2 and 3) show that species richness and availability of both prey categories (rodents and birds) was higher, nearly by orders of magnitude, in both human-altered zones than in primary rainforest. We attribute this to the variety of vertebrate and invertebrate prey, which is more abundant in heterogeneous landscapes. In addition, as suggested by *Lozano et al. (2003)*, feral cats use a wide range of habitat components to meet their different activity requirements (e.g., hunting, resting), and this landscape offers a mixture of agricultural features with secondary growth, infrastructure and potential human subsidies (*Ferreira et al., 2011*). Our data clearly support such a tendency to forage relatively close to human settlements, however we were not able to determine from our records whether a photographed animal was feral or domestic.

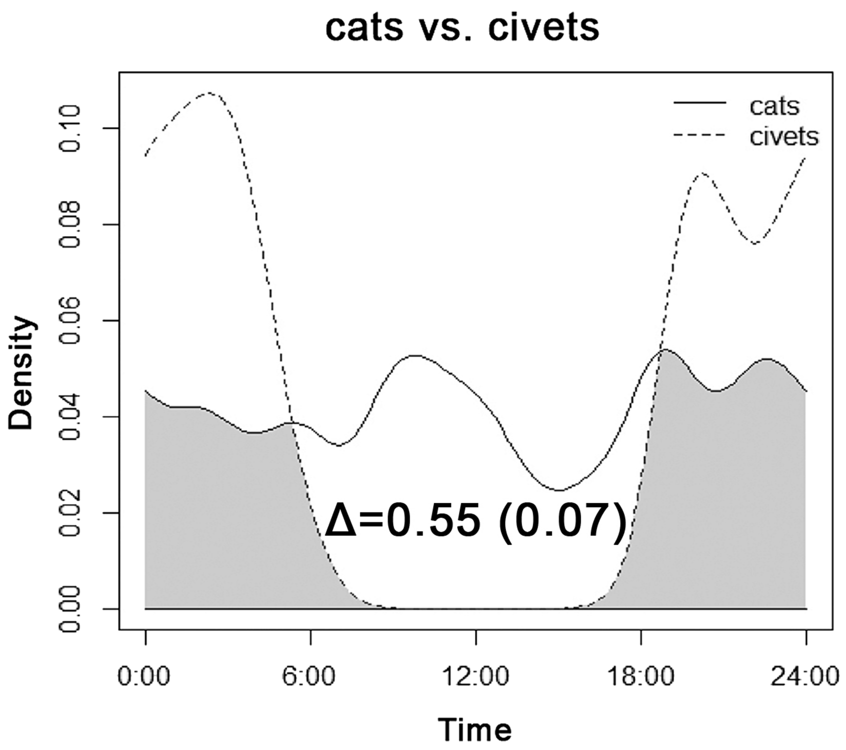

Figure 6 **Overlap between the diel activity patterns of cats and both species of civets at all sites of their occurrence.**

Although the diel activity pattern of cats was roughly consistent over 24-h periods (Fig. 6), a detailed analysis of zones revealed a decline in diurnal activity in the vicinity of villages, in contrast to an apparent activity peak before noon in Zone II (Fig. 3). Both Zones II and III offered more-or-less the same number of prey species (Table 2). Compared with Zone II, we hypothesize that more uniform diurnal activity of relatively abundant dogs dissuaded cats from daytime foraging in Zone III (Fig. 4). Also subsidies provided by humans in villages could influence cats to remain inactive in shelters and forage at night. We did not detect any sign of cats being spatially excluded by dogs, but our results support findings that cats optimize their timing of hunting behavior to when dogs are less active, hence avoiding potentially dangerous encounters (*Brook, Johnson & Ritchie, 2012*; *Wang & Fisher, 2012*). Cats were more diurnal in Zone II. This could be explained by the same factor, because the zone-specific relative abundance index of dogs was two times lower than the index of cats than in Zone III (Table 3). So cats could respond both to lower disturbance from dogs and to higher diurnal availability of rodents in Zone II (Fig. 4). Other prey not detected by cameras such as insects or lizards might also be present (*Bonnaud et al., 2011*).

Prey species showed shifts in diel activity patterns between sites where cats were, or were not, present (Fig. 5). When cats were absent, rodents tended to forage visibly by day, while the activity of ground-dwelling birds peaked about 4 h later. It is difficult to interpret the shift in bird activity; data from sites without cats were considered too scarce to perform a reliable analysis. Rodents shift their activities to become nocturnal if cats are present and more diurnal (*Doherty et al., 2015*). This raised the question of whether almost 500 years of cat presence in the Philippines has driven adaptive mechanisms of prey and competitors to cope with a new predator or not. Our results suggest that this already happened, similar to the 4000-year history of the dingo in Australia (*Carthey & Banks, 2012*). Nevertheless, we believe that further research is needed, especially throughout all seasons.

Knowledge of feral cat diet is paradoxically the least researched in tropical habitats with the richest terrestrial biodiversity (*Doherty et al., 2015*; *Doherty, Bengsen & Davis, 2015*). Our findings reveal the first tempo-spatial co-occurrences between feral cats and their potential prey in a typical mixture of Philippine landscapes. We suggest feral cats' temporal avoidance of dogs as the apex predator. We confirm that camera traps are capable of capturing small-bodied fauna, ground-dwelling birds and highly elusive species, such as *Sus philippensis*, as well. Endangered Philippine fauna exposed to invasive species should rapidly become the target of a broad and long-term camera-trapping inventory survey. For an in-depth knowledge of the dietary intake of feral cats in the Philippines, DNA analysis of scat is recommended as a priority for researchers (*Nogales et al., 2013*). In addition, collared and GPS-tracked cats would provide information about habitat use and the size of home ranges. Finally, attention should be paid to the cultural value of cats kept as pets within Philippine society, to inform eradication strategies.

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ADDITIONAL INFORMATION AND DECLARATIONS

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The authors declare there are no competing interests.

Author Contributions

- Vlastimil Bogdan and Tomáš Jůnek conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Pavla Jůnková Vymyslická conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, reviewed drafts of the paper.

Field Study Permissions

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Data Availability

The following information was supplied regarding data availability:

Jůnek, Tomáš (2016): Dataset from Bohol. Figshare. https://dx.doi.org/10.6084/m9.figshare.2245810.

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5.3. Density and abundance estimates

Jůnek, T., Jůnková Vymyslická, P., Hozdecká, K., & Hejcmanová, P. (2015).

Application of Spatial and Closed Capture-Recapture Models on Known Population of the Western Derby Eland (Taurotragus derbianus derbianus) in Senegal.

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RESEARCH ARTICLE

Application of Spatial and Closed Capture-Recapture Models on Known Population of the Western Derby Eland (*Taurotragus derbianus derbianus*) in Senegal

Tomáš Jůnek[1]*, Pavla Jůnková Vymyslická[1], Kateřina Hozdecká[2], Pavla Hejcmanová[2]

1 Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Prague 6 –Suchdol, Prague, Czech Republic, **2** Department of Animal Science and Food Processing, Faculty of Tropical AgriSciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Prague 6 –Suchdol, Prague, Czech Republic

* tjunek@fzp.czu.cz

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Abstract

Camera trapping with capture-recapture analyses has provided estimates of the abundances of elusive species over the last two decades. Closed capture-recapture models (CR) based on the recognition of individuals and incorporating natural heterogeneity in capture probabilities are considered robust tools; however, closure assumption is often questionable and the use of an M_h jackknife estimator may fail in estimations of real abundance when the heterogeneity is high and data is sparse. A novel, spatially explicit capture-recapture (SECR) approach based on the location-specific capture histories of individuals overcomes the limitations of closed models. We applied both methods on a closed population of 16 critically endangered Western Derby elands in the fenced 1,060-ha Fathala reserve, Senegal. We analyzed the data from 30 cameras operating during a 66-day sampling period deployed in two densities in grid and line arrays. We captured and identified all 16 individuals in 962 trap-days. Abundances were estimated in the programs CAPTURE (models M_0, M_h and M_h Chao) and R, package secr (basic *Null* and *Finite mixture* models), and compared with the true population size. We specified 66 days as a threshold in which SECR provides an accurate estimate in all trapping designs within the 7-times divergent density from 0.004 to 0.028 camera trap/ha. Both SECR models showed uniform tendency to overestimate abundance when sampling lasted shorter with no major differences between their outputs. Unlike the closed models, SECR performed well in the line patterns, which indicates promising potential for linear sampling of properly defined habitats of non-territorial and identifiable herbivores in dense wooded savanna conditions. The CR models provided reliable estimates in the grid and we confirmed the advantage of M_h Chao estimator over M_h jackknife when data appeared sparse. We also demonstrated the pooling of trapping occasions with an increase in the capture probabilities, avoiding violation of results.

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Introduction

The size of wild or human-managed populations of animals is a crucial parameter directly involving a wide range of activities, from conservation to commercial strategies.

One popular tool for researchers, mainly in the last two decades, is capture-recapture (CR) analysis of closed animal population parameters, in which data is processed from camera traps. The recognizability of individual animals based on their natural markings is an essential clue for software such as CAPTURE [1] and MARK [2] implementing the Lincoln-Petersen estimator [3] and, more recently, for spatially explicit capture-recapture (SECR) models [4] which overcome the limitations of predecessors. A widely employed non-invasive method which enables estimation of abundances and densities from assumed closed populations was developed for large striped or specked felids, such as tigers [5,6], jaguars [7,8], leopards [9], ocelots [10], pumas [11], cheetahs [12], European lynxes [13], bobcats [14] and margays [15].

