Biological Conservation 201 (2016) 160–168

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Aging traits and sustainable trophy hunting of African lions

Jennifer R.B. Miller [a,*], Guy Balme [a], Peter A. Lindsey [a,b], Andrew J. Loveridge [c], Matthew S. Becker [d,e], Colleen Begg [f], Henry Brink [g], Stephanie Dolrenry [h], Jane E. Hunt [c], Ingela Jansson [i], David W. Macdonald [c], Roseline L. Mandisodza-Chikerema [j], Alayne Oriol Cotterill [k], Craig Packer [l], Daniel Rosengren [m], Ken Stratford [n], Martina Trinkel [o], Paula A. White [p], Christiaan Winterbach [q], Hanlie E.K. Winterbach [q], Paul J. Funston [a]

[a] Panthera, 8 West 40th Street, 18th Floor, New York, NY 10018, USA
[b] Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
[c] Wildlife Conservation Research Unit, Zoology Department, Oxford University, Tubney House, Abingdon OX135QL, UK
[d] Zambian Carnivore Programme, Box 80, Mfuwe, Eastern Province, Zambia
[e] Conservation Biology and Ecology Program, Department of Ecology, Montana State University, 310 Lewis Hall, Bozeman, MT 59717, USA
[f] Niassa Carnivore Project, The Ratel Trust, Cape Town, South Africa
[g] Selous Lion Project, PO Box 34514, Dar es Salaam, Tanzania
[h] Department of Biological Sciences, Conservation Conflict Research Institute, University of Cape Town, Rondebosch 7701, South Africa
[i] Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE- 901 83 Umeå, Sweden
[j] Zimbabwe Parks and Wildlife Management Authority, PO Box CY140, Causeway, Harare, Zimbabwe
[k] Ewaso Lions, PO Box 14996, Nairobi 00800, Kenya
[l] Department of Ecology, Evolution & Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, MN 55108, USA
[m] Frankfurt Zoological Society, Bernhard-Grzimek-Allee 1, 60316 Frankfurt am Main, Germany
[n] Ongava Research Centre, Ongava Game Reserve, PO Box 58, Okaukeujo, Namibia
[o] School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville Campus, Private Bag 54001, Durban 4000, South Africa
[p] Center for Tropical Research, Institute of the Environment and Sustainability, University of California Los Angeles, 619 Charles E. Young Drive East, Los Angeles, CA 90095, USA
[q] Centre for Wildlife Management, University of Pretoria, Pretoria, South Africa

ARTICLE INFO

Article history:
Received 14 March 2016
Received in revised form 17 June 2016
Accepted 3 July 2016
Available online xxxx

Keywords:
Age-based hunting quota
Age determination
Minimum age threshold
Panthera leo
Pre-mortem aging
Sustainable harvest

ABSTRACT

Trophy hunting plays a significant role in wildlife conservation in some contexts in various parts of the world. Yet excessive hunting is contributing to species declines, especially for large carnivores. Simulation models suggest that sustainable hunting of African lions may be achieved by restricting offtakes to males old enough to have reared a cohort of offspring. We tested and expanded criteria for an age-based approach for sustainably regulating lion hunting. Using photos of 228 known-age males from ten sites across Africa, we measured change in ten phenotypic traits with age and found four age classes with distinct characteristics: 1–2.9 years, 3–4.9 years, 5–6.9 years, and ≥7 years. We tested the aging accuracy of professional hunters and inexperienced observers before and after training on aging. Before training, hunters accurately aged more lion photos (63%) than inexperienced observers (48%); after training, both groups improved (67–69%). Hunters overestimated 22% of lions <5 years as 5–6.9 years (unsustainable) but only 4% of lions <5 years as ≥7 years (sustainable). Due to the lower aging error for males ≥7 years, we recommend 7 years as a practical minimum age for hunting male lions. Results indicate that age-based hunting is feasible for sustainably managing threatened and economically significant species such as the lion, but must be guided by rigorous training, strict monitoring of compliance and error, and conservative quotas. Our study furthermore demonstrates methods for identifying traits to age individuals, information that is critical for estimating demographic parameters underlying management and conservation of age-structured species.

