The distribution and numbers of cheetah *(Acinonyx jubatus)* in southern Africa (#19233)

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The distribution and numbers of cheetah *(Acinonyx jubatus)* in southern Africa

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Assessing the numbers and distribution of threatened species is a central challenge in conservation, made difficult because the species of concern are rare. For some predators, this may be compounded by the fact that they are sparsely distributed over large areas. Such is the case with the cheetah *Acinonyx jubatus.* The IUCN Red List process solicits comments, is democratic, transparent, widely used, and has recently assessed the species. Here, we present additional methods to that process and provide quantitative approaches that may afford greater detail and a better benchmark against which to compare future assessments. The cheetah poses challenges, but also affords unique opportunities. It is photogenic, allowing the compilation of thousands of crowd-sourced data. It is also persecuted for killing livestock, enabling estimation of local population densities from the numbers persecuted. Moreover, persecution means that data on livestock densities can provide a direct prediction on where the species may or may not occur. Compilations of extensive telemetry data coupled with >20,000 observations from 39 sources show that free ranging cheetah were present across approximately 789,700 km^2 of Namibia, Botswana, South Africa, and Zimbabwe (56%, 22%, 12% and 10% respectively) from 2010 to 2016, with an estimated adult population of 3,500 animals. We identified a further 742,800 km^2 of potential cheetah habitat within the study region with low human and livestock densities, where another ~3,200 cheetah may occur. Our population estimate is 19% lower than the IUCN's current assessment, supporting the recent call for the uplisting of this species from vulnerable to endangered status. Unlike many previous estimates, we make the data available and provide explicit information on exactly where cheetahs occur, or are unlikely to occur, and do so within a limited time span. We stress the value of gathering data from public sources although these data were largely restricted to well-visited protected areas. There is a contiguous, transboundary population of cheetah in southern Africa, known to be the largest in the world. We suggest that this population is more threatened than believed due to the concentration of about 55% of free ranging individuals in two ecoregions. Indeed, this area overlaps with private ranch lands with high persecution risk.

The distribution and numbers of cheetah *(Acinonyx jubatus)* in southern Africa

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Abstract

Assessing the numbers and distribution of threatened species is a central challenge in conservation, made difficult because the species of concern are rare. For some predators, this may be compounded by the fact that they are sparsely distributed over large areas. Such is the case with the cheetah *Acinonyx jubatus.* The IUCN Red List process solicits comments, is democratic, transparent, widely used, and has recently assessed the species. Here, we present additional methods to that process and provide quantitative approaches that may afford greater detail and a better benchmark against which to compare future assessments. The cheetah poses challenges, but also affords unique opportunities. It is photogenic, allowing the compilation of thousands of crowd-sourced data. It is also persecuted for killing livestock, enabling estimation of local population densities from the numbers persecuted. Moreover, persecution means that data on livestock densities can provide a direct prediction on where the species may or may not occur.

Compilations of extensive telemetry data coupled with >20,000 observations from 39 sources show that free ranging cheetah were present across approximately 789,700 km^2 of Namibia, Botswana, South Africa, and Zimbabwe (56%, 22%, 12% and 10% respectively) from 2010 to 2016, with an estimated adult population of 3,500 animals. We identified a further 742,800 km^2 of potential cheetah habitat within the study region with low human and livestock densities, where another ~3,200 cheetah may occur.

Our population estimate is 19% lower than the IUCN's current assessment, supporting the recent call for the uplisting of this species from vulnerable to endangered status. Unlike many previous estimates, we make the data available and provide explicit information on exactly where cheetahs occur, or are unlikely to occur, and do so within a limited time span. We stress the value of gathering data from public sources although these data were largely restricted to well-visited protected areas. There is a contiguous, transboundary population of cheetah in southern Africa, known to be the largest in the world. We suggest that this population is more threatened than believed due to the concentration of about 55% of free ranging individuals in two ecoregions. Indeed, this area overlaps with private ranch lands with high persecution risk.

Introduction

Assessing how many individuals of a species remain, mapping where they are, estimating declines in numbers, and also, understanding their causes, are core activities for conservation science. Although entirely familiar, these activities can pose challenges, especially for large predators that are sparsely distributed across large areas. We address these challenges for the cheetah *Acinonyx jubatus* in southern Africa, noticing that the IUCN Red List (henceforth Durant et al. 2015) has addressed these same questions for the global cheetah population in its listing and an accompanying paper (Durant et al. 2016). The Red List process solicits comments, is democratic, transparent, and widely used. Here, we present additional methods to that process to provide quantitative approaches that may afford greater detail and a better benchmark against which to compare future studies. We chose the cheetah as a case study because it affords unique opportunities and Durant et al. (2016) recommend an up-listing of the cheetah to “endangered” status. We aim to provide an independent process to evaluate their results that uses other approaches, some new data, and alternative assessments of the data analysed.

Durant et al. (2016) estimate approximately 7,100 adult cheetahs across Africa and Asia, with five separate subspecies (Krausman & Morales 2005). Of these, approximately 4,300 cheetahs (61%) live in southern Africa and 2,300 cheetahs (32%) in eastern Africa. Historically, cheetahs roamed large parts of sub-Saharan Africa, but have been widely extirpated, now residing in only 22% of their historical range (Durant et al. 2016). Durant et al. (2016) recommend the IUCN status be changed from “vulnerable” to “endangered.” This acknowledges an on-going declining population and >75% of the species’ range exists outside protected areas where they are exposed to greater threat due to high levels of human persecution.

Several aspects of the cheetah’s biology make appraisals challenging. Cheetahs are cryptic, occur over a variety of habitats (Sunquist & Sunquist 2002) and at variable, though usually low, densities (Boast & Houser 2012; Dalerum et al. 2008; Funston et al. 2010). All important population parameters, such as survival rates and inter-birth intervals vary with several factors, including competing predators (Marnewick et al. 2009; Wachter et al. 2011) and degree of human persecution (Marker et al. 2003). Such factors differ across study areas, thus hampering extrapolation (Mills & Mills 2014). Many studies have been limited to small areas and few animals (e.g. Boast et al. 2011). [Van der Meer, (2016) is an exception.] The necessary population data to assess status, threats, and population trends adequately across landscapes are consequently hard to obtain. Thus, independent approaches could lead to different conclusions on how many cheetahs remain. In this situation, it may be particularly valuable to gather verifiable information from as wide a variety of sources as possible and to be explicit about how these data are converted into range maps and population estimates.

Fortunately, all big cats are photogenic; the cheetah particularly so. This affords an opportunity to incorporate crowd-sourced data across large areas to document the range and numbers of cheetahs. Citizen science is emerging as an important tool in cheetah monitoring (Marnewick et al. 2014, Van der Meer 2016), complementing traditional research methods such as interview surveys (Stein et al. 2012) and tracks-and-signs based methodologies (Keeping 2014). We add such data to those from GPS-tracking and remote wildlife cameras. Simultaneously, some research programmes expand to national and regional scales, providing important landscape level information where most cheetahs reside.

The Range Wide Conservation Program (RWCP) for the cheetah and African wild dog L*ycaon pictus* (IUCN/SSC 2007, 2012, RWCP & IUCN/SSC 2015) has collated much of the existing knowledge on cheetah distribution and numbers. In regional workshops, experts revise the range extent, assess threats, estimate population sizes, and set suitable conservation strategies and priorities. For areas with little or no sampling effort, the assessment relies on expert opinions to inform the potential status of the species. A recent appraisal of the IUCN status assessment protocol suggested that additional mechanisms are required to determine the cheetah's conservation status adequately, particularly outside of protected areas (Durant et al. 2016). This prompts questions such as whether alternative approaches might be necessary for the cheetah and if other methods can assist in poorly sampled regions or those outside PAs. We have four aims:

(1) The first aim was to provide an independent assessment from previous efforts, driven by maximum data gathering, and including a wealth of information previously not considered. We

present a data-based appraisal and analyse the largest set of cheetah information collected to date. We do so over a narrow time interval that reflects the average adult lifespan. We outline the current known range of the species in southern Africa while also providing an evidence-based update of population sizes using an ecoregion based approach to scale up density estimates based on habitat suitability.

