Estimating spotted hyaena (*Crocuta crocuta*) population density using camera trap data in a spatially-explicit capture-recapture framework

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Honours Thesis

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Abstract

Species-specific population data are important for the effective management and conservation of wildlife populations within protected areas. However such data are often logistically difficult and expensive to attain for species that are rare and have large ranges. Camera trap surveys provide a non-invasive, inexpensive and effective method for obtaining population level data on wildlife species. Provided that species can be individually identified, a photographic capture-recapture framework can be used to provide density estimates. Spatially-explicit capture-recapture (SECR) models have recently been developed, and are currently considered the most robust method for analysing capture-recapture data. Camera trap data sourced from a leopard survey performed in uMkhuze Game Reserve, KwaZulu-Natal, South Africa, was analysed using SPACECAP, a Bayesian inference-based SECR modelling program. Overall hyaena density for the reserve was estimated at 10.59 (sd=2.10) hyaenas/100 km^2, which is comparable to estimates obtained using other methods for this reserve and some other protected areas in southern Africa. SECR methods are typically conservative in comparison to other methods of measuring large carnivore populations, which is somewhat supported by higher estimates in other nearby reserves. However, large gaps in time between studies and the variety of historical methods used confound comparisons between estimates. The findings from this study provide support for both camera trap surveys and SECR models in terms of deriving robust population data for spotted hyaenas and other individually recognisable species. Such data allows for studies on the drivers of population and distribution changes for such species in addition to temporal and spatial activity patterns and habitat preference for select species. The generation of accurate population data for ecologically important predators provides reserve managers with robust data upon which to make informed management decisions. This study shows that estimates for spotted hyaenas can be produced from an existing survey of leopards, which makes photographic capture-recapture methods a sensible and cost-effective option for the less charismatic species. The implementation of standardized and scientifically robust population estimation methods such as SECR using camera trap data would contribute appreciably to the conservation of important wildlife species and the ecological processes they support.

Introduction

Conservation biology is a crisis discipline (Soulé 1985), which in the face of drastic global declines in wildlife populations (Dirzo *et al.* 2014, WWF International *et al.* 2014) has become exceedingly relevant in the modern context. Despite the distressing losses of biodiversity and associated ecosystem services (Díaz *et al.* 2006, Cardinale *et al.* 2012, Dirzo *et al.* 2014), the field is largely under-resourced (Possingham *et al.* 2001, Wilson *et al.* 2006, McDonald-Madden *et al.* 2008), with the result that conservation decisions are often made on the basis of triage (Bottrill *et al.* 2008, McDonald-Madden *et al.* 2009, Bottrill *et al.* 2009). As a result, evaluating and selecting species for conservation has become hugely important, and the field of population biology is essential to informing modern conservation efforts (Simberloff 1988, Marsh & Trenham 2008). There is an ongoing need to add to and update existing population data. If well-maintained, databases such as the IUCN Red List (IUCN; http://www.iucn.org) can enable conservation practitioners to make informed and effective decisions (Rodriguez *et al.* 2006). Thus, population data have a vital role to play in combatting the current global biodiversity crisis.

Frustratingly, population data are not typically easy to obtain, with various challenges posed by both the ecology and habit of the target species. Surveying wide-spread species can be logistically problematic, and species that live at low densities are often difficult to account for due to low encounter probabilities (e.g. McCarthy *et al.* 2008). For territorial animals with exclusive home ranges these factors can work in tandem to complicate the data collection process (Balme *et al.* 2009). Sampling can be further challenged when species are nocturnal, solitary or of a shy disposition (Balme *et al.* 2009).

Conservation efforts on all scales are typically attempted on a limited budget (Possingham *et al.* 2001, Wilson *et al.* 2006, McDonald-Madden *et al.* 2008), meaning that these logistical challenges are usually compounded by financial constraints. The costs of population data collection may be particularly pertinent for long-term monitoring projects that rely on repetitive surveys rather than once-off estimates (Nichols & Williams 2006). It is thus essential to develop optimal methods that produce the highest quality data with the resources available (Rondinini 2008), prioritizing accurate, precise and repeatable data collection techniques. This return-on-investment approach (Murdoch *et al.* 2007) will ensure that management can be effectively informed despite limited resources.

Camera trapping is a passive, non-invasive method for sampling wildlife, and is especially useful for surveys of cryptic, nocturnal species (Balme *et al.* 2009). While the start-up costs (i.e. the costs of the cameras) may be expensive, there is little labour required; hence, camera trapping is a comparatively inexpensive option for long-term monitoring. Motion-triggered cameras are deployed in the landscape, typically along pathways where the animal of interest is thought to be most active (see O'Connell *et al.* 2010). The photographic 'capture' of an animal by these remote cameras can yield a wide variety of information for biologists (Trolliet *et al.* 2014) and camera trap surveys have outperformed other biodiversity survey tools in their ability to inventory mammals across a wide range of environmental conditions (Silveira *et al*. 2003). At the most basic level camera traps can produce occurrence and distribution data for many species in an area, in some cases disproving the supposed extinction of certain species (Brink *et al.* 2002). Distribution data from camera traps can be further analysed to investigate habitat preference, distribution drivers, and responses to disturbance such as habitat fragmentation (Lomolino & Perault 2001, Farhadinia 2004, Zielinski *et al*. 2005, Linkie *et al.* 2006).

The applicability of camera trap data is dramatically enhanced when the study species has a distinct pelage pattern, or other visually discernible markings. This enables the surveyor to distinguish between individuals, negating the problem of multiple captures of the same animal being considered as separate individuals. Camera traps can thus be used to compile capture histories of individuals, which can be analysed in a closed capture-recapture (CR) framework to generate abundance and density estimates (e.g. Karanth & Nicholls 1998, Heilbrun *et al.* 2006, Thorn *et al*. 2009). Camera trap data can also be combined with open CR models to measure demographic characteristics such as survivorship and population turnover (Karanth *et al.* 2006, Mondal *et al.* 2012).

Karanth and Nichols (1998) developed the first camera trap studies using closed CR analyses to study tigers *Panthera tigris* in India. While this was an advance on previous methods, there were a number of shortcomings. In particular it proved problematic to define the area that had been sampled (Karanth *et al.* 2010), the accuracy of which is essential for deriving accurate density estimates. Solutions to this problem included applying a buffer to each trap representing either half the width of an estimated home range size (Soisalo & Cavalcanti 2006), or when this information is unavailable then it is common practice to use the mean maximum distance moved (MMDM) or half that (HMMDM) of an animal in the survey as a substitute for home range (Karanth & Nicholls 1998). Soisalo and Cavalcanti (2006), however, exposed the tendency of this proxy to under-estimate actual movement, which can result in overestimates of density when applying these ad-hoc buffers. It is also worth noting that MMDM is heavily influenced by how far apart the traps within the grid are set (Dillon & Kelly 2007), which can further diminish the accuracy of estimates using this method.

Camera trap surveys are also typically limited by the need to account for imperfect detection (MacKenzie *et al.* 2005). Assuming that all animals in the area have been captured puts the estimate at risk of a false-negative error (assuming there is no individual where there is in fact one). Camera grids being used for capture-recapture analysis have historically been required to be rigid, with cameras typically spaced at distances less than the minimum home range size of the target to avoid the potential of an individual existing within the grid without exposure to a proximate trap (Karanth *et al.* 2010). This constrains the geographical spread of the survey area due to an inevitably limited number of available cameras (Kays & Slauson 2008, O'Brien 2010).

Spatially-explicit capture-recapture (SECR) methods have recently been developed to overcome some of these drawbacks and to improve on the rigour of these earlier surveys (Borchers 2012). SECR explicitly incorporates the movement of individual animals relative to the trap grid in the modelling framework, creating potential activity centres for each individual. The model applies a probability of detection at each trap for each individual, assuming that the further away the activity centre is from a camera trap, the less likely it is for that individual to be captured there. The application of a biologically-based buffer as opposed to an ad hoc movement estimate enables the model to produce a more robust density estimate than non-spatial CR models (Noss *et al.* 2012, Blanc *et al.* 2013). SECR models are robust to changes in camera spacing (Sollmann *et al.* 2012), meaning trap arrays no longer need to be organized in a rigid, grid-like pattern. SECR estimation methods can be performed using either a likelihood-based approach (Borchers & Efford 2008) or Bayesian inference (Royle *et al.* 2009). Camera trap CR surveys have been shown to be more accurate than other traditional methods used to measure large carnivore populations (Balme *et al.* 2009). While spatially-explicit methods have been shown to be more precise than non-spatial models and do not have the same tendency to overestimate densities (Noss *et al.* 2012, Blanc *et al.* 2013), no comparison between SECR methods and other estimation methods not utilizing camera traps on a known reference population exists, therefore comparing accuracy and precision is currently impossible. However for methods utilizing camera traps SECR is currently considered the most accurate, precise and robust method to use when investigating population densities.

