Biological Conservation 192 (2015) 268–275

Contents lists available at ScienceDirect

Biological Conservation

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

Big cats kill more livestock when wild prey reaches a minimum threshold

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ARTICLE INFO

Article history:
Received 22 April 2015
Received in revised form 8 August 2015
Accepted 23 September 2015
Available online xxxx

Keywords:
Acinonyx
Human-carnivore conflict
Livestock predation
Panthera
Predator–prey
Prey biomass
Puma

ABSTRACT

Livestock predation by big cats, i.e., lion (*Panthera leo*), tiger (*Panthera tigris*), leopard (*Panthera pardus*), jaguar (*Panthera onca*), snow leopard (*Panthera uncia*), puma (*Puma concolor*), and cheetah (*Acinonyx jubatus*), creates conflicts with humans which challenge biodiversity conservation and rural development. Deficiency of wild prey biomass is often described as a driver of such conflicts, but the question "at which level of prey density and biomass do big cats begin to kill livestock?" still remains unanswered. We applied logistic regression to meta-data compiled from recent peer-reviewed scientific publications and show that cattle predation is high when prey biomass is $<812.41 \pm 1.26$ kg/km^2, whereas sheep and goat predation is high at $<544.57 \pm 1.19$ kg/km^2, regardless of sizes of study areas and species, body masses, and population densities of big cats. Through mapping cases with known prey biomass and case-specific comparison of actual vs. threshold-predicted livestock predation we confirm the reliability of these thresholds in predicting livestock predation by big cats. The map also demonstrates that some protected areas of India, Nepal lowlands, and South Africa contain sufficient prey that makes big cats less likely to kill livestock, but in other sampled areas prey biomass is not high enough and the probabilities of livestock predation are moderate to high. We suggest that these thresholds represent important landmarks for predicting human–felid conflicts, identifying conflict hotspots, and setting priorities for targeted conservation actions. It is essential to maintain and restore wild prey to forestall local extinctions of big cats.

1. Introduction

Mammalian carnivores inflict socio-economic losses to rural livelihoods, mainly due to predation on domestic livestock, and are intensively wiped out because of retaliatory or preventive persecution (Treves and Karanth, 2003; Baker et al., 2008; Gusset et al., 2009; Loveridge et al., 2010). These losses and arising human–carnivore conflicts are particularly strong for small-scale households and near protected areas, thus challenging a synergy between rural development and biodiversity conservation (Treves and Karanth, 2003; Bauer and de Iongh, 2005; Namgail et al., 2007; Baker et al., 2008; Lagendijk and Gusset, 2008; Dar et al., 2009; Loveridge et al., 2010). Encroachment of carnivore habitats by expanding human populations is a potential spark for new conflicts, which deteriorate the complex functioning of the environment at all levels, from individuals to ecosystems (Ripple et al., 2014). Big cats, namely the lion (*Panthera leo*), tiger (*Panthera tigris*), leopard (*Panthera pardus*), jaguar (*Panthera onca*), snow leopard (*Panthera uncia*), puma (*Puma concolor*), and cheetah (*Acinonyx jubatus*), are among the best-known carnivores responsible for conflicts with humans (Inskip and Zimmermann, 2009). Retaliatory killing, poaching and prey loss are the main threats for these species, of which six are classified by the IUCN Red List of Threatened Species as "Endangered" to "Near Threatened" and only puma is still common having the "Least Concern" status (Macdonald et al., 2010).

