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Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East

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ABSTRACT

Wild tiger numbers continue to decline despite decades of conservation action. Identification, conservation and restoration of tiger habitat will be a key component of recovering tiger numbers across Asia. To identify suitable habitat for tigers in the Russian Far East, we adopted a niche-based tiger habitat modeling approach, including biotic interactions with ungulate prey species, human activities and environmental variables to identify mechanisms driving selection and distribution of tiger habitat. We conducted >28,000 km of winter snow tracking surveys in 2004/2005 over 266,000 km^2 of potential tiger habitat in 970 sampling units ($\sim$171 km^2) to record the presence of tracks of tigers and their ungulate prey. We adopted a used-unused design to estimate Resource Selection Probability Functions (RSPF) for tigers, red deer, roe deer, sika deer, wild boar, musk deer and moose. Tiger habitat was best predicted by a niche-based RSPF model based on biotic interactions with red deer, sika deer and wild boar, as well as avoidance of areas of high human activity and road density. We identified 155,000 km^2 of occupied tiger habitat in the RFE in 17 main habitat patches. Degradation of tiger habitat was most extreme in the southern areas of the Russian Far East, where at least 42% of potential historic tiger habitat has been destroyed. To improve and restore tiger habitat, aggressive conservation efforts to reduce human impacts and increase ungulate densities, tiger reproduction and adult survival will be needed across all tiger habitat identified by our tiger habitat model.

1. Introduction

The precipitous decline in wild tiger (*Panthera tigris*) numbers over the past century has received wide attention (Dinerstein et al., 2007; Walston et al., 2010) and has generated a recent high-profile global conservation response (Global Tiger Initiative, 2010). In 2010, the political leaders of the 13 tiger range nations met in St. Petersburg and boldly committed to “double the number of wild tigers across their range by 2022”. Habitat loss is generally recognized as one of the three key threats driving the tiger decline (along with poaching and prey depletion) with an estimated 93% of tiger habitat lost in the last century (Dinerstein et al., 2007). One of the primary means to achieve the Global Tiger Initiatives bold goal is the identification, conservation and restoration of tiger habitat (Dinerstein et al., 2007; Smith et al., 1998; Wikramanayake et al., 2011).

Many large-scale habitat-modeling exercises are often forced to rely on incomplete information about habitat parameters. With few exceptions, it has only been recently that extensive

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countrywide surveys have been conducted to fully map tiger distribution (Jhala et al., 2011; Miquelle et al., 2006; Wibisono et al., 2011). Yet, even with these extensive surveys, the next step of identifying high quality habitats for tigers has not always been conducted, making it difficult to prioritize habitat conservation. For instance, the earliest tiger habitat modeling identified 1.5 million square kilometers of suitable habitat across tiger range using coarse landcover-based information (Wikramanayake et al., 1998). Subsequent conservation planning identified 20 Global priority tiger conservation landscapes (TCL's) necessary to secure the fate of tigers (Dinerstein et al., 2007). Yet, Walston et al. (2010) suggested prioritizing within these TCL's to protect putative source sites based solely on their protected status and potential to hold breeding females. This 'source site' strategy was quickly criticized with, again, large-scale analyses that suggest that achieving the GTI objective of doubling wild tiger populations requires conserving much more than just these core areas (Wikramanayake et al., 2011). Despite the advances in the political will to conserve tigers with the Global Tiger Initiative, however, we still do not have rigorous empirical identification of the basic components of tiger habitat in many TCL's, an understanding of habitat quality, nor empirical evidence of what differentiates sites where reproduction is actually occurring from other tiger habitat. Without a stronger foundation for tiger habitat ecology and conservation, the debate about whether core sites or an entire TCL is required will remain unresolved, potentially distracting conservation efforts.

It is widely acknowledged that, aside from anthropogenic factors, prey abundance and distribution (Karanth et al., 2004) are the key factors driving demography of large carnivores (Carbone and Gittleman, 2002; Karanth et al., 2004; Miquelle et al., 1999; Mitchell and Hebblewhite 2012). Large carnivores such as tigers are habitat generalists, and therefore habitat may be more aptly defined from a niche-based perspective (Gaillard et al., 2010; Mitchell and Hebblewhite, 2012), i.e., as the abiotic and biotic resources and conditions that are required for occupancy, reproduction, and, ultimately, demographic persistence (Gaillard et al., 2010; Mitchell and Hebblewhite, 2012). Most previous tiger habitat modeling approaches used instead a functional habitat mapping approach based, necessarily, on broad-scale landcover or vegetation (Linkie et al., 2006; Wikramanayake et al., 2004). Such approaches are limited in their ability to provide a mechanistic understanding of habitat or identify parameters associated with high reproductive rates or adult female survival, e.g., high quality habitat. We hypothesize that a niche-based approach provides a conceptually stronger method to understand the drivers of habitat selection, and are therefore potentially more valuable for conservation planning. Practically, however, detailed information on prey abundance, especially over large landscapes, is rare. Yet there is a growing recognition in large carnivore and tiger habitat modeling of the importance of understanding prey distribution at large landscape scales for conservation (Barber-Meyer et al., 2013; Hebblewhite et al., 2012; Zhang et al., 2013).

