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# Methods for lion monitoring: a comparison from the Selous Game Reserve, Tanzania

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## Abstract

The Selous Game Reserve in Tanzania is believed to contain Africa's largest population of lions (*Panthera leo*), making it a popular destination for trophy hunters and photographic tourists. However, a lack of recent data has raised concerns about the conservation status of this iconic population, so we collected two types of population data between 2006 and 2009. First, we identified 112 individual animals in an 800 $km^2$ study area in the photographic tourism part of Selous, giving a density of 0.14 individuals $km^{-2}$. This density estimate was similar to results using the same method from 1997 to 1999, but the adult sex ratio has decreased from 1 male : 1.3 female in 1997 to 1 male : 3 females in 2009. Second, using buffalo calf distress calls, we conducted call-up surveys to census lions in three hunting sectors in the west, east and south of Selous and in the northern photographic area. Estimated adult lion densities varied from 0.02 to 0.10 $km^{-2}$, allowing an overall population estimate of 4,300 (range: 1,700–6,900). Our results highlight the value of call-ups in surveying cryptic hunted carnivores but stress the importance of long-term projects for calibrating the responses to call-ups and for measuring trends in demography and population size.

*Key words:* Lions (*Panthera leo*), Selous, call-ups, density, monitoring, population

## Résumé

La Réserve de gibier de Selous, en Tanzanie, doit héberger la plus grande population de lions (*Panthera leo*) du monde, ce qui en fait une destination très populaire auprès des chasseurs de trophées et des touristes de vision. Cependant, le manque de données récentes suscitait des inquiétudes quant au statut de conservation de cette population emblématique, et nous avons donc collecté deux types de données sur cette population entre 2006 et 2009. Nous avons d'abord identifié individuellement 112 animaux sur une zone d'étude de 800 km² dans la partie du Selous vouée au tourisme photographique, ce qui correspond à une densité de 0,14 individu/km². Cette estimation de densité était comparable aux résultats obtenus avec la mÁme méthode en 1997-1999, mais le sex-ratio des adultes était passé de 1 mâle : 1,3 femelle en 1997 à 1 mâle : 3 femelles en 2009. Ensuite, en utilisant les appels de détresse des jeunes buffles, nous avons mené une étude avec enregistrements globale pour faire le recensement des lions dans trois secteurs de chasse à l'ouest, à l'est et au sud de Selous, et dans la zone de tourisme de vision au nord. La densité estimée des lions adultes variait de 0,02-0,10/km², ce qui équivaut à une population totale estimée à 4 300 (entre 1 700 et 6 900). Nos résultats soulignent la valeur des enregistrements dans la recherche concernant des carnivores chassés cryptiques, mais ils montrent bien l'importance de projets à long terme pour calibrer les réponses à ce type de comptages et pour mesurer les tendances en matière de démographie et de taille des populations.

## Introduction

Adaptive management and conservation of natural ecosystems require effective monitoring of biodiversity, including regular surveys of wildlife abundance (Lindenmayer & Likens, 2009). Such surveys should use cost-effective and efficient techniques but should also generate reliable estimates that can detect temporal and spatial trends in wildlife abundance (Danielsen *et al.*, 2009). These surveys are particularly important when managing exploited

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species, as harvesting increases the risk of populations becoming economically, or in extreme cases, biologically unviable (Adams, 2004; Milner-Gulland, Bunnefeld & Proaktor, 2009). This situation is illustrated by the African lion (*Panthera leo*), which provides an important source of trophy-hunting revenue for management agencies that fund their activities through sustainable utilization. However, the lion is a top predator that lives at low densities and is particularly vulnerable to overharvesting because of infanticide by replacement males (Whitman *et al.*, 2004; Caro *et al.*, 2009; Packer *et al.*, 2009). Thus, it is important to identify and develop effective monitoring methods to help ensure the long-term biological and economic viability of these populations.