(2) We assess the value of additional data gathering methods and the data themselves in delineating cheetah range and population status. We collect verifiable data from a wide array of public, private, and research sources across Botswana, Namibia, South Africa, and Zimbabwe, a contiguous region harbouring most remaining cheetahs (Durant et al. 2016).

(3) We establish a rigorous standard of data provenance. Existing range maps arise from a combination of direct observations and expert opinion, and so incorporate extensive experience. That said, one cannot readily interrogate a location to know whether a species was observed there and, if so, when and by whom, or whether its presence was inferred. The results we present provide such provenance.

(4) Finally, in addition to estimating cheetah range, we estimate population based on persecution levels and study estimates of cheetah density. Combined with demographic and life history information of cheetahs, we produce a Leslie matrix model to predict the densities of cheetah necessary to sustain known off-take levels.

Methods

Data sources for distribution

Botswana, Namibia, South Africa, and Zimbabwe harbour the largest free ranging populations of cheetah in the world — i.e. those whose movements are not effectively obstructed by fencing (Durant et al. 2015). This region also includes a managed cheetah meta-population (i.e. those within fenced areas), particularly in South Africa (Purchase et al. 2007).

We gathered cheetah distribution information from a broad range of sources. We approached over 90 colleagues asking for data on GPS/VHF telemetry locations, direct sightings, camera trap records, intensive spoor surveys with experienced local trackers, and presence-absence questionnaires. We supplemented these data with information from government wildlife departments (their survey data), additional observations from RWCP's Pan-African cheetah sightings database, verifiable records from the public and non-governmental organizations, and an extensive literature survey. We also included cheetah records from commercial and communal conservancies managed for tourism, wildlife or livestock purposes, hunter and farmer associations, as well as amateur, semi-professional and professional wildlife photographers. The public data mining (i.e. crowd-sourced data) for the survey period entailed an intensive search in English, German, and Afrikaans of online image and video repositories, social media sites, as well as different citizen science mapping efforts (Supplemental Information 1). Finally, we consulted the scientific and other literatures on cheetahs in southern Africa and geo-referenced published information for which we had no access to original data. Again, we searched publications in English, German, and Afrikaans. We conducted literature searches in the Web of Science, the IUCN Cat Specialist Group Library and Google Scholar using "cheetah" and "Acinonyx jubatus" as search terms (Supplemental Information 1). We classify "research data" as original and processed records sourced from the environmental research community (either as raw or published data). The public supply "crowd-sourced data" of cheetah observations

Our records span from 01 January 2010 to 30 April 2016, giving a survey period of 2,312 days, or 6.4 years. This time frame broadly reflects the average lifespan of a free ranging adult cheetah in southern Africa (see below). The exact location data, subject to sensitivity caveats, are stored on Dryad.

Distribution Mapping

For distribution mapping, we set out with the single assumption that cheetah historically occurred everywhere in the study area except for Etosha Pan in Namibia (RWCP and IUCN/SSC 2015). We carefully examined all distribution data for reliability (Supplemental Information 2).

Cheetah presence data were collected as point or polygon data. Data were converted to raster with 10 x 10 km spatial resolution. A pixel size of 100 km^2 balances the need to protect the exact GPS coordinates of sensitive data, and its edges are only marginally longer than the average daily distance moved by a female cheetah (Wilson et al. 2013). One of the smallest published cheetah home range estimates was 126 km^2 for a coalition of three males in Kruger National Park (Broomhall et al. 2003). Assuming these cheetahs were observed in the very center of a 100 km^2 presence pixel, their home range would extend into adjacent pixels. Therefore, we classified all pixels adjacent to observed free range cheetah presence as likely presence for a conservative estimate of cheetah distribution.

For a maximum distribution estimate, we determined areas with possible cheetah presence within historical species range. Beginning with areas without recent cheetah observations, we employed a three-step process for determining potential cheetah range. First, we selected a threshold of human and livestock densities above which cheetah were unlikely to reside. Second, we removed ecoregions considered inhospitable to resident cheetah populations. Finally, we used spatial clustering and adjacency to remove small, isolated patches of potential habitat. Zimbabwe was the only exception to this process due to the exhaustive survey by Van der Meer (2016).

In the first step, we reviewed the distribution of presence points in relation to four interrelated factors – human population density, and densities of three major livestock species: cattle (*Bos taurus*), sheep (*Ovis aries*), and goats (*Capra hircus*). High human population density is likely to preclude resident cheetahs (Woodroffe 2000). In both Africa and in South Asia, wild ungulate populations decline in areas with high livestock density due to resource limitation or where landowners are hostile toward wild ungulates (Berger et al. 2013, Georgiadis et al. 2007, Madhusudan 2004, Ogutu et al. 2009). Such decreases could limit potential densities of wild prey for the cheetah (Winterbach et al. 2015). Increased livestock density also increases the risks of human conflict for the cheetah. Farmers often are intolerant of conflict and many will attempt to kill or remove cheetah after only one or two predation incidents (Weise 2016). We identified the distribution of these covariates within free range presence areas and calculated thresholds of human or livestock densities at levels that included more than 85% of free ranging cheetah presence points. Presence points above this threshold may represent outliers (e.g. potentially a non-resident individual). We applied these values to areas without data to identify potential cheetah range. Pixels below threshold values remained potential range, whereas those above the threshold were removed. We then filtered three ecoregions within the historical range as unlikely to contain resident individuals – i.e. Namib Desert, Kaokoveld Desert, and Makgadikgadi Halophytics. Although we did observe cheetah in these ecoregions, they mostly occurred along the periphery of these areas and, historically, have been characterised as thinly scattered or only seasonally resident due to prey scarcity in these ecoregions (Myers 1975, Klein 2006). In the final step, we removed patches of potential habitat with less than 300 km^2 (3 pixels) of core habitat where these patches are adjacent to areas excluded as cheetah habitat. We did so as our population analysis revealed that the weighted mean density of cheetah in this area of potential habitat was 0.47/100 km^2 meaning that 300 km^2 would support approximately one resident individual.

Data sources for other variables

We obtained human population data from the 2015 LandscanTM High Resolution Global Population Data Set (Bright et al. 2015) and livestock data from 2007 Gridded Livestock of the World (GLW) v3.0 (Robinson et al. 2014). Botswana conducted a countrywide aerial survey in 2013 that estimated livestock densities (DWNP 2013). It provides considerably more detail and may be preferable to the GLW source, but it combines sheep and goats, and equivalent data sources were unavailable for other countries in our study area. We used the Terrestrial Ecoregions of the World (Dinerstein et al. 2017) dataset to describe distinct habitats within cheetah range. We obtained protected area data from the World Database on Protected Areas (WDPA) (IUCN and UNEP 2016).

Density estimates

We searched the scientific literature for any data recorded during the survey period that allowed estimates of cheetah densities. We collated published information with on-going surveys and re-analysed the data already published to increase sample sizes and improve accuracy. We excluded repeat studies of the same areas, and considered only the most recent results.

