AMUR TIGER PREDATION AND ENERGETIC REQUIREMENTS IN THE RUSSIAN FAR EAST: NEW INSIGHTS FROM GLOBAL POSITIONING SYSTEM COLLARS

By

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Amur tiger predation and energetic requirements in the Russian Far East: new insights from Global Positioning System collars

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ABSTRACT

The IUCN Red List has classified all subspecies of tigers (*Panthera tigris*) as endangered with prey depletion being widely recognized as one of the primary drivers of tiger declines. Due to substantial energetic requirements, tigers can only survive and reproduce in areas with healthy prey populations. This may be particularly important for Amur tigers (*P. t. altaica*) in the Russian Far East, living at the northern limits and with the lowest prey densities of any tiger population. Few studies have been able to rigorously investigate annual prey requirements for any tiger population. We deployed Global Positioning System (GPS) collars on Amur tigers to study annual kill rates and energetic requirements in the Russian Far East. We captured and radio-collared 5 adult tigers from 2009 – 2011 in and around the Sikhote-Alin Biosphere Zapovednik (Reserve) in the Russian Far East. We used GPS locations and 62 known kill sites to build a logistic regression model to predict kills from GPS location clusters. Our top model for predicting kill sites included a temporal component and fidelity to site as covariates (overall classification success 87.11%; ROC = 0.854). Empirical evidence suggests Amur tigers made a kill once every 8.3 days (95% CI 7.2–9.4) and consumed an average of 7.5 kg/day (95% CI 7.4–7.6). We then used empirical movement rates and activity budgets derived from GPS data to estimate the daily energetic requirements for tigers to maintain a subsistence diet. Overall movement rates averaged 888.3 meters/hour, and 6.6 km/day. Our energetics model suggests an average male tiger needs to consume a minimum of 4.9 kg/day, a non-reproductive tigress 3.6 kg/day, and a reproductive tigress raising an average sized litter 7.3 kg/day to maintain a positive energy balance. These are minimum estimates, but clearly illustrate the importance of large ungulate prey because maximum tiger reproduction may require 300% above the average sustenance requirements. This information is critical for conservation and emphasizes that success of current efforts to reverse tiger declines will be defined by managers' ability to conserve large ungulates to ensure an adequate prey base for recovering tiger populations.

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policy with me and offered constructive suggestions and helpful advice at every step. I feel privileged to have Joel and Mike on my graduate committee.

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CHAPTER 1: INTRODUCTION

In an unprecedented action to save a rapidly diminishing wildlife species, government leaders from all 13 tiger range countries gathered in St. Petersburg, Russia in November 2010 to discuss efforts to save tigers (*Panthera tigris*) from extinction (Global Tiger Recovery Program 2010). At the end of this 3-day meeting, all 13 leaders endorsed the Global Tiger Recovery Program, with a primary goal of doubling the number of wild tigers by 2022. Although tigers are consistently threatened throughout their range, the primary threats to tiger populations vary between and within tiger range countries. For example, Amur tigers (*P. t. altaica*) in the Russian Far East live in mostly large, contiguous blocks of forest but the prey populations they rely on are declining (Miquelle et al. 1999), whereas tigers in some SE Asian countries often have plenty to eat but little room for dispersal or range expansion due to habitat loss and fragmentation (Wikramanayake et al. 1998).

There will not be one solution to bringing back the world's tigers; rather it will take a variety of conservation measures taken in a variety of places. Within this multitude of conservation actions, however, sufficiently high ungulate densities are the foundation on what any recovering tiger population depends. Poaching and legal subsistence hunting have led to the empty forest syndrome (Redford 1992) throughout much of Asia where intact forests are depopulated of large ungulate prey – the main prey required for persistence of tiger populations. Recently, Hayward et al. (2012) reviewed the literature to define the preferred prey and preferred prey weight ranges of tigers and this information will help land managers develop strategies that benefit these key prey species. What remains to be clearly defined are the prey requirements and kill rates of tigers.

Many studies have addressed this aspect of tiger ecology (Sunquist 1981; Yudakov & Nikolaev 1987), but none have harnessed the recent technological advances in our field to rigorously estimate kill rates across all seasons. Russian scientists have been publishing research of Amur tigers for almost a century (Baikov 1925) and the first empirically-derived kill-rate estimate was published nearly 40 years ago by extrapolating winter observations into an annual estimate (Yudakov 1973). Many others have built on these pioneering efforts, primarily relying on snow tracking methods that became so popular in the temperate climate that is unique to Amur tigers (Kovalchuk 1988; Kucherenko 1993; Pikunov 1988; Zhivotchenko 1979). In 1992, the Wildlife Conservation Society and the Siberian Tiger Project started deploying Very High Frequency (VHF) collars on tigers and investigating annual food habits (Miquelle et al. 1996), but small prey items may be underrepresented using this approach and a kill rate was unestimable from these summer data. Intensive snow-tracking studies of individual tigers, such of those of Yudakov and Nikolaev (1987), should provide the most precise data on winter kill rates, assuming kills are not missed during tracking sessions. Unfortunately, recent research has highlighted the dangers of extrapolating large carnivore kill rates collected only during winter without adjusting for expected seasonal differences (Metz et al. 2012; Sand et al. 2008). Recent advances in Global Positioning System (GPS) collars have enabled researchers to gain detailed predation data that was used to estimate kill rates for a variety of large felids (Cavalcanti & Gese 2010; Knopff et al. 2010).

My Master's thesis is the first project to use GPS technology to expand existing scientific knowledge of year-round tiger-prey dynamics in the Russian Far East, to improve kill-rate estimation methods, and contribute practically to sustainable wildlife management. This thesis is divided into two main chapters concerning Amur tiger kill rates and prey requirements. In chapter 2, I developed methods for estimating kill and consumption rates from GPS data to estimate annual kill rates on large ungulates in the Russian Far East. I then compare our results to previous estimates of tiger kill rates from snow tracking in the Russian Far East and VHF tracking in Chitwan National Park, Nepal, as well as to other GPS-based kill rate estimates from other large felids. This exploration of annual kill rates offered insights into summer predation patterns and the risks of extrapolating kill rate estimates from winter to annual estimates of tiger's impact on large ungulates.

These annual consumption rate estimates from a tiger population living in a protected area with an adequate prey base adds to the understanding of tiger-prey dynamics. However, more information is needed to aid in the recovery of tiger populations across their largely unprotected range where prey densities are often suppressed through poaching and legal hunting. Determining the threshold consumption rate for survival and reproduction is important as we guide prey population recovery across tiger range because an impoverished prey base may not support reproduction (Karanth & Stith 1999). Accordingly, in chapter 3, I develop an energetics model to estimate the prey requirements for tigers to survive and reproduce in the wild. I used empirically-derived movement rate estimates and activity budgets from GPS data to estimate tiger energetic requirements. I then determined the consequences of these requirements in terms of predicted prey requirements in single and multi-prey communities. Quantifying the energetic requirements of tigers allows scientists and managers to estimate nutritional carrying capacity (Hobbs 1989; Laundre 2005), estimate the impact of tigers on prey, and develop science-based conservation recommendations (Odden & Wegge 2009).