Tanzania's Selous Game Reserve (SGR) exemplifies this need. SGR is believed to hold the country's largest lion population, and SGR's principal source of conservation income derives from trophy hunting (Baldus, 2004, 2009). However, the population has not been surveyed recently, creating a number of issues that relate to lion trophy hunting. For example, recent efforts to up-list the African lion from Appendix II to Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) argued: 'that the largest population of free-ranging African lions in Tanzania, that in the Selous Game Reserve, has not been the subject of recent direct population survey and population estimate is of concern' (CITES, 2004 CoP 13 Prop. 6). There have only been three studies of lions in SGR, one in the 1970s and two in the 1990s (Rodgers, 1974; Creel & Creel, 1997; Spong, 2002). Furthermore, recent work from Tanzania has highlighted the negative impact of trophy hunting on lion populations (Packer *et al.*, 2011a), thereby stressing the need for monitoring to establish baseline data in hunting areas. Here, we describe a study that provides new data on the population status of lions in SGR.

Various methods have been used to count lions, such as roar counts (Rodgers, 1974), mark-resighting (Smuts, 1976; Castley *et al.*, 2002), spoor transects (Stander, 1998; Funston *et al.*, 2010), audio playback response surveys, referred to hereafter as 'call-ups' (Ogutu & Dublin, 1998; Ferreira & Funston, 2010), and individual identification (Pennycuick & Rudnai, 1970). Individual identification has been the preferred method for long-term research projects on lions (Schaller, 1972; Packer *et al.*, 2005a). However, individual identification may not be feasible when population estimates are required over large areas and/or are needed quickly, for example, to set hunting quotas or understand human–wildlife conflict patterns (Lichtenfeld, 2005). To this end, a number of indirect measures have been developed to estimate relative lion abundances, and the current preferred indirect method in East Africa is call-ups (Ogutu, Bhola & Reid, 2005; Whitman *et al.*, 2006; Kiffner *et al.*, 2009). We therefore combined individual identification in the photo-tourism section of SGR with call-up surveys over a broader area to determine: (i) lion population trends from a study population that has been intensively studied from 1997 to 1999 and again from 2007 to 2009; (ii) whether a rapid assessment of the SGR's hunted lion population can provide meaningful results.

## Materials and methods

### *Study area*

Selous Game Reserve covers 47,500 km$^2$, making it Africa's largest protected area (Baldus, 2009), and it may support the largest lion population in Africa (Bauer & Van Der Merve, 2004). SGR supports one of Africa's largest big game populations and has developed a considerable reputation as a premium trophy-hunting destination despite being a large and inaccessible area infested with tsetse flies (Leader-Williams & Hutton, 2005; Baldus, 2009). SGR was originally subdivided into 47 hunting blocks in the 1970s (Leader-Williams, Kayera & Overton, 1996) but more recently, four of these blocks in the north, covering 6% of SGR, have been set aside for photographic tourism (Fig. 1). We resumed intensive research on lions within an 800-km$^2$ section of this photographic area of the Matambwe sector in northern SGR (marked Study Area in Fig. 1), wherein a similar study was conducted from 1997 to 1999 (Creel & Creel, 1997; Spong *et al.*, 2002). The Matambwe study area consists of a mosaic of wooded savannah, miombo woodland and *Combretum* thickets (Spong, 2002). Four other areas of roughly 100 km$^2$ were less intensively surveyed using call-ups in 2009 (marked Call-up Areas in Fig. 1; A–D). As 100 km$^2$ represents 1–2 pride territories (see results), we felt that this was an appropriate sampling regime.