To estimate the total regional population of cheetah, we used existing estimates for Zimbabwe (Van der Meer 2016) and Kruger National Park (NP) (Marnewick et al. 2014). We stratified the remainder of cheetah presence (and its buffer) by ecoregion and multiplied that area by the density estimates for that ecoregion for the interval of this study. Where direct estimates were not available, we applied densities derived from similar ecoregions. Finally, we applied the same approach as above for possible range areas.

We also created a per pixel (100 km^2) density estimate for cheetah presence areas to understand how concentrated the cheetah population is. For most areas, densities were calculated using the ecoregion approach. In Kruger, we determined density using the cheetah count and park area. However, we cannot assume that cheetah density in Zimbabwe was consistent across known presence areas. Therefore, we calculated an ecoregion based estimate for Zimbabwe to estimate the % of cheetah in each ecoregion, then assigned the total cheetah count (from Van der Meer 2016) accordingly.

If A_i is the # of presence pixels in Zimbabwe from ecoregion i, D_i is the estimated density of cheetahs for Ecoregion i, and C_v represents the Van der Meer (2016) Zimbabwe cheetah count, then Z_j is the estimate of cheetah population density in ecoregion j of Zimbabwe:

$$Z_j = \frac{C_v D_j}{\sum_{i=1}^{n} A_i D_i}$$

for n ecoregions containing cheetah presence points in Zimbabwe.

Data sources for off-take estimates

We defined persecution as the effective removal of cheetah from the free ranging population via lethal control or captivity. During the assessment period, we recorded details of cheetah persecution on 185 commercial farmland properties across nine regions in Namibia over an area of 19,184 km^2 (median size = 65.5 km^2), or approximately 5.4% of the commercial farmland of the country (Mendelsohn 2006). Persecution data were recorded during direct, on-site carnivore consultations with land managers as part of a conflict research programme. The land use and management characteristics recorded for this sample were similar to those previously reported for commercial farmland across Namibia (Mendelsohn 2006; Lindsey et al. 2013a, 2013b) (Supplemental Information 3). Persecution data usually included information on age and sex of the cheetah (Supplemental Information 4).

Leslie Matrix model

Leslie Matrix models calculate growth rates for age-structured populations and so require information on several life history parameters (Caswell 2001). With a long history and widely used, these models have varied practical applications that include assessing the management options for highly threatened species (Fujiwara & Caswell, 2001), such as whether contraception would be a practical way to slow elephant growth rates (Whyte et al. 1998). Using life history parameters, we estimated potential population growth rates. We used these models to estimate by how many females the population can be reduced per year while still permitting a constant population size over time. We then compared these results with persecution data.

We employed a simple model that required only the age at first reproduction, inter-birth interval, number of cubs that reached adulthood, and adult survival rates. We searched the literature for all relevant life history data. Due to variations in methodology, terminology, and ecological conditions, we created a regional average of the data. We ran the Leslie Matrix model using various parameter combinations of the life history parameters to test sensitivity, i.e. a range of possible annual growth rates. These models consider only female population growth rates. The model assumed there will always be sufficient males to breed with all females, thus we did not separately model males. The model is implemented in a Microsoft Excel spreadsheet (Supplemental Information 5).

Results

Cheetah presence observations

We received cheetah monitoring data from 39 sources. They included 66 distinct data sets and studies that ranged from local to national scale. Data included records from >30 independent camera trap surveys (often across multiple years), 10 spoor survey programmes (including multiple sites and years), nine farmland studies across the four countries, summarised positional data from >2.7 million GPS- and VHF-telemetry locations representing 208 free ranging collared cheetahs, and communal conservancy monitoring data. In addition, we geo-referenced published cheetah information of four predator research programmes for which we had no access to the original data. We supplemented research data with verifiable crowd-sourced data (e.g. blogs, news media, social media, citizen science platforms and wildlife photographers). Of all direct point observations (n=20,070), 89.2% (*n*=17,901) had exact latitude and longitude information while we geo-referenced 2,169 observations (10.8%) to the nearest verifiable locations, i.e. a known water hole or road junction (Supplemental Information 2). We discarded >25,000 possible public cheetah records that could not be verified for lack of reliable time, location, and/or species evidence.

The majority of cheetah presence observation pixels were determined using research data (Table 1; Supplemental Fig. 1). Crowd-sourced point data uniquely contributed 12.9% of presence pixels of free ranging cheetahs and corroborated an additional 10.8% of presence pixels. 69.2% of pixels attributed to crowd-sourced data were in IUCN I-IV protected areas and an additional 13.7% were in other protected areas. In contrast, research point data were found primarily outside protected areas with only 18.9% found in IUCN I-IV protected areas and an additional 10.7% in other protected areas.

Range

Data on cheetah presence in free range habitat encompassed 789,800 km^2 of southern Africa (Table 2; Fig. 1), including the buffer around verified presence. The largest range portion occurred in Namibia (55.6%), the least in Zimbabwe (10.4%) (Table 2). Namibia also had the largest portion of its area in cheetah range (53.5%). Of the current known free range in southern Africa, 18.4% is formally protected (IUCN categories I-IV) and an additional 27.6% by the remaining categories (V-VII). Occurrence records suggest that cheetah populations in these four countries are linked across international boundaries (Fig. 1) and 13.6% of the documented free-range presence falls into the Kavango Zambezi Transfrontier Conservation Area.

In South Africa, 50 fenced reserves across nine provinces comprised a managed meta-population, with a total size of 11,721 km^2 (Fig. 1). Note, due to our spatial resolution, the estimated area is slightly larger than this at approximately 13,000 km^2.

Cheetahs are generally not observed in areas with human densities > 25 people per km^2, or where there are > 10 cattle or >5 sheep or > 5 goats per km^2 (Supplemental Information 6). We apply these thresholds across the remainder of the study area where no presence information was available. Areas within historical range and below these thresholds, i.e. possible presence areas, comprised another 742,800 km^2 (Fig. 2). In contrast, most of South Africa, eastern Botswana, and the northern part of Namibia adjacent to Angola are above these thresholds, suggesting cheetah absence.

In sum, we confirmed free ranging cheetah across 789,800 km^2; when the fenced population is included this increased to 802,800 km^2, and when we included possible presence areas, this increased to 1,545,600 km^2.

Persecution

On Namibian farms (n=185), 26.5% of land managers actively persecuted cheetahs while 49.7% considered the species as causing conflict (Supplemental Information 4). On these properties, managers trapped a total of 245 cheetahs during the survey period, of which 17 were translocated (Weise et al. 2015), 32 were placed into permanent captivity, and 196 were killed (146 verified plus 50 reported). This resulted in an effective annual removal of 0.59 cheetahs per 100 km^2 over all ages and sexes, 0.30 adult cheetahs per 100 km^2 per year, including 0.10 breeding age females (Supplemental Information 4). Persecution was skewed towards adult males (32.9% of all aged and sexed animals) and sub-adult males (26.7%) compared to adult females (17.1%) and sub-adult females (23.3%), but not significantly different across ages and sexes (χ^2 = 3.51, d.f. = 3, *p* = 0.318). We suspect higher removal of males is likely a consequence of coalition behaviour and relative ease of trapping males at marking trees.

The primary income sources of the farm managers influenced levels of cheetah persecution. Commercial wildlife farming and hunting operators had a disproportionately high impact on cheetah removal, while recreational land uses appeared most tolerant (χ^2 = 41.2, d.f. = 4, *p* < 0.001). The few least-tolerant land managers had a disproportionately high impact on cheetah removal. Ten farm owners removed 71.9% of all persecuted cheetahs; possibly inducing local population sinks. The three most intolerant managers (two wildlife ranchers and one cattle owner) contributed 50.0% to persecution, including one manager accounting for 36.0% of all removals (Supplemental Information 4).