I develop the tiger energetics model using data from Amur tigers, but also demonstrate its application to Bengal tigers (*P. t. tigris*) in the Bangladesh Sundarbans. It is our hope that this model will allow conservationists to estimate prey requirements and assess which suite of prey is likely to ensure survival and successful reproduction. This information is critical for global tiger recovery efforts, as tiger distribution and dispersal is likely defined by females' ability to acquire sufficient energy to successfully rear young to independence. The conservation implications of this research could help steer conservation efforts to focus on protecting preferred prey populations as a key component of tiger conservation and recovery in an effort to meet the goals of the Global Tiger Recovery Program.

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CHAPTER 2: ESTIMATING AMUR TIGER (*PANTHERA TIGRIS ALTAICA*) KILL RATES AND CONSUMPTION RATES USING GLOBAL POSITIONING SYSTEM COLLARS.

Fewer than 3,500 wild tigers (*Panthera tigris*) remain in the world (Walston et al. 2010). The Global Tiger Recovery Program, a collaborative initiative endorsed by all 13 tiger range countries, aims to double wild tiger numbers globally by 2022 (Global Tiger Recovery Program 2010). Primary threats to tiger persistence include habitat loss and fragmentation across Asia in areas that hold some of the densest and fastest growing human populations in the world (Wikramanayake et al. 1998), over-hunting of prey species (Karanth & Stith 1999; Miquelle et al. 1999b), direct killing of tigers for traditional Chinese medicine (Nowell 2000), and retaliatory killing after tiger-human conflicts (Miquelle et al. 2005a). Roughly ten percent of the world's tigers inhabit the Russian Far East, with one interconnected population representing the vast majority of Siberian, or Amur tigers (*P. t. altaica*). In contrast to other tiger subspecies, tiger range in the Russian Far East consists of large contiguous forests with relatively low human densities. Thus, the primary short-term threats to Amur tigers are not necessarily habitat loss and fragmentation, but declines in ungulate prey caused by unsustainable poaching and hunting (Miquelle et al. 1999b) and direct tiger poaching (Chapron et al. 2008).

Annual ungulate surveys from 1998 to 2009, following Hayward et al. (2002), have documented a steady decline in ungulate prey populations throughout Amur tiger habitat (Miquelle et al. 2007). Uncertainty over actual densities and potential causes for declines of ungulates has resulted in a potential dilemma. Less than 15% of the remaining 156,000 km^2 of tiger habitat in the Russian Far East is protected and hunting of large ungulates – the same species which tigers depend upon - is both legal and a traditional source of protein for local villagers in the remaining unprotected 85% (Miquelle et al. 1999a). In a classic example of conflict between hunters and carnivores, Russian hunters claim that tigers are reducing the amount of prey, yet conservationists maintain over-hunting and poaching is the cause of the reduced prey base. Because Amur tigers require large forested areas (Goodrich et al. 2008) with sufficient ungulate prey and low human disturbance to survive (Kerley et al. 2002) and reproduce (Goodrich et al. 2010; Kerley et al. 2003), tigers and people must find a way to co-exist in the multiple-use forests of the Russian Far East (Miquelle et al. 2005a).

Legal ungulate harvest by human hunters is managed by the Provincial Wildlife Departments of Primorye and Khabarovsk by allocating a harvestable surplus of ungulates to both humans and tigers based on an estimated annual predation rate by the tiger population (Miquelle et al. 2005a). A key to minimizing conflict is the acquisition and application of reliable scientific information about annual prey requirements of Amur tigers to help land managers identify the ungulate densities required to sustain viable tiger populations. Unfortunately, data on kill rates and prey requirements of wild tigers are difficult to obtain, particularly during snow-free months or elsewhere in tiger range. Annual kill rates by Amur tigers are currently estimated by extrapolating winter kill rates from intensive snow tracking efforts (Pikunov 1988; World Wildlife Fund 2002; Yudakov & Nikolaev 1987). Recent research has highlighted the dangers of extrapolating large carnivore kill rates collected during winter without adjusting for expected seasonal differences (Knopff et al. 2010; Metz et al. 2012; Sand et al. 2008). Varying estimates of Amur tiger prey composition (Miquelle et al. 1996; Pikunov 1988; Yudakov & Nikolaev 1987) and kill rates derived from snow tracking methods exist in the Russian literature (Table 2-1). Radio-tracking using Very High Frequency (VHF) technology provides some advantages over snow tracking, but is also limiting because small prey items may be quickly consumed (and therefore underrepresented in VHF datasets) and because intensive monitoring is logistically and financially difficult (Miller et al. 2010). VHF-based kill-rate estimation methods have been applied to tigers in Chitwan, Nepal, but not to any other tiger population (Table 2-1). Recent advances in Global Positioning System (GPS) collars have enabled carnivore researchers to gather detailed location data that can be used to estimate kill rates (e.g., Anderson & Lindzey 2003; Knopff et al. 2009; Webb et al. 2008).

Ultimately, from the tiger's perspective, the goal of allocating prey to tigers based on annual kill rates through management is to ensure that tigers maintain a consumption rate sufficient to survive and reproduce. While kill rate is an important ecological parameter, ultimately it is the consumption rate that matters most for tiger conservation. Metz et al. (2012) showed that interpretations of predation varied significantly depending on the metric used to quantify kill rates. For example, kill rates of wolves (*Canis lupus*) in Yellowstone were highest in summer if looking at kill rate as the number of animals killed per unit time but lowest in summer if looking at kill rate as the biomass acquired per unit time (Metz et al. 2012). Conversion of kill rates (number of prey killed per unit time) to consumption rates (kg of prey consumed per unit time) allows for comparisons between sexes or to studies with different prey species (and sizes) available.

Anderson and Lindzey (2003) were the first to use GPS collars to estimate large felid kill rates. Knopff et al. (2009) built on these pioneering efforts and developed predictive logistic regression models in combination with field efforts to successfully predict >95% of cougar (*Puma concolor*) kills ≥ eight kg. Application of these methods to estimate kill rates of other large cats species also include jaguars (*P. onca*), where Calvancati and Gese (2010) used GPS collars to provide some of the first robust kill-rate estimates of jaguars. While these methods are becoming widespread throughout the carnivore research community for a variety of felids (Appendix A), they have yet to be applied to estimate kill rates of tigers. GPS collars have been deployed on Amur tigers only recently (Miller et al. 2010; Rozhnov et al. 2011) and understanding how kill rates estimated through GPS collars compare to those estimated through snow tracking or VHF technology is important to understanding the accuracy of each method and perhaps for adjusting past estimates for subsequent time series analyses.

Here, for the first time, we develop methods for estimating Amur tiger kill rates and consumption rates from GPS data to estimate annual kill rates on large ungulates in the Russian Far East (Anderson & Lindzey 2003; Knopff et al. 2009; Sand et al. 2008; Webb et al. 2008). We used clusters of locations obtained from GPS collars to detect and examine putative tiger kill sites. Next, we developed a logistic regression model to predict kill sites of ungulate prey from clusters of locations to understand the extent to which GPS-based statistical models predict field observations of kill rates. We then tested whether we could predict kill sites of large ungulate prey using a two-step logistic regression model (Knopff et al. 2009). Despite potential seasonal differences in kill rates because of differential prey size availability, actual intake or consumption rates may remain the same because of seasonal variation in prey size (Metz et al. 2011; Sand et al. 2008). Therefore, we converted kill rates to consumption rates (kg/tiger/day) to understand the energetic consequences of changes in kill rates. Finally, we compared our GPS-based kill rates to previous estimates of tiger kill rates from snow tracking in Russia and VHF tracking in Nepal, as well as to other GPS-based kill rate estimates from other large felids.