### *Intensive study of lions based on individual identification*

We conducted intensive searches for lions, (except during the rainy season of March to May) between 2006 and 2009 in the Matambwe study area. We produced

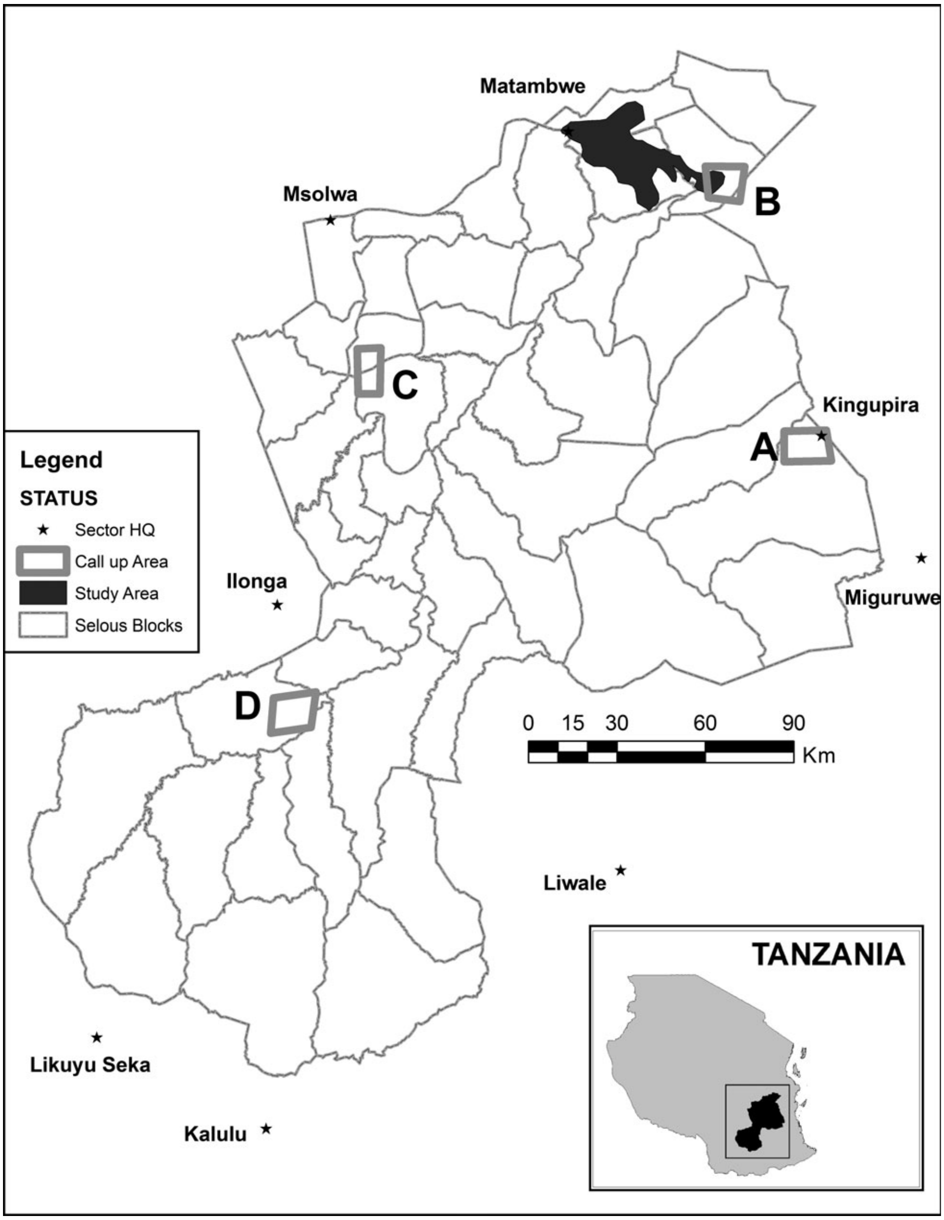


**Fig 1** The Selous Game Reserve, showing the main study area and location of call-ups areas

individual photographic identification cards for each lion using whisker spot patterns, nose scars and colour, tongue rips, tooth breakage and wear, body size and any other relevant features (as described by Pennycuick & Rudnai, 1970). We recorded group composition and Global Positioning System (GPS) location at each lion sighting. Lions are the most social species among felids, and cubs of either sex are totally dependent on their mothers for food and protection until 2 years of age (Schaller, 1972), so we categorized animals that were 2 years old or less as cubs and older animals as adults.