Albeit the density and biomass of livestock exceed those of wild prey manifold, big cats would prefer to kill wild prey to avoid human retribution (Loveridge et al., 2010). When prey, especially medium-sized and large ungulates, becomes scarce due to population declines or seasonal migrations felids increase predation on livestock to survive (Polisar et al., 2003; Bauer and de Iongh, 2005; Azevedo and Murray, 2007; Kumaraguru et al., 2011; Mondal et al., 2011; Amador-Alcalá et al., 2013; Zhang et al., 2013; Kabir et al., 2014). In some areas, cats kill livestock mostly during the wet season when prey disperses into lush vegetation, regains fitness and thus becomes less available, whereas livestock enters these areas for uncontrolled grazing (Polisar et al., 2003; Patterson et al., 2004; Kissui, 2008). In other areas, livestock predation is minimal during winter when prey attains high densities in certain areas with little snow (Dar et al., 2009) or it is maximal during the dry season when limited cover decreases hunting success, prey moves away and livestock concentrates around a few waterholes (Schiess-Meier et al., 2007). Overall, the relationships between prey availability and livestock predation by big cats appear to be straightforward, but some more intricate cause-and-effect patterns are also possible. For example, Harihar et al. (2011) found out that the natural recovery of prey after relocation of local people has led to a sharp rise, and not a decline as expected, of livestock predation by leopards because recovering tigers displaced them closer to villages. Moreover,

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http://dx.doi.org/10.1016/j.biocon.2015.09.031
0006-3207/

Suryawanshi et al. (2013) concluded that snow leopard predation on livestock may intensify with more abundant prey, presumably because higher stock of prey supports a greater number of cats. Therefore, these authors recommend that prey recovery programs should be accompanied by strengthening livestock protection measures.

If the causality between wild prey scarcity and increased livestock predation is real, then a new question arises: at what threshold levels of prey density/biomass are attacks on livestock triggered? We did not find such information in the scientific literature. Such a threshold may vary with the species, body masses and population densities of big cats, as well as with size of the study areas. Although being similar in regard to obligatory meat eating, big cats may differ in livestock predation patterns due to species-specific ecological properties. For example, snow leopards are known for surplus killing and group-living lions might be expected to kill more livestock than other cats, which are solitary (Jackson et al., 2010; Loveridge et al., 2010). Livestock predation can also be allometric, because large-bodied big cats select cattle and buffaloes, and smaller species usually prefer sheep, goats, and juveniles of larger species (Dar et al., 2009; Zarco-González et al., 2013; Kabir et al., 2014). Population density of felids and other carnivores is positively related to prey biomass and this relationship is so strong that it allows estimating carnivore densities and carrying capacity from current prey resources (Carbone and Gittleman, 2002; Hayward et al., 2007; Carbone et al., 2011). However, this rule relies only on bottom–up processes (carnivores controlled by prey) and fails when ever-increasing top–down processes (carnivores controlled by humans, e.g., via poaching) limit carnivore numbers while prey remains sufficient (Khorozyan et al., 2008; Kiffner et al., 2009; Zhang et al., 2013; Bauer et al., 2014). Unlike other big cats, cheetah density is related more to competition with larger competitors than to prey availability (Carbone and Gittleman, 2002; Carbone et al., 2011). Sizes of study areas are inversely related to carnivore and prey densities, so they can mediate the strength of predator–prey relationships and livestock predation (Carbone and Gittleman, 2002). For instance, for practical reasons prey populations are often studied in relatively small high-density enclaves or protected areas, which may represent the areas of low predation on livestock (Biswas and Sankar, 2002).

In this paper, we (a) study the linkage between livestock predation by big cats, wild prey biomass and above-mentioned confounders, (b) identify and estimate the minimum thresholds of prey biomass that move predation rates up, and (c) discuss these thresholds as a potentially useful metric for assessing and predicting human–felid conflicts.