Anthropogenic factors are as important as prey abundance and distribution in determining habitat quality, since virtually the entirety of large carnivore habitat today is under the influence of humans (Crooks et al., 2011; Ripple et al., 2014). This is especially true for wild tigers who face the booming economies and burgeoning human populations of Asia, given that human activity is known to decrease adult and cub survival (Kerley et al., 2002). Therefore, the best approach to defining quality tiger habitat for conservation planning would combine large-scale measures of abiotic conditions, prey resources, and human activity. Such an approach would provide a means of not only identifying habitat, but may allow definition of breeding habitat as well as a means for assessing risk for habitat across the landscape, further assisting the conservation process.

This is an ambitious goal for tigers because of the challenges of collecting range-wide information on prey. Fortunately, there is an opportunity to adopt this approach in the Russian Far East, the only country where tigers have recovered from the verge of extinction, providing a valuable opportunity to assess habitat requirements in a recovered population. Rough estimates suggest that a population in 1940 of only 30–40 Amur tigers (*P. tigris altaica*) recovered to an estimated 430–500 in 2005 (Miquelle et al., 2006). This recovery process has been documented via large-scale surveys that have attempted to map distribution and estimate tiger numbers based on the distribution and abundance of tracks in the snow (Miquelle et al., 2006). While there are multiple problems with converting information on track abundance into population estimates (Hayward et al., 2002; Miquelle et al., 2006; Stephens et al., 2006), the information obtained during recent surveys, where track locations of both tigers and prey have been carefully mapped, provide an extensive data set for determining habitat quality for tigers in the Russian Far East.

We used existing data on location of tracks, collected during a 2005 survey over the entire 266,000 km^2 range of tigers in the Russian Far East to identify biotic and abiotic drivers of tiger habitat. Conducting such an analysis for the entire Amur tiger population in Russia is particularly challenging because preferred prey, forest types, and human densities vary greatly across the range of tigers. For instance, while wild boar (*Sus scrofa*) appear to be a preferred prey throughout tiger range (Hayward et al., 2012), sika deer (*Cervus nippon*) are the primary prey only in the southern part of Amur tiger range, while red deer (*Cervus elaphus*) are the most common prey item for Amur tigers further north (Miquelle et al., 2010). Incorporation of such variability with regionalized modeling may better predict habitat. Thus, our goals were to: (1) estimate non-prey based habitat parameters that best define potential habitat for Amur tigers using resource selection probability function (RSPF) models (Boyce and McDonald, 1999); (2) develop a suite of RSPF models for ungulate species that could be incorporated into the process of modeling tiger distribution; (3) test the biotic interaction hypothesis that including prey distribution and abundance in RSPF models for tigers improves predictive power of such models; (4) test for regional differences in prey-based resource selection by Amur tigers; (5) use data on the occurrence of females with cubs (family groups can be easily distinguished from track characteristics) to test the hypothesis that tiger habitat quality is correlated with habitat for successful reproduction of Amur tigers in Russia; and finally (6) to operationally define tiger habitat and use the outcomes of this process to identify priority areas of high risk for habitat conservation.

2. Methods

2.1. Study area

Our study area was defined by the range of Amur tigers in the Russian Far East, an area of 266,000 km^2 (Miquelle et al., 1999) in the provinces of Primorye and Khabarovsk, with 95% in the Sikhote-Alin mountains and 5% in the Changbaishan mountains along the Russian–Chinese border (Fig. 1). There are probably less than 400 adult and subadult tigers in Russia (Miquelle et al., 2006), and less than 20 in China (Hebblewhite et al., 2012). This Tiger Conservation Landscape (TCL) (Dinerstein et al., 2007) represents a merger zone of two bioregions: the East Asian coniferous-deciduous complex and the northern boreal (coniferous) forest, resulting in a mosaic of forest, bioclimatic and human land-use types. Mountains in the Sikhote-Alin range from 500 to 800 m (max 1200 m). Over 72% of Primorye and southern Khabarovsk is forest covered. The original dominant forest was a mixture of Korean pine (*Pinus*