Within the Matambwe study area, we fitted two adult females with very high frequency radio collars from 25 October 2007 to 28 August 2009 and one adult female with a GPS collar from 27 February 2008 to 31 August 2008. The GPS collar recorded three locations (or fixes) a day, at 19:00, 01:00 and 08:00 hours, and allowed ranging data to be collected during the wet season for the first time in SGR. The collared females were from three different prides. Anaesthesia to fit and remove collars was induced for around an hour by 300 mg of ketamine and 8 mg of medetomidine. The medetomidine was reversed using 40 mg of atipamezole. All lions were up and moving within 1 h of the reversal.

*Call-up surveys*

Buffalo (*Syncerus caffer*) distress calls are known to attract lions (Kiffner *et al.*, 2007), so we played a recording lasting 4 min and 20 s between 06:00 and 08:00 hours and again between 17:00 and 20:00 hours at call-up sites during 2009. We used an MP3 player to play recordings at full volume four times in every 40 min with a six-minute period of silence between call-ups. The MP3 player was attached to a 12-volt FA2 (HiVi Inc, Arcadia, CA, USA) amplifier and two 8-ohm speakers (SRX-220, Ahuja, New Delhi, India) facing opposite directions from each other and mounted on the roof of the vehicle, about 2 m above the ground.

Call-ups have limitations as a sampling technique (Whitman, 2006) including the following: (i) male lions are more likely to respond than females, (ii) response is sensitive to the lions' initial distance from the speakers and (iii) response is sensitive to the location of the speaker within the pride's territory. Therefore, the technique should be calibrated prior to sampling. Consequently, we carried out fourteen calibration experiments to thirteen males, 24 females and 25 cubs, where the distance from the lion to the speaker was varied randomly from 500 m to 1,500 m. The maximum distance was restricted to 1,500 m because responses were not elicited in three trial runs at distances of 3,000, 2,500 and 2,000 m. Only at 1,500 m did the lion look in the direction of the speaker and begin moving towards it. Therefore, the effective response radius was 1.5 km for lions in SGR, equivalent to sampling an area of 7.065 $km^2$ ($\pi r^2$) at each call-up site. We also used these results to calculate the call-up response probability, which reflects the likelihood that a group would approach the calls. The call-up calibrations were mainly carried out in open woodland, which is the predominant habitat type in the SGR. It should also be noted that call-ups can only be used for research purposes in Tanzania; hunters are not allowed to use the technique to attract lions.

We used four call-up areas for the actual survey (marked A to D in Fig. 1), and individual call-up sites were spaced at least 3 km apart. At each call-up site, we recorded the start and end time, GPS coordinates, habitat and the presence of any incoming lions, spotted hyaena (*Crocuta crocuta*) and wild dog (*Lycaon pictus*). As soon as the lions approached the car, the playback was stopped to prevent habituation. We also took photographs and whisker spot drawings of each lion to ensure that animals were not double-counted between sites.

*Data analysis*

We estimated the territory size of each lion pride based on at least 60 GPS fixes that were collected at least 24 h apart, as a previous study from SGR suggested this as a minimum sample of independent observations for accurately measuring territory extent (method as in Spong, 2002). We then used the ArcGIS 9.3 (ESRI, Redlands, CA, USA) GIS software to map lion distributions and Hawth's tools ArcGIS extension to calculate territory area based on the adaptive kernel method (Beyer, 2004). The 50% contour was defined as the core of the territory and the 90% contour as the outer boundary of the territory (as used by Spong, 2002). We used the SPSS for Windows (version 17.0, SPSS Inc., Chicago, IL, USA) statistical package to carry out *t*-tests to determine whether pride territory size differed from a previous study in 1996–1999 (Spong, 2002). None of the individual lions were the same between the two studies.