SPACECAP (Gopalaswamy *et al*. 2012) is a recently developed Bayesian SECR modelling program that functions in the R statistical environment (R Development Core Team 2010). SPACECAP has already been effectively used to generate density estimates for a number of species, especially medium-large mammals, including leopard *Panthera pardus* (Chase-Grey *et al.* 2013), serval *Leptailurus serval* (Ramesh & Downs 2013), brown hyaena *Parahyaena brunnea* (Kent & Hill 2013), striped hyaena *Hyaena hyaena* (Athreya *et al.* 2013), Scottish wildcat *Felis silvestris silvestris* (Kilshaw *et al*. 2014), and ocelot *Leopardus pardalis* (Rodgers 2014). Though the use of these techniques is increasing, there are still many species which could benefit from such analysis that remain unstudied. An opportunity exists to reverse data deficiency for a number of species, provided that they can be individually identified in a photographic capture. One such example is the spotted hyaena *Crocuta crocuta*.

With the exception of the Kalahari Transfrontier Park (Mills 1990) and to a lesser extent Kruger National Park (Mills, 1985, Henschel & Skinner 1987, 1990), spotted hyaenas are largely understudied within protected areas in southern Africa and thus few reserves have baseline population data. For example, in uMkhuze Game Reserve, KwaZulu-Natal, the only population study on spotted hyaenas was undertaken by Skinner *et al.* (1992). They performed call-ups and baiting in 1989, following the method described by Whateley (1981), and estimated 38 individuals in their study area existing at 13 hyaenas/100 km^2. Current reserve management is therefore limited by the outdated nature of the information available on their spotted hyaena population.

Population estimates for spotted hyaenas are often derived using different methods, which limits the extent to which they can be effectively compared. The estimates that do exist (Table 3, also Table 1 in Appendix) are generally obtained using one of three methods: call-ups (e.g. Mills & Gorman 1997, Mills *et al.* 2001, Ogutu *et al.* 2005, Graf *et al*. 2009), track counts (e.g. Funston *et al*. 2010) and long-term studies where researchers recognize individual animals (Höner *et al.* 2005, Holekamp *et al*. 2012). Call-ups are performed by playing sounds known to attract hyaenas (usually distress sounds of their prey or calls of conspecifics; Mills *et al.* 2001) from designated sampling points. Using a predetermined calibrated response distance, one can then divide the mean number of respondents by the sampling area around each point (Mills et al. 2001). Track count estimates are achieved by counting the number of spoor found on transects of known distance.

Each of these methods has its drawbacks. Call-ups and track counts do not generally account for individual hyaenas, and have large associated errors. Call-ups in particular do not successfully attract cubs or sub-adults, which results in underestimates (Mills *et al*. 2001, Graf *et al*. 2009). Animals are also readily habituated to the call-ups, so surveys may become ineffective if used too frequently (Mills *et al*. 2001). Glen & Dickman (2003) found that track counts were highly inaccurate for estimating red fox *Vulpres vulpres* abundance and much more open to interpretation than SECR models. While long-term studies enable researchers to identify individuals and become familiar with the population, they are not feasible for every reserve, particularly outside protected areas where conservation needs are often greatest (Miller & Hobbs 2002), and require long-term investment of time and finances. These studies often account for a small number of hyaena clans, and therefore the size of the areas for which they generate density estimates is limited (eg. Holekamp *et al.* 1992). This represents a poor return-on-investment for the most basic population data, but an excellent return for behavioural studies. The use of vastly different techniques each with their own associated pros and cons of each method has resulted in widely differing density estimates for the species across Africa (Table 1 in Appendix).

Camera traps are not a new tool for studying hyaenas. Studies using camera traps have previously analysed members of the Hyaenidae with regard to a number of ecological factors, including occupancy (Thorn *et al.* 2009), habitat use and preference (Petorelli *et al*. 2009, Abade *et al.* 2014), as well as impacts on rangeland management (Kauffman *et al*. 2007). Density estimates have been performed for both striped (Athreya *et al*. 2013) and brown hyaena (Kent & Hill 2013), and recently for the spotted hyaena by Henschel *et al.* (2014), producing an estimate of 15.39 hyaenas/100 km^2 in the Odzala-Kokoua National Park in the Republic of Congo. To my knowledge, This was the first study to my knowledge to use camera traps to estimate population density for spotted hyaena; however, they used non-spatial CR models to analyse their data. They also used unpaired camera trap stations, resulting in uncertainty of multiple individual identities due to the capture of only one flank. Their effort was nevertheless a worthwhile foray into the use of such techniques for the species, and has confirmed that spotted hyaenas can be individually identified with sufficient confidence from camera trap photographs. However, there are clear improvements to be made to the study design; specifically, the application of SECR is likely to improve the rigour of population estimates.

The primary objective of this study was to use an existing camera trap survey established for leopard in KwaZulu-Natal to perform the first SECR analyses for spotted hyaena within a protected area. This study fills a knowledge gap in conservation management for this ecologically important species within the study site, and could provide an easily performed, relatively cheap, non-invasive, informative and rigorous alternative survey method with which to standardize population analyses for the species in southern Africa.

Methods

Study species

The spotted hyaena *Crocuta crocuta* Erxleben 1777 (Hyaenidae) is a large predator and scavenger indigenous to much of sub-Saharan Africa. They are monospecific and the largest of the Hyaenidae, with unique spot patterns on each individual (Höner *et al.* 2005, East & Hofer 2013). Hyaenas have significant ecological influence on other sympatric large predators such as lion *Panthera leo*, cheetah *Acinonyx jubatus*, and wild dog *Lycaon pictus*, including the direct effects of resource conflict, kleptoparasitism and mortality (Cooper 1991, Carbone *et al.* 1997, Palomares & Caro 1999, Carbone *et al.* 2005), as well as consequent spatial avoidance (Creel & Creel 1996, Durant 1998, 2000a, 2000b, Creel & Creel 2002, Hayward & Hayward 2007). The spotted hyaena's dual foraging ability of hunting and scavenging makes them particularly important to ecosystem functioning. Thus while spotted hyaenas are able to bring down prey in weight classes matched only by lion (Hayward & Kerley 2008) they are much better than lions at both osteophagy and cracking large bones. Richardson *et al*. (1986) demonstrated that species of vulture that rely on crushed bone fragments for their calcium uptake experienced elevated levels of osteodystrophy and stunted bone formation in chicks when spotted hyaenas were not present. Spotted hyaenas are significant ecological role-players, however it is indicative of the neglect they have suffered in both academic study and conservation that their vast ecological influence on sympatric large carnivores and species of other trophic levels were ignored in the recent review of the world's largest predators (Ripple *et al.* 2014). Spotted hyaenas are in fact declining due to anthropogenic pressures of habitat destruction and direct persecution, though they are still classified as of Least Concern by the International Union for Conservation of Nature (IUCN) (Höner *et al*. 2008).

Study site

uMkhuze Game Reserve (hereafter uMkhuze) is a 360 km^2 protected area in northern KwaZulu-Natal, South Africa (Figure 1). It is managed by KZN Ezemvelo Wildlife, and hosts all the members of the Big 5, as well as cheetah, wild dog and spotted hyaena. The reserve is characterized by Western Maputaland sandy bushveld, with a matrix of woodland, bushland and wooded grassland (Scott-Shaw & Escott 2011). The eastern edge of uMkhuze is heavily populated, which is a likely source of poaching pressure along this boundary (G Balme, Panthera, pers. comm.). A habitat mask was drawn up for the area using ArcGIS 10.1 (ESRI 2010), where pixels of 0.336 km^2 that contained fewer than three human settlements were considered suitable habitat, and those with three or more were unsuitable for spotted hyaenas (G Balme, Panthera, pers. comm.).

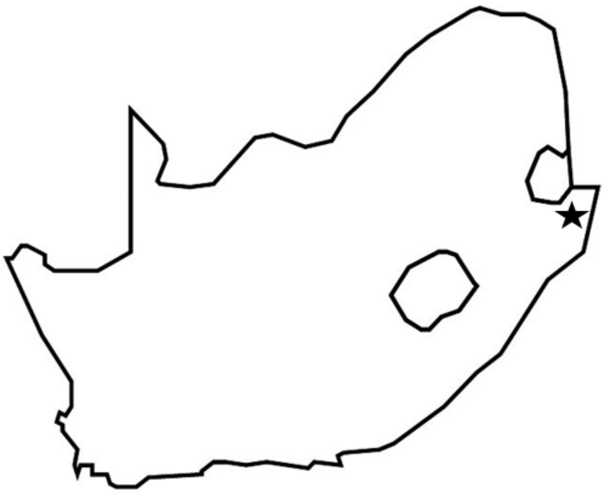

Figure 1: Location of uMkhuze Game Reserve, KwaZulu-Natal, indicated on a map of South Africa by a star.