STUDY AREA

We conducted our research in and around the 4,000 km^2 Sikhote-Alin Biosphere Zapovednik (SABZ), which has harbored as many as 35 tigers (Smirnov & Miquelle 1999). The SABZ was founded in 1935 and is maintained as an International Union for Conservation of Nature (IUCN) Class I protected area near the village of Terney, Primorski Krai (province), in the Russian Far East (Figure 2-1). SABZ is closed to the public and access is strictly limited to Zapovednik (Reserve) staff and visiting scientists. Inside the Reserve, hunting is illegal and poaching is relatively low, whereas prey populations outside of SABZ are exposed to legal hunting and high poaching rates (Miquelle et al. 2005b). Within SABZ, the Sikhote-Alin Mountains parallel the Sea of Japan with elevations reaching 1,600 m, but most peaks are < 1,200 m. SABZ occurs in the Far Eastern temperate climatic zone and is characterized by strong seasonality with dry, cold winters (mean = -14°C, January in Terney), strong winds, moderate snowfall (mean = 1,190 mm snow in Terney per winter), and warm and humid summers (mean = 15°C, July in Terney; Goodrich et al. 2001). Average annual precipitation is 788 mm (Goodrich et al. 2001). Dominant vegetation communities within SABZ include oak (*Quercus mongolica*) forests along the coast and mixed conifer-deciduous forests at higher elevations including Korean pine (*Pinus koraiensis*), larch (*Larix komarovii*), birch (*Betula* spp.), and mixed forests of spruce (*Picea ajanensis*) and fir (*Abies nephrolepis*). The primary tiger prey species in SABZ include red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), sika deer (*C. nippon*), and roe deer (*Capreolus pygargus*; Miquelle et al. 1996). Amur tigers in SABZ also opportunistically prey on moose (*Alces alces*), musk deer (*Mochus moschiferus*), ghoral (*Nemorhaedus caudatus*), brown bear (*Ursus arctos*), Asiatic black bear (*U. thibetanus*), wolf, red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), badger (*Meles leucurus*), lynx (*Lynx lynx*), and domestic dog (*C. familiaris*; Miquelle et al. 1996).

METHODS

General field methods

We deployed GPS collars on tigers captured in and around SABZ from 2009 – 2010 using modified Aldrich foot snares (Goodrich et al. 2001). Tigers were anaesthetized with Zoletil® (UM IACUC # AUP 043-09; Lewis & Goodrich 2009) and fitted with VECTRONIC GPS Plus (Berlin, Germany), LOTEK 4400 (Newmarket, Ontario, Canada), or Iridium GPS collars (LOTEK and VECTRONIC).

Predicting tiger kill and consumption rates with GPS data

We combined GPS data collection with field investigation of potential kill sites to estimate tiger kill rates as the number of days between kills (days/kill/tiger) and in terms of consumptions rates (kg/tiger/day). To estimate the number of kills, we processed GPS location data into clusters and ground-searched most of the largest clusters as putative kill sites. Previous research on wolves indicated that a fix-rate of one location/2 hours was sufficient to locate 90% of large ungulate winter kills in the field (e.g., elk and moose; Webb et al. 2008), whereas 95% of mountain lion kills were confirmed at a fix-rate of one location/4 hours (Anderson & Lindzey 2003). We programmed collars to obtain locations at intervals of 90, 120, 180, or 360 minutes. After uploading GPS data, we used the program SaTScan (Boston, Massachusetts, USA; Webb et al. 2008) to identify potential kill sites and to guide field sampling in a systematic manner. For all analyses, we defined a cluster as two or more locations within 100 m and 48 hours of each other. To ground-truth clusters identified by SaTScan, we located kill sites by physically searching GPS clusters for approximately 30 minutes or until we determined if the site contained prey remains. During winter, we located kill sites by uploading GPS data from collars and snow-tracking GPS-collared tigers to clusters in the field. During snow-free months, we relied on GPS data uploads and cluster searches to locate kill sites. We attempted to search putative kill sites for prey remains within one to two weeks of receiving location data to avoid scavenged or decomposed kills (Sand et al. 2008; Webb et al. 2008). We visited a subset of non-clustered GPS locations to verify our sampling technique did not underestimate potential kill sites. We also collected data during an intensive sampling period where we searched every location during a two-week period in the summer to verify presence or absence of small prey remains. Following field work, we used a Python script (Python Software Foundation, Hampton, NH) to revise the assigned clusters using a more reliable rule-based algorithm developed for identifying GPS location clusters from mountain lion collar data (Knopff et al. 2009). We then used these new clusters generated by the Python script throughout subsequent logistic regression analyses to predict kills at sites we were unable to investigate.

We used multiple logistic regression (Hosmer & Lemeshow 2000) to model the presence or absence of a kill at Python-generated GPS clusters. To correct for potential missed kills, we used multiple logistic regression to estimate kills at clusters we were unable to field sample (Anderson & Lindzey 2003; Knopff et al. 2009; Webb et al. 2008). We measured six potential spatio-temporal predictor variables of kills for each GPS cluster: 1) hours: the total number of hours between the first and last locations in the cluster; 2) days: the number of 24 hour periods when at least one fix was obtained within the cluster; 3) average distance: the average distance away from the cluster center that all points were located; 4) radius: the difference between the cluster center and the furthest point away; 5) multiday binary: a dichotomous variable that separated clusters into those with locations across multiple 24-hour periods and those with all locations within a single 24-hour period (e.g., Knopff et al. 2009); and 6) percent fidelity: the percentage of locations over the duration of the cluster that fell within the cluster. We estimated the effects of these variables using logistic regression to predict the presence (1) or absence (0) of a kill (Pr(Kill)) following:

$$\mathrm{Pr\ (Kill)} = \frac{exp^{(\beta 0\ +\ \beta 1*\mathrm{Days}\ +\ \beta 2*\mathrm{Radius}\ +\ \beta\ 3*\mathrm{X3}\ +\ \dots\ \beta\ 8*\mathrm{X8})}}{1+\ exp^{(\beta 0\ +\ \beta 1*\mathrm{Days}\ +\beta 2*\mathrm{Radius}\ +\beta 3*\mathrm{X3}\ +\ \dots\beta 8*\mathrm{X8})}} \qquad \text{(Equation 1)}$$

where β_0 is the intercept, and β's are the coefficients of the effects of the covariates, X_i, on Pr(Kill). To eliminate collinearity, we excluded variables that were correlated at $r \geq 0.7$ (Webb et al. 2008). We developed a set of a-priori candidate models using combinations of non-collinear predictor variables, fit them to the data, and assessed model support with Akaike's Information Criteria (AIC; Burnham & Anderson 1998). We summed AIC weights (Σw_i) from the top ten models to rank support among predictor variables influencing the probability a cluster contained a kill site. We conducted all analyses using Stata 11.0 (Stata Corp, College Station, TX).