Estimating densities from persecution data

The Leslie Matrix model does not need to explain the full range of population parameters, but to understand the most optimistic conditions for population growth. The *greatest* possible growth rate corresponds to the *lowest* densities of cheetahs that can support a given level of persecution were the population not to decline. First, we review the parameters gleaned from the literature, then estimate growth rates, and then calculate minimum densities of cheetah needed to support known persecution levels.

In Serengeti National Park, Kelly et al. (1998) estimated the age of first reproduction at 2.4 years (=29 months), essentially 2 years plus the estimated 90 to 95 day gestation period known from both captive and free ranging cheetahs (Brown et al. 1996, Eaton 1974). Kelly et al. (1998) estimated the inter-birth interval for the same area at 20.1 months (n=36). Marker et al. (2003) reported a range of 21-28 months (mean=24, n=6) for Namibian farmland.

The number of cubs reaching independence (at approximately 17 months) varied more substantially across data sources. Some studies observed the same cubs from their detection in the lair to independence, whereas other studies observed cubs detected at any age to independence (Frame & Frame 1976, McVittie 1979, Morsbach, 1986a, b, Laurenson 1992, 1994, Laurenson et al. 1995, Kelly et al. 1998, Marker et al. 2003, Pettorelli & Durant 2007, Marnewick et al. 2009, Wachter et al. 2011, Mills & Mills 2014). Weise et al. 2015). The presence of carnivore species, particularly large ones such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), can be a major factor affecting the survival of cubs (Laurenson 1994, Wachter et al. 2011). For some Namibian ranchlands without these species, the range of young cheetahs raised to independence varied from 1.3 (Marker et al. 2003) to 3.2 cubs surviving to 14 months (Wachter et al. 2011). In the Kgalagadi Transfrontier Park, Mills and Mills (2014) estimated 1.5 cheetahs survived to independence (45% of an average litter size of 3.4). In the Serengeti, Pettorelli and Durant (2007) recorded an average of 3.8 cubs raised to independence over five years, which represent two reproductive cycles.

Adult female survival was also reported in different ways either as averaged life spans or as annual survivorship. Kelly et al. (1998) recorded an average life span of 6.2 years for the Serengeti, whereas Marnewick et al. (2009) estimated an annual survivorship of 89%, corresponding with an average lifetime of 5.7 years for the Kruger National Park.

Using the most optimistic scenario of demographic factors influencing population growth in a Leslie Matrix model (29 months at first reproduction, a 20 month inter-birth interval, 3.2 cubs raised to independence, and a 6.2 year life span for adult females) cheetah populations can grow at 30% per year. When manipulating a single parameter at a time, the growth rate fell to 25% when the inter-birth interval increased to 24 months, to 24% when a reduced life span of 5.7 years is used, and to 10% when only 2.0 cubs survive to independence.

For this most optimistic scenario, a density of 0.33 reproductive females per 100 km^2 would sustain the known persecution rate of 0.1 females per 100 km^2 per year without population decline. With lower growth rates, a higher density of animals would be required.

Densities

We sourced 14 empirically determined local to regional cheetah density estimates, covering 286,417 km^2, or approximately 36% of the area known to support free ranging cheetahs (Fig.

3a; Table 3). Estimated densities varied from 0.18 - 0.70 individuals per 100 km^2 (Table 3). The mean density across study sites was 0.43 ± 0.06 S.E. cheetahs per 100 km^2. Weighting the mean by the area surveyed (mean calculated from total number of 100 km^2 sample blocks with measured density) yielded an overall density of 0.47 ± 0.00 S.E. cheetahs per 100 km^2.

Under managed conditions, the densities on 50 fenced cheetah reserves in South Africa ranged from 0.11 – 15.0 individuals per 100 km^2 (Supplemental Information 7). Nearly all reserves contained at least 1.0 cheetah per 100 km^2 (88.0%, *n*=44) while 21 reserves contained 5.0 cheetah per 100 km^2 or more. Only 14 of the reserves reported cubs — hence evidence for breeding. The densities from managed reserves are not included in calculations of free ranging populations.

Including densities based on cheetah counts in Zimbabwe and Kruger National Park, the density of free ranging cheetahs varies from 0.09 per 100 km^2 in the Zambezian Dry Miombo and Baikaiea Woodlands to more than 2.0 per 100 km^2 in the Kruger National Park (Fig. 3b). When study density estimates were applied across ecoregions in presence areas without cheetah monitoring, the minimum estimated density was 0.18 per 100 km^2 in Baikaiea Woodlands and Flooded Grasslands and the maximum estimated density was 0.51 per 100 km^2 in Xeric Savanna and Mopane Woodlands, with a weighted mean density of 0.36 cheetah per 100 km^2 in the same area. By comparison, the IUCN status assessment used an average density of approximately 0.35 adults per 100 km^2.

Population

Based on known (Table 3) and inferred densities calibrated to ecoregion types with measured densities (Table 4), we estimated 3,500 free ranging adult cheetahs in southern Africa with a maximum additional 3,176 cheetahs in potential habitat areas. At the end of July 2017, 176 adult cheetahs lived in fenced reserves in South Africa.

Our estimates of free ranging cheetah numbers are of three kinds. First, across Zimbabwe Van der Meer (2016) estimated 150-170 free ranging adults, of which 104 were individually recognized as 52 males, 30 females, 22 of unknown sex, plus approximately 60 cubs. Using this study, we estimate 160 resident individuals in Zimbabwe. Marnewick et al. (2014) estimated 412 adults in Kruger National Park in South Africa (2008-2009 data). This falls outside our study period but the count was included because we consider it the most reliable estimate of cheetah population in the area. Second, we applied cheetah densities to areas of known range based on their ecoregion (Table 4; Fig. 3b). We predict approximately 2,928 cheetahs in these areas. We estimated the highest number of cheetahs (1,397 individuals) in the Kalahari Xeric Savannah ecoregion which covers 273,800 km^2 of connected habitat in Namibia, Botswana, and north-western South Africa (Fig. 3a). The second highest number was 468 animals in the Angolan Mopane Woodlands covering 99,600 km^2. Third, and not included in the estimate of 3,500 individuals, another 742,800 km^2 may hold cheetahs. This possible range spans ecoregions with densities ranging from 0.18 to 0.51 cheetahs per 100 km^2 (Fig. 3b). If cheetah fully occupied possible range, this would add another approximately 3,176 animals, suggesting a maximum adult population of 6,676 individuals in the four study countries.

Discussion

Our objective was to provide independent estimates of cheetah distribution and abundance in southern Africa, considering additional data sources and processes not often used for this purpose, e.g. crowd-sourced information, estimates of cheetah persecution, and maps of human impact.

Our population estimate for confirmed cheetah range is lower than that produced by the RWCP and IUCN/SSC. In Zimbabwe, both studies relied on Van der Meer (2016) and we found few additional data using alternative sources. In removing expert opinion from our assessment of "confirmed" cheetah range, and using observation data for this category only, we arrived at a much smaller portion of known cheetah distribution (also see paragraph below) than previously proposed. Consequently, our estimate of approximately 3,500 adult cheetahs is 19% less than the 4,300 adults estimated by the RWCP and IUCN/SSC (2015), supporting Durant et al.'s (2016) call for up-listing to "endangered" status. Yet, if we added areas where we did not record cheetahs, but suggest they may occur, our overall estimate would rise to approximately 6,676 adults. As it is unlikely that all of these possible presence areas contain cheetahs, we urge greater caution in applying the upper end of our population estimate as opposed to its low limit, which is based on verified observations.