Data collection

Panthera, a non-government organisation based in New York which focuses on the conservation of wild felids, runs regular camera trap surveys in KwaZulu-Natal as part of a long-term project to monitor the population trends of the provincial leopard population. One site which is surveyed on an annual basis is uMkhuze. Cameras traps were placed along roads and game paths well used by leopards (and other carnivores) in order to maximize captures. Trap sites were equipped with two white flash Panthera digital cameras in order to capture both flanks of the animal. Cameras were either fixed to trees or tied to metal stakes driven into the ground. Vegetation was cleared from the field of view when necessary, and cameras were placed roughly 30-50 cm off the ground. A total of 82 cameras were deployed at 41 stations, 2-3 km apart. Every camera was checked roughly once per week with faulty or missing cameras and flat batteries being replaced. In addition all images on memory cards were downloaded during each visit to avoid saturation and to minimise potential data loss as a result of card failure. Each survey ran for 45 days to satisfy the SECR condition of population closure (Karanth *et al.* 1998). I used data from the 2013 survey which was run from the 12th of June to the 26th of July 2013.

Data curation

Captures of spotted hyaenas were separated out using the software package Camera Base 1.6 (M. Tobler, San Diego Zoo Institute for Conservation Research, USA 2012) which is freely available online. This program reads the External Image File (EXIF) data for each image, including time, date and camera identification tag, and builds a capture history for each image. Captures at a single site were considered independent if the photographs were separated by a minimum of 30 minutes, or if the picture was clear enough to conclude from the spot patterns that it was a different individual (O'Brien *et al*. 2003). Individual identification of hyaenas relies primarily on variation in spot patterns on the flanks and upper legs and I thus retained all side-on images while discarding photographs of the front or rear of the animal.

Once this filtering process was complete the images were cropped to exclude the head, hindquarters, and lower legs to produce standardised flank images in preparation for matching. Care was taken to minimize background featuring in the cropped image. Image rotation was used where necessary to achieve this. The first stage of matching was conducted with the freeware Wild-ID program (Bolger *et al.* 2012). At this stage the threshold matching score for hyaenas had not been calibrated, so the matching was done only by eye with no regard to the match score computed by the program (Figure 2). The calibration of this score is addressed later in this thesis. Only the top-ranked image in each Wild-ID comparison was accepted or rejected (Bolger *et al*. 2012).

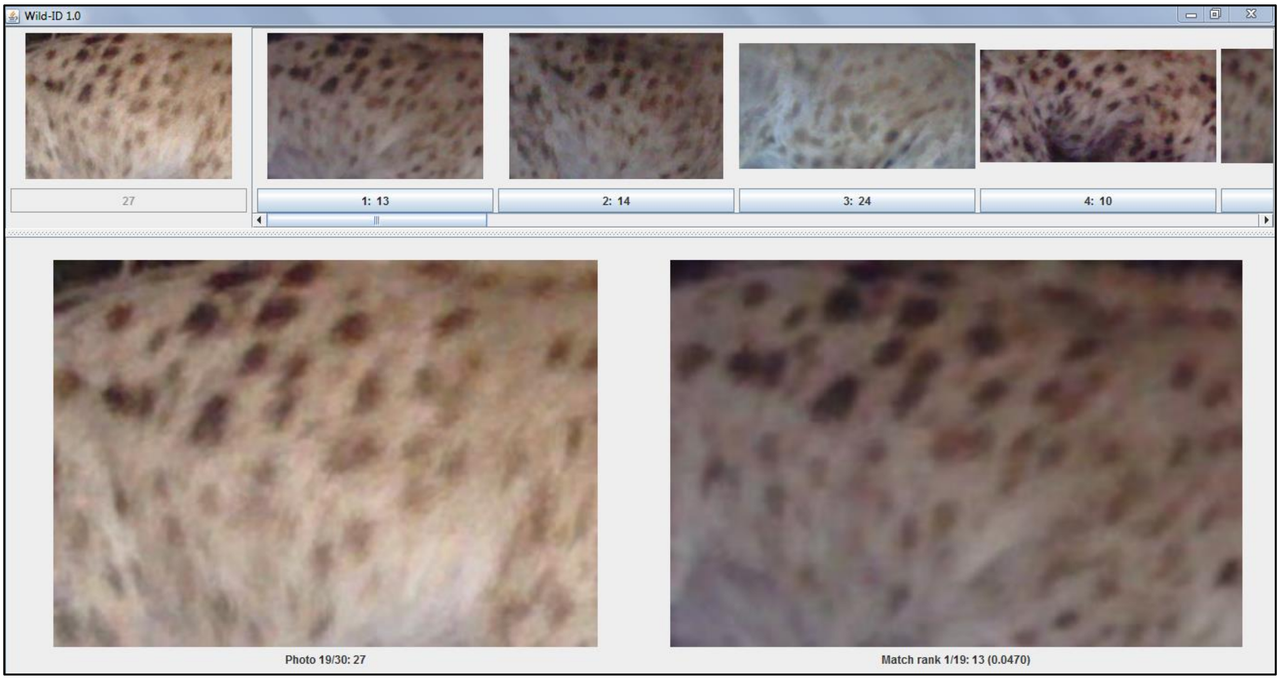

Figure 2: Wild-ID interface (Bolger *et al.* 2012) showing a matching pair. The Scale Invariant Feature Transform (SIFT) function computes a 'match score' (shown as 0.0470 underneath the right-hand picture in parentheses). The higher the score, the more likely the two images are a matching pair.

Confirmed matches in Wild-ID were paired in the Camera Base database using the 'Compare' function (Figure 3). Thereafter, I extracted the best photograph of each flank from each individual and reran the data through Wild-ID to further reduce overestimates and missed matches. The final matches were again paired in Camera Base, yielding a total number of individuals within the dataset with confidence that no outstanding matches remained. Since some captures only successfully photographed one flank, particular individuals could only be compared with others with the same flank. It is not safe to assume that individuals captured only with their right flank and others with their left are distinct individuals, therefore all individuals identified only by the one flank for which there were fewer captures were removed before proceeding with the SECR analysis.

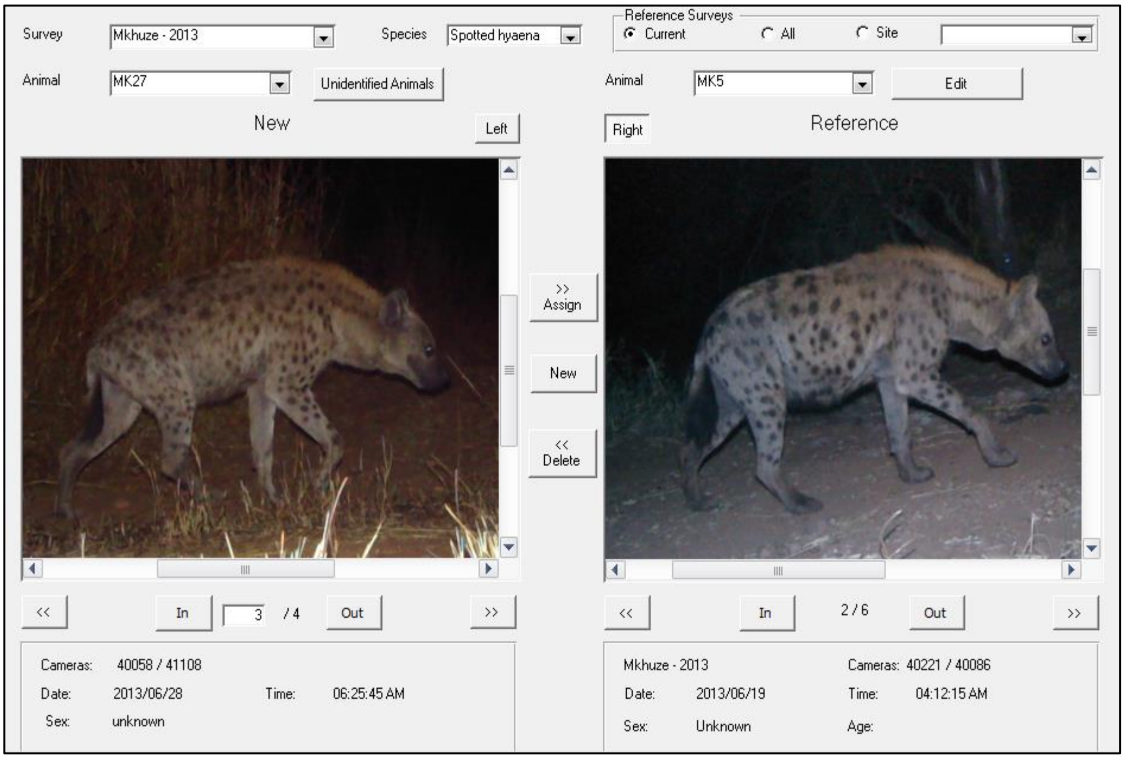

Figure 3: The Camera Base interface, displaying the 'Compare Photos' window used for pairing images. The current window shows a comparison between MK27 (left) and MK5 (right), two separate individuals. Note the healed snare wounds around the necks of both individuals.