To distinguish large prey kill sites from small prey kill sites (40 kg cut-point; Chundawat et al. 1999) we used sequential multiple logistic regression (e.g., Knopff et al. 2009) to first determine the probability a cluster contained a kill (i.e., equation 1 above), and a second model for predicting small prey kills (0) vs. large prey kills (1). Finally, following Cavalcanti and Gese (2010), we tested the relationship between the inter-kill interval and weight of observed kills or size of predicted kills. To evaluate the inter-kill interval of known kills, we compared the time from the first location in a kill site cluster to the first location at the next kill site with the estimated weight of the observed kill. To evaluate the inter-kill interval of predicted kills, we compared the time from the first location in a predicted kill site to the first location in the following predicted kill site with the predicted size (large or small) of the kill.

We used sensitivity and specificity curves to classify predictions from the top kill vs. non-kill and small vs. large kill regression models (Hosmer & Lemeshow 2000; Knopff et al. 2009). The cut-point for the probability of a cluster being a kill has a direct bearing on model performance and estimated kill rates. Previous work has selected cut-points arbitrarily or obtained values based on sensitivity and specificity curves (Knopff et al. 2009; Webb et al. 2008; Zimmerman et al. 2007). A cut-point that maximizes sensitivity will correctly classify most kill sites but may incorrectly classify a high proportion of non-kill sites, thereby overestimating the predicted kill rate. Conversely, a cut-point that maximizes specificity will correctly classify most non-kills but may incorrectly classify many kill sites as non-kills, thereby underestimating the predicted kill rate. We selected a cut-point value that maximized overall prediction success to determine if a cluster contained a probable kill site in the first model or a probable large prey kill site in the second model (Hosmer & Lemeshow 2000; Liu et al. 2005).

To estimate the kill rate for each tiger, we took the sum of predicted kills vs. non-kills (and large vs. small kills) and estimated kill rate as the number of predicted kills divided by the number of days of continuous monitoring. We calculated kill-rate variance using a design-based ratio estimator (Hebblewhite et al. 2003; Thompson 2002).

We estimated consumption rates by converting our kill-rate estimates into kg prey consumed/tiger/day. To do this, we multiplied the predicted kill rates by the proportion of each prey species in our field-verified sample and the corresponding average prey species weights across different sex and age classes. The average weights of primary prey species in and around SABZ have been reported for all sex and age classes (Bromley & Kucherenko

1983; Danilkin 1999; Appendix B). Because of variation in digestibility and our lack of ability to conduct feeding trials, we relied on literature where such procedures have been studied. For instance, the edible portion of whole white-tailed deer (*Odocoileus virginianus*) carcasses fed to captive cougars was estimated to be about 77-79% (Ackerman et al. 1986; Hornocker 1970). Because red deer, wild boar, and sika deer are all larger than white-tailed deer, and larger animals have proportionally more consumable biomass, we used the higher estimate and assumed that 79% of a tiger prey carcass was edible. Tigers that are not disturbed by humans rarely leave edible portions of a carcass (Kerley et al. 2002). As human disturbance in the backcountry of the SABZ is limited, we assumed tigers consumed 79% of each prey item. As with kill rates, we used a design-based ratio estimator to calculate variance in consumption rates (Hebblewhite et al. 2003; Thompson 2002).

RESULTS

From 2009 to 2010, we captured and collared two adult females, two adult males, and one sub-adult female (Appendix C). These five tigers were each monitored from 0 to 481 days, with a combined total of 697 days from all tigers (Appendix C). We obtained between 0 and 3,433 locations from each tiger, with a total of 6,191 locations out of 6,666 attempts for an overall fix rate of 92.9% (Appendix C). Unfortunately, human-tiger conflicts and technology failures limited data collection. The first collar malfunctioned soon after the adult tigress (Pt94) was released and did not gather any data, nor was Pt94 observed again. Pt90 was an adult male captured during fall 2009, but data from this collar could not be downloaded until the collar retrieved after this tiger was killed during a human-tiger conflict in January 2010. Post-mortem analysis showed Pt90 was infected with canine distemper virus when he was killed. Pt97 was a sub-adult female captured in the fall of 2009 and was monitored for five weeks before she died from unknown causes in SABZ. Pt99 was a tigress captured in a human-tiger conflict situation in February 2010 and translocated into a remote forested area with healthy prey populations (Miller et al. 2011). Pt100 was a young adult male captured in fall of 2010 in SABZ whose collar malfunctioned 99 days after capture. Despite these challenges our data are reflective of the range of fates of wild Amur tigers, many of which die of human-caused mortality (Goodrich et al. 2008) or are involved in human-tiger conflicts (Goodrich et al. 2011).

As our focus was predicting kill rates and consumption rates of healthy adult tigers, we chose to screen out locations when tigers were known or believed to be unhealthy or dependent on mother. Canine distemper virus in domestic dogs indicated that infection of the central nervous system was evident three weeks following infection (Greene & Appel 2006). Therefore, we only used the first 45 days of data from Pt90 during our analyses, omitted Pt97 because there was evidence she was traveling with her mother during part of the time we monitored her, and excluded two months of data from Pt99 while she was recovering from gunshot wounds sustained in a poaching attempt (Miller et al. 2011). Thus, we used data from three tigers (Pt90, Pt99 and Pt100) for development of predictive tiger kill-rate models (Table 2-2). Both Pt90 and Pt100 lived in and around SABZ, but Pt99 lived exclusively in unprotected, multiple-use forests. We estimated 588 unique clusters representing potential kill sites or beds and investigated 225 clusters (range 6–171 per tiger), resulting in 62 observed kills (range 1–47 per tiger; Table 2-2). Two of these kills (both were badgers) were located at single locations during our investigation of a subset of non-clustered GPS locations (n = 273). All other kills were found at clusters of 2 or more locations. Of our total observed kills, 29% were wild boar, 21% were red deer, and 30.7%

were roe deer (Table 2-3). Among known wild boar kills, 44.4% were adults, 50% subadults and piglets, and 5.6% could not be accurately classified (Appendix B). Red deer kills consisted of 69% adults and 31% subadults and calves (Appendix B). Among known roe deer kills, 52.6% were adults, 21.1% subadults, and 26.3% could not be accurately classified (Appendix B). Looking at large ungulate kills of known age classes by season, only 6 of 16 (37.5%) observed summer kills and 7 of 15 (46.7%) winter kills were juveniles (Appendix B). Overall, ungulate species represented 83.9% of all tiger kills with non-ungulate prey comprising the remaining kills (Table 2-3).