While the differences between our estimate of the cheetah's distribution and that produced by the RWCP and IUCN/SSC may appear small, they have important implications for conservation. We estimated the known cheetah range to be 789,800 km^2 in the four countries (802,800 km^2 when including fenced reserves) — an area based exclusively on confirmed data but which included an adjacency buffer around verified free range presence. We further speculated that cheetahs may occur across another 742,800 km^2 due to suitable habitat and low human and livestock densities, resulting in a total possible range of 1,545,600 km^2. For the same four countries, Durant et al. (2015) estimate 1,149,000 km^2 of confirmed and 245,000 km^2 of possible presence, a total of 1,394,000 km^2. Much of this difference arises from Durant et al. (2015) using expert opinion to inform areas where data are sparse. While this is understandable, particularly for protected areas, using an expert system approach to range mapping raises issues about supporting evidence. On the other hand, we appreciate that our approach is correlative and does not provide causal evidence to indicate why cheetahs may or may not live at certain densities. In addition, the global data set of livestock densities (Robinson et al. 2014) may have inaccuracies at local scales.

An important difference between our study and the RWCP process is in how we choose to present the data, which include many sensitive records. In addition to summarised GPS records from collared individuals, we compiled more than 20,000 observations, and plotted them into a 10 km x 10 km grid. This allowed us to publicly display them (Fig. 1). IUCN maps do not provide this level of detail although the information is collected by the RWCP and used in mapping. This has some important consequences in framing questions for research that may improve future assessments of the species' status.

First, our approach is explicit about the sampling bias. This allows us to understand where estimates are derived from research and where estimates were based on expert opinion.

Across much of central and eastern Botswana there are only scattered observations (Fig. 1). Given how sparsely populated and inaccessible this area is, it is perhaps sensible to presume that the species is present throughout this area. Nonetheless, not explicitly linking presence data to potential range may have the effect of discouraging surveys in places where presence is based on assumption. The IUCN map also occasionally extends the cheetah's range 100 - 200 km outside our known records. It is possible we may have missed data supporting these extensions, but if not, verified observations and new surveys in these areas would be most important. We propose that the commercial ranch lands in south-eastern Namibia and northern South Africa, and ranch lands in north-western, central, and eastern Botswana should be areas of particular research interest.

Second, our approach permits discussion about where cheetahs might be and we can ask detailed questions concerning the uncertainty of our analyses. Adding all possible areas of cheetah presence more than doubles our population estimate. This is an unlikely scenario, hence this upper estimate serves to highlight the need for further research in such areas rather than providing a realistic assessment of the current status of the species. One important uncertainty stems from the few observations in central Botswana in the Kalahari Xeric Savannah and Kalahari *Acacia-Baikiaea* Woodland ecoregions. Documenting presence here is important; based on the ecoregion densities this area could contain a maximum of around 1,100 cheetahs. Other important areas are southern Namibia and northern South Africa, where habitat in Gariep Karoo and Kalahari Xeric Savannah could support another 1,200 cheetahs.

Third, as a corollary to evaluating assumptions about where cheetahs might be, one may evaluate our assumptions about where they are unlikely to be found. While the absence of evidence for cheetahs should not be automatically equated with evidence for their absence, combined with other data (e.g. Fig. 2) it can be suggestive. High densities of humans and their livestock likely preclude permanent cheetah presence and we excluded these areas from possible range. Reliable observations in such areas would be important in confirming or refuting this assumption, as well as for building a better understanding of the factors that restrict the cheetah's range. Such exercises are beyond the scope of this paper, but further refinements are necessary at national scales. Similarly, there is a need to calibrate local density estimates to the cheetah's unique spatial ecology (e.g. Keeping 2014).

Fourth, we found that known cheetah populations are remarkably concentrated. About 55% of the known population are located within approximately 400,000 km^2, consisting of 259,600 km^2 of the Kalahari Xeric Savannah and 143,600 km^2 of the Namibian Savannah Woodlands. Thus, while cheetah range may be contiguous across the four study countries in southern Africa, most individuals are highly concentrated in a particular portion of that range. Much of the Kalahari Xeric Savannah overlaps with privately owned range lands, an area of higher risk for human-wildlife conflict and associated persecution. Within the core high density cheetah range in Kalahari Xeric Savannah between Kgalagadi Transfrontier Park and Central Kalahari Game Reserve (see Fig 3B), Botswana recently relinquished 8,230 km^2 of Wildlife Management Areas for planned livestock expansion. The continued large-scale conversion of conservation lands will almost certainly exacerbate conflict and negatively impact the southern African free-ranging cheetah population.

Value of crowd-sourced data

We provide an extensive and replicable process to gather data from public sources (Supplemental Information 1). Reliable crowd-sourced information uniquely contributed 12.9% to our distribution estimate, sometimes being the only available information for specific areas (e.g. Etosha National Park in Namibia). Furthermore, it was essential in assessing cheetah status in Zimbabwe (Van der Meer 2016). Nevertheless, we should not expect crowd-sourced data across all of cheetah range. Such data did add to our knowledge, but originated largely from protected areas and within areas the RWCP process classified as extant range (85.3% of crowd-sourced observations were within extant range, and 76.9% from protected areas). Indeed, the crowd-sourced data were even more restricted, being primarily available for well visited protected areas. Knowing the patterns of crowd-sourced data can be beneficial in understanding biases in our assessment processes (Boakes et al. 2016). For the cheetah, obtaining crowd-sourced data can assist in assessing numbers in parks with high tourist volumes (see Marnewick et al. 2014), and [illegible]d free up valuable research effort to focus on unprotected lands where most cheetah occur and are more vulnerable.

Off-take data and the Leslie Matrix model.

We provide some of the most detailed off-take records for large carnivores. These data are from commercial ranch lands in Namibia and are not applicable to all areas of range in southern Africa (e.g. protected areas). Nevertheless, our data indicate the importance of documenting persecution hot spots as only a single or few land managers can eliminate large numbers of animals. The implications are that conservation efforts should focus on such hot spots to prevent continued unsustainable removal, and that education should attempt to reach all cheetah custodians, as otherwise, locally concentrated persecution efforts may continue to inflict substantial losses.

Secondly, these detailed data allow us to estimate cheetah population densities required to sustain these levels of off-take without population decline. For the Kalahari Xeric Savannah, the Leslie Matrix model suggested a density of 0.66 adult cheetahs per 100 km^2 (at equal sex ratio) was necessary to support the level of persecution we observed. This was only slightly lower than the density recorded in this area (0.7; Table 3).

Now, the density estimate based on persecution would have been substantially higher had we used demographic parameters that were typical for cheetahs rather than their optimal ones for growth. Were that the case, one explanation might be that there are far more cheetahs in this area than currently recognised. This may be unlikely. So, yet another alternative might be the high off-take might be causing declining cheetah densities. Our off-take data may involve animals drawn into local population sinks, meaning an area larger than the sampled area is supporting this loss. In addition, the high numbers of animals killed in Namibia possibly reflect a period when cheetahs might have been unusually abundant because of above average rainfalls (Climate Change Knowledge Portal 2017), supporting high prey densities between 2009-2012. These considerations underline the uncertainties of assuming an overall and constant density estimate. All that said, the most parsimonious explanation is that the close similarity of the two estimates (0.66, 0.7) is that the cheetahs are just holding their own in an area of relatively high productivity but in the face of intense persecution.

Conclusion

Our approach demonstrates the value of crowd-sourced information although these data largely originate from protected areas with high visitor volumes. Thus, it did not assist in answering the critical question of how cheetahs are faring outside of protected areas. This suggests that research effort could focus on unprotected landscapes where most cheetah occur and are more vulnerable, while encouraging the use of citizen science particularly for protected areas.