Such long-lived, medium- to large-sized mammals are suitable subjects for closed population CR analysis thanks to their potential to meet one of its basic requirements, namely constancy of population size during the study period. Conducting a camera trap study in time periods as short as possible in order to minimize births, deaths and migration should satisfy the closure assumption, in terms of species demography. Regarding geographical closure, especially for felids and other animals with enormous home ranges, attention should be paid to the appropriate spatial design of sampling grids [5,16,17]. Researchers seeking reliable estimates must also take into consideration that the probability of capturing wild-ranging animals may also naturally vary among sampled individuals with regard to their age, social status, sex, fitness, etc. [18], and even among species [19,20]. Heterogeneity will cause underestimation of abundance if a model assuming uniform capture probability is applied [21]. Attempting to cope with defective sources of heterogeneity in capture or detection probabilities, a consensus about the robustness of application of the jackknife estimator, M_h [21] predominates in numerous studies [5,8,9,12,22]. However, drawbacks in the accuracy of the estimates, which originate from the small sample size (i.e. few captures and recaptures), were examined [3,16,23,24]. For example, Chao [25] pointed out that the jackknife estimator usually underestimates the population size when data is sparse and proposed modified M_h Chao estimator. The results can be biased also because camera traps along the border of deployment could detect animals whose home ranges lie predominantly outside the selected area and which are not representatives of the surveyed population [26]. Additionally, an average capture probability of the sampled animals ($\hat{p}$) lower than 0.1 could severely violate the reliability of the results [16]. As modeled [17], the use of an M_h jackknife estimator may result in over- or under-estimations of real abundance when the heterogeneity is high. Several authors [5,10,14] overcame this obstacle and raised the $\hat{p}$ value by pooling capture occasions, which, on the other hand, could theoretically disrupt the assumption of population closure if applied over a long period.

A recent approach which incorporates the location-specific capture histories of marked individuals is the spatially explicit capture-recapture, SECR [4]. The basic assumption is that the source of variability in the detection of individuals is the proximity of a detector to the center of activity. SECR deals with accidental visits along edges of the trapping array, and the estimated density of animals refers to the study area [4]. Likelihood-based SECR modeling allows multiple detections of individuals per trapping occasion, even from polygons or linear transects [27]. Despite widespread use of the method among a scientific audience [28–31], empirical evaluations of its outputs are rare [32–34].

In light of the direct application of abundance estimates in the conservation of wild-ranging animals, we focused on analyzing related sources of bias in a marginalized subject, ungulates. An exemplary species, which manifests white markings that are noticeable, lifelong and unique to each individual, is the Western Derby eland (*Taurotragus d. derbianus*), a critically endangered subspecies of one of the world's largest antelopes (IUCN 2008). In particular, its 10 to 18 vertical stripes, present on each flank in a barcode-like pattern, provide a convenient clue for the identification of individuals from photographs. Images of both flanks are illustrated in taxon's studbook identification cards [35], which annually list every Derby eland in the semi-captive breeding program in the fenced reserves of Bandia and Fathala in Senegal [36].

Capture-recapture models are surprisingly poorly adopted for herbivores [37]. Instead, ungulates are a common subject of camera-trap surveys which implement relative abundance indices [38–40], which refer to trends and changes in the population rather than to the real size [41]. In this study, we applied for the first time a nonspatial and spatial CR models on a closed population of marked antelope. Our goal was to empirically determine the most appropriate model, which will enable reliable estimates of abundance based on proposed detector array, duration of sampling and density of cameras. We estimated the Derby eland's abundance using the programs CAPTURE (models M_h and M_0) and R, package secr (basic *Null* and *Finite mixture* models) [42], in two different densities of camera traps in the line and grid placement derived from the x-matrix covering the entire reserve of Fathala. The results, which change with the variable duration of the trapping period, were compared with the known real abundance. We also tested the pooling of trapping occasions and its impact on results and compliance with the closed model assumptions. Our findings will support researchers, conservationists and managers in choosing an appropriate procedure in an effort to estimate the population size of large identifiable ungulates in similar conditions.

Methods

Ethics Statement

Our study took place in the private reserve of Fathala with the agreement of the Fathala Tourism Company and the Society for the Protection of the Environment and Fauna in Senegal. We located all cameras strictly on private soil within the fenced area of the reserve. The non-invasive nature of the method neither disturbed the animals nor involved a direct encounter with them. No bait was used.

Study area and taxon

Our study took place from May to September 2013 in the Fathala reserve, a sanctuary and part of the UNESCO site Delta de Saloum National Park on the western coast of Senegal (GPS coordinates of the main gate are 13°38'27.9"N; 16°25'51.9"W). The vegetation of the sanctuary consisted of Sudano-Guinean savanna with *Andropogon guayanus* and *Pennisetum purpureum* dominating in the undergrowth [43]. The largely flat topography is eroded by one wadi, a seasonal river valley crossing the northern part of the reserve in an east-west direction. The wadi contains running superficial water only at the peak of the rainy season, which lasts from July to September.

The fenced 10.6-km^2 section of the reserve was occupied, together with the Derby eland, by other species of African ungulates (Table 1).

Altogether, 16 Derby elands (real density = 1.51 animals per 1 km^2) inhabited the studied section during the entire trapping period. The population consisted of 13 adult males, two adult females and one juvenile male. Each animal or part thereof photographed by a camera trap was manually compared with the pattern of white-striped flanks depicted in the African studbook [35]. Following Nežerková [44] we used these morphological criteria in the process of identification: number, position and shape of stripes, white markings on head, dimension and shape of horns (Fig 1). Sex was determined based on external genitalia and dimensions of

Table 1. List of species of ungulates captured by camera traps in the Fathala reserve.

Species	Common name	Order	Family
Syncerus caffer	African buffalo	Cetartiodactyla	Bovidae
Hippotragus equinus	roan antelope	Cetartiodactyla	Bovidae
Kobus ellipsiprymnus	waterbuck	Cetartiodactyla	Bovidae
Taurotragus oryx	common eland	Cetartiodactyla	Bovidae
Tragelaphus scriptus	bushbuck	Cetartiodactyla	Bovidae
Taurotragus derbianus	Derby eland	Cetartiodactyla	Bovidae
Giraffa camelopardalis	giraffe	Cetartiodactyla	Giraffidae
Ceratotherium simum	white rhinoceros	Perissodactyla	Rhinocerotidae
Equus quagga	plain zebra	Perissodactyla	Equidae

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horns. Two observers (T. J. and K. H.) independently analyzed all the images, and only consensual identifications were included in the dataset.

Camera trapping tools and design

We used 30 Ltl Acorn 5210MC (Shenzhen Ltl Acorn Electronics Co., Ltd., China) weatherproof infrared (IR) digital camera traps operating in photo mode with a resolution of five megapixels. The IR flash was used in attempt to avoid disturbance of animals, although images taken at night are only back and white and not as readable as those from white flash [45]. Units were placed in a grid with a regular span of 500 m throughout the entire reserve, avoiding facilities and fences. The placement pattern was designed to generate data from a) the entire grid, b) reduced grid of 14 cameras, c) a single line of eight cameras and, d) a reduced line of four camera traps crossing every habitat transversely (Fig 2).

Every final location of a camera trap varied within a 5-meter GPS error from the preliminary defined points, which enabled us to set each trap up to 10 meters from the nearest animal trail in use. Pursuant to findings from our pilot testing of camera traps in the reserve during a 2-week period in February 2013, units were tightened to tree trunks or large bushes between 1.0 and 1.5 m in height. A motion PIR sensor and 52-degree-wide camera lens faced as perpendicular as possible to the trail and north- or southwards to minimize activation of the trigger by direct sunshine. Every camera trap was covered by a flat sheet metal roof as a protection against rain and sun.

Camera trap units were programmed to be in single photo mode with a 0-second interval between two consecutive images which, in the case of the selected model of camera trap, meant a real minimal interval of 6 seconds. Units operated 24 hours a day, and a built-in infrared flash enabled black-and-white photographs to be taken without disturbing the animals. The sensitivity of the motion sensor was set at ‘normal’. Units operated without any maintenance, with a power supply of 8 AA alkaline batteries.

The time schedule was set to allow for at least two months of trapping, beginning on May 11th, 2013, before the rainy season. Units were collected on September 21st, 2013. We experienced a malfunction of four cameras due to battery leakage. Comparing the minimal lengths of the cameras’ operational period, we were finally able to utilize the data from 26 camera traps for computation in CAPTURE. These devices functioned for 66 days; each day was considered a trapping occasion. In secr, we processed the data from all 30 cameras with application of the *usage* function, which treats the varying detector-specific effort.

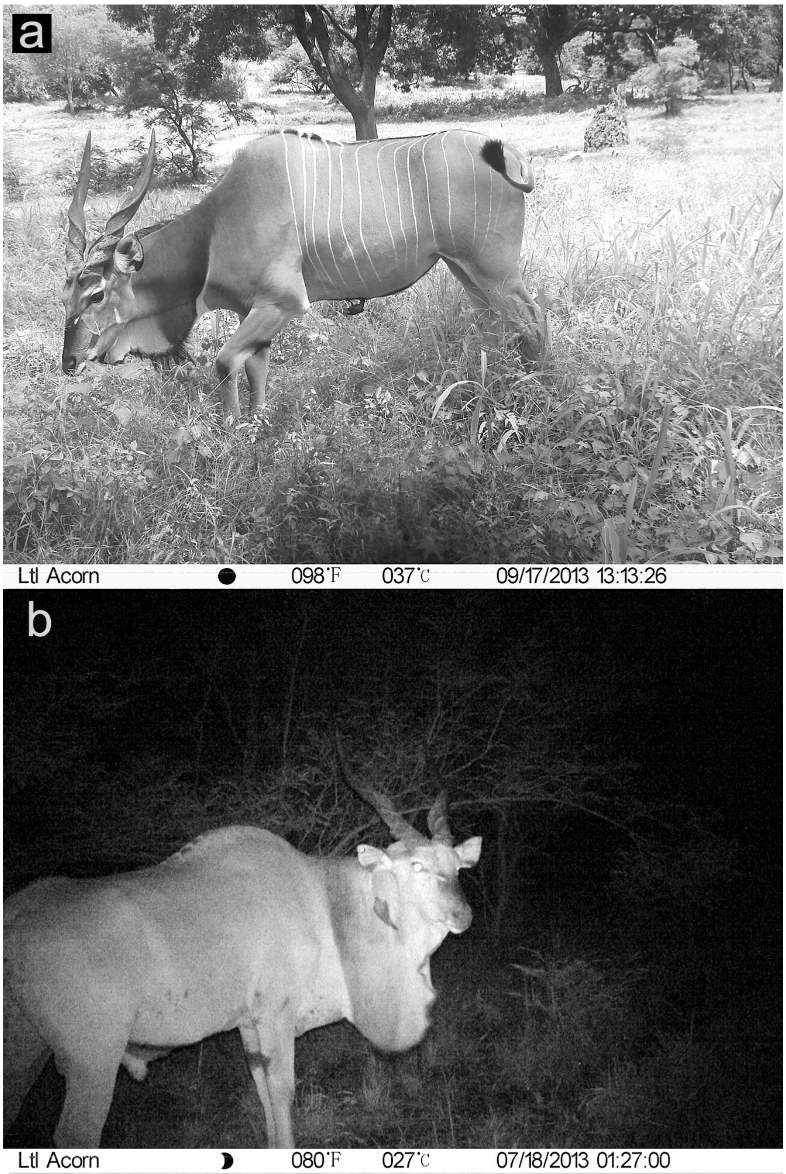

Fig 1. Photographs of a Derby eland female in the daytime (a) and a male at night (b) taken by camera traps in the Fathala reserve, illustrating the poor visibility of markings in the night shot.