Calibration of Wild-ID match score acceptance threshold

The use of automated pattern recognition software could expedite the analysis of camera trap data as it negates the time-consuming job of manually identifying images, which is also prone to human error. Wild-ID (Bolger et al. 2012) is a commonly used pattern recognition program that is freely available online. Wild-ID has been used to match images for many species, including such varied animals as Southern red-bellied toads *Melanophryniscus cambaraensis*, wildebeest *Connochaetes taurinus*, Jollyville Plateau salamanders *Eurycea tonkawae*, and giraffe *Giraffa camelopardis* (Bolger *et al.* 2012, Caorsi *et al.* 2012, Morrison & Bolger 2012, Bendik *et al.* 2013). Wild-ID uses a scale-invariant feature transformation (SIFT) (Lowe 2004) to recognize patterns in images, and then computes a probability score of two photographs being a match. The photographs are then evaluated visually for similarity on the program interface with the guide of the match score. The threshold match score for positively matched images of spotted hyaenas has not yet been calibrated. However, if this can be established and the program is found to consistently and accurately match spot patterns for this species then the human element in the matching process can be removed.

To calibrate the match score acceptance threshold for spotted hyaenas the Wild-ID outputs were compared to the manually-performed matches of multiple human observers. A 30 photograph sub-sample of the dataset was presented in both digital and hardcopy forms to 17 independent volunteers who each attempted to match flank patterns by eye, thereby forming an estimate of the total number of hyaenas in the subset. The subset was restricted to photographs of only the right flank to avoid invalid comparisons. I assumed the mean of these estimates to be the 'true' number of individuals present in the 30 photographs. I compared this value to the Wild-ID outputs generated using a range of minimum threshold match scores. In this context, the Wild-ID match score for spotted hyaenas can then be defined as the score at which the Wild-ID software output equals the 'true' value. I, as someone who now has extensive experience dealing with such images, estimated the total in the sub-sample to be 22 individuals.

SECR analysis

Capture histories for individuals were exported from Camera Base into Microsoft Excel (Microsoft Corporation 2010) in preparation for the impending SECR model. This information, along with the habitat mask for uMkhuze and the UTM data for the camera trap locations were entered into SPACECAP 1.0 (Gopalaswamy *et al*. 2012). SPACECAP uses Bayesian inference to generate a total and pixel-specific density estimate. Pixel values were then used in ArcGIS to construct a map of density distribution across the study site (Figure 6). The model was set (as recommended by Gopalaswamy *et al.* 2012) at 50 000 iterations, with a burn-in of 1000 and no thinning.

Results

Capture success

The survey lasted 1827 trap nights, generating 174 photographs of spotted hyaena taken between 19h03 and 07h06. These images comprised 127 independent captures, 106 (83.5 %) of which could be used for identification purposes (Figure 4). These included 79 images of right flanks and 74 of left flanks. The matching process produced a total of 45 uniquely identified individuals, of which 20 had captures of both their flanks. Of those identified by only one flank, 17 were identified from the right flank and 8 from their left. The latter were discarded from the model inputs, leaving 37 individual hyaenas for the model inputs. The number of captures per individual ranged from 1-10, with a mean of 2.49 (sd=2.26).

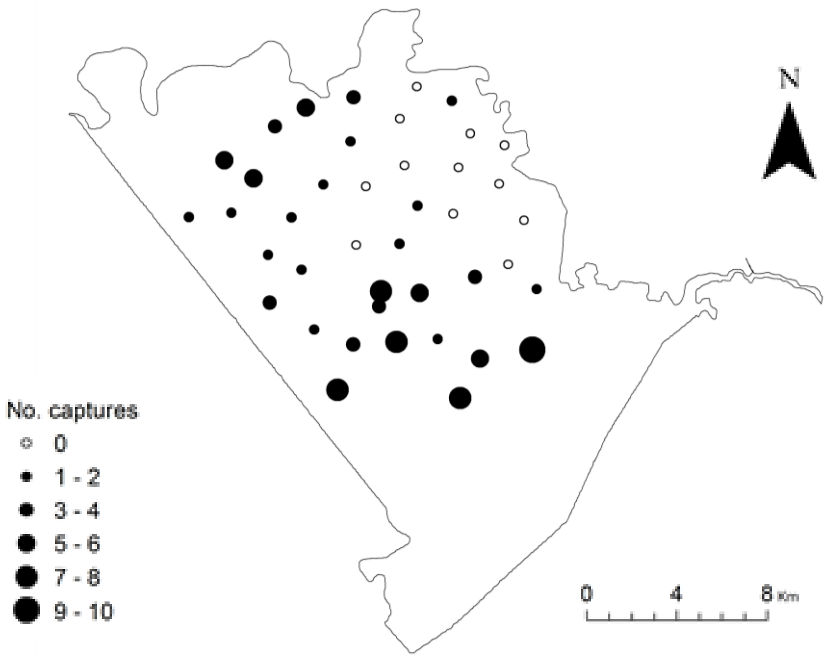

Figure 4: Map of capture success at trap site locations. Circles denote trap site location and are scaled to number of spotted hyaena captures over the 45 day survey.

The capture frequency (the number of 24-hour sampling occasions each individual was captured) ranged from 1-9, with a mean of 2.33 (sd=1.87). While no cubs were captured, there was a seemingly good range of sub-adults (with characteristic black fur on the legs and belly) to adults represented in the catalogue of individuals.

The rate of photographic captures remained fairly steady as the survey progressed (Figure 5). The growth in numbers of unique individuals being added to the dataset was steady for the first 15 trap nights, after which the rate of addition slowed, reaching an eventual total on the 38th trap night of 37 individuals (Figure 5).

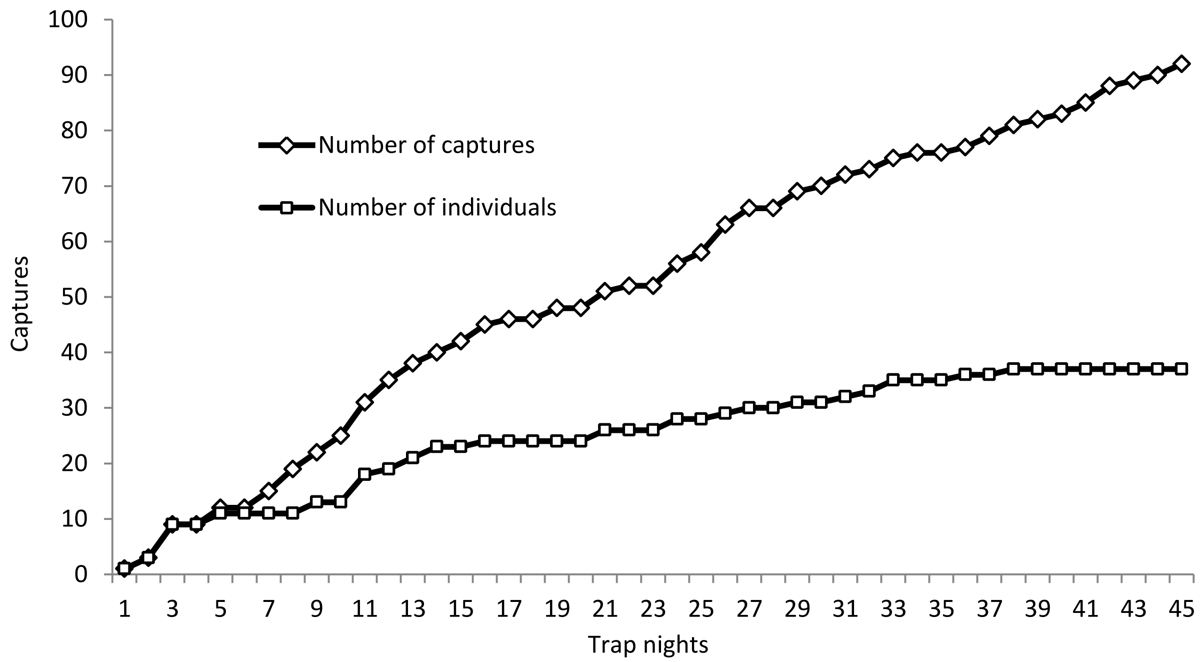

Figure 5: Cumulative numbers of independent captures and unique individuals in the survey dataset with increasing trap nights across 41 camera trap stations.