2. Materials and methods

2.1. Literature

We retrieved peer-reviewed English language scientific articles and book chapters dated 2000–2014 through the ISI Web of Knowledge (http://www.webofknowledge.com) and the IUCN/SSC Cat Specialist Group Digital Library (http://www.catsg.org). Only recent publications were considered to assure the most accurate and consistent data on predictors and confounders, especially on prey biomass, prey density, and cat density, which are particularly demanding for up-to-date research techniques. As information on wild prey density and its derivate prey biomass was a priori assumed to be most limited in livestock predation studies, we used the search words "panthera*livestock", "acinonyx*livestock", "puma*livestock", "panthera*prey density", "acinonyx*prey density" and "puma*prey density". These combinations gave us more output than if we used narrower options, e.g., "panthera*livestock*prey density", because the "*prey density" combination revealed control studies without livestock predation. In an array of publications that met these criteria, we selected those which contained at least some of the predictors and confounders (see below) or held sufficient information so that we could calculate them (Appendix A). Original data are provided in Appendix B. Each publication contained one livestock predation/no predation case (one study area for one big cat species) or more cases (2–5 study areas for a species, e.g. different protected areas in a puma study by Donadio et al. (2010) in which each protected area was considered a separate case). We took the cases as independent if they described different big cat species, areas and/or study periods in the same area. Otherwise, we considered the cases as dependent and lumped them into a single case.

2.2. Input data

The numbers of livestock killed per year, which are reported in publications, usually do not represent actual livestock losses to carnivores. They come mostly from interviews and also from carnivore diets, livestock carcasses, farm reports and authority appraisals for compensation. Interviews may underestimate losses if remote or less and accessible villages are under-represented, if villagers forget cases or if they are reluctant to share information (Holmern et al., 2007; Kissui, 2008). On the other hand, villagers may overestimate losses if they assign other mortality causes to carnivore attacks, if they perceive carnivores as evil disproportionally to actual threat or if they want to attract attention or get compensation (Holmern et al., 2007; Gusset et al., 2009; Suryawanshi et al., 2013). Such biases are common, since in most cases villagers do not get compensations for losses and therefore they are not obliged to accurately document them. Although some authors try to minimize these biases by field verification of reported losses, it is applicable only to the most recent and identifiable cases and when verifying researchers are available on place (Azevedo, 2008; Kabir et al., 2014). Feces and livestock records suffer from low detection probabilities and underestimate livestock losses (Bagchi and Mishra, 2006; Sollmann et al., 2013; but see Wegge et al., 2012). Authority appraisals also tend to underestimate losses because they record only the most recent cases confirmed by carcasses or other irrefutable evidence (Sangay and Vernes, 2008). Farm reports are the most accurate, but their published data are only few (Patterson et al., 2004; Schiess-Meier et al., 2007; Wegge et al., 2012). As a result, inaccurate data on livestock losses may hide a relationship between livestock losses and predictors, which is present but goes undetected (type II error of false negatives, non-detections or underestimations; Zarco-González et al., 2013).

To overcome these issues, we considered livestock predation rates in terms of binary response variables: probability of cattle predation (*CP*) and probability of sheep and goat predation (*SP*). We lumped sheep and goats as "shoats" as they usually graze together and chose cattle and shoats because of their ubiquitous predation by big cats (Inskip and Zimmermann, 2009; Loveridge et al., 2010). We coded *CP* and *SP* as 1 if predation was high and 0 if it was none or minimal as described in references. If a livestock species was not taken, we coded it as 0 only if that species was bred, i.e. available for predation. Alternatively, we left *CP* or *SP* blank, as in the case of shoats not bred on cattle ranches (Rosas-Rosas et al., 2008).

Although the published numbers of livestock kills can be inaccurate, they allow getting an impression of whether livestock losses in a study are high or low, especially when they are discussed further by the authors. Our recent studies (Khorozyan et al., 2015a, in press) showed that the numbers of killed livestock are random and unpredictable while the binary data of high and low predation can be well described and predicted by variables. Dietary studies routinely use the correction factors that estimate the proportions of the numbers of livestock consumed to the numbers of all prey consumed, which are also useful for classifying livestock predation as high or low (Marker et al., 2003; Azevedo, 2008; Athreya et al., in press). The main criterion that we used to separate the cases of high and low predation was whether the studied big cat species depended on livestock as staple food (high