Our results demonstrate how concentrated cheetah records are within southern Africa. A mere 400,000 km^2 contain approximately 55% of the known population, much of it on unprotected lands. That this area corresponds with high levels of persecution generates a concern that the stronghold is 'hollowing out' and highlights how precarious the situation is for this species. We also show the impact of a few landowners on overall cheetah persecution. Our independent assessment, with an estimated adult population of approximately 3,500 animals, therefore supports the conclusion of Durant et al. (2016) to review the cheetah's threat status and consider uplisting the species to endangered status.

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Figure 1

Cheetah distribution in the study area in southern Africa.

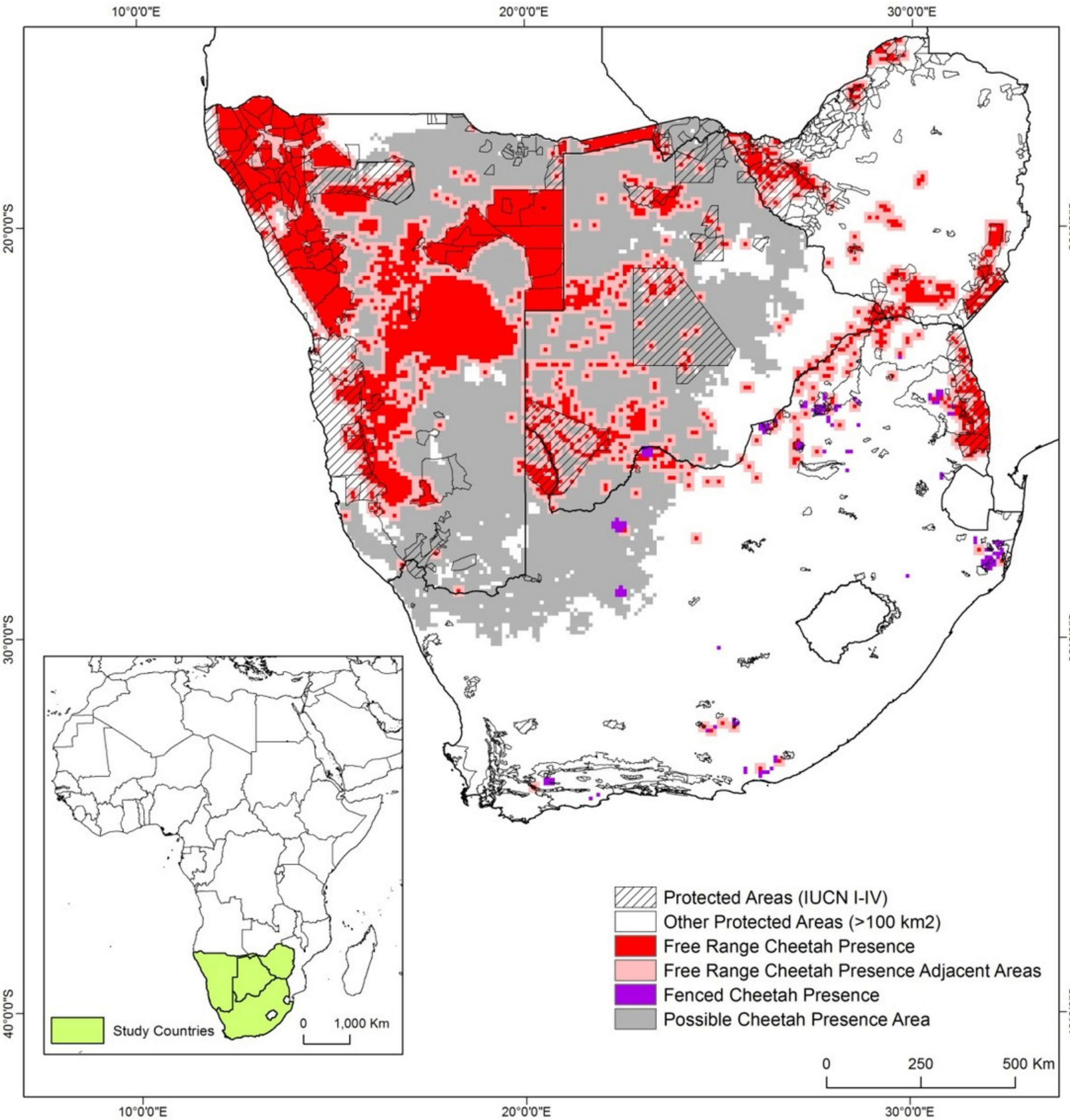

Figure 2

Known cheetah presence in relation to human and livestock densities. Clockwise from top left: densities as numbers per km of people, cattle, sheep, and goats.

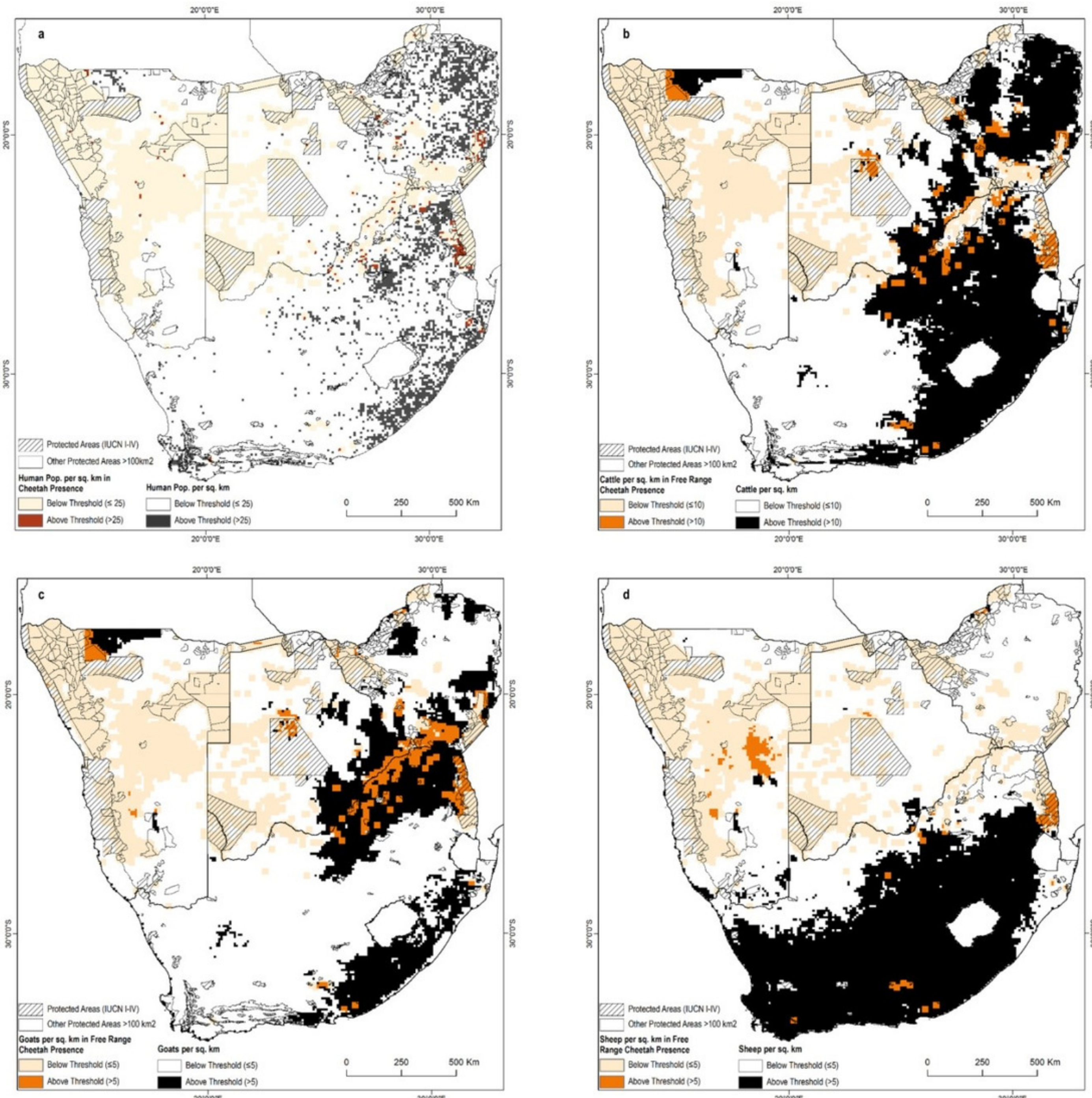

Figure 3

A) Locations of cheetah density estimates overlaid on the major ecosystem types in the study area. B) Estimated cheetah densities in presence and possible presence areas.