Calibration of Wild-ID matching score

The 30-photograph subset was analysed by 17 participants. Their estimates ranged from 10-24 individual hyaenas, with a mean of 19.24 (sd=3.5) (Figure 6).

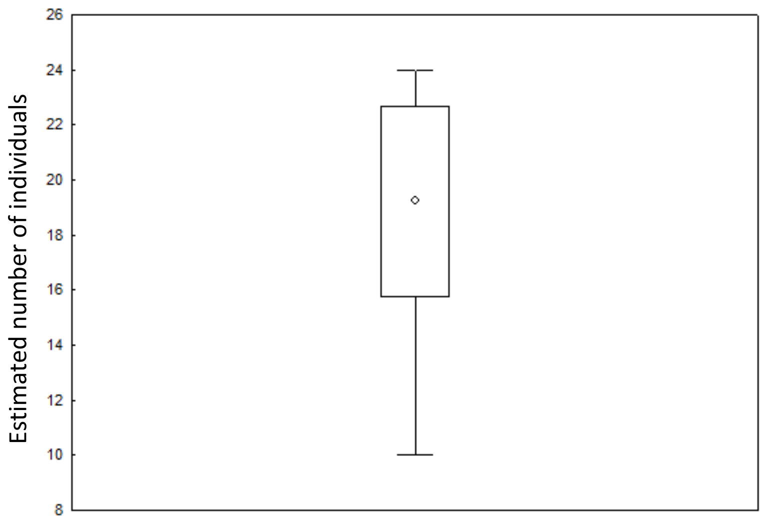

Figure 6: Box-and-whisker plot of independent estimates (n = 17) of spotted hyaena totals from a 30-photograph set. Circle = mean, box = standard deviation, whiskers = minimum-maximum.

The Wild-ID estimates for the number of individuals in the 30-photograph subset differed greatly with small changes in the match score acceptance threshold applied (Table 1). The match score threshold had to be greatly reduced (<0.001) to produce outputs similar to the mean of the independent estimates.

Table 1: Wild-ID outputs (estimate of total individuals) from 30 photographs at different acceptance threshold match scores.

Match Score	Output
0.08	28
0.06	25
0.04	23
0.02	23
0.002	23
0.001	20

Model results

The model in SPACECAP reported a Bayesian p-value of 0.62, which confirms model adequacy (Gopalaswamy *et al.* 2012). The summary statistic z scores (Table 2) indicate successful convergence of the Monte Carlo Markov Chains (MCMCs). The estimate of density for spotted hyaenas in uMkhuze is 10.59 (sd=2.10) hyaenas/100 km^2.

Table 2: Summary statistics of the model run in SPACECAP.

Parameter	Posterior Mean	Posterior SD	95% Lower Interval	95% Upper Interval	z score
σ	3410.701304	426.6406	2620.334	4212.331	-0.3543
Lam0	0.009265642	0.001984	0.005773	0.013182	1.0709
Psi	0.160815819	0.033659	0.097877	0.229505	0.3819
N	166.1068163	32.93037	103	231	0.3389
Density	0.105905211	0.020996	0.066945	0.148554	-

Lam0 is the intercept of expected encounter frequency, σ is the ''range parameter'' of the species, Psi is the ratio of the number of animals present within the space S to the maximum allowable number, N is the number of activity centres located in S, Density is N divided by S. D is reported as N/km^2.

Density across the park varied widely (Figure 7). The north and north-east of the park were particularly devoid of hyaenas, while the southern and western areas supported much higher densities.

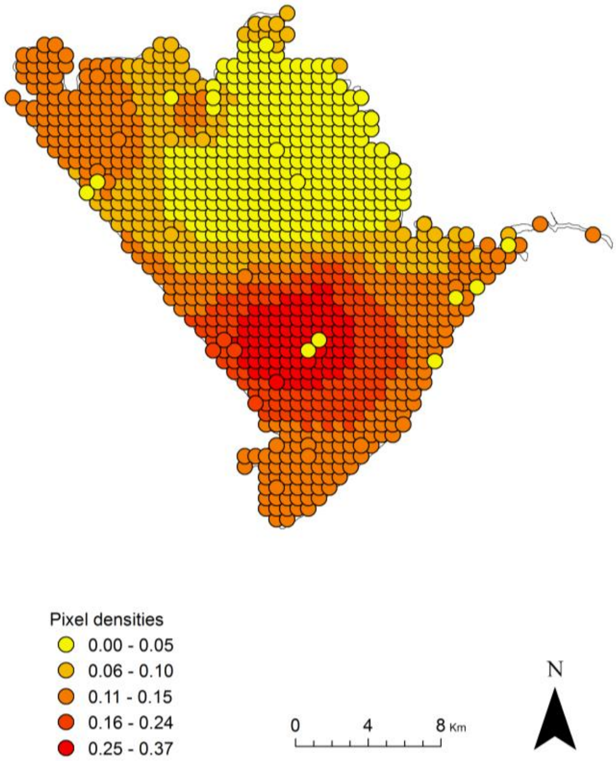

Figure 7: Pixel-specific density distribution of spotted hyaenas across uMkhuze Game Reserve, KwaZulu-Natal, based on spatially-explicit capture rates. Pixel-specific densities generated by SPACECAP are designated by colour gradient (1 pixel = 0,336 km^2).

Discussion

Camera traps as an effective tool for studying spotted hyaenas

As with Henschel *et al*. (2014), I found that it is possible to individually identify spotted hyaenas using photographs collected through camera trapping. This opens up a range of research possibilities for the species, the foremost being the derivation of population density estimates using a method which is non-invasive, easily repeatable and based on sound science. The data for this study were sourced from a camera trap survey originally intended to estimate the density of leopards in uMkhuze. However, as leopard and hyaenas have similar ranging patterns (East & Hofer. 2013, Hunter et al. 2013) I was able to use the 'by-catch' images from this survey to generate a reliable estimate of population density for hyaenas. The fact that the rate of addition of new individuals to the dataset slowed and stopped before the survey ended (Figure 5) is a good indication that hyaena populations can be thoroughly sampled using this study design (Wegge *et al.* 2004). The possibility exists to do similar work for a number of other individually-distinguishable large carnivores, for example, endangered cheetahs and African wild dogs. This highlights the ability of camera traps to simultaneously monitor a range of species, which is particularly important for animals such as hyaenas which are often ignored in research and conservation (Ray *et al.* 2005). Such species can essentially 'piggyback' on better-funded research programs targeting more charismatic species. In KwaZulu-Natal, camera trap surveys are undertaken annually at several sites to monitor leopard population trends across the province. Data from these surveys could easily be used for a province-wide examination of hyaena numbers without any additional costs. This is particularly true of the leopard surveys, as they are typically equipped with two cameras per site to capture both flanks of the animal, which facilitates the identification of individual hyaenas. While individual identification with both flanks improves the data quality immensely, surveys with unpaired cameras such as that by Henschel *et al.* (2014) have shown that useful records and analyses can still be performed with a single camera per trap site. The possibility therefore exists for very many other camera trap studies conducted throughout hyaena range to yield important population estimates for this species and others, all at minimal cost.