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Estimates of abundance

We tested closure of the Derby eland population in the reserve by direct observation of all 16 animals before and after the study, with no change detected.

For estimation of abundance via nonspatial CR analyses, we used the time-tested program CAPTURE. For each recognized Derby eland we generated a capture history, which consisted of a row of 66 numbers, marked 1 if the animal was photographed within the occasion, or 0 if it was not. All available models of the software, differing in assumptions of capture probabilities,

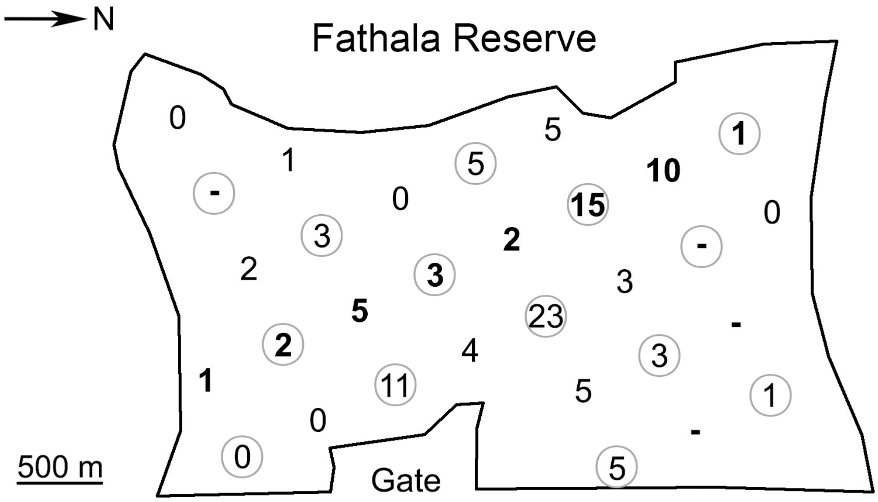

Fig 2. Map of camera trap placement in the Fathala reserve during the sampling period, showing the number of independent captures of an identified Derby eland by a particular camera trap. Bold numbers highlight the analyzed line of camera traps, circles highlight reduced grid and line; dashes denote malfunctioning cameras.

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were used. In every processed test, the models M_h (capture probability differs among animals, usually considered realistic), which use the jackknife estimator, as well as M_0 (assuming constant capture probability) were determined to be appropriate by CAPTURE's goodness-of-fit test. Our estimated population size ($\hat{N}$) from both models was reported number of captured animals, standard error of estimate (*SE*), capture probability ($\hat{p}$), coefficient of variation of estimates ($CV = SE[\hat{N}]/\hat{N}$) and lower and upper values of 95% confidence intervals. The closure test was also processed by CAPTURE.

We computed the estimations of Derby eland abundance ($\hat{N}$) using spatially explicit analyses of density estimates in the R language (version 3.1.2, R Development Core Team, 2014) in the package secr (version 2.9.3, [42]). We employed two models—the *Null* model, where detection is affected only by the use of space, and the 2-class *Finite mixture* model (hereinafter *h2*), which allows for the modeling of variation in detection probability among individuals. For each analysis we compared both models with use of the Akaike Information Criterion (AIC) to test which model is preferable. We defined habitat mask, which span within the borders of the reserve and was composed of the number of detectors corresponding with the analyzed density of camera traps (i.e. 30 or 14) with the buffer width of 100 m. For the line arrays, only eight, respectively four cameras were marked as "1" in the secr *usage* argument, remaining 22, reps. 10 had the zero value. The *usage* argument was used also for the determination of every detector's daily functional state. The detector type for analysis was set as 'proximity', which allows multiple detections of individuals on the same occasion. Our sampling area was relatively small and uniform, and we expected the distribution of home range centers to be homogenous. Therefore, distribution was selected as 'Poisson'. The detection function was equal to half-normal because we assumed that probabilities of capture increase linearly with the proximity of a camera trap to the home range of an individual. We estimated population size ($\hat{N}$) using expected *E (N)* as the volume under a fitted density surface. The value is then equal to the density ($\hat{D}$) multiplied by the area of the region; the standard error is a product of the same equation [42].

Results

Identification

We accumulated data from a total of 1,716 trap-days from 26 camera traps. During a trapping period of 66 days, our devices took 16,911 photographs, of which 358 (2.1%) were images of Derby elands or parts thereof. We subsequently recognized 192 events of non-identified Derby elands' encounters with camera trap. Finally, we were able to identify 108 independent captures of 16 Derby eland individuals, scoring a 56.3% success rate in recognition. Hence, the trapping rate was 6.29 (detections of individuals/100 trap-days) and the average trapping effort resulted in 15.9 trap-days per one capture. We needed 962 trap-days to capture and recognize all 16 Derby elands inhabiting the reserve (Fig 3). The first identified animal was photographed in the first day of monitoring, which is equal to 26 trap-days. We successfully distinguished 1 juvenile male, 2 females and 13 adult males.

Abundance estimates

The assumption of the Derby eland's population closure during the study period was proven by the goodness-of-fit test in CAPTURE (z = -0.382, P = 0.351).

CAPTURE's model M_h was selected as the most appropriate for every pattern, as it scored 1.00 in the selection criterion, followed by M_0. The suggested estimator was the jackknife

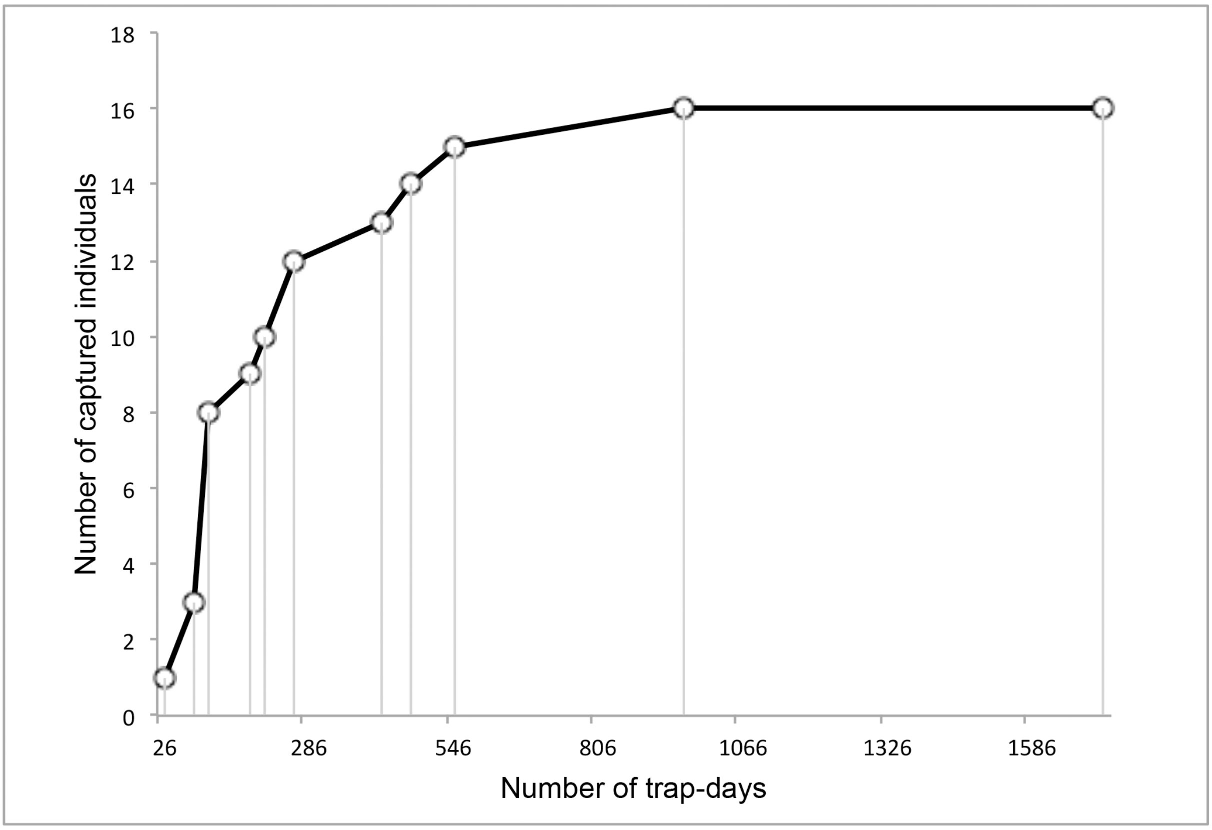

Fig 3. Development of cumulative captures of identified Derby elands in the Fathala reserve.

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Table 2. Average capture probabilities ($\hat{p}$) of Derby elands for the full and reduced grid and line placement patterns (CAPTURE, models M_0, M_h and M_h Chao).