See Table 3 for the source of the density estimates.

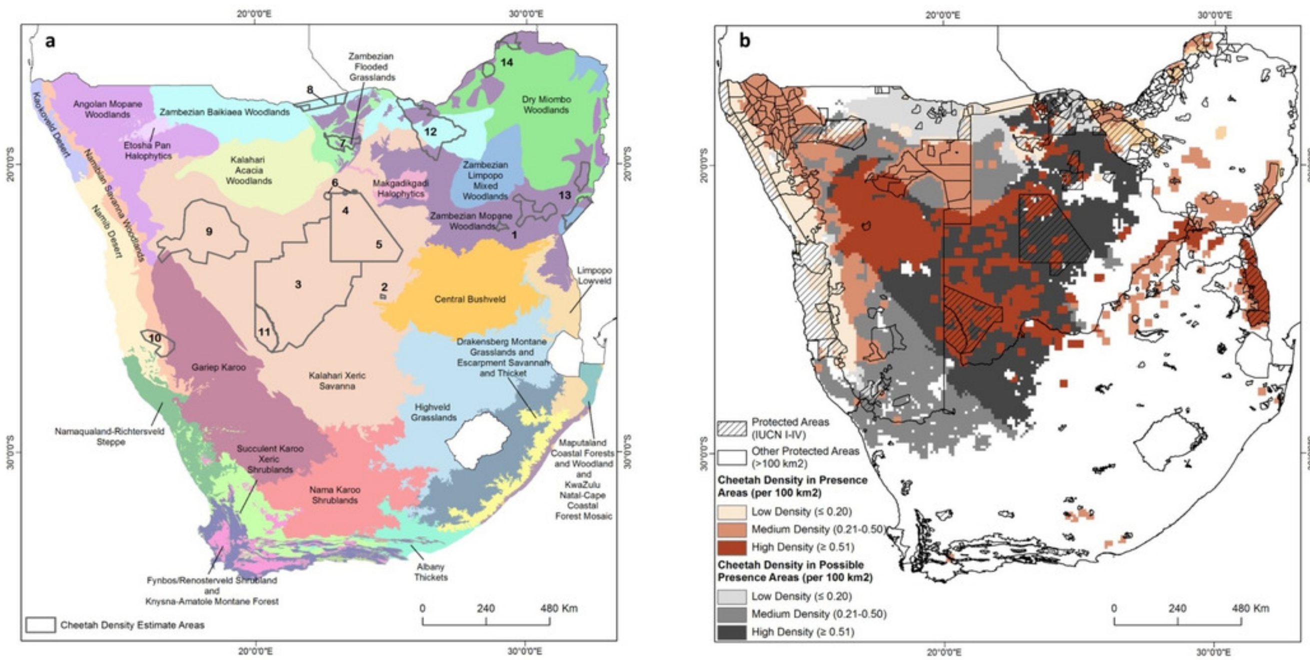

Table 1(on next page)

Area (in 100 km^2) of data contributions per country and within protected areas.

Table 1: Area (in 100 km^2) of data contributions per country and within protected areas.

	Research Data	Research Data in IUCN I-IV Protected Areas (% of Total Research)	Research Data in all Protected Areas (% of Total Research	Crowd Sourced data	Crowd Sourced Data in IUCN I-IV Protected Areas (% of Total Crowd Sourced)	Crowd Sourced Data in all Protected Areas (% of Total Crowd Sourced)	Corroborated Data (i.e. both sources)	Corroborated Data in IUCN I-IV Protected Areas (% of Total Corroborated)	Corroborated Data in all Protected Areas (% of Total Corroborated)
Botswana	388	105 (27.1%)	105 (27.1%)	27	19(70.4%)	19(70.4%)	26	18 (69.2%)	18 (69.2%)
Namibia	767	117 (15.3%)	190 (24.8%)	34	23 (67.6%)	28 (82.4%)	8	4 (50.0%)	5 (62.5%)
South Africa	117	11 (9.4%)	42 (35.9%)	140	105 (75.0%)	126 (90.0%)	40	31 (77.5%)	39 (97.5%)
Zimbabwe	148	36 (24.3%)	84 (56.8%)	40	20 (50%)	27 (67.5%)	127	45 (35.4%)	78 (61.4%)
Total	1420 (76.2%)			241 (12.9%)			201 (10.8%)		

Table 2(on next page)

Area of cheetah distribution (in 100 km^2) across countries and protected areas.

Table 2: Area of cheetah distribution (in 100 km^2) across countries and protected areas.

	Botswana	Namibia	South Africa	Zimbabwe	Total Study Area	Protected Areas IUCN I-IV	All Protected Areas	Kavango–Zambezi (KAZA)
Free range cheetah presence	441 (11.1%)	2897 (73.2%)	289 (7.3%)	333 (8.4%)	3,960	605 (15.3%)	2,353 (59.4%)	562 (14.2%)
Presence buffer	1297 (32.9%)	1497 (38.0%)	652 (16.6%)	492 (12.5%)	3,938	870 (22.1%)	1,297 (32.9%)	515 (13.1%)
Fenced metapopulation	0	0	130	0	130	6(4.6%)	46 (35.4%)	0
Possible cheetah presence	3069 (41.3%)	2956 (39.8%)	1403 (18.9%)	NA	7,428	738 (9.9%)	1,066 (14.4%)	1,284 (17.3%)
Total presence without metapopulation	1738 (22.0%)	4394 (55.6%)	941 (11.9%)	825 (10.4%)	7,898	1,475 (18.7%)	3,650 (46.2%)	1,077 (13.6%)
Total presence with metapopulation	1738 (21.6%)	4394 (54.7%)	1071 (13.3%)	825 (10.3%)	8,028	1,481 (18.4%)	3,696 (46.0%)	1,077 (13.4%)
Total cheetah presence area with possible areas	4807 (31.1%)	7350 (47.6%)	2474 (16.0%)	825 (5.3%)	15,456	2,219 (14.4%)	4,762 (30.8%)	2,361 (15.3%)
Percent country with cheetah presence (with metapopulation)	30.0%	53.5%	7.7% (8.8%)	21.1%	26.2% (26.7%)			

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Table 3(on next page)

Cheetah density estimates across the study area in southern Africa from 2010-2016. See text for explanation of the difference between mean and weighted mean.

Table 3: Cheetah density estimates across the study area in southern Africa from 2010-2016. See text for explanation of the difference between mean and weighted mean.