Predicting tiger kill rates with GPS data

Our best model for differentiating clusters that contained tiger kill sites from non-kill clusters included multiday binary and percent fidelity to the site (Table 2-4). The top model showed that the probability a cluster contained a kill increased when a tiger spent over 24 hours at a site and as fidelity to the site increased ($P \leq 0.005$; Table 2-5). Covariates were ranked in the following order based on summed variable importance weights (Σw_i) of the top ten models: 1) percent fidelity to the site $\Sigma w_i = 0.970$, 2) clusters that contained locations from multiple days (Multi Day Bin) $\Sigma w_i = 0.916$, 3) average distance from each location to the cluster center $\Sigma w_i = 0.217$, 4) radius of cluster $\Sigma w_i = 0.204$, 5) hours at the site $\Sigma w_i = 0.077$, and 6) number of 24 hour periods with at least one location at the site $\Sigma w_i = 0.003$. We used only the top model (AIC weight = 0.514) because model averaging would have included collinear variables, which included days, hours, and multiday binary, as well as average distance and radius. The top model for predicting kill sites from non-kill sites fit the data well (Likelihood ratio χ^2 score of 101.31 [P-value < 0.0001], pseudo $R^2 = 0.38$, and receiver operating characteristic [ROC] score of 0.854). The maximized probability cut-off for which we considered a cluster a probable kill site was 0.45, which corresponded to an overall classification success of 87.11% (Appendix D).

The number of days at a site was the only predictive variable in our top model for discriminating small prey from large prey kill sites ($P \leq 0.005$; Table 2-6). Our top model suggested that kill rates of large prey increased with increasing days spent at the site (Table 2-5). Despite a low AIC weight, we chose to use only the top model (AIC weight = 0.284), instead of multi-model inference, because model averaging would have included collinear variables. Considering summed variable importance weights (Σw_i) of the top ten models, covariates were ranked in the following order: 1) days at the site $\Sigma w_i = 0.775$, 2) average distance from each location to the cluster center $\Sigma w_i = 0.314$, 3) percent fidelity to the site $\Sigma w_i = 0.224$, 4) hours spent at the site $\Sigma w_i = 0.189$, and 5) radius of cluster $\Sigma w_i = 0.164$. The multiday binary variable did not appear in any of the top 10 models, $\Sigma w_i = 0.0$. Our top model for predicting small prey from large prey kill sites fit the data well (Likelihood ratio χ^2 score of 32.58 [P-value < 0.0001], pseudo $R^2 = 0.38$, and ROC score of 0.895). The optimal probability cut-off for which we considered a cluster a large prey kill site was 0.50, which corresponds to an overall classification success of 88.71% (Appendix D).

We evaluated the relationship between the inter-kill interval and weight of observed kills (and size of predicted kills) using all data from Pt100 and two sets of data from Pt99, one before the poaching attempt and one after a two month recovery period. The average inter-kill interval between observed small prey kills (7.25 days) was shorter than the inter-kill interval between large prey kill sites (9.25 days), but the relationship was not strong (1-tailed t-test; $P = 0.091$). The average inter-kill interval after predicted small prey kill sites (7.07

days) was shorter than the inter-kill interval of predicted large prey kill sites (9.45 days; 1-tailed t-test; P = 0.047).

Comparing Empirical and Predicted Kill Rates and Consumption Rates

Monitored tigers made an average of 0.11 kills per day (95% CI 0.086 – 0.134; SE = 0.006), or one kill every 9.1 days (95% CI 7.13 – 11.07; SE = 0.46). Extrapolating our results to an annual rate for an individual tiger, these observed kill rates would result in an average of 40.1 kills/year (95% CI 31.4 – 48.8; SE = 2.02). Across tigers, observed kill rates averaged 0.032 (SE = 0.005) boar/day/tiger, 0.023 (SE = 0.002) red deer/day/tiger, and 0.034 (SE = 0.003) roe deer/day/tiger; and 0.02 other prey/day/tiger (SE = 0.001; Table 2-3). Extrapolating to an annual rate for an individual adult tiger, these observed kill rates would result in an average of 11.6 boar/year (SE = 1.88), 8.4 red deer/year (SE = 0.67), 12.3 roe deer/year (SE = 0.93), and 7.8 other prey/year (SE = 0.52). Observed consumption rates from all monitored tigers averaged 6.47 kg/day/tiger (95% CI 6.17 – 6.77; SE = 0.07), and was composed of 36.39% boar, 38.99% red deer, 15.34% roe deer, and 9.28% of all other prey items (Table 2-3).

Our logistic regression model predicted slightly higher kill rates than observed in the field, mostly due to six kills predicted by the model that were missed during field sampling. Predicted kill rates resulted in an average of one kill every 8.29 days (95% CI 7.21 – 9.38; SE = 0.25), or 0.12 kills/tiger/day (95% CI 0.105 – 0.136; SE = 0.0037). Extrapolating these predicted kill rates to an annual estimate results in an average of 44 prey killed/tiger/year (95% CI 38.2 – 49.8; SE = 1.34). Our limited sample size restricted the ability to extend this model to predict kill rates of individual prey species. Converting these predicted kill-rate estimates into overall predicted consumption rates results in an average of 7.5 kg/day/tiger

(95% CI 7.36 – 7.63; SE = 0.03), or an average of 2,735.8 kg/year/tiger (95% CI 2,687.9–2,783.7).

DISCUSSION

We report estimated annual kill and consumption rates of tigers at the northern edge of their natural range using a combination of GPS collars and field validation. Annual tiger kill rates in and around SABZ averaged 8.29 days/kill, which corresponded to 7.5 kg/day consumption rates for adult tigers. These kill-rate estimates were relatively low compared to estimates from other published studies in Russia and Chitwan National Park, Nepal (Table 2-1). Our kill-rate results are more similar to estimates in other parts of tiger range than they are to most Russian studies. In radio-telemetry studies based in Chitwan National Park, a solitary female tiger was reported to make a kill every 7.3 – 9.1 days (Sunquist 1981) and a female with two 6–10 month-old dependent cubs was reported to make a kill every 5 – 6 days (Table 2-1; Seidensticker 1976). Several studies have attempted to estimate the amount of prey consumed by tigers and our estimates of annual tiger consumption rates in and around SABZ (7.5 kg/day; 95% CI 7.4 – 7.6; SE = 0.03) were only slightly higher than consumption rate estimates in Chitwan National Park, Nepal (males 6–7 kg/day, females 5–6 kg/day; Sunquist 1981) and Kanha National Park, India (5–7 kg/day/tiger; Schaller 1967). Snow tracking-based studies of tiger kill rates in Russia have produced highly variable estimates, ranging from 3.86 – 10.14 days/kill, with an overall average of 6.2 days/kill (95% CI 4.0 – 8.5; SE = 0.91; Table 2-1). Winter estimates based on snow tracking resulted in higher, but overlapping, estimates (5–15 kg/day/tiger; Pikunov 1988). Consumption rate estimates of captive tigers (males 6 kg/day, females 3–4 kg/day) were only slightly lower than preliminary estimates from the field (Yudin 1990). Only one study reported a lower kill-rate estimate than ours (Zhivotchenko 1979) and another reported an estimate very similar to ours (Kovalchuk 1988).