We estimated density of lions for each of the four study areas by: (i) multiplying the number of call-up sites by the estimated sampling area of 7.065 $km^2$ to estimate the total survey area, (ii) dividing the number of individuals responding to the call-ups by the area sampled and (iii) dividing by the probability of lions responding during fourteen calibration call-ups. We then calculated the mean and standard deviation of the estimated adult densities for each of the four study areas. Finally, we multiplied these density estimates by the total area of SGR to estimate the total number of adults, using the cub-to-adult ratio from Matambwe to estimate total population size. However, this estimate does not account for habitat heterogeneity or varying hunting pressures in different parts of SGR.

## Results

*Lion density from individual recognition:*

Over 2,079 lion sightings were made of 162 different individual lions from 2006 to 2009 representing thirteen prides. Nineteen of the individuals were nonresident or nomadic, and eight individuals were only seen on one occasion. A total of 112 individually recognized lions were present in the 800 $km^2$ Matambwe study area in August 2009, equivalent to a density of 0.14 lions $km^{-2}$. This represents a minimum number of individuals in the study area, as there could be nomadic males missed by the study. Despite changes in the individual composition of prides, this density has remained similar to density estimates collected between 1997 and 1999 (Spong, 2002; Spong *et al.*, 2002). These results initially appear different from another study of lion densities in SGR, which focused on an area of only 90 $km^2$ near Lake Manze (Fig. 2) and recorded a lion density of 0.28 $km^{-2}$ (adult density of 0.13 $km^{-2}$) between 1991 and 1994 (Creel & Creel, 1997). However, this small area still supports similarly high lion densities, as it forms part of three different pride territories.

Based on data from 1997 to 1999 and 2006 to 2009, the mean number of adults per pride was 4.9 ± 0.9 (mean ± SD throughout the paper), and the mean number of cubs was 3.4 ± 0.9. The breakdown of the population in terms of adult males, adult females and cubs by age-sex class shows that males made up on average 31% of the adult population (Table 1). Mean coalition size was 2.2 ± 1.4 individuals (range 1–5 males, $n$ = 29 coalitions). Average female pride size was 3.3 ± 1.4 individuals (range 1–7 females, $n$ = 39 prides). The adult sex ratio between males and females decreased between 1997 and 2009, and the difference between number of males to females in 1997 and 2009 was significant ($P$ = 0.026, Fisher's exact test), but the proportion of cubs remained fairly constant (Table 1).

### *Pride territories*

The results from the GPS fixes showed that most lion territories are centred near lakes and rivers (Fig. 2). The mean core area was relatively small at 12.7 ± 6.4 $km^2$ (Table 2) but the entire territory of a pride covered a mean area of 48.5 ± 11.2 $km^2$. Thus, the core areas covered an average of 25 ± 0.06% of the entire territory. The exclusiveness of the core pride areas was 81% in this study, which was not significantly higher than the 52% found in the previous study (df = 8, $t$ = 1.749, $P$ = 0.118).

Comparison of pride territory area between this study and a study from 1996 to 1999 (Spong, 2002) showed no significant difference (df = 8, $t$ = −0.317, $P$ = 0.760). When compared to the Serengeti National Park (Mosser *et al.*, 2009), SGR contains smaller prides in smaller territories. In SGR, prides comprised 3.3 ± 1.36 adult females in territories of 48.5 ± 11.2 $km^2$, while in

