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Detecting declines of apex carnivores and evaluating their causes: An example with Zambian lions

Elias Rosenblatt [a,b,*], Matthew S. Becker [a,b], Scott Creel [a,b], Egil Droge [a,b], Thandiwe Mweetwa [a,c], Paul A. Schuette [a,b], Fred Watson [a,d], Johnathan Merkle [a], Henry Mwape [a]

[a] Zambian Carnivore Programme, Mfuwe, Eastern Province, Zambia
[b] Department of Ecology, Montana State University, Bozeman, MT 59717, USA
[c] School of Natural Resources and the Environment, University of Arizona, Tuscon, AZ 85721, USA
[d] Division of Science and Environmental Policy, California State University Monterey Bay, CA 93955, USA

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A B S T R A C T

Large carnivores are in rapid global decline, with a broad array of consequences for the ecosystems they inhabit. To efficiently detect and address these declines requires unbiased and precise demographic data. Unfortunately, the characteristics that make large carnivores extinction-prone also pose serious challenges to obtaining these data. Rapid survey methods exist, but provide only relative measures of abundance, cannot detect declines before they become large, and provide little or no information about the causes of decline. African lions (*Panthera leo*) are declining throughout their range, making accurate monitoring of remaining populations urgent. We provide statistically rigorous estimates of population size, trends, survival rate and age–sex structure from Zambia's South Luangwa lion population from 2008 to 2012, just prior to cessation of hunting in 2013. Mark-recapture models fit to data from intensive monitoring of 210 individual lions in 18 prides and 14 male coalitions indicated a declining population, low recruitment, low sub-adult and adult male survival, depletion of adult males, and a senescing adult female population. Trophy hunting was the leading cause of death, with 46 males harvested. Based on these data we recommend continuing the hunting ban at least to 2016 to allow recovery, with substantially reduced quotas, age-limits, and effective trophy monitoring mandated thereafter should hunting resume. Similar data from intensive monitoring of key Zambian lion populations is required to evaluate effects of the hunting ban and provide management guidance. Effectively integrating intensive long-term monitoring and rapid survey methods should be a priority for future management and monitoring of carnivore species.

1. Introduction

The decline and extinction of large carnivores is one of the most pervasive human impacts on earth's ecosystems (Vitousek et al., 1997). While our understanding of carnivores' strong ecological effects continues to broaden (Estes et al., 2011), losses continue to accelerate, and the majority of the world's large carnivores are currently threatened (Ripple et al., 2014). Large carnivores are typically low-density, wide-ranging, and elusive, with a propensity to conflict with humans; consequently, these species are very sensitive to human impacts even in protected areas, and often require large areas of relatively intact, contiguous tracts of habitat (Woodroffe and Ginsberg, 1998; Brashares et al., 2001; Woodroffe, 2000; Cardillo et al., 2004; Creel et al., 2013). Demographic data are of prime importance to inform and guide conservation efforts, but the characteristics that make large carnivores extinction-prone also hinder the collection of these data, particularly when populations are small and declining.

Population monitoring to describe dynamics typically yields data constrained by a trade-off between scale and precision. Intensive long-term studies of known individuals provide good precision (e.g. Packer et al., 1998; Peterson, 1999; Kelly and

Abbreviations: GMA, Game Management Area; IOA, indices of abundance; SLNP, South Luangwa National Park; ZAWA, Zambia Wildlife Authority; ZCP, Zambian carnivore programme.

* Corresponding author at: Department of Ecology, Montana State University, Bozeman, MT 59717, USA. Tel.: +1 406 994 5646.

E-mail addresses: elias@zambiacarnivores.org (E. Rosenblatt), matt@zambiacarnivores.org (M.S. Becker), screel@montana.edu (S. Creel), egil@zambiacarnivores.org (E. Droge), thandiwemweetwa@gmail.com (T. Mweetwa), paul@zambiacarnivores.org (P.A. Schuette), fwatson@csumb.edu (F. Watson), johnathan@zambiacarnivores.org (J. Merkle), hmwape@gmail.com (H. Mwape).

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Durant, 2000), but are rare and relatively small scale due to their logistical difficulty, expense, and time-consuming nature (Durant et al., 2007). Consequently, a variety of rapid and economical survey methods have been developed to monitor large carnivore populations, including spoor counts (Van Dyke et al., 1986; Stander, 1998; Houser et al., 2009; Funston et al., 2010; Ferreira et al., 2013; Bauer et al., 2014; Midlane et al., 2014), audio lures (Ogutu and Dublin, 1998; Mills et al., 2001; Kiffner et al., 2008; Ferreira and Funston, 2010; Cozzi et al., 2013; Groom et al., 2014), camera trapping (Karanth and Nichols, 1998; Jackson et al., 2006; Balme et al., 2009; Karanth et al., 2011; Schuette et al., 2013), distance sampling (Durant et al., 2011), detection dogs (Smith et al., 2001), extrapolation from prey density (Karanth et al., 2004), and noninvasive genetic surveys (Kohn et al., 1999; Creel et al., 2003; Mondol et al., 2009; Creel and Rosenblatt, 2013). While these survey methods avoid some of the constraints inherent to intensive monitoring of known individuals, they often provide population estimates with confidence intervals so broad that they provide little guidance for management and conservation. Large (or unmeasured) variance in estimates of population size remains a substantial impediment to detecting carnivore declines, prioritizing areas for conservation, and assessing the effectiveness of management actions.