Occasions	Grid			Grid reduced		
	M_0	M_h	M_h Chao	M_0	M_h	M_h Chao
11	0.113	0.117	0.096	0.113	0.117	0.096
22	0.106	0.105	0.099	0.083	0.078	0.066
33	0.101	0.101	0.101	0.070	0.062	0.070
44	0.097	0.091	0.091	0.076	0.067	0.067
55	0.100	0.100	0.100	0.066	0.062	0.066
66	0.096	0.096	0.096	0.064	0.061	0.064
	Line			Line reduced		
11	na	na	na	na	na	na
22	0.011	0.018	0.011	na	na	na
33	0.020	0.027	0.024	0.010	0.015	0.010
44	0.023	0.024	0.022	0.017	0.025	0.021
55	0.033	0.035	0.035	0.018	0.024	0.022
66	0.040	0.034	0.036	0.022	0.025	0.023

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except for the grid and reduced grid at 44 occasions, where M_h scored 0.95 and 0.93 after M_0. The 95% confidence limits of selected models did not include the true value in three cases of M_h—the grid (44 occasions) and in the reduced grid (55 and 66 occasions) when the lower limit scored identically 17. In the grid, all three models produced the estimated the size of Derby eland population identically 16 animals at 66 occasions with a lowest value of $SE = 0.15$ in M_0 Chao. In the line pattern for the same trapping period, only M_h Chao scored 16 individuals ($SE = 2.3$). As seen in Table 2 and Table 3, the shorter trapping period lasted, the more variable results CAPTURE's models produced. The sparse data of the shortest periods of both line patterns resulted in higher estimates in M_0 and noticeably lower in M_h. Estimator of Chao performed results in between these two models (Fig 4), however, all closed models finally underestimated real size in the reduced line pattern—M_0 ($\hat{N} = 14$, $SE = 2.7$), M_h ($\hat{N} = 12$, $SE = 3.0$), M_h Chao ($\hat{N} = 13$, $SE = 2.2$).

The M_h model's estimated average probability of capture ($\hat{p}$) reached the verified threshold of reliability 0.1 of the CR estimates only in the grid pattern and at 11 trapping occasions in the reduced grid (Table 2). As mentioned above, low capture probability can be increased by the pooling of capture occasions. Therefore, we undertook a trial computation of the line pattern

Table 3. Developments of the mean capture probability ($\hat{p}$) of Derby elands depending on the pooling of 66 capture occasions in the line placement patterns (CAPTURE, model $M_{h,}$).

Pooling	Captured	$\hat{N}$	*SE*	$\hat{p}$	95% *CI*
none	14	17	2.6	**0.034**	15–27
2 days	14	17	2.6	**0.066**	15–27
3 days	14	17	2.5	**0.099**	15–26
6 days	14	17	2.4	**0.193**	15–25
11 days	14	17	2.2	**0.304**	15–25

$\hat{N}$ denotes estimated abundance

doi:10.1371/journal.pone.0136525.t003

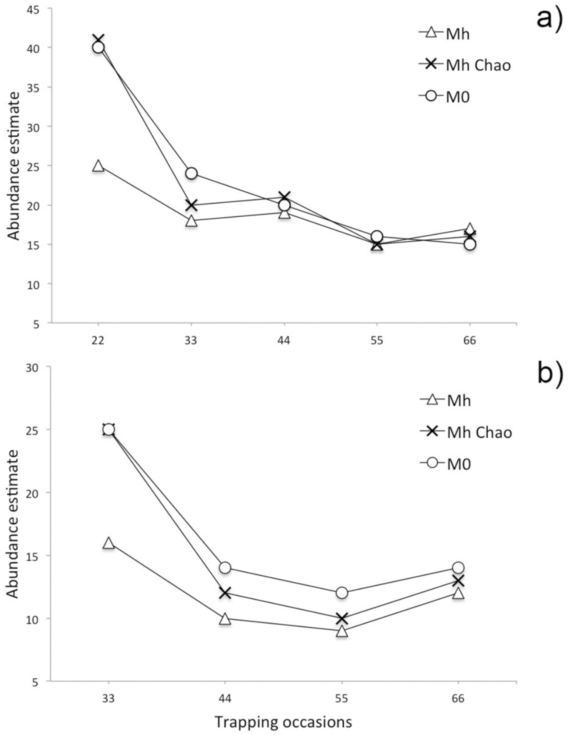

Fig 4. Development of abundance estimates provided by closed (M_0, M_h, M_h Chao) during 66 trapping occasions in a) the line and b) reduced line camera trap placement.

doi:10.1371/journal.pone.0136525.g004

data pooled out of 2, 3, 6 and 11 days (33, 22, 11 and 6 occasions), resulting in an increase of the parameter $\hat{p}$ from 0.034 to 0.304 (Table 3).

We did not recognize major differences between chosen SECR models outputs. As tested using AIC, the *h2* mixture model was never preferred in each computation. Both models along with rising sampling period consistently decreased their initially overestimated abundances to the nearly real size value. The models in the grid at 66 occasions scored equally $\hat{N}$ = 16.1, *SE* = 4.1, in the reduced line the *h2* model was slightly more precise ($\hat{N}$ = 15.4, *SE* = 5.4) than the *Null* model ($\hat{N}$ = 15. 1, *SE* = 5.3). Generally, the *h2* model performed similarly better when data appeared sparse (Tables 4 and 5).

Detailed parameters of estimates for 11 to 66 trapping occasions in the CR and SECR models are shown in Tables 4 and 5. With the increasing duration of sampling, standard errors decreased with narrowing confidence intervals in all models and arrays (with one exception of M_h at 66 occasions in the reduced grid). Our test specified 66 days (1,716 trap-days) as the sufficient period for appropriate abundance estimation in the grid and line pattern regardless of the detector/animal ratio. Mainly SECR, but also CR models reached almost the real size of 16 Derby elands no matter the ratio was 1.88 (grid) or 0.25 (reduced line) (Fig 5).

Discussion

Our results demonstrated the successful application of camera-trapping for the identification of Western Derby eland individuals. However, we found that the infrared mode for pictures taken at night did not provide clear results. We needed 37 days (962 trap-days) to identify all

Table 4. Estimations of abundance ($\hat{N}$) of Derby elands with parameters within different durations of sampling for the full and reduced grid and line placement patterns using *Null* model in secr and M_0 in CAPTURE.

Grid		SECR *Null*				CAPTURE M_0			
Oc.	***N***	$\hat{N}$	***SE***	***CV***	***95% CI***	$\hat{N}$	***SE***	***CV***	***95% CI***
11	12	**19.1**	6.9	0.36	10–38	**15**	3.3	0.22	12–27
22	15	**16.6**	4.4	0.27	10–28	**16**	1.4	0.09	16–22
33	15	**15.7**	4.1	0.26	9–26	**15**	0.7	0.05	15–15
44	16	**16.4**	4.2	0.25	10–27	**16**	0.4	0.03	16–16
55	16	**16.2**	4.1	0.25	10–26	**16**	0.2	0.01	16–16
66	16	**16.1**	4.1	0.25	10–26	**16**	0.9	0.06	16–16
Grid reduced									
11	12	**19.0**	6.8	0.36	10–38	**15**	3.3	0.22	12–27
22	14	**17.8**	5.2	0.29	10–31	**16**	2.1	0.13	15–24
33	15	**17.5**	4.8	0.27	10–30	**16**	1.5	0.09	16–23
44	15	**15.9**	4.2	0.26	10–27	**15**	0.7	0.05	15–15
55	16	**17.0**	4.3	0.26	10–28	**16**	0.7	0.04	16–16
66	16	**16.7**	4.3	0.25	10–27	**16**	0.5	0.03	16–16
Line									
11	3	na	na	na	na	na	na	na	na
22	9	**27.2**	19.9	0.73	8–98	**40**	34.5	0.86	15–189
33	12	**22.9**	9.7	0.42	10–51	**24**	9.2	0.38	16–57
44	13	**20.1**	7.0	0.35	10–39	**20**	5.2	0.26	15–38
55	14	**16.9**	4.8	0.29	10–29	**16**	2.2	0.14	15–25
66	14	**15.3**	4.2	0.28	9–26	**15**	1.2	0.08	15–21
Line reduced									
11	3	na	na	na	na	na	na	na	na
22	4	na	na	na	na	na	na	na	na
33	8	na	na	na	na	**25**	20.6	0.82	10–115
44	9	**22.0**	13.2	0.60	7–65	**14**	6.1	0.43	10–38
55	9	**19.1**	10.2	0.54	7–51	**12**	4.2	0.35	9–29
66	11	**15.1**	5.3	0.35	8–30	**14**	2.7	0.19	12–24

Oc. denotes number of trapping occasions, *N* is number of captured individuals

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16 Derby elands at a density nearly one-hundred times higher than could be expected [46] in the taxon's last stronghold, Niokolo Koba National Park in Senegal, an endangered UNESCO World Heritage Site. The black-and-white photographs made the distinction of white stripes on the pale fur of the antelope difficult. Hence, only daytime images could be examined. Application of the selected camera traps will constrain the sampling of free-ranging animals which tend to be nocturnal or crepuscular.

The solution would comprise the employment of camera traps equipped with a white flash. Karanth [5], using a white flash in Nagarahole, India, captured 10 tigers in 387 trap-nights with an estimated density of about 0.14 tigers per 1 km^2. We achieved the same number of Derby elands in 208 trap-days but with a real density of 1.51 individuals per 1 km^2. Nevertheless, negative behavioral responses, such as the potential avoidance of camera traps [47], should first be tested for a particular taxon and location. The invisibility to humans of the infrared light spectrum protects camera traps from theft, which is not a trivial argument in areas accessible by the public. Researchers must also take into consideration the duration of recharging of

Table 5. Estimations of abundance ($\hat{N}$) of Derby elands with parameters within different durations of sampling for the full and reduced grid and line placement patterns using models allowing for heterogeneity in capture probabilities (*h2*, *Finite mixture* model in secr, M_h and M_h Chao in CAPTURE).