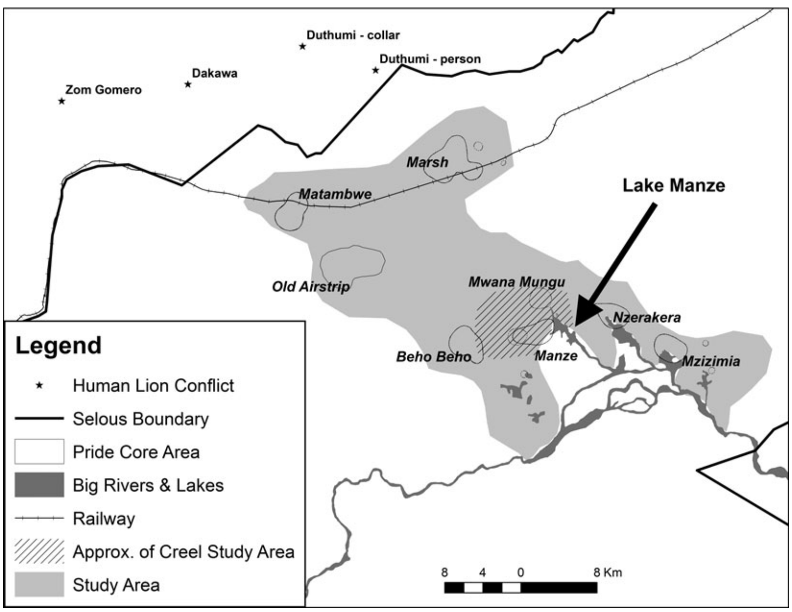


**Fig 2** Core areas of lions in Matambwe sector of Selous Game Reserve (SGR) from 2006 to 2009, and points marking human-lion conflict in areas bordering SGR during the same period

**Table 1** Composition of the lion population in the Matambwe sector of Selous Game Reserve by age and sex class from 1997 to 2009. Adults are over 2 years old, cubs up to 2 years

| Year | Adult female (%) | Adult male (%) | Cub (%) | Adult sex ratio M : F |
|---|---|---|---|---|
| 1997 | 36.0 | 28.1 | 36.0 | 1 : 1.28 |
| 1999 | 45.3 | 18.9 | 35.8 | 1 : 2.40 |
| 2007 | 48.0 | 21.6 | 30.4 | 1 : 2.23 |
| 2009 | 50.4 | 16.8 | 32.7 | 1 : 3.00 |
| Mean | 44.9 ± 6.3 | 21.3 ± 4.9 | 33.7 ± 2.7 | – |

**Table 2** Lion territories in Matambwe sector of Selous Game Reserve from 2006 to 2009

| Pride | No. of fixes | Area ($km^2$) | | Proportion exclusive | | Core area accounts for % of total |
|---|---|---|---|---|---|---|
| | | 50% | 90% | 50% | 90% | |
| Matambwe | 99 | 9.4 | 41.3 | 1.00 | 1.00 | 0.23 |
| Marsh | 70 | 17.6 | 62.4 | 1.00 | 1.00 | 0.28 |
| Nzerakera | 61 | 7.0 | 46.2 | 0.81 | 0.71 | 0.15 |
| Manze | 65 | 8.2 | 35.1 | 0.48 | 0.36 | 0.23 |
| Old airstrip | 559 | 21.4 | 56.8 | 1.00 | 0.97 | 0.38 |
| Mean | | 12.7 | 48.4 | | | 0.25 |

Serengeti, prides comprised 4.64 ± 0.18 adult females in 56 $km^2$ territories (range 15–219 $km^2$).

*Call-up surveys*

During the fourteen trials to calibrate the call-up surveys, 77% of males ($n$ = 10), 63% of females ($n$ = 15) and 8% of cubs ($n$ = 2) responded within the 40-min period. Consequently, call-ups only appear effective for sampling adults, which showed an average response probability of 0.73 ± 0.58. Lions either responded as a group, or not at all, leading to large standard deviations. The results of call-up surveys played in the four call-up areas in SGR show that more lions responded in the north and west (Table 3). The Matambwe call-up site, in the north of SGR, had an estimated adult density of 0.09 $km^{-2}$ (Table 3), which was similar to the adult density recorded through individual identification in the 800-$km^2$ study area from 2006 to 2009. The Msolwa call-up site recorded the highest density of lions, while the Kingupira area recorded the lowest density (Table 3). Interestingly, the areas with the highest densities are also the areas with the highest hunting pressures in the late 1990s (see Packer *et al.*, 2011a).