This problem is exemplified with Africa's largest carnivore, the lion (*Panthera leo*), which has declined throughout its range (Riggio et al., 2012) due to a combination of prey depletion and habitat loss, direct conflict and retaliatory killing, wire-snare poaching, and trophy hunting (Yamazaki, 1996; Ogada et al., 2003; Loveridge et al., 2007, 2010; Bauer et al., 2013; Packer et al., 2009, 2011; Becker et al., 2013a; Groom et al., 2014). The broad range of threats to lion population viability creates an urgent need for accurate data to describe population trends, identify underlying demographic changes and understand their causes. To assess lion density and monitor trends through time, indices of abundance (IOA; Conroy, 1996) such as spoor counts (Stander, 1998) have been widely adopted. While spoor counts can provide unbiased estimates of lion population size, the precision of these estimates must be carefully considered in assessments of lion and other large carnivore populations. As noted by Midlane (2014), the coefficient of variation has been calculated incorrectly in a sequence of studies that have used spoor counts to estimate lion density, in a manner that substantially over-estimates the method's precision (Stander, 1998; Funston et al., 2010; Ferreira et al., 2013; Bauer et al., 2014). Consequently, the ability of spoor counts to describe and evaluate trends in lion populations has been overstated. Another common lion monitoring strategy employs audio playback experiments (i.e. call-in surveys). These population estimates also have low precision and can be biased by variation in detection probability and methodology (Mills et al., 2001; Whitman, 2006; Kiffner et al., 2009; Brink et al., 2012; Cozzi et al., 2013). While IOA for lions and other carnivores are important conservation tools, precise estimates of population density, trends and vital rates and information about the probable causes of demographic patterns still depend primarily on intensive monitoring of known individuals.

Zambia is one of eight remaining African countries containing a lion stronghold (Riggio et al., 2012); however its lion populations are geographically and numerically limited by human encroachment, direct mortality due to wire-snare poaching by-catch, prey depletion due to poaching, trophy hunting, disease, and human-lion conflict (Yamazaki, 1996; ZAWA, 2009; Becker et al., 2013a, 2013b; Berentsen et al., 2013; Watson et al., 2013, 2014; Midlane et al., 2014; Lindsey et al., 2014). The relative importance of these factors, their trends through time, and the associated demographic impacts on lions are poorly understood. In response to growing concern over the status of Zambian lions and a lack of data on population size, distribution, and trends, the Zambia Wildlife Authority (ZAWA) developed a National Conservation Strategy and Action Plan for the Lion, with the overall intent being "... to establish a science-based Conservation Strategy and Action Plan for the African Lion" (ZAWA, 2009). In January 2013, the government of Zambia enacted a ban on lion trophy hunting due to concern over potentially excessive quotas, alleged mismanagement, possible lion declines, and a lack of scientific data to assess the status of lions and other species (Mfula, 2013). To address these issues we use data from intensive monitoring of known individuals in a five-year (2008–2012) study of lions in South Luangwa National Park (SLNP) and the adjacent Lumimba and Lupande Game Management Areas (GMAs) to estimate age- and sex-specific survival rates and population size, density and growth rate using mark-recapture models. We use these results to evaluate lion management policies in Zambia, and more broadly as an example of the importance of intensive monitoring for detecting, understanding and addressing large carnivore declines.

2. Material and methods

2.1. Study area and data collection

Our 2775 km^2 intensive study area was located along the eastern boundary of SLNP and the adjoining Lupande and Lumimba GMAs, which collectively support a substantial portion of Zambia's largest lion population and its prime photo tourism and trophy hunting area (Fig. 1; ZAWA, 2010). While national parks are strictly protected, GMAs are IUCN Category VI areas that serve as buffer zones to national parks and allow human settlement and a variety of natural resource-based uses (Dudley, 2008; Chomba et al., 2011), including trophy hunting of male lions (Yamazaki, 1996; Becker et al., 2013b; see Section 4.3). Our study area thus encompassed two wildlife management regimes, with associated variations in human influence, available habitats, and potential prey.

The study area included a mosaic of edaphic grassland, deciduous riparian forest, miombo (*Brachystegia* spp) woodland, mopane (*Colophospermum mopane*) woodland and scrubland, dry deciduous forest, and undifferentiated woodland (Astle, 1988; Astle et al., 1969; White, 1983). The perennial Luangwa River forms most of the eastern border of the park, though lions and other wildlife move freely between SLNP and adjacent GMAs. The Luangwa valley experiences two distinct seasons: a rainy season (December–April) with extensive flooding and a dry season (May–November). Within the dry season, there is a cold dry season (May–August) and a hot dry season (September–November). Both wildlife and human activity is centered along the Luangwa River at the boundary of SLNP and adjacent GMAs, particularly during the height of the dry season when water is severely restricted.

We recorded all lion sightings from intensive monitoring of known individuals in 18 prides and 14 male coalitions (hereafter referred to as 'coalitions') from 2008 to 2012, during which all lions were individually-identified using whisker-spot patterns, scarring, and tooth breakage (Pennycuick and Rudnai, 1970; Becker et al., 2013a). Since mid-2009, with permission from the Zambia Department of Veterinary and Livestock Development and ZAWA, we radiocollared one adult female lion in each of eight resident prides and one adult male lion in each of five resident male coalitions, using a combination of VHF and GPS collars. Because lions live in stable social units, VHF radio collars allowed regular resighting of uncollared individuals in our focal study groups, allowing for close monitoring of population size and survival. Data from peripheral, uncollared prides and coalitions sighted opportunistically were used in conjunction with sighting data from the collared resident prides and coalitions, with the presence or absence of a collar considered in statistical analysis.