Grid		**SECR *h2***				**CAPTURE M_h**				**CAPTURE M_h Chao**			
Oc.	***N***	$\hat{N}$	***SE***	***CV***	**95% *CI***	$\hat{N}$	***SE***	***CV***	**95% *CI***	$\hat{N}$	***SE***	***CV***	**95% *CI***
11	12	**19.1**	6.9	0.36	10–38	**14**	3.6	0.25	12–29	**17**	6.5	0.38	13–44
22	15	**17.0**	4.6	0.27	10–29	**16**	2.9	0.18	16–34	**17**	2.6	0.16	16–29
33	15	**15.7**	4.1	0.26	9–26	**15**	3.8	0.25	15–15	**15**	0.0	0.00	15–15
44	16	**16.4**	4.2	0.25	10–27	**17**	1.5	0.09	17–24	**17**	1.3	0.08	16–24
55	16	**16.2**	4.1	0.25	10–26	**16**	2.1	0.13	16–16	**16**	0.0	0.00	16–16
66	16	**16.1**	4.1	0.25	10–26	**16**	0.9	0.06	16–16	**16**	0.0	0.00	16–16
Grid reduced													
11	12	**18.8**	6.8	0.36	10–37	**14**	3.6	0.25	12–29	**17**	6.5	0.38	13–44
22	14	**17.7**	5.1	0.29	10–31	**17**	3.6	0.21	15–32	**20**	6.5	0.32	16–47
33	15	**17.6**	4.8	0.27	10–30	**18**	2.6	0.15	16–28	**16**	1.5	0.09	15–23
44	15	**16.1**	4.3	0.26	10–27	**17**	2.4	0.14	16–27	**17**	3.7	0.22	16–37
55	16	**17.0**	4.3	0.26	10–28	**17**	1.7	0.10	17–25	**16**	0.5	0.03	16–19
66	16	**16.6**	4.2	0.25	10–27	**17**	4.2	0.25	17–44	**16**	0.5	0.03	16–19
Line													
11	3	na	na	na	na	na	na	na	na	na	na	na	na
22	9	**27.2**	19.9	0.73	8–98	**25**	8.9	0.36	15–53	**41**	39.6	0.97	14–220
33	12	**23.2**	9.9	0.43	10–52	**18**	4.6	0.25	14–34	**20**	7.5	0.37	14–49
44	13	**20.5**	7.1	0.35	11–40	**19**	4.6	0.24	15–35	**21**	7.5	0.36	15–50
55	14	**17.8**	5.4	0.31	10–32	**15**	7.1	0.48	15–63	**15**	1.5	0.10	15–22
66	14	**15.5**	5.1	0.33	8–29	**17**	2.6	0.15	15–27	**16**	2.3	0.14	15–26
Line reduced													
11	3	na	na	na	na	na	na	na	na	na	na	na	na
22	4	na	na	na	na	na	na	na	na	na	na	na	na
33	8	na	na	na	na	**16**	6.3	0.39	10–38	**25**	23.6	0.94	10–134
44	9	**22.1**	12.9	0.58	8–64	**10**	3.4	0.34	9–26	**12**	4.9	0.41	9–33
55	9	**18.7**	9.4	0.50	7–47	**9**	3.0	0.34	9–27	**10**	2.6	0.26	9–22
66	11	**15.4**	5.4	0.35	8–30	**12**	3.0	0.25	12–30	**13**	2.2	0.17	12–22

Oc. denotes number of trapping occasions, *N* is number of captured individuals

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the white flashbulb, which constrains the trigger speed of the camera, and discharging of the power supply. This is an important fact, considering that 97.9% of the images taken depicted other species of animals living in the Fathala reserve. Cameras were also triggered by moving vegetation waving in the wind, or by flying insects such as unidentified species of butterflies, moths, termites or flies, and even by spiders hiding in the proximity of the trap's sensors.

We benefited from the knowledge of the Derby elands flank patterns listed in the identification cards in the African studbook [35]. This economized on material costs because instead of being in pairs, standard in surveys of large cats [5,8,20], cameras could be set in a single placement only and the process of identification was faster.

We successfully tested the accuracy of CR and SECR estimates for the chosen distinctive species of large antelope in conditions of dense wooded savanna in West Africa. Both methods were sensitive to the duration of trapping, hence, the sparsity of capture-recapture data [25]. Unlike the CR models, SECR provided a consistent decline of estimates to the true value. In

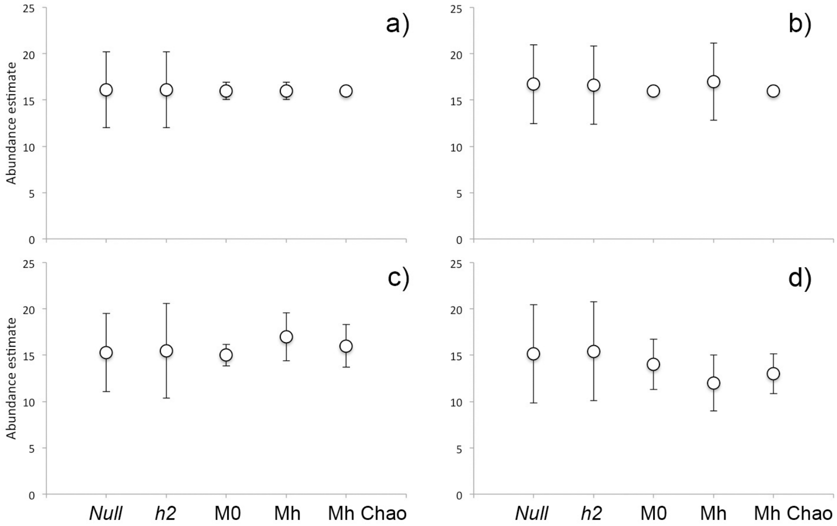

Fig 5. Comparison of abundance estimates ($\hat{N}$) of Derby elands in the Fathala reserve gained from spatially explicit capture-recapture (*Null* and *h2* models) and closed CR models (M_0, M_h, Mh Chao) at 66 trapping occasions in a) the grid, b) reduced grid, c) line and, d) reduced line camera trap placement. Whiskers denote standard errors.

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grid patterns, all models performed well relatively soon, in 22 days, but cameras already caught almost all Derby elands within this period. In the line arrays, where only part of the population was recorded, the poorer data meant for CR model both over- and under-estimation, whereas SECR models showed the same declining pattern with almost no differences between *Null* and *h2* model. The period of 66 days of sampling, which should ensure the closure assumption in the case of large mammals, proved a sufficient time for reliable estimates in all patterns for the SECR. The CAPTURE did not reach the true abundance yet in the reduced line. We can conclude, that spatially explicit models served reliably even within the range of density 0.004 to 0.028 camera trap/ha, or 7.5-times divergent ratio of number of camera traps per one Derby eland. This is a crucial argument because if we are able to properly model the area of habitat of the focal taxon, and we expect its rough density, the calculation of our trapping effort, design and costs is hereby intuitive. Despite being promising, the suggested method requires further examination, mainly in terms of the spatial and temporal distribution of target species and sources.

Use of the jackknife estimator in CR analyses is an intuitive and widely recommended rote in the literature [5,8,9]. We did not confirm the expected underestimation of abundances with the use of model M_0, with the only exception in the reduced grid. Conversely, estimates were higher for the shortest trapping occasions especially in the line patterns. As suggested [23,25], poorer and sparse capture data affect the jackknife estimator performance and the estimator of Chao brought better results and higher estimates. Anyway, in the scantiest design (reduced line), M_0 worked the best, which indicates only minor heterogeneity in Derby eland's capture probabilities.

As we demonstrated, capture probabilities did not vary among models M_0, M_h and M_h Chao within each array. This indicates minor differences in spatial use of the studied area by focal animals as well as strict satisfaction of the closed model assumptions. The increasing trend in capture probabilities (Table 2) confirms the conclusion of Tobler [30] that the only way to improve estimates, besides utilizing more detectors, is to extend the survey period. Unlike the latter authors, we showed that the pooling (or collapsing) of trapping occasions could reasonably influence parameters without leaving the results poorer or more biased.

Based on our findings, the results gained from secr demonstrate a negative bias between the accuracy of abundance estimates and the number of trapping occasions. The *Null* and *Finite mixture* models equally overestimated true values when the number of occasions was lower, particularly in the line arrays. Performed SECR computations confirmed outputs of AIC and CR models, which did not support the use of the model incorporating the variation in detection probabilities (*h2*). Due to the use of IR camera traps, we did not expect even any behavioral response to the detectors.

We did not fulfill the scenario of underestimation of density (and abundance) demonstrated by Gerber and Parmenter [33]. The unmodeled variation in SECR tends to produce outputs that are overly precise and biased [48]. A negative bias has been described when the ranging pattern differs between sexes [30], when spatial resource use affects the movement of animals [49], or when home ranges are asymmetric [50]. To date, no study has estimated the home range size of the Derby eland. With the use of available data of its sister species, the Common eland (*Taurotragus oryx*), an adult male could occupy an area of 6 to 71 km^2 and a female 34 to 360 km^2 [51]. Our 10.6 km^2 study site might therefore be relatively disproportionate to 16 Derby elands and their home ranges. However, we fully satisfied the suggestion of Tobler [30] that the camera polygon for a density study should cover no less than the size of one home range.

We confirmed that the x-matrix placement of camera traps covering the entire sampling area produces accurate outcomes in both the spatial and nonspatial capture-recapture models, even in the case of small-sized populations. Especially for fenced game reserves, where migrants do not violate the closure assumption, the CR model remains a reliable and approachable tool for researchers and managers, however old-fashioned it may be. We highlight the potential of the line pattern, the estimates from which closely reached the real population size, along with adequate capture probability when pooling was applied. However, both the poorer data and line distribution of detectors constrained nonspatial models and the advantages of the secr, which defines the habitat mask, became clear. The linear pattern and the secr models may become more topical for the Western Derby eland and other species inhabiting areas, in fact refuges, geographically restricted in human-populated landscapes as found in Africa [52,53]. With reasonable costs, cameras can span parts of a large area, such as the Niokolo Koba National Park (9,130 km^2), when set on the most frequented trails and crossing a properly modeled and homogenous area of taxon occurrence, where the density is reasonable [54]. The technique can sample 'oscillating' herds of herbivores on a low budget relative to conventional but bias-sensitive counting methods such as aerial census [55,56] or distance sampling [57,58]. West and Central African national parks contend with a lack of funding as well as a fundamental knowledge of the real size of animal populations [44,59–63]. The data obtained would provide a valuable foundation for conservation plans and actions to manage the protected areas.

Supporting Information

S1 Data. Fathala Data.zip. Source data for analysis in CAPTURE and SECR models.
(ZIP)

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Author Contributions

Conceived and designed the experiments: TJ PH. Performed the experiments: TJ PJV KH. Analyzed the data: TJ KH. Contributed reagents/materials/analysis tools: TJ PH. Wrote the paper: TJ PJV PH.