**Table 3** Lion densities ($km^{-2}$) in different areas of Selous Game Reserve based on call-up data

| Sector | Block | Habitat[a] | Dates | No. of call-ups | Area Sampled ($km^2$) | Lions seen | No. of call-ups with lions | Estimated adult lion density ($km^{-2}$) | Hyena seen | Wild dog seen |
|---|---|---|---|---|---|---|---|---|---|---|
| Kingupira (**A**) | LL1 | Cl wd | 26/01–02/02/09 | 21 | 148.4 | 2 | 2 | 0.02 | 26 | 21 |
| Matambwe (**B**) | Z1 | Cl wd | 12/02–17/02/09 | 20 | 141.3 | 9 | 1 | 0.09 | 18 | 4 |
| Msolwa (**C**) | K4/5 | Wd Gr R | 21/06–25/06/09 | 12 | 84.8 | 6 | 2 | 0.10 | 17 | 0 |
| Ilonga (**D**) | LU2 | Op Wd R | 28/06–02/07/09 | 12 | 84.8 | 3 | 1 | 0.05 | 7 | 8 |

[a]Habitat categories: 'CL wd' is closed woodland with grassland clearings; 'Wd Gr R' is wooded grassland by river; 'Op Wd R' is open woodland by river.

This call-up study sampled 459 $km^2$ or <1% of the total area of SGR. The estimated density of lions in the area sampled was 0.06 adult lions $km^{-2}$, which would be equivalent to a total population of ~2,850 adult lions and a total population with cubs of ~4,300 lions with an estimated range of 1,700 and 6,900 individuals.

## Discussion

The importance of the SGR's lion population is recognized by conservationists and trophy hunters alike, hence the need for up-to-date data on demography and population status. Individual recognition surveys in the intensive study area and call-up surveys over a more extensive area provided an update on lion population trends in the photo-tourism sector and allowed an overall estimate of lion numbers throughout SGR. We estimate that the total number of lions in SGR is 4,300 individuals based on call-up surveys, with a range of 1,700–6,900 individuals. Although these density estimates are important, they should be viewed with caution. Previous studies have shown that the response probability of lions clearly falls with distance, stressing the importance of calibrating the results (Whitman *et al.*, 2006). Our calibrations suggested a maximum response distance of 1.5 km, but it is worth noting that, if the response radius was increased to 2.5 km (as used by Ogutu & Dublin, 1998) or 3.5 km (as used by Kiffner *et al.*, 2009), our lion density values would drop from 0.06 adult lions $km^{-2}$ to 0.02 or 0.01 adult lions $km^{-2}$. However, the similar density estimates derived from the individual recognition study and the call-up survey in Matambwe (Area B, Fig. 1) strongly support our calibration curve and hence our SGR population estimate.

Our results suggest that the Msolwa and Matambwe sectors have higher lion densities than the Kingupira and Ilonga sectors (Fig. 1; Table 3). Lion densities and territory size follow a pattern of preferred prey availability (Van Orsdol, Hanby & Bygott, 1985; Hayward, O'brien & Kerley, 2007; Hayward *et al.*, 2009), and our recorded lion call-up densities follow this pattern of prey distribution, as the north and northwest have higher densities of prey species (TWCM, 1998; Caro *et al.*, 2009) and explains why the northern and western hunting blocks are considerably smaller than the southern and eastern blocks (B. Nicholson in Matthiessen, 1981). Blocks in the western Selous (in Msolwa and Ilonga) experienced very high hunting pressures in the late 1990s and then subsequent declines in hunting off-take in the early 2000s (Brink, 2010; Packer *et al.*, 2011a). However, by 2009, parts of the Msolwa sector had some of the highest lion densities in SGR (see Table 3). It is thought that the overharvesting of the late 1990s led to a scarcity of lions to hunt, which made it difficult to attract clients to the blocks, allowing lion populations there to recover by 2009. The fact that a block in the heart of the Msolwa sector stopped hunting lion in 2002/2003 due to overhunting probably helped this recovery (R. Ramoni, Pers comm.). It is also of interest that more wild dogs were sighted in areas with low lion densities, supporting suggestions of competition between the two species (Creel & Creel, 1996; Creel, Spong & Creel, 2001; see Table 3).