Despite some overlap, our estimates are lower than most previously reported results, likely due to both methodological and ecological differences. Intensive snow-tracking studies of individual tigers, such of those of Yudakov and Nikolaev (1987), should provide the most precise data on kill rates, assuming kills are not missed during tracking sessions. It is possible to push tigers from kills while tracking, however, after which a large percentage of tigers do not return to kills, causing them to eat less from each kill and kill more frequently (Kerley et al. 2002). In some instances, high kill rate estimates may have been associated with snow tracking that displaced tigers from kills, reducing consumption rate/kill of tigers and forcing tigers to kill more. This suggests that kill rates of undisturbed tigers in our study area may be lower than previously recorded. Our intensive field sampling, guided by both GPS collars and snow tracking, still occasionally missed kills, thereby underestimating kill-rates. Thus, snow tracking-based estimates may have overestimated kill rates because animals were chased from kills, whereas our telemetry-based estimates may have underestimated kill rates due to missed kills. We were, however, able to estimate our success rates for finding kills and hence correct our empirical kill-rate estimates.

Ecologically, a reduced prey base could be responsible for some of the differences between previous estimates and our results. With declining ungulate populations, Amur tiger kill rates would also be expected to decline (as is well known with wolves, Vucetich et al. 2011). Thus, the differences we observed could be a real effect of declining prey populations in the Russian Far East (Miquelle et al. 1999b). Variation in the body sizes of prey killed could also contribute to discrepancies between kill-rate estimates and consumption-rate estimates. Cavalcanti and Gese (2010) found jaguar kill rates decreased and the amount of time between kills increased with increasing body size of prey. In contrast, we only found a moderately strong relationship between the inter-kill interval and size of prey killed. Differences between kill-rate and consumption-rate estimates are often due to larger bodied prey being killed during winter and an increase in smaller neonate prey being killed during summer. For example, Metz et al. (2012) found a peak in number of prey killed by wolves during the summer months, but a peak in biomass acquisition during winter months. Metz et al. (2012) point out that wolves in Yellowstone killed larger prey in the winter and smaller prey in the summer but interpretations of differences in seasonal kill rates can vary depending on whether it is expressed as numbers of prey or biomass of prey.

Despite our limited sample size, we conducted a preliminary comparison of summer vs. winter kill rates to evaluate potential effects of seasonal changes in prey availability on consumption rates. We found both consumption rates (6.6 kg/day/tiger in summer vs. 8.8 kg/day/tiger in winter) and kill rates (9.4 days/kill/tiger in summer vs. 7.1 days/kill/tiger in winter) were lower during summer months. Additionally, our model predicted an increase in large bodied prey killed during the winter months (52.8% vs. 62.5% of kills in summer and winter, respectively). Similar to Metz et al. (2012), our model predicts that tigers may also be preying on juvenile ungulates and smaller, non-ungulate prey during summer, reducing their consumption rates while increasing their kill rates. Our higher consumption rates predicted during winter corresponds well with the theory that biomass acquisition should be greater in the winter due to the additional energetic requirements from thermoregulatory demands (Chapter 3). The higher consumption rates we observed during winter could also be due to losses to avian scavengers, as Yudakov and Nikolaev (1987) suggested an average of 15% of all kills were lost to scavengers.

Our diet composition results differ from previous research on Amur tiger predation patterns. For example, Miquelle et al. (2010b) report that red deer and wild boar collectively accounted for 63–92% of all kills from 6 sites across tiger range in Russia. In contrast, only 50% of our confirmed kills were red deer or wild boar, and only 57.4% of predicted kills were classified as large prey. These differences could arise from recent declines in red deer and wild boar populations documented in our study area due to increased poaching, especially outside protected areas. For example, recent monitoring efforts show an approximate 50% reduction in red deer abundance over the past decade (Miquelle et al. 2010a). There are also potential methodological differences leading to disparate prey composition estimates. For example, our GPS-based sampling techniques are more likely to locate small prey kill sites compared to the snow tracking and VHF radio-telemetry techniques used by Miquelle et al. (1996). Many of the kills reported by Miquelle et al. (1996) were located during winter months, when most small prey species are hibernating. Additionally, most of Miquelle et al.'s (1996) research was based in and around SABZ, an area known for harboring healthy red deer and wild boar populations, whereas much of our sample comes from one tiger outside protected areas, where large-bodied prey populations are likely reduced because of hunting and poaching. For example, Pt99 represented 75.8% of our total prey sample, all of which were located outside of protected areas. Only 48.9% of Pt99's kills were large-bodied prey, whereas 66.7% of all other kills were large-bodied prey items. Certainly, a larger sample of Amur tigers inside protected areas, including differing sex and age classes, would improve precision of our estimates, increase the understanding of the effect of protected areas on ungulate prey, and allow us to better generalize to broader populations of interest.

We found that multiple 24 hour periods and strong fidelity to a site to be the most important factors in determining if a GPS cluster contained a kill site. For example, if a tiger spent over 24 hours localized at a site and 80% of the locations fell within the cluster, there was a 75% chance that site contained a kill (Figure 2-2). Similarly, Anderson and Lindzey (2003) determined that the most influential parameter predicting cougar kills from GPS data was the number of nights spent at a cluster, with cougars that spent two nights at a cluster having a 94% chance of being on a kill. Knopff et al. (2009) found the most important variable for predicting cougar kill sites to be the number of points at a cluster (corrected to account for variation in fix success), which equates with time spent at a site. Webb et al. (2008) found that the two most important variables used to distinguished wolf kills from non-kill clusters were the number of days spent within 100m of a cluster and the number of GPS locations (i.e., hours) within 100m of the cluster center. We also determined that if a tiger spent four days at a site, there was a 90% chance that site contained a large-bodied kill (Figure 2-2). Clearly, identifying long periods of localized activities can be a simple method of locating large-prey kill sites for large predators (Miller et al. 2010).

Several recent studies have used either multinomial logistic regression or sequential logistic regression to predict kill rates of specific prey species (Knopff et al. 2009) or different prey sizes (Webb et al. 2008). We did not use multinomial logistic regression because previous studies have shown limited utility of this approach and also because we had small sample sizes for most prey species. Instead, we attempted to predict kills of different prey sizes using multiple logistic regression and found the total number of days spent at a cluster to be the most important factor in determining if a cluster contained a large prey. Despite challenges in predicting specific prey species composition at kill sites from GPS data, our model proved to be very good at predicting large prey kill sites from small prey kill sites. As such, our model could be particularly useful for systems dominated by a single prey species where adults and calves could be easily differentiated.

Our results have several limitations, the most obvious being a small sample size of collared tigers. To minimize the effects of some unique circumstances encountered by our collared tigers and learn what healthy tigers do, we removed data from tigers that were known or believed to be unhealthy or dependent offspring. As a result of Pt99 being shot and injured, we removed two months of data from our analyses. During these two months of recovery, we monitored Pt99 via GPS collar and intensive snow tracking. Her consumption rates dropped from the predicted average of 7.8 kg/day to an observed 2.9 kg/day while she recovered. While removing some locations reduced our effective number of kills even further, these results convinced us removing some locations strengthened the overall power of our study and also provided anecdotal evidence of the energetic costs of wounding by humans on tigers.