Whilst the application of camera traps in this study proved successful, there were some factors that should be noted and considered in future studies. In some instances the animals were captured a significant distance from the trap, which reduced the image quality to unusable levels when cropped. This was particularly problematic in my study as all captures were made at night. To counter this problem, trap sites could be selected where the width of the path does not exceed the effective flash distance of the camera. There were also instances where only one flank of the animal was captured, which reduced the number of usable captures for the model. It is possible that the two cameras at these sites were too staggered and the flash of the first camera may have scared away the animal before it could trigger the second camera. This was evidenced in some captures where the image of one flank was of a seemingly calm hyaena and the other of it running. In some cases the hyaenas walked past both cameras and only one was triggered, which could be a fault in the setup of the camera sensitivity, or again a result of the animal escaping in fright. It is possible that trap avoidance may be reducing recaptures as the hyaenas learn the locations of the trap sites. This was hypothesized by Wegge *et al.* (2004) to be the reason for progressively fewer captures of tigers as camera trap surveys progressed. However, the rate of captures in this survey did not decrease (Figure 5), even after a period of over a month in which hyaenas may have learnt the camera locations. This does not support the presence of trap shyness in the uMkhuze hyaenas. However, there are other valid investigations to be made before declaring this as fact. Specific avoidance of one trap does not preclude hyaenas from being captured at other sites. Therefore, one could assess shyness by looking at the location of recaptures of an individual animal. If it is found that animals are found repeatedly being recaptured at a single trap site then it would seem unlikely that trap avoidance is playing a role. However, if an animal is only recaptured at different sites then it would warrant further investigation into this possible cause of error in the design. CR models in programs such as CAPTURE (Rexstad & Burnham 1991) can incorporate heterogeneity in the models in the form of behavioural response variables (eg. Wegge *et al.* 2004, du Preez *et al.* 2014, also see Otis *et al.* 1978), which may be applicable in future models of spotted hyaenas. One last factor to note regarding the applicability of camera traps for the study of this species is that the cameras failed to capture any cubs, presumably because they do not move far from the den site. However, this is also a problem for call ups which, in addition to missing cubs, have a low rate of capture for juveniles and sub-adults (Mills *et al.* 2001, Graf *et al.* 2009), which was not the case using camera traps.

The fact that hyaenas at the study site were only captured after dark could indicate two possible scenarios. The first is that hyaenas in uMkhuze are entirely nocturnal. The second is that hyaenas are avoiding trails during the day time. A study in the protected Masai Mara Reserve, Kenya (Kolowski *et al.* 2007), showed that 96 % of activity took place during hours of darkness. This is consistent with the data, and the first scenario. However, there is also support in the literature for the second scenario. Kolowski & Holekamp (2008) found that when dense vegetation was available that the hyaenas actively selected for these patches, especially during the day time. However, the traps in this study were situated mostly in dense vegetation, as leopards prefer this habitat (Bailey 1993); hence, if hyaenas were using these areas during daytime they would likely have been captured. The first scenario therefore seems the most likely in the case of uMkhuze.

Mills *et al.* (2001) suggested that camera trap surveys are unsuitable for large protected areas such as the Kruger National Park, South Africa, because of the logistics of establishing and maintaining a camera trap grid that covered the entire park. While it is clearly logistically easier to perform surveys using call-ups or spoor counts over large areas, they are no longer the most robust methods available. It is therefore recommended that the results of such surveys in large areas such as Kruger National Park are validated using smaller camera trap surveys in representative areas. It is also possible to sample representative portions of the park with regard to population drivers (which could be investigated using data from studies such as this in smaller reserves) such as rainfall, dominant vegetation or geology, and then extrapolating this over the larger area with regard to the variables chosen. Study sites could be selected far enough apart to avoid cross-sampling of populations, and spaced out across the park to ensure good coverage. While camera trap grids can be laborious to maintain, there is little reason why this study approach should not be applicable to spotted hyaenas.

Application of the SECR method

The main objective of this study was to determine whether data from camera trap surveys could be used in a SECR framework to estimate spotted hyaena population densities. Initial indications suggest this proved a success, and bodes well for the collection of accurate data on this species as well as others which are individually identifiable. The strength of the model was confirmed in two ways. First, the Bayesian p-value reported by SPACECAP (which has a possible range of 0-1, with values close to either extreme being indicative of poor model fit (Gopalaswamy *et al.* 2012)) was 0.62, indicating adequate model fit. It is also similar to other p-values reported by studies using SPACECAP (e.g. Chase-Grey *et al.* 2013). Second, the z-score statistics for the model parameters (see Table 2) are required to be <1.6 to be confident of Monte Carlo Markov Chain (MCMC) convergence (Gopalaswamy *et al.* 2012). They are all well under this threshold, again showing that the model ran successfully. These statistics support the applicability of SECR methods to populations of spotted hyaenas.

Though still within the acceptable range, the lam0 parameter (capture probability value; Table 2) is low compared to SECR models for other large mammals such as leopards (eg. Athreya *et al.* 2013, Chase-Grey *et al.* 2013). This is most likely a reflection of low recapture rates for many of the individuals in the study (mean=2.49 (sd=2.26)). There are a number of ways in which the study design could be changed or manipulated in order to combat this dearth of recaptures in order to produce higher lam0 values. Future surveys that target hyaenas may be improved by having a greater density of cameras within the same sample area, if camera units are available. Another option is to identify more optimal sites to set up traps in order to maximize the probability of hyaena captures, as well as ensure that cameras are set with a high sensitivity and appropriately placed so as not to either counter flash each other nor to be so staggered as to miss the opposite flank on the second camera. du Preez *et al.* (2014) showed that baited trap sites with single cameras were more effective than unbaited, paired traps in producing photographs for identification in leopards. Baited trap surveys produced 1.4-1.5 times more individuals than unbaited ones, and also increased the frequency of captures by 4.8-6.2 times. This had understandable consequences for the SECR models they ran. They argue that despite the increase in captures the home range estimates of area and shape for each leopard were relatively unchanged between survey types, which is an essential input for the model. Incorporating a greater number of individuals in the baited model increased the population estimates, and show that unbaited surveys are perhaps underestimating true leopard populations (but see Balme *et al.* 2014). It is probable that similar situations exist for spotted hyaenas. The species is possibly even better suited to baiting than leopards as they are effective scavengers and have highly adapted olfactory senses to locate carrion (Mills 1984). In addition, though baits were sponsored for their study, du Preez *et al.* performed the baited survey for substantially less money than the unbaited survey, mostly because of the reduced number of cameras needed. While the communal feeding of hyaenas may confuse the individual identification process by crowding images and creating visual blocks, the method warrants some investigation. The penultimate way to increase recaptures could be to extend the survey period. This does risk violating the requirement of population closure (Kendall 1999), however it is possible to test for closure of the population, and surveys running for more than 45 days could test at different lengths of time to establish the maximum time of a survey that does not do so. Lastly, Gopalaswamy *et al.* (2012) intimated that later versions of SPACECAP will incorporate analyses of open populations, which may be suitable for this species.

Mills *et al*. (2001) expressed further doubt over the suitability of camera traps as tools to survey hyaena populations due to the fact that spotted hyaena do not regularly travel on the same paths, adopting a more random movement pattern within their territory than other large mammals. This may be limiting the number of recaptures at a particular camera site for an individual hyaena, as opposed to animals such as leopards that routinely patrol the perimeters of their territory using the same paths and therefore could be captured multiple times at the same stations. However when cameras are set up in a large grid array the possibility of a hyaena being caught elsewhere should increase (comparative to leopards) as the animal travels within its territory and encounters other trap stations in the vicinity. The regularity of leopard movement would conversely limit the number of trap stations they are exposed to. The precision of an SECR model is contingent on the availability of movement data supplied by recaptures, in which case the irregular movement of hyaenas and subsequent recaptures at different trap sites may in fact be increasing the applicability of this method for the species, not decreasing it as Mills *et al.* suggest.

One species-specific limitation in terms of SECR model applicability is the lack of sex-specific movement data. Spotted hyaenas are unfortunately monomorphic, and therefore impossible to sex confidently using an image alone. Models for sexually dimorphic species are at an advantage in that the models can incorporate sex-specific differences in movement and capture probability (Sollmann *et al.* 2011). There is some evidence of sexually dimorphic movement patterns in spotted hyaenas. Boydston *et al.* (2005) found that dispersing males in particular may adopt more of a wandering habit than those with greater site-fidelity, and that males in general move further afield than females. This may be influencing the rate of recaptures for individuals, but without the ability to confidently sex individuals from an image alone this is an unavoidable source of error.