Selous Game Reserve lion densities are similar to the 0.1 adults $km^{-2}$ recorded in South Africa's Kruger National Park (Funston *et al.*, 2003) and comparable to the 0.07 lions $km^{-2}$ in similar miombo habitat of Tanzania's Katavi National Park (Caro, 1999). However, areas with higher biomass of preferred prey not surprisingly also support higher densities of lion (Hayward, O'brien & Kerley, 2007); Kenya's Masai Mara supports 0.2–0.3 lions $km^{-2}$ (Ogutu & Dublin, 1998), and Tanzania's Ngorongoro Crater supports 0.3 lions $km^{-2}$ (Kissui, Mosser & Packer, 2010). Lion densities vary temporally, spatially and with different management regimes. For example, densities in the 250 $km^2$ Ngorongoro Crater have varied from 0.04 to 0.40 lions $km^{-2}$ from 1963 to 2003 (Kissui & Packer, 2004). Similarly, studies from an area of 2,500 $km^2$ in the Serengeti have shown that lion density has varied over time (Packer *et al.*, 2005a) and is also habitat dependent, with adult densities varying from 0.03 to 0.06 $km^{-2}$ in the short grass plains to 0.2–0.3 $km^{-2}$ in woodland edge habitats by rivers. This Serengeti population had on average larger prides in larger territories than our Matambwe study population. Moreover, recent work from Zimbabwe showed a decrease in lion territory size following a moratorium on trophy hunting (Davidson *et al.*, 2011).

Matambwe supported a total lion density of 0.14 $km^{-2}$ in 2009, and this density appears to have changed little since 1997. Furthermore, the Matambwe densities also match those predicted through computer modelling of lion densities across Africa (Loveridge & Canney, 2009). This initially suggests that lions are successfully conserved in the region. However, human–lion conflict, particularly man-eating, is a problem in this area (see Packer *et al.*, 2005b, 2011b), and two of the three collared lions were lost during our study, and their collars were subsequently found in bordering villages (Fig. 2; Dakawa and Duthumi). While we could not determine whether the deaths were a result of human–lion conflict, such conflict has been reported in the area: a lion killed a person on 6 June 2008 (Fig. 2; Duthumi), and a subadult male lion was killed on 3 September 2008 (Fig. 2; Zom Gomero). A further cause of concern comes from comparisons of the sex ratio of the Matambwe lion population, which has changed from 1 male to 1.3 females in 1997 to one male to three females in 2009. Such changes in the sex ratio are often indicative of unsustainable male trophy hunting (Rodgers, 1974; Loveridge *et al.*, 2007), which tie in with recent studies of lion trophy hunting off-take from SGR and across Tanzania showing that hunting decreased by 50% between 1998 and 2008, with the steepest declines occurring where hunting is most intensive (Packer *et al.*, 2009, 2011a,b). However, comprehensive data from Serengeti National Park have shown lions can recover relatively quickly (~5 years) from large-scale population losses as long as their prey-base and habitat remain intact (Packer *et al.*, 2005a), and our baseline data from the Msolwa sector may also support such evidence.

The need for rapid assessments of lion populations is often driven by political pressure, such as a response to increased human–wildlife conflict or drops in the number of trophy lions being shot. However, there is no quick way to collect such data, and long-term studies will always be needed when studying these cryptic carnivores. This requires high levels of consistent funding and support, which precludes their widespread application. Our results show the value of call-up surveys, which are relatively inexpensive and can be used to census shy animals such as those hunted individuals from SGR. However, our results also show the value of combining call-ups with a detailed individual identification project. For example, it is only through these more intensive studies that we could calibrate the response distances in the hunting blocks, confirm that the Matambwe population has remained relatively stable for more than a decade, but that there has been a marked change in the adult sex ratio. This last point is vital because the main driver for studying lion populations in SGR is the concern over unsustainable trophy hunting (Rodgers, 1974; Creel & Creel, 1997; Packer *et al.*, 2011a). Moreover, recent work suggests that spoor transects have the potential to offer much more reliable lion census data at comparatively low costs (Funston *et al.*, 2010), and this will be the focus of future lion monitoring efforts in SGR.

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