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6. Commentary on results

Desire and need to observe what our own eyes cannot reach belong among the intrinsic instincts of a researcher. And the more so when data can be automatically recorded in the same moment. Camera traps can be considered as such an extended sense, which allow for previously unprecedented insight. This fact has been proven by thousands of publications recently generated on data generated with the use of these autonomous detectors. The camera trap has become a standard monitoring tool of zoologists and conservationists globally. In the so called era of Sixth Mass Extinction driven by human (Dirzo *et al.* 2014) an unbiased source of biodiversity data, such as those obtained from camera traps, are crucially needed for effective application of conservational strategies and their evaluation (O'Connell, Nichols & Karanth 2010; Ahumada *et al.* 2011).

As for every no-matter-how-perfect scientific method, the pros and cons of whole camera trapping hardware and software system must be thoroughly tested and its limits identified. This mantra appears particularly important in still developing models of analysis. Researchers using camera traps should be aware of proper project designing to present reliable results (Marcus Rowcliffe *et al.* 2011; Rovero *et al.* 2014). Relative availability of camera traps on the market encourages also practitioners from management of protected areas or enthusiasts to use it but data might not be useful for deeper investigations and comparative studies leaving their effort unfortunately wasted.

Camera traps provide researcher with photographs or videos. Capturing video is both a power and storage demanding process, which significantly shortens the operating time of the device. Long-term monitoring hence relies on photographs. However static, such records contain, besides the objects captured and previously located GPS coordinates also file metadata such as date and time of capture, moon phase and usually temperature. A researcher can probe the image from different points of view and seek answers on these basic questions: what is captured, where is the object captured, and when is the object captured. Variables such as for example moon phase, seasons, distance from the source of disturbance or/and attractant, co-occurrence with other species, and vice versa offer a playground for postulating numerous hypotheses. The following text will describe our investigation of the three most common approaches in the camera-trapping field rising up from this triple inquiry.

The basic biodiversity measure for any studied area is the list of species found there. Especially for reserves, national parks and any other protected and managed areas the inventory of mammals, usually the main living attractants for visitors, is needed (Gaston *et al.* 2008; Rowcliffe & Carbone 2008).

Not only can all protected areas profit out of tourism, nor are they all managed sustainably. Populations of large-bodied mammals dropped within protected areas in Africa by 59% on average between 1970 and 2005 (Craigie *et al.* 2010). Mainly the regions of West and Central Africa face a dramatic decline in their fauna. Anthropogenic destruction of habitat, overhunting, diseases, and creating barriers such as fences and roads are the most important drivers of the fragmentation of protected areas and biodiversity decline (Newmark 2008; Bouché *et al.* 2011). Projected net biodiversity loss for the majority of the West Africa is expected to exceed 25% by 2095 (Newbold *et al.* 2015). Megafauna and large carnivores are considered the most vulnerable to defaunation, with consequences for the trophic cascade (Dirzo *et al.* 2014; Ripple *et al.* 2015, 2016). For example the largest terrestrial animal, the African elephant (*Loxodonta africana*), has lost 33% of its West- and 76% of its Central African population since 1980 (Bouché *et al.* 2011).

The camera trap is an ideal tool for monitoring wildlife in conditions of relatively open and clear savannah. A several months lasting period of dry season secures longevity of equipment, deployment of cameras can be logistically easier than in a dense rain forest. Nonetheless, in contradiction just to tropical rain forests, no systematic long-term monitoring of biodiversity has been yet introduced to this ecosystem of high eco-touristic importance.

One of the largest, most western and also troubled conservation areas in West Africa is the Niokolo-Koba National Park (NKNP) in Senegal, a UNESCO World Heritage Site and Biosphere Reserve since 1981 (UNESCO 2017). Similar to other reserves in the region, the community of large mammals, both predators and herbivores, in the NKNP has vanished in recent decades. The park has been listed as UNESCO World Heritage in Danger since 2007 due to mainly illegal pasture, poaching, bush fires, and a succession of invasive plants. The relatively easily accessible Park in a stabile country has a viable economic potential. But, despite the existence of a reporting system, a lack of systematic knowledge persists regarding medium- to small-bodied elusive species, along with analyses of drivers in distribution. Our camera-trapping inventory in a Park's core area was therefor a logical move to redress (**Chapter 5.1.**).

The goals of our camera-trapping study were: (1) inventory of all mammalian species of the core area of the NKNP, (2) to evaluate sampling efforts and estimate species richness, (3) estimate species occupancy (Ψ), and (4) determine the best ecological and environmental predictors (distance from the nearest rivers, a passable road, and the park's border) of Ψ and detection probability (p) as species response patterns to these predictors.

We monitored the Park's core area of 1,025 km^2. A regular grid containing 41 camera trap locations had a 5-km span (density of one camera per 25 km^2). Four locations had to be omitted, data from two cameras could not be obtained due to their malfunction, but from altogether 35 camera traps we registered 1,876 trap days out of 2,590 possible (72.4%). The average duration of camera traps functioning was 52.1 days. In total 33,909 photographs were taken, 3,734 (11%) contained animals or parts thereof, and four pictures showed alleged poachers. One camera captured on average 10.1 species (ranging from 1-18 species).

We recorded and identified 35 species of mammals (Chapter 5.1., Table 1). The species accumulation curve (Chapter 5.1., Fig. 3) showed a steep increase in the number of species detected in the first 200 trap days; 1,000 trap days resulted in 87.6%, or 30.7 recorded species with an on-going slow progression of the curve. We have thus confirmed the proposed reliability of 1,000 trap days for the detection of rare species (O'Brien 2011), and our 87.6% of recorded species is similar to those from tropical forests differing in detector arrays (Tobler *et al.* 2008; Bernard *et al.* 2013; Bogdan, Jůnek & Jůnková Vymyslická 2016; Bowler *et al.* 2016). To our knowledge, no comparative data is unfortunately available for the savannah.

The most recorded species with more than 50 independent events of capture were these (in descending order): Guinea baboon (*Papio papio*, Fig. 1), crowned duiker (*Sylvicapra coronata*), common warthog (*Phacochoerus africanus*), Western bushbuck (*Tragelaphus scriptus*) and roan antelope (*Hippotragus equinus*). Sixteen species (46%) we reported less than in five events.

Figure 1. Guinea baboon was the most captured species in the Niokolo-Koba National Park. The species did not seem to avoid camera traps; could these detectors, on the contrary, attract this attentive primate?

We can conclude, that the main benefit of our study was listing and analysing the small-bodied vigilant species (e.g. mongooses, wildcat *Felis silvestris*, rodents) and medium-sized mammals with significant ecological and eco-tourism importance, such as aardvark, honey badger, West African wild dog, serval (*Leptailurus serval*), caracal (*Caracal caracal*), African civet (*Civettictis civetta*), and the common crested porcupine. These species were unreported in previous ground and aerial surveys in the past probably due to the then chosen methodology (Galat *et al.* 1992; Renaud *et al.* 2006).

On the other hand, we missed at least three medium- to large-sized species (hippopotamus, Buffon's kob, and lion). To encounter hippopotamus, our camera traps were simply not close enough to rivers. The presence of lions was confirmed through our observations of fresh tracks, but the same as for other rare gregarious species (Derby eland, hartebeest, wild dogs), we suggest that the camera-trapping sampling effort should be considerably intensified by a denser array of detectors. Contrary to known low density of lions (Henschel *et al.* 2014; Kane, Morin & Kelly 2015), the absence of relatively abundant Buffon's kob is difficult to explain. We can only speculate that seasonal changes in habitat preferences or the species-specific pressure of poachers targeting the surveyed area might be considered.

We endeavoured to employ the most appropriate statistical models. Because of their ability to account for multiple sources of uncertainty, hierarchical models are increasingly popular; occupancy-detectability estimation and modelling represents one of the classical fields of their application. We analysed the data using a Bayesian hierarchical modelling framework enabling future updates via specification of informative prior distributions for model parameters in future. Some studies (Tobler *et al.* 2015; Bowler *et al.* 2016) do report the important convergence as well as goodness-of-fit measures, but some do not (Rovero *et al.* 2014), which makes their results questionable. Therefore, we included a check of both convergence (the $\hat{R}$ and multiple $\hat{R}$ statistics) and goodness of fit (the Bayesian *p*-value based on the Pearson χ^2 statistic). As we tested, the Royle-Nichols type Multi-species abundance-detectability model with known N (MSA-N) was the only one with both satisfactory convergence and reasonable fit, similar to other studies (Tobler *et al.* 2015; Bowler *et al.* 2016). However, the multi-species occupancy-detectability (MSO) model was the only one that could be used for species richness estimation given the observed number of species and generally low detectability.

The mean occupancy (Ψ) and detectability (p) was 0.364 and 0.058, respectively, with highest occupancy values for the common warthog, Western bushbuck, and crowned duiker. Only six species showed a significant response in occupancy to environmental covariates: common crested porcupine exhibited an increasing probability of occurrence with increasing distance from the nearest road and river; Egyptian mongoose was found to have a higher occupancy probability closer to the NKNP border as well as farther from the nearest road; Northern lesser galago (*Galago senegalensis*) tended to occupy sites more distant from rivers; spotted hyena (*Crocuta crocuta*) occupied sites closer to rivers, but farther from roads; Western oribi had higher occupation probability closer to the roads, but farther from the NKNP border (although, as mentioned, it had a relatively poor fit); and finally, Western reedbuck (*Redunca redunca*) preferred sites more distant from roads.

These results gained from the predicted occupancy, however, need to be drawn carefully. The large confidence intervals indicate a high uncertainty related to the effect of environmental covariates on the species occupancy. More data is needed for more precise estimates. This can be ensured by either a denser camera trap network or longer observation period. The effect of environmental covariates thus remains rather unclear.

Being aware of mentioned imperfections, we still believe that our approach was the most transparent possible and correct. We hope that occupancy and species richness analyses providing comparative data will be widely employed for vanishing savannah wildlife. All the more so when the only World's systematic biodiversity camera-trap monitoring in tropical rainforests (Beaudrot *et al.* 2016) reports surprisingly positive animal demography results. Emerging asymmetry with alarming Living Planet Index reports (WWF 2014, 2016b) call for our vigilance from premature optimism.