1. Introduction

Trophy hunting can play a significant role in wildlife conservation by incentivising the conservation of animals and land in exchange for recreational use. In Africa, hunting motivates the retention of vast blocks of state property for wildlife, generates over US$200 million annually across >20 countries, and encourages wildlife-based land uses on large areas of community and private lands (Di Minin et al., 2015; Lindsey et al., 2007; Naidoo et al., 2016). However, poorly managed hunting can negatively affect animal populations by reducing genetic variation, increasing stress levels, changing animal behavior, and driving species decline (Aryal et al., 2015; Burke et al., 2008; Keehner et al., 2015; Packer et al., 2009; Rodríguez-Muñoz et al., 2015). Excessive

* Corresponding author.
E-mail address: jmiller@panthera.org (J.R.B. Miller).

http://dx.doi.org/10.1016/j.biocon.2016.07.003
0006-3207/

trophy hunting has recently led to localized unsustainable exploitation of ecologically and economically-important species, including elephants (Selier et al., 2014), leopards (Pitman et al., 2015), and lions (Bauer et al., 2015). The negative impacts of hunting in some areas contributed to 'Cecil-gate' in 2015, prompting global public outcry and scrutiny over the use of trophy hunting as a management tool (Di Minin et al., 2015; Lindsey et al., 2016). In light of this recent media spotlight and increasing anthropogenic threats to species, science-based techniques are urgently needed to guide the sustainable management of harvests if trophy hunting is to continue.

Most harvested species, particularly long-lived large mammals, exhibit age and sex specific rates of survival and reproduction (Milner-Gulland et al., 2007). Thus, age is a common metric used to guide the sustainable harvest and management of wildlife, including large carnivores, ungulates, and fish (Balme et al., 2012; Bender et al., 1994; Berkeley et al., 2004; Garel et al., 2006; Gipson et al., 2000; Hiller, 2014; Hoefs and Konig, 1984; Lundervold and Langvatn, 2003). Age-based hunting addresses the age-structured nature of populations by harvesting animals at certain age thresholds, which, in combination with conservative quotas, can help reduce negative demographic impacts (Whitman et al., 2004). The success of age-based hunting depends on hunters' abilities to accurately age individuals, and requires traits that indicate relevant age thresholds and are easily discernible in the field. These indicators of age would be equally useful to enforcement authorities for ensuring that trophies meet permitted age thresholds. Because age structure is critical to understanding the dynamics of wildlife populations, determining precise indicators of age at biologically-important life stages is also useful for wildlife research, management and conservation (Delahay et al., 2011; Van Horn et al., 2003). Here we investigate age determination and aging accuracy for African lions in an effort to test the feasibility of using age-based trophy hunting regulations to manage and conserve threatened and economically significant species.

Lions are one of the most highly desired big game trophy species, and ensuring ecological and economic sustainability of lion hunting has been recently prioritised at national and international levels (Lindsey et al., 2013). Lion hunts attract some of the highest mean prices of all trophy species (US$24,000–125,000 per hunt) and produce 5–17% of national gross trophy hunting income in countries where lion hunting is allowed (Lindsey et al., 2012, 2007). Yet lion numbers are declining rapidly: the global population has decreased by as much as 42% over the past 21 years (3 generations) to 20,000–35,000 individuals (Bauer et al., 2015; Riggio et al., 2012). In many areas, excessive trophy harvests have contributed to declines in the southern and eastern African subspecies (Groom et al., 2014; Loveridge et al., 2007; Packer et al., 2011, 2009; Rosenblatt et al., 2014). Concerns over lion population decline led Australia and France in 2015–2016 to ban lion trophy imports and resulted in the United States uplisting some lion subspecies to 'Endangered' on the Endangered Species Act (Milman, 2015; U.S. Fish and Wildlife Service, 2015; Vaughan, 2015).