The SECR-generated estimate in context

The SECR model generated a density estimate of 10.59 (sd=2.10) hyaenas/100 km^2 for the study area. Importantly, this is the first published population estimate for this reserve in over 20 years. The previous estimate by Skinner *et al.* (1992) used a call-up method described by Whateley (1981) and was based on data collected in 1989. Their estimate of 13 hyaenas/100 km^2 is within the upper 95 % confidence level for my estimate. SECR models are accurate, precise and robust estimators of large mammal population densities (Noss *et al.* 2012, Blanc *et al.* 2013); hence it is interesting to see how the SECR-generated estimate for spotted hyaenas at uMkhuze compares to the wider literature for the species. There are a number of other protected areas in southern Africa that report estimates using other methods that are similar in magnitude to that of this study (Table 3). These include Moremi Game Reserve in Botswana (Cozzi *et al.* 2013), Kruger National Park in South Africa (Mills 1985, Henschel & Skinner 1987, Mills *et al.* 2001) as well as Zambezi National Park and Lemco Ranch in Zimbabwe (Bowler 1991). Interestingly, these studies all used the method of call-ups. Notably, the two reserves closest to the study site, Hluhluwe Game Reserve and Imfolozi Game Reserve, were also surveyed using call-ups, yet produced estimates of 4 and 5 hyaenas/100 km^2 respectively (Whateley & Brooks 1978, Whateley 1981). These estimates are much higher than both the old and new estimates for uMkhuze despite the similar vegetation, prey and competitors present across all three. However, one must be cautious of using the similarities and disparities in estimates as reason to validate or criticize methods. The long spans of time between estimates bring with them natural fluctuations in population, changes in reserve management and other variables that will all have their own effects on the populations present. Furthermore, comparing across reserves is not often a valid comparison due to differences in vegetation, animal communities and the management strategies. Lastly, without a single study on a known reference spotted hyaena population comparing methods and their estimates one cannot compare the efficacy of one method compared to another with any fairness. This should be a research priority for this species, with the well-documented populations in East Africa providing a good opportunity for this work.

Table 3: Density estimates for spotted hyaena populations in southern African protected areas.

Country	Locality	Year	Population	Area (km^2)	Density ($/km^2$)	Method	Source
Botswana	Savuti, Chobe NP	1986-88	43	>100	<0.4	Clan/territory	Cooper (1989)
Botswana	Moremi GR	2013	244	1800	0.144	Call ups	Cozzi *et al.* (2013)
South Africa	uMkhuze GR	1989	38	~250	0.13	Call-ups	Skinner *et al.* (1992)
South Africa	Kalahari Gemsbok NP	1972-1980	80	10 000	0.008	Call-ups	Mills (1990)
South Africa	Timbavati NR	1975	11	>25	<0.4	Clan/territory	Bearder (1977)
South Africa	Hluhluwe GR	1975-77	9	13	0.5	Call-ups	Whateley & Brooks (1978)
South Africa	Umfolozi GR	1979-81	14	39	0.4	Call-ups	Whateley (1981)
South Africa	Mavumbye, Kruger NP	1982-84	11	130	0.08	Clan/territory	Henschel & Skinner (1987)
South Africa	Kruger NP	1984	1269-3886	19220	0.07-0.2	Call-ups	Mills (1985)
South Africa	Kruger NP	2001			0.03-0.2	Call-ups	Mills *et al.* (2001)
Zimbabwe	Hwange NP	1991	-	-	>0.17-0.18	Call-ups	Bowler (1991)
Zimbabwe	Zambezi NP	1991	-	-	>0.13	Call-ups	Bowler (1991)
Zimbabwe	Matetsi Safari Area	1991	-	-	>0.03-0.25	Call-ups	Bowler (1991)
Zimbabwe	Matetsi CA Area	1991	-	-	>0.04	Call-ups	Bowler (1991)
Zimbabwe	Gwaai Valley ICA	1991	-	-	>0.04	Call-ups	Bowler (1991)
Zimbabwe	Lemco Ranch	1991	-	-	>0.1	Call-ups	Bowler (1991)
Zimbabwe	Gonarezhou NP south	1991	-	-	>0.22	Call-ups	Bowler (1991)
Zimbabwe	Gonarezhou NP north	1991	-	-	>0.05	Call-ups	Bowler (1991)

Wild-ID as a tool for individual identification

The calibration of the threshold acceptance match score for spotted hyaenas failed due to a lack of agreement over the number of individual hyaenas represented in the 30 photographs. The independent estimates by individuals ranged so extensively that the assumption of the mean as the 'true' number of individuals is rendered senseless. This lack of accord is most likely due to the fact that those involved in the sample were inexperienced, possibly with a poor understanding of what constituted a matched pair. It would not be scientific to draw any conclusions from these data with regard to the true number of individual hyaenas contained in the data provided.

However, these results do speak to the apparent human error inherent in the identification process. The issue of certainty of population estimates derived by researchers based only on the own estimation of the number of individuals captured must be called into question. Certainly there is value in the idea that an 'expert' will deliver the best possible individual estimate, however it is not apparent in the papers published using this method how much experience the people performing these analyses have had. Perhaps the justification of why the estimates of total individuals in the camera trap data should be trusted should be mandated and made explicit in future studies on individually identifiable animals. One possibility is to show statistical repeatability of matches among several observers before such an estimate is accepted (see Lessells & Boag 1987). After rechecking my matches from the 30-photograph sample I am still convinced that there are 22 individuals, however without someone available with equal or greater experience in identifying hyaenas by their spot patterns with whom to cross-check, the certainty with which that can be declared the true value must also still be questionable.

Unfortunately, it is not possible for the pattern recognition software package Wild-ID to replace the human element in the matching process. In addition to there not being a safe estimate of the true number of individual hyaenas in the subsample, the outputs of Wild-ID at different match score thresholds were not useful as they were highly disparate with small changes to the match score. If one were hypothetically to ignore the sizeable variation around the mean of the independent estimates and still accept this as the 'true' number of individuals then one would need to accept matches at a score <0.001 to reach this number (Table 1). At this point a majority of the images being accepted as matches were, in my 'expert' opinion, beyond doubt different individuals.

It is probable that the variation in both the independent estimates and the Wild-ID outputs are as a result of small sample sizes (n=17 and 30 respectively). With regard to the independent estimates, if one were to decide only to use experienced individuals to conduct the independent estimates then one must be content with a reduced sample size. It is more practical to increase the number of pictures used in the experiment, but this does increase the time taken to complete these estimates exponentially, and participants would most likely require some compensation for the arduous undertaking to make it worthwhile. Ideally one would test the relationship between experience and accuracy by seeing how many 'runs' through such a sample dataset it takes for a group to reach consensus. The time taken could then be used as a standard threshold at which the label of 'expert' is attributed, standardizing the quality of estimates and increasing confidence in these studies.

It is not recommended on the basis of these results that the match score function of Wild-ID is used to automatedly accept matches. This is disappointing as it would reduce survey analysis time substantially and potentially remove biases associated with human error. The applicability of pattern recognition also has other more far-reaching applications (eg. Hiby *et al.* 2009) which are now hampered for this species However, the interface of Wild-ID is user-friendly and can still be used to conduct manual matches by eye, but should be complemented by further comparisons using other platforms to minimize missed matches as per my methods.

Recommendations for future study

While my findings are useful, the potential application of the data I both used and produced extends much further. While these exceed the scope of an Honours project, I propose that three further investigative-type studies be undertaken. These studies require very little extra data, making them easy to initiate. Such investigations will give further insight into the population biology of spotted hyaenas in this reserve, and could provide novel information for surveying and management of populations across their range.

The influence of 'edge effects' on density distribution

It is possible to identify trends in density across the area using the map generated by SPACECAP (Figure 7). It is recommended that further study is conducted into the lower densities in the northern and eastern regions of the reserve as well as the reasons for the concentration of hyaena populations in the interior of the reserve. Woodroffe & Ginsberg (1998) outline the detrimental consequences (termed 'edge effects') for large carnivores that events occurring outside of small protected areas can have for populations within them. They found that species which ranged widely and thus often had territories extending outside protected area boundaries were most likely to go extinct regardless of population size. This was primarily as a result of conflict with local populations. These edge effects could explain the trends in density observed in the density map generated for uMkhuze. Balme *et al*. (2010) demonstrate this exact process occurring with leopards in the Phinda-uMkhuze reserve complex. The expectation, therefore, is that similar processes are affecting the spotted hyaena populations. As evidence for the supposed edge effects manifesting in this population, a number of hyaenas in the study bore old snare-inflicted neck scars (see Figure 3) and others were photographed with snares still attached. It is expected that densities should be lower nearer to park edges, as the surrounding communities persecute hyaenas when they range beyond the reserve as well as snare hyaenas inside the park, either accidentally while trapping for illicit bushmeat or intentionally for the illegal traditional medicine trade (McKean & Mander 2007). It is predicted that hyaenas will be photographed more frequently with snares and snare wounds along the edges of the park, and that the index of snared animals should be inversely related to the density of animals in that area.

Discernment of population drivers

While snaring and edge effects may be exerting influence on the uMkhuze hyaena population, there are other ecological variables that are no doubt influencing hyaena populations as well. Abade *et al.* (2014) found that spotted hyaena presence was best explained by precipitation and proximity to rivers, while Kolowski and Holekamp (2009) found that hyaenas were selecting for vegetated patches and shrublands. However, the density and distributions of hyaenas, like wild dogs (Mills & Gorman 1997), are likely controlled at least in part by other ecological factors such as prey availability, presence of competitors such as lion and leopard, and human activity. The data for many of these factors are available (see Woodgate 2014), and can be analysed in context with the density map produced through SPACECAP (Figure 7). While these studies used other carnivore presence and abundance data collection techniques such as GPS-fixed observations and telemetry data, the camera trap data used for this study is also applicable. This ecological information is paramount for the formulation of good management policy and effective conservation.