Country	Survey Method	Study Area (km^2)	Land use	Data collection	Habitat Description	Ecoregions	Numbers per 100 km^2	Study
Botswana	camera trapping	240	predominantly commercial ecotourism and private holiday purposes with limited farming activities	Dec 2012 – Oct 2013	mopane veld, savanna	Zambezian Mopane Woodlands	0.61	1
Botswana	camera trapping	180	mineral extraction	Oct - Dec 2010	open semi-wooded savannah mixed with a moderate to thick bush - *Acacia* and *Boscia* spp	Kalahari Xeric Savanna	0.51	2
Botswana	spoor survey - calibrated to day range and stratified by demographic group	109,612	conservation and tourism, communal pastoralism, limited fenced ranching	Feb 2011 – Dec 2015	*Acacia* - *Boscia* tree dominated savanna interspersed with prominent mineral pans	Kalahari Xeric Savanna	0.57	3
Botswana	spoor survey analysed with refined Funston et al. (2010) carnivore density formula	4,900	conservation and tourism	Nov-12	salt pans, riverine woodland, scrubland, open grassland	Kalahari Xeric Savana	0.2	4
Botswana	spoor survey analysed with refined Funston et al. (2010) carnivore density formula	54,645	conservation and tourism	2014	shrubby savannah and grassland	Kalahari Xeric Savanna	0.25	5
Botswana	spoor survey analysed with refined Funston et al. (2010) carnivore density formula	1,060	game ranching	2014	Kalahari Xeric Savannah (Acacia - Boscia tree dominated) interspersed with prominent mineral pans	Kalahari Xeric Savanna	0.59	6
Botswana	camera trapping & tourist observations	2,700	conservation and tourism	Oct 2008 - Jul 2011;	mopane woodland, mixed woodland and floodplain	Zambezian Mopane	0.6	7

				subsequent monitoring	habitat (7%)	Woodlands		
Namibia	spoor survey analysed with Funston et al. (2010) formula	5,794	conservation with partial communal user rights	Jul-14	rivers and floodplains of the Kavango and Kwando rivers, sandy ridges and omurambas of teak (*Burkea* spp) and mixed woodlands	Zambezian Baikiaea Woodlands	0.19	8
Namibia	camera trapping with SCR modelling analysis	46,349	mixed cattle, smallstock, game farming, hunting and tourism	2012 – 2016	Acacia-dominated highland savannah with Kalahari Desert transition	Kalahari Xeric Savanna and Gariep Karoo	0.7	9
Namibia	camera trapping with SCR modelling analysis	6,445	mixed farming and tourism	2016	Namib Desert with mountain ranges	Namibian Savanna Woodland, Namib Desert and Gariep Karoo	0.2	10
South Africa	long-term intensive monitoring of known or collared individuals	6,000	conservation and tourism	2006-2012; subsequent monitoring	Kalahari Desert, sand dunes, shrubby grassland, open tree savannah	Kalahari Xeric Savanna	0.7	11
Zimbabwe	sighting reports collected via interviews and citizen science platform, monitoring of known individuals through photographs collected via citizen science	23,340	predominantly hunting and tourism, some subsistence farming	2012-2015	diverse range of terrain and vegetation types, predominantly woodland and scrubland (most common species Acacia, Zambezi teak, *Combretum* spp., *Terminalia cericea* and Mopane) with some patches of grassland.	Zambezian Baikiaea and Zambezian Mopane Woodlands	0.18	12
Zimbabwe	sighting reports collected via interviews and citizen science platform, monitoring of known individuals through photographs collected via citizen science	17,423	hunting, cattle farming, tourism	2012-2015	deciduous woodland savanna dominated by Mopane and Acacia, traversed by seasonal river-lines and associated riparian vegetation. Scattered open grassland areas in between.	Zambezian Mopane Woodland and Limpopo Mixed Woodland	0.51	13

Zimbabwe	sighting reports collected via interviews and citizen science platform, monitoring of known individuals through photographs collected via citizen science	7,729	tourism, some hunting	2012-2015	floodplains of the Zambezi river, woodland dominated by Mopane and Miombo. Patches of open woodland and grassland.	Zambezian Mopane Woodlands and Dry Miombo Woodlands	0.19	14
Overall		**286,417**		2010-2016	**Mean**		**0.43 (0.06 S.E.)**	
					Weighted Mean		**0.47 (0.00 S.E.)**	

1) Brassine & Parker (2015); 2) Boast et al. (2011); 3) Keeping (2016); 4) Maude (2014) extended analysis; 5) Maude (2014) extended analysis; 6) Maude (2014); 7) Broekhuis (2012); 8) Funston et al. (2014); 9) Institute for Zoo and Wildlife Research farmland survey 2012-2016; 10) Institute for Zoo and Wildlife Research farmland survey 2016; 11) Mills (2015); 12- 14) Van der Meer (2016)

Table 4(on next page)

Numbers and densities of free-range cheetahs.

Table 4: Numbers and densities of free-range cheetahs.

Location	Presence Area* (100 km^2)	Possible Presenc Area (100 km^2)	Inferred Density	Cheetah Population	Possible Additional Cheetah Population	Footnote
Direct estimates						
Zimbabwe	825			160		1
Kruger NP	168			412		2
Indirect estimates						
Kalahari Xeric Savanna	2738	3166	0.51	1397	1615	3
Angolan Mopane Woodlands	996	385	0.47	468	181	4
Kalahari Acacia Woodlands	616	444	0.47	290	209	4
Namibian Savannah Woodlands	480	95	0.20	96	19	5
Namib Desert	396		0.20	79	0	5
Gariep Karoo	333	1575	0.36	120	567	6
Central Bushveld	317	59	0.46	146	27	7
Zambezian mopane woodlands	265	531	0.51	135	271	8
Zambezian Baikiaea Woodlands	251	776	0.18	45	140	9
Kaokoveld Desert	153	0	0.20	31	0	5
Zambezian Flooded Grasslands	112	137	0.18	20	25	9
Limpopo Lowveld	79		0.47	37	0	4

Etosha Pan Halophytics	48		0.20	10	0	5
Albany Thickets	29		0.47	14	0	4
Namaqualand-Richtersveld Steppe	29	235	0.47	14	110	4
Highveld Grasslands	17		0.47	8	0	4
Nama Karoo Shrublands	14	13	0.47	7	6	4
Makgadikgadi Halophytics	13		0.20	3	0	5
Miscellaneous habitats (<10,000 km^2)	18	12	0.47	8	6	4
Totals	7897	7428		3500	3176	

Footnotes

1 From Van der Meer (2016), who found cheetahs mostly in areas of Zambezian *Baikiaea* and Mopane Woodlands ecoregions (See Fig. 1)

2 From Marnewick et al. (2014). Kruger NP is classified as mostly Mopane Woodlands.

3 Density is a weighted average of estimate #s 2,3,4,5,6,9 and 11 from Table 1.

4 We have no specific estimates of cheetah densities for this ecoregion, however we know this is a highly suitable habitat, so we use the overall weighted density estimate from Table 1.

5 We used the density estimate # 10 from Table 1.

6 We used the average density of Kalahari Xeric Savanna and Namib Desert under the assumption that this ecoregion should have an intermediate density.

7 We used the average density of Kalahari Xeric Savanna and Mopane Woodlands under the assumption that this ecoregion should have an intermediate density.

8 Density is a weighted average of estimate #s 1, 7, 13 from Table 1. Density sample 14 also contains Zambezian Mopane Woodlands but this sample seems to be more representative of the Dry Miombo ecoregion in Zimbabwe, already accounted for in Van der Meere (2016)

9 Density is a weighted average of estimate #s 8 and 12 from Table 1.

* Areas include buffers (see text)