From an ecology point of view, I consider camera-trapping the most exciting for its ability to analyse tempo-spatial occurrences of animals. And also, the most challenging to interpret. In the article presented in **Chapter 5.2.,** I report our study of invasive predators along with the first camera-trapping inventory of terrestrial wildlife in a typical mixture of Philippine landscapes on Bohol island.

Similarly to other major World's archipelagos, the nature of the Philippines faces multiple environmental issues including deforestration, pollution, human overpopulation and, last but not least, the introduction of invasive plant and animal species. Domestic cat (*Felis catus*) is considered the most damaging potentially invasive carnivore mammal for native fauna (Lowe *et al.* 2000). The cat threatens or drives to extinction at least 175 vertebrate species on about 120 islands worldwide (Medina *et al.* 2011). Parallel occurrence of cat prey species as mice (*Mus musculus*) or rabbits (*Oryctolagus cunuculus*) is known to exacerbate the negative impact of feral cats on endemic mammals (Nogales *et al.* 2013). Filipinos have kept cats for hundreds of years as pets, we can therefor expect that they will affect local wildlife. To our knowledge, assessment of the role of the cat has not been made in the Philippines, also there has been no camera-trapping inventorying survey conducted on Bohol.

The design of our study - opportunistic placement of camera traps on used trails - was adapted to the aim of the most frequent capturing of cats, known as preferable users of pathways (Doherty, Bengsen & Davis 2015). Inventory of terrestrial vertebrates therefor reflects the presence of such microhabitat dwellers rather than a standardized cross-section of species from randomized sampling array. Hence we were not able to analyse such population parameters as occurrence (ψ), neither our capture events cannot be considered as an independent *sensu stricto*. Reported events, however, served well as a basis for the relative abundance indices of recorded species and for the following analysis of their diel activity patterns.

We were able to record and identified 18 out of 22 (81.8%) known ground-dwelling mammalian, avian, and reptilian species occurring on Bohol. This rate corresponds well with results from inventories in other Tropics (Tobler *et al.* 2008, Bernard *et al.* 2013). Also an initial steep shape of the species accumulation curve (Chapter 5.2., Fig. 2) confirm the robustness of the approach, because we captured the most of the selected species in the first 1,000 trap days. This value is considered a reliable threshold enabling the detection of rare species (O'Brien 2011).

The list of recorded species contains 30 taxa, from which include 10 mammals, one reptile (*Varanus cumingi*) and 19 birds (Chapter 5.2., Table 2). During 2,885 trap days the most frequent native species was the barred rail (*Gallirallus torquatus*), recorded in 183 events. The most recorded carnivore was the domestic cat (180 events), domestic dog (144 events) and the common palm civet (59 events). We did not record four expected ground-dwelling bird species: *Megapodius cumingii, Coturnix chinensis, Turnix sylvaticus* and *Gallinago megala.* Conversely, we succeeded with confirmation of the Philippine warty pig (*Sus philippensis*) survival (Fig. 2). Probably a male individual that was captured only once on August 9th (6:35 pm) in a mud wallow in the interior of primary forest in the Rajah Sikatuna Protected Landscape. This subspecies on Bohol is considered to be close to extinction (Oliver

1993), DNA analysis is, however, needed to confirm or falsify genuineness of wild-ranging animals due to possible hybridization with domestic pigs.

Figure 2. Photographs from camera traps set on the Philippine island of Bohol depict a) domestic cat, b) domestic dog, c) Malay civet, and d) Philippine warty pig.

As we expected, the cat as an opportunistic generalist was absent inside the primary forest, where no subsidies from human are available. Cats generally prefer a heterogeneous habitat with linear features like roads, tree lines etc. (Crooks 2002; Bengsen, Butler & Masters 2012), but relatively homogeneous primary forest may offers countless minor paths, which a researcher seeking the best locations for camera traps can miss. Given to increasing number of our capture events closer to human settlements the first explanation is preferable. Occurrence of the cat in human-altered zones reflected, nearly by orders of magnitude, higher species richness and availability of rodents and birds as a prey.

Since we have described occurrences of prey, predators and competitors, what can their diel activity pattern actually tell us about mutual interferences? Overlapping curves of 24-h activity patterns is a relatively novel tool implying the tendencies of species to collide or avoid each other (Ridout & Linkie 2009).

We found the diel activity pattern of cats roughly consistent over 24-h periods (Chapter 5.2., Fig. 3). However, a decline in diurnal activity in the vicinity of human settlement comparing to an apparent activity peak before noon in a zone of rural landscape was revealed.

The cat had three possible competitors in the studied area – native common palm civet and Malay civet, and the domestic dog. The first two native predators are actually omnivorous with a distinctive nocturnal activity pattern (Jennings *et al.* 2009). Still, they forage in the habitat of cats, and given their size we consider them as competitors. Nonetheless, cats did not show any temporal avoidance, which indicates no interspecies competition. Cat and these viverrids have co-evolved during almost a 500-year co-existence in the Philippines (Jubair 1999). For a more comprehensive view of a tempo-spatial niche partitioning, as known from e.g. between Sumatran felids (Sunarto *et al.* 2015), a camera-trapping study should be extended on Negros, home of the Visayan leopard cat (*Prionailurus bengalensis* ssp. *rabori*), which is a direct regional competitor of the domestic cat (IUCN 2016).

The domestic dog, on the other hand, seemed to influence the daily budget of the cat. We did not find direct spatial exclusion of cats. Our results, however, support findings that cats optimize their timing of hunting behaviour to periods when dogs are less active, hence they avoid potentially dangerous encounters (Brook, Johnson & Ritchie 2012; Wang & Fisher 2012). Also the zone-specific relative abundance indices support the theory, because RAI values of cats and dogs differed noticeably between rural Zone II (4.57/2.53 for cats) and urban Zone III (13.52/14.66 for dogs). Cats in Zone II, where dogs were relatively to cats two times less numerous than in Zone III, were much more diurnal. So cats could respond to lower disturbance from dogs by shifting their activity peak to daylight.

Analysis of the overlap between cats and prey categories of rodents and ground-dwelling birds did not reveal any significant preference of temporal co-occurrences of cats with particular prey. In rural zone cats overlapped more with ground-dwelling birds ($\Delta=0.61$) and less with rodents ($\Delta=0.48$), in urban zone III the values were reversed ($\Delta=0.40$, resp. $\Delta=0.62$). Interestingly, the zone-specific relative abundances of prey categories was in direct opposition to what we can expect – cats always overlap more with such prey, which has a lower abundance index compared to the second prey. We can argue, that cats with an activity peak in rural area will prefer to forage for birds, while in urban sites will more search for rodents, which are active at night. Also, zone-specific relative abundance index might be a misleading parameter due to the chosen nonrandomized array of camera traps. Finally, and more generally, I would suggest the evaluation of the parameter of the overlap itself. The hypothesis of the arm races between predator and prey implies that prey would not get stuck on a place to be caught up by a predator (Dawkins & Krebs 1979), why hence the overlap would be representative in interspecies relationships? Also, other prey not captured by cameras such as insects or lizards might also be present on monitored sites and could influence our results undetected (Bonnaud *et al.* 2011). For an in-depth knowledge of the dietary intake of feral cats in the Philippines, and as a reference for the interpretation of overlaps, I recommend the DNA analysis of scat as a priority for researchers (Nogales *et al.* 2013).

The knowledge of feral cat diet and behaviour in general is paradoxically the least researched in tropical habitats with the richest terrestrial biodiversity (Doherty *et al.* 2015; Doherty, Bengsen & Davis 2015). We confirmed that the camera trap is a useful tool for monitoring small-bodied fauna and ground-dwelling birds even in dense and dusky tropical rainforest. We revealed the first tempo-spatial co-occurrences between feral cats and their potential prey in the Philippines, where local fauna is exposed to invasive species. Last but not least, I would like to point out the difficulty in making conclusions based on the analysis of overlaps, which despite seeming intuitiveness remains a challenge for future investigators.

One of the most applicable outputs of the camera trapping are abundance and/or density estimates. Animal species with a remarkable colour pattern unique to individuals (e.g. tigers, jaguars, leopards) are an ideal objects for capture-recapture estimates of population parameters (Karanth 1995; Silver *et al.* 2004). In the article in **Chapter 5.3.**, I presented our application of camera traps on the closed population of the Western Derby eland in the fenced Fathala Reserve on the Western coast of Senegal. Similarly to tigers, this critically endangered taxon shows an individually unique pattern of white stripes on the flanks (Fig. 3). Each of the 16 elands kept in the reserve were also listed in a studbook with both flanks depicted (Brandlová 2013). For my purpose of empirical testing of the reliability of abundance estimates ($\widehat{N}$), the herd in semi-captive conditions thus served as an ideal object.