Optimization analyses

Multiple studies have looked at the effect of different spatial arrays on the robustness of SECR estimates (Dillon & Kelly 2007, Maffei & Noss 2008, Sollmann *et al.* 2012). The findings from these studies contributed to the optimization of the use of limited cameras within a trapping grid for each of their study species. The camera trap survey used in this study was relatively lengthy and sampled the majority of the reserve. It is thus possible using the data to begin hyaena-specific optimization of study protocols to save time and money for future surveys. The total number of cameras in our dataset can be reduced and the spatial array manipulated to find a minimum density of cameras needed across an area to produce robust estimates. In addition to this, the optimization of survey length can also be investigated by manipulating the data to simulate the survey being run for different length periods and then comparing model outputs. Thereafter a recommendation of study length can be made as to the minimum length required for an accurate survey of this nature for this species. A random exclusion of one camera at each trap site can also test the validity of unpaired camera traps as a setup in this method. These tests could culminate in a recommendation on how to perform the cheapest and least resource-intensive population survey for this species without compromising on accuracy, which can then be implemented in other areas within Africa.

Conclusion

This study has shown that spotted hyaenas are readily identified in camera trap images to individual-level through spot patterns, which enables analysis of existing populations through capture-recapture methods using camera trap data. An SECR model on an existing population was successfully run, proving the efficacy of the method for the species. In addition to probable (but currently untested) improvements in the accuracy and precision of estimates, SECR methods are likely to be less expensive, labour intensive and time-consuming than other techniques. Management of the species across its range is stymied by a lack of up-to-date population-level data as well as contrasting methods used to generate existing estimates that are not easily comparable. It is therefore recommended that future studies adopt spatially-explicit capture-recaptures as the method of choice for spotted hyaena population analysis in the interest of standardization, as it can be performed in conjunction with projects on other sympatric, individually identifiable species with existing camera trap studies (such as leopards). Small changes to the study design are suggested in order to increase the number of recaptures, which should consequently improve the precision of the model, though the model was successful and any changes made are improvements rather than fixes. Disappointingly, Wild-ID was not successful as an automated pattern matching application, but this may be as a result of sample size and expertise of those estimating the true number of individuals in the calibration sample. The results of the SPACECAP model could easily be used as the foundation on which further research into population drivers and spotted hyaena ecology could be based. The use of spatially-explicit capture-recaptures could therefore open up a plethora of possibilities for study into this oft-neglected, understudied and ecologically important species.

Acknowledgements

I would like to acknowledge both my supervisors, Prof Justin O'Riain and Dr Guy Balme. Justin gave valuable feedback on draft versions of this thesis, and was a useful sounding board during project development. Guy's expertise and experience with these types of analyses in particular was integral to its success. I would like to thank him for his expert guidance throughout the project, and especially for putting up with me in those moments when I was a bit slow on the uptake or was struggling with some very basic functions on new programs. The project could also not have taken place without the work of Panthera and WildlifeACT who supplied the cameras, set up the trap array, performed the camera maintenance and agreed to share the data. I would like to thank Zoë Woodgate for helping to catalogue the data, separating out rare hyaena captures from seemingly endless impala and crested guineafowl, as well as delivering useful comment on my drafts, and generally being a great lab mate and even better friend. The whole of the Honours group were willing to help me maintain a semblance of sanity by chatting over endless cups of tea. The second year Zoology students who helped with the independent estimates were very enthusiastic, as well as being timeous with their returns. Jenny Leonard, Angela Ferguson and Nick de Blocq van Scheltinga delivered useful comments on draft versions of this thesis. My Biological Sciences Honours course was funded by a National Research Fund (NRF) Innovation Scholarship, for which I am very grateful.

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Appendix

Table 1: Estimates of spotted hyaena densities from published literature (adapted from Hofer & Mills 1998 and Graf *et al*. 2009)

Country	Locality	Year	Population	Area (km^2)	Density (km^{-2})	Method	Source
Botswana	Savuti, Chobe NP	1986-88	43	>100	<0.4	Clan/territory	Cooper (1989)
Botswana	Moremi GR	2013	244	1800	0.144	Call-ups	
Burkina Faso	Nazinga Game Ranch	1991	20-100	940	0.02-0.1		G.W. Frame (pers. comm. as in Hofer & Mills 1998)
Central African Republic	Northern part	1980-88	100-1000	35 000	0.003-0.03		A.A. Green (pers. comm. as in Hofer & Mills 1998)
Guinea-Bissau	Comoe NP	1978	100	11 500	0.009		Kronberg-Bericht (1979)
Guinea-Bissau	Dulombi Reserve	1990	-	213.3 km of transects	0.8 faeces/10km	Faeces counts	Paris (1991)
Kenya	Nairobi NP	1968-72	<10	114	<0.09		Rudnai (1979)
Kenya	Kitengela CU	1974-75	>40	568	>0.07		Rudnai (1979)
Kenya	Nairobi NP	1976	>30	114	>0.26		Rudnai (1979)
Kenya	Masai Mara GR	1992	45	70	0.6	Clan/territory	Holemkamp *et al*. (1992)
Kenya	Aberdare NP	1992	-	-	1.3	Call-ups	Sillero-Zubiri & Gotelli (1992)
Kenya	Masai Mara	2005	-	-	0.4	Call-ups	Ogutu *et al*. (2005)
Malawi	Liwonde NP	?	50	540	0.09		R. Bhima (pers. comm. as in Hofer & Mills 1998)
Namibia	Half of Namibia	1972/82/92	2000-3000	400 000	0.005-0.0075		E. Joubert (pers. comm. as in Hofer & Mills 1998)
Namibia	Etosha Pan	1979-86	68	1430	0.05		Gasaway *et al*. (1991)
Namibia	Namib along Kuiseb	1977-79	18	3080	0.006		Tilson *et al*. (1980)
Republic of Congo	Odzala-Kokoua NP	2007			0.1539	Camera trap C-R	Henschel *et al.* (2014)
South Africa	uMkhuze GR	1989	38	~250	0.13	Call-ups	Skinner *et al*. (1992)
South Africa	Kalahari Gemsbok NP	1972-1980	80	10 000	0.008		Mills (1990)
South Africa	Timbavati NR	1975	11	>25	<0.4	Clan/territory	Bearder (1977)
South Africa	Hluhluwe GR	1975-77	9	13	0.5	Call-ups	Whateley & Brooks (1978)
South Africa	Umfolozi GR	1979-81	14	39	0.4	Call-ups	Whateley (1981)
South Africa	Mavumbye, Kruger NP	1982-84	11	130	0.08	Clan/territory	Henschel & Skinner (1987)
South Africa	Kruger NP	1984	1269-3886	19220	0.07-0.2	Call-ups	Mills (1985)
South Africa	Kruger NP	2001			0.03-0.2	Call-ups	Mills *et al.* (2001)
Tanzania	Central Serengeti	1987-92	45	56	0.8	Clan/territory	Hofer & East (1993)
Tanzania	Ngorongoro Crater	1966-68	378	220	1.7	Call-ups	Kruuk (1972)
Tanzania	Serengeti "source"	1986	5214	8100	0.6		Hofer & East (1995)
Tanzania	Ngorongoro Crater	2005	-	-	0.89	Count/study area	Höner *et al*. (2005)
Tanzania	Selous GR	1994	-	2600	0.32		Creel & Creel (1996)
Zimbabwe	Hwange NP	1991	-	-	>0.17-0.18	Call-ups	Bowler (1991)
Zimbabwe	Zambezi NP	1991	-	-	>0.13	Call-ups	Bowler (1991)
Zimbabwe	Matetsi Safari Area	1991	-	-	>0.03-0.25	Call-ups	Bowler (1991)
Zimbabwe	Matetsi CA Area	1991	-	-	>0.04	Call-ups	Bowler (1991)
Zimbabwe	Gwaai Valley ICA	1991	-	-	>0.04	Call-ups	Bowler (1991)
Zimbabwe	Lemco Ranch	1991	-	-	>0.1	Call-ups	Bowler (1991)
Zimbabwe	Gonarezhou NP south	1991	-	-	>0.22	Call-ups	Bowler (1991)
Zimbabwe	Gonarezhou NP north	1991	-	-	>0.05	Call-ups	Bowler (1991)