As mentioned above, an innovative way in which ungulates are managed in the Russian Far East is that the harvestable surplus is allocated to both humans and tigers. Hunters are key stakeholders in tiger conservation in the Russian Far East as hunting is an important recreational and subsistence tradition in Russia, with over 60,000 registered hunters in the Russian Far East who rely on multiple use lands. Wildlife management organizations are responsible for managing hunting, controlling poaching, and conducting surveys of game species on leased hunting territories which encompass about 85% of Amur tiger habitat. Our results suggest that kill rates of Amur tigers may have recently declined, potentially as a result of methodological differences or lower prey densities. As our research shows, tiger kill rates and consumption rates of ungulates may differ between seasons. Therefore, extrapolating snow-tracking based kill-rate estimates over the entire year may lead to an overestimate of annual harvest of ungulates by both humans and tigers. Finally, our results show promise for estimating kill rates and prey requirements of tigers in southern Asia where snow-tracking is not possible. Given that most published estimates of kill rates of tigers are from Amur tigers (Table 2-1), GPS collars may provide a crucial tool to better understand prey requirements to conserve tiger populations.

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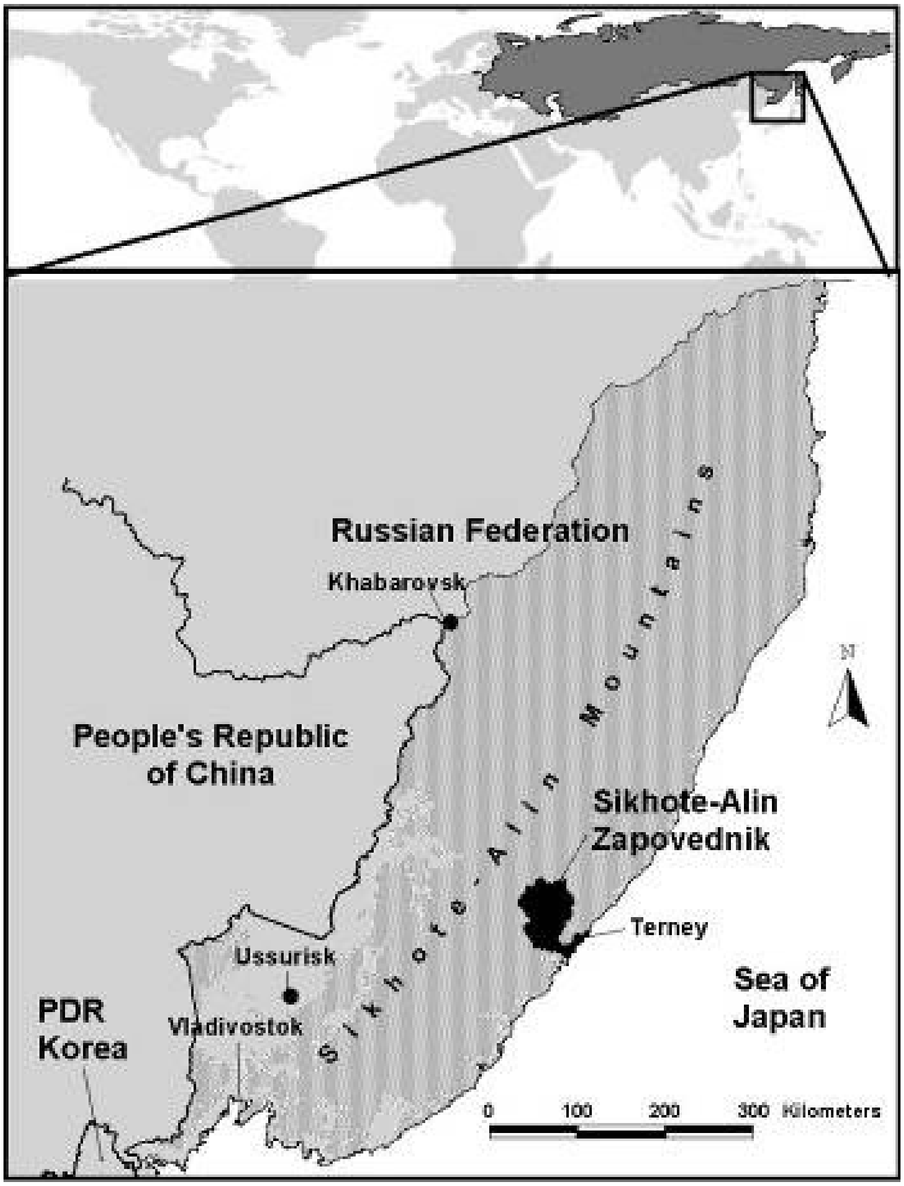

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Figure 2-1. Our study was focused in and around the 4,000 km^2 Sikhote-Alin Biosphere Zapovednik, Russian Far East, 2009–2011.

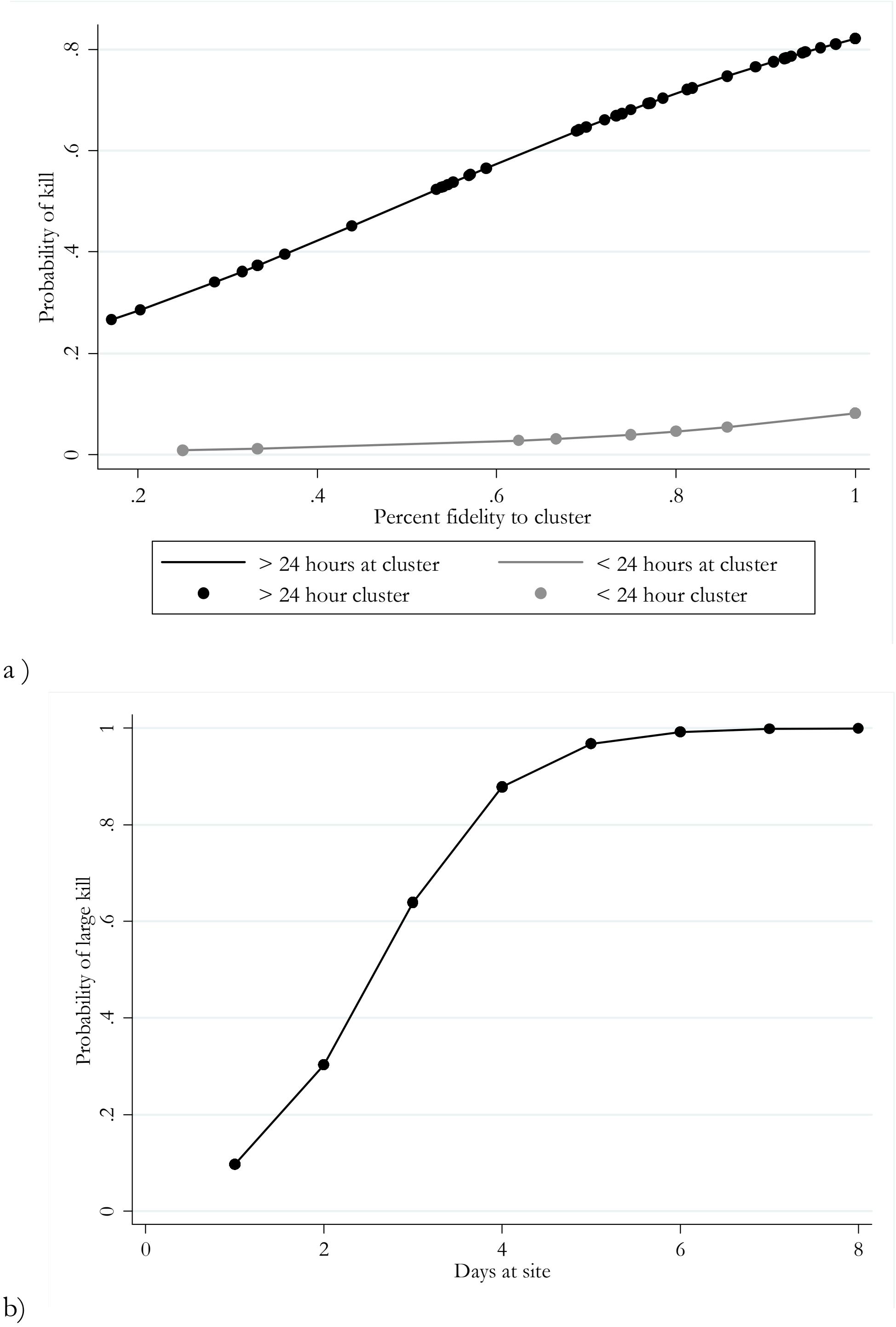

Figure 2-2. Predicted probability of Amur tiger (*Panthera tigris altaica*) a) kill sites as a function of days on a cluster and fidelity to site and b) large kills (> 40kg) versus small kills as a function of number of days on a cluster in the Russian Far East, 2009–2011.

Table 2-1. A review of published studies focusing on annual tiger kill rates on prey populations in Russia and Chitwan National Park, Nepal.

	Kills/Year			Days/Kill			
Study	Low	High	Range	Low	High	Mean	Range
Kovalchuk (1988)	40	50	(40–50)	9.13	7.30	8.22	(7.3–9.13)
Kucherenko (1977)	55	58	(55–58)	6.64	6.29	6.47	(6.29–6.64)
Kucherenko (1993)	65	75	(65–75)	5.62	4.87	5.25	(4.87–5.62)
Pikunov (1983)	90	100	(90–100)	4.06	3.65	3.86	(3.65–4.06)
Pikunov (1988)	75	81	(75–81)	4.87	4.51	4.69	(4.51–4.87)
Yudakov (1973)	70	75	(70–75)	5.21	4.87	5.04	(4.87–5.21)
Zhivotchenko (1979)	36	36	(36–36)	10.14	10.14	10.14	(10.14–10.14)
Sunquist (1981)*	40	50	(40–50)	9.13	7.30	8.22	(7.3–9.13)
Seidensticker (1976)*	61	73	(61–73)	5.98	5.00	5.49	(5–5.98)
This Study	38.9	50.6	(38.9–50.6)	9.38	7.21	8.29	(7.21–9.38)

* Study site located in Chitwan National Park, Nepal.

Table 2-2. Summary of data used during analyses of Amur tiger (*Panthera tigris altaica*) kill rates and consumption rates (CR) on and near Sikhote-Alin Biosphere Zapovednik, Russia, from 2009–2011.

Tiger ID	Sex	Days Monitored	Locations	Fix %	Clusters Searched	Kills	Observed Days/Kill	Predicted Days/Kill	Observed CR	Predicted CR
Pt90	Male	45	477	89.7	6	1	45	15	0.63	4.14
Pt99	Female	420	2,988	90.4	171	47	8.94	7.92	6.34	7.84
Pt100	Male	99	1,660	96.6	48	14	7.07	8.25	9.69	7.54
Total	3	564	5,125	92.2	225	62				
Mean		188	1,708.3	92.2	75	20.67	20.34	10.39	5.55	6.51
SD		202.72	1,256.20	3.796	85.74	23.714	21.380	3.994	4.581	2.053
Ratio Estimator							9.10	8.29	6.47	7.50
Ratio SD							0.648	0.358	0.099	0.043

Table 2-3. Prey species located at Amur tiger (*Panthera tigris altaica*) kill sites identified from logistic regression-directed cluster sampling of GPS-collared tigers in the Sikhote-Alin Mountains, Russian Far East, 2009–2011.

Prey Species	Number of kills located	Percentage of total kills	Percent biomass[1]	Kills/Day (SE)
Wild boar (*Sus scrofa*)	18	29.0	36.39	0.032 (0.005)
Red deer (*Cervus elephus*)	13	21.0	38.99	0.023 (0.002)
Roe deer (*Capreolus pygargus*)	19	30.7	15.34	0.034 (0.003)
Sika deer (*C. nippon*)	1	1.6	2.29	0.002 (0.009)
Musk deer (*Mochus moschiferus*)	1	1.6	0.27	0.002 (0.009)
Brown bear (*Ursus arctos*)	1	1.6	3.04	0.002 (0.009)
Asiatic black bear (U. *thibetanus*)	1	1.6	1.76	0.002 (0.009)
Feral dog (*Canis familiaris*)	3	4.8	0.78	0.005 (0.007)
Badger (*Meles leucurus*)	4	6.5	0.87	0.007 (0.006)
Livestock (*Bos taurus*)	1	1.6	0.27	0.002 (0.009)
Total	62	100	100	0.11 (0.006)

[1] Percent biomass was calculated by multiplying each prey item by our weight estimates for the corresponding age class and then dividing by overall consumption estimates.

Table 2-4. The top 10 multiple logistic regression models for predicting Amur tiger (*Panthera tigris altaica*) kill sites in the Russian Far East from clusters not associated with a kill site.

Model Description	N	K	Log Likelihood	ΔAICc	AIC Weights	Evidence Ratio – Compared to Best Model
Multi Day + % Fidelity	225	3	-81.80	0.000	0.514	1.000
Multi Day + Avg distance + % Fidelity	225	4	-81.75	1.96	0.193	0.375
Multi Day + Radius + % Fidelity	225	4	-81.80	2.07	0.183	0.356
Hours + % Fidelity	225	3	-84.29	4.96	0.043	0.084
Hours + % Fidelity + Avg Distance	225	4	-84.11	6.68	0.018	0.035
Hours + % Fidelity + Radius	225	4	-84.25	6.97	0.016	0.031
Multi Day	225	2	-86.38	7.10	0.015	0..029
Multi Day + Avg Distance	225	3	-86.28	8.95	0.006	0.011
Multi Day + Radius	225	3	-86.38	9.15	0.005	0.010
Days + % Fidelity	225	3	-86.91	10.21	0.003	0.006

Table 2-5. Beta coefficients from the top multiple logistic regression models used to predict Amur tiger (*Panthera tigris altaica*) kill sites from non-kill sites at clusters of locations, and predict Amur tiger small prey kill sites from large prey kill sites in the Russian Far East.

	Pr (Kill, No Kill)			Pr (Large kill, small kill)		
Covariate	Coefficient	SE	P-value	Coefficient	SE	P-value
Constant (β_o)	-5.47	1.096	<0.0005	-3.65	0.971	<0.0005
Multi Day	3.94	0.479	<0.0005			
Binary						
% Fidelity	3.05	1.063	0.004			
Days				1.41	0.371	<0.0005

Table 2-6. The top 10 multiple