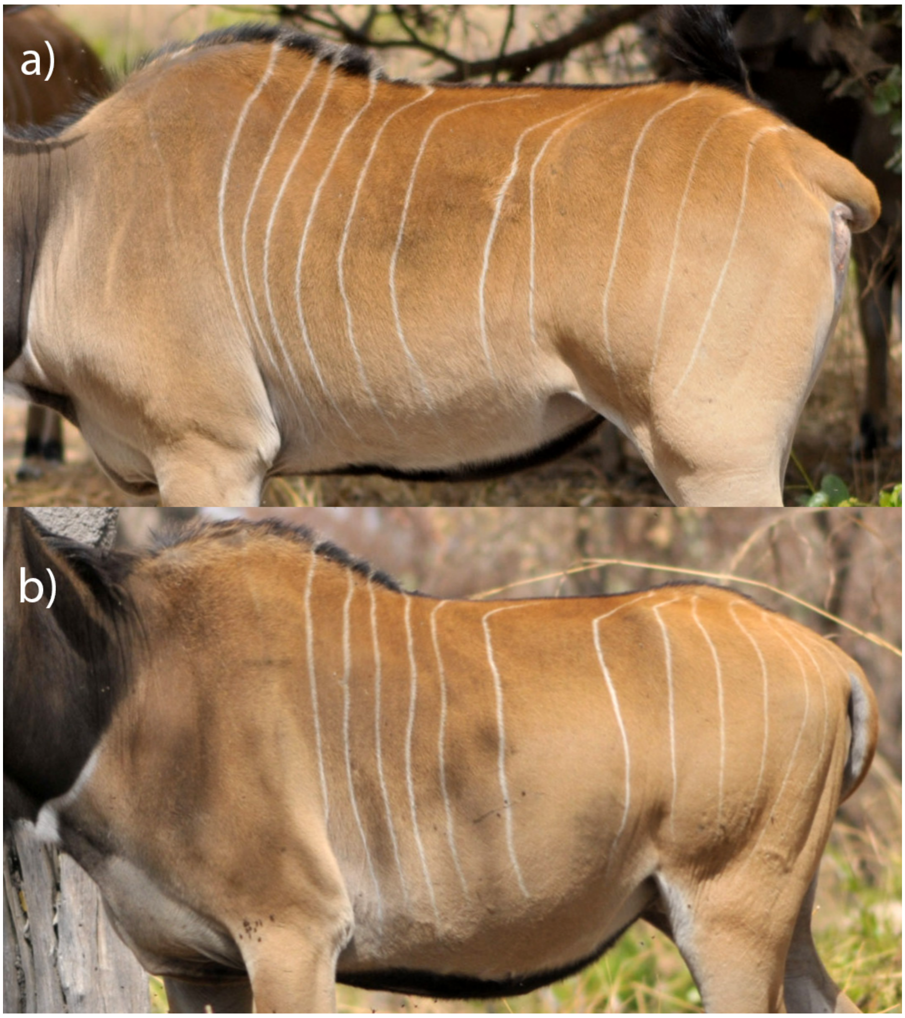

Figure 3. An example of unique markings on flanks of two Derby eland individuals. Note the number of stripes (12 at a), 13 at b) and their shape.

The closed capture-recapture models (CR) based on the recognition of individual animal were successfully introduced for the estimates of populations of tigers in India (Karanth 1995) with a logical extension on other marked felids worldwide (Harmsen *et al.* 2009; Garrote *et al.* 2012; Sunarto *et al.* 2015). As a reference population data source researchers used the calculation of the number of tigers given by the extent of the inhabitable habitat with prey available (Karanth & Nichols 1998; Gopalaswamy *et al.* 2012) divided by home range size. The CR estimates reflected the latter method and local knowledge, which resulted in a general consensus of the robustness of the camera-trapping approach. Natural low densities of tigers as apex predators, however, can produce scarce data and a high level of heterogeneity in the detection of individual tigers, which results in malfunctions of recommended CR estimators, as modelled (Harmsen, Foster & Doncaster 2010).

Lack of empirical evaluation of the method was the inspiration for our study on the known population of analogically bar-coded Derby elands. The test appeared more topical thanks to the newly incoming method of spatially explicit capture-recapture (SECR) models overcoming the limitations of the closed ones. SECR is based on the location-specific capture histories of individuals and should perform well for surveys dealing with the migration of the target animals. We tested the most common models of abundance estimates: for (1) CR M_0, M_h and M_h Chao computed in the program CAPTURE, and (2) for SECR basic *Null* and *Finite mixture* models run in R, package secr.

We recorded and identified the whole population of 16 individuals in 962 trap-days. Only daytime pictures could be used in the analysis due to the poor visibility of white stripes on animal flanks taken during a night in the infrared flash mode of the camera. We successfully processed our data via CR and SECR analyses. Both approaches provide us with estimates close to the real size of the eland population tested. Results were even reliable in half of the duration of our test, which meant 33 days. Generally, CR models performed in a more accurate way and in shorter tested periods than SECR models. Interestingly, we did not find CR model M_0 to produce underestimated results in comparison with jackknife M_h. This is expected (Harmsen, Foster & Doncaster 2010), because jackknife models are designed to positively reflect heterogeneous detectability of each animal driven by different age, sex, personality, etc. But our model M_0 resulted in an even higher abundances for the shorter trapping occasions, and was more accurate when the analysed array of camera traps was linear. This implies that particular individuals did not vary in the spatial use of the surveyed area, and that assumption of closure was fulfilled, as we personally confirmed after the survey.

SECR models, on the other hand, showed increasingly biased results with shorter duration of the monitoring, i.e. the number of trapping occasions. Both array of camera traps, line and polygonal grid one, produced in tested SECR models overestimated abundances when the number of occasions was lower. The *Null* model resulted in reliable estimates from both array of cameras. The *Behavior* model, counting with behavioural response to detectors, produced reasonable estimates only in the grid. Our results suggest that the number of detectors and duration of sampling are crucial factors, even in a homogenous habitat with a high density of animals. Nevertheless, we have to be aware of already described sources of bias, which are affecting of movement of animals by spatial use of resources (Royle *et al.* 2013), and asymmetry of individuals' home ranges (Ivan, White & Shenk 2012). Unfortunately, we did not have data to investigate these variables.

Studies aiming on estimates of abundances of such low-density animals, as large carnivores or critically endangered eland, commonly face very low capture probabilities ($\hat{p}$) of individuals. This parameter negatively influence the reliability of results and the improvement can rely only on the employment of more detectors or an extension of the survey period, which can collide with population closure (Kendall 1999; Tobler & Powell 2013). As we successfully demonstrated, pooling (or colliding) of trapping occasions could reasonably improve parameters from $\hat{p}$ values of 0.034 to 0.304 The results remained solid as seen in Chapter 5.3., Table 3.

We can conclude that both methods performed well. But especially in the case of small-sized population at fenced game reserves, the CR models remain for researchers and practitioners a reliable and approachable tool with a user-friendly computing environment. In terms of cost efficiency of camera-trapping, we should highlight the potential of the limited number of detectors in line array, the estimates from which were accurate, along with adequate capture probability when pooling was used.

The importance of camera-trapping and abundance estimates reliability has recently become a topical issue, and accidentally for species which whole CR modelling successfully started - tigers. As reported in July 2017 (Hindustan Times 2017) with reference to Singh & Sen (2015), the population of tigers was declared to be increasing for the first time after an era of their mitigation, which is shedding positive light on the conservation strategy in India. Regardless the statement scientists implementing CR estimates on this species did react and questioned the published absolute numbers of tigers (The Hindu 2016). This can be possible due to the simple fact, that monitoring with camera traps is much more effective than any other, thus a certain number of tigers could previously remain undetected. Also, numbers of tigers were considered rising only in India, where their densities, mainly within protected areas, are much higher than in any other parts of the species range. Therefore detection probabilities allow for representative estimates. On the very different habitat, boreal Chinese-Russian Far East, however, tigers occur in such low densities as 0.6–1.4 tigers/100 km^2 (Karanth & Nichols 1998), that camera traps outside reserves will hardly encounter single individuals in to-be-closed trapping period (Jůnek & Jůnková Vymyslická, unpublished data). The extremely large home range of a male Amur tiger even exceeds an area of local protected landscapes, which would logically result in such low detectability making any CR estimates impossible.

As we can see, the initially studied tiger shows us at the same time how misleading the generalization of the CR method on a single species can be. Researchers should be aware of the fact, that they could face analogous situation with species of their interest and that capture probability is a key parameter worth anticipating.

I conclude that camera traps serve as a reliable, cost efficient, durable and evolving tool for zoological research. Low-end cameras are affordable even for enthusiasts. Nonetheless, the wide use of these detectors is not necessarily equal to the production of data applicable for science. I would like to highlight several issues which researchers considering application of camera traps should become familiar with.

The market is nowadays full of brands and types of camera traps with prices ranging approx. between 100 and 700 U.S. dollars. A buyer has to count with the fact that the cheapest ones can tend to certain level of heterogeneity in performance. The reaction and triggering time of two units may differ, set up values can be performed with varying delays, power supply can be differently consumed, and rate of malfunctioning cameras in the field is unpredictable. Unfortunately, based on own experience, even threefold expensive cameras malfunctioned in a similar way.

Large scale monitoring requires a large number of detectors; price is thus an important factor. A researcher should be able to compromise reliability of equipment (and outputs) and an expected risk of damage usually such as theft from human intruders, destruction by animals, bushfires, moisture, or heat causing leakage of batteries.

Capturing in night is enabled by in-build flashlight. An infrared lamp does not disturb animals or attract people; on the other hand, produced images are often not clear and sharp compared with those from white flashlights. For such marks, as stripes on tiger or eland, poor visibility of these features from infrared images is a crucial obstacle. To my knowledge, no study has yet proved a significant effect of white or infrared flashlight on animals. We could expect, that white light will be a source of disturbance, but we also can oppose that wild animals are familiar with similar, and much powerful events – lightning.

This leads us to the non-invasive presupposition of the method. Known avoidance of camera traps is known (Schipper 2007) and especially the recent use of the method in canopy (Olson *et al.* 2012; Bowler *et al.* 2016) is worthy of critical attention. But there exists an undetermined opposite source of bias – camera trap as an attractant. Primates are notorious examiners of camera traps wherever they encounter them. From my experience, chimpanzee, mona monkeys, green monkeys, patas monkeys, Guinea baboons actively investigated our equipment. I consider the assessment of this phenomenon an important topic for researchers seeking real independence of capturing events.

The final comments urge researchers for both environmental and moral responsibility. Camera-trapping produces a large amount of empty batteries. A proper recycling process should be assured even for rechargeable accumulators, particularly in remote study areas. Camera traps also come into contact with body fluids such as saliva, or are inhabited by various invertebrates (e.g. spiders, ants, termites). Translocations of such equipment into new biome should be accompanied with careful disinfection. And lastly, we should be aware of the law dealing with the protection of personal data. In the Czech Republic, there is the Act No. 101/2000 Coll., which specifies handling of images from camera-trapping. We can expect future tightening of such regulations worldwide. This will be an obstruction to deal with when, specifically, alleged poaching should be targeted (Fig. 4). Anyway, even if some developing tropical country does not employ such ID protection, it is our moral duty towards our hosts to be discreet.

Figure 4. A suspected poacher captured in the Niokolo-Koba National Park. Could the photograph be used in court as evidence or does the Senegalese law protect man's identity?

7. References

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