Modelling studies that have assessed the impact of age-based trophy hunting on lion demography indicate that sustainable trophy hunting may be achieved by restricting offtakes to males old enough to have reared their first cohort of offspring, or ≥5 years of age (note that harvesting females is not sustainable; Edwards et al., 2014; Packer et al., 2009; Whitman et al., 2007, 2004). Following these guidelines, Tanzania, Zimbabwe and Niassa National Reserve in Mozambique began implementing age-based hunting restrictions in 2007–2013. In these on-going programmes, age restrictions are paired with quotas revised annually based on compliance with age limits, whereby operators that harvest males equal or older than 5–6 years are 'rewarded' the following year with an equal or higher quota, and operators harvesting males <4–5 years are 'punished' with reduced quotas (age limits vary between countries; Begg and Begg, 2012; Mandisodza et al., 2009; Wildlife Division, 2012). The implementation of age restrictions has resulted in reduced lion quotas and harvests in all three countries in which they have been implemented. Reduced harvests may be due to greater selectivity on the part of hunters, and/or due to the relatively low number of old male lions in hunted populations. Some professional hunters, safari operators, and conservationists have resisted the implementation of age restrictions, citing insufficient scientific evidence for which physical traits are the most reliable indicators of lion age, and disputing the practicality of accurately aging lions in the field.

Age-based hunting systems require simple methods for aging quarry *pre-mortem* in the field with high precision. In the case of lions, the harvest of younger males (<5 years) has a particularly significant impact due to the removal of individuals before they have raised a litter of cubs to independence and the associated risk of infanticide following the removal of pride males (Whitman et al., 2004). In the countries where age restrictions on lions are in place, lion ages are assessed *post-mortem* based on teeth size, wear, and development (often using dental radiographs) and skull ossification (using weight and cranial sutures; Ferreira and Funston, 2010a; Smuts et al., 1978; Wildlife Division, 2012). The utility of various potential aging cues *pre-mortem* is currently less clear. Only one trait has been suggested as a reliable *pre-mortem* indicator of age: nose pigmentation, which grows darker as lions age (Whitman et al., 2004). However, the correlation between nose pigmentation and age has only been studied in the Serengeti population of lions and doubt has been raised as to whether the relationship holds across Africa (Lindsey et al., 2013). Furthermore, nose darkness can be challenging to assess in the field under varying light and visibility, especially from a distance.

A more practical and effective strategy for aging lions *pre-mortem* would be to identify a suite of traits that that can be collectively referenced to accurately estimate a lion's age, as has been recently done for leopards (Balme et al., 2012). Because professional hunters often use camera trap photographs to identify animals suitable for trophy hunting, and wildlife managers and researchers use photographs to study individuals and monitor populations, characteristics that are easily identifiable from photographs would be especially useful in aging individuals. Previous studies have identified several candidate traits (Ferreira and Funston, 2010a). Males' manes grow with age, however length can be influenced by injury, testosterone, and nutrition (Smuts, 1980; West and Packer, 2002). Mane colour typically darkens with age but can vary with ambient temperature (West and Packer, 2002; West et al., 2006). Facial scarring and slack jowl also increase with age, with older individuals appearing pockmarked and loose-jowled (Schaller, 1972; Smuts, 1980; West et al., 2006). In order for these traits to be used as reliable indicators of age, the relationship with age should ideally show low variation between individuals and across regions to establish consistent aging guidelines. Furthermore, practitioners should be able to easily grasp associations between traits and age to achieve high aging accuracy.

We aimed to identify distinct phenotypic traits for determining *pre-mortem* age and to test the utility of these traits for accurately aging male lions. Using an extensive photo dataset of known-age male lions from ten long-term study sites across eastern and southern Africa, we examined associations between physical characteristics and age in a suite of traits between individual lions and across regions. Finally, we tested how accurately practitioners could age lions with varying levels of hunting experience as well as before and after training. We discuss the applicability of our results for use in the conservation and management of harvested large carnivores and their broader implications for the future conservation of lions and other threatened and economically significant species.

2. Methods

We collected 601 high resolution photographs (≥150 dpi) of 228 known-age male lions (1–16 photos per individual and 92 individuals with >1 photo) from ten long-term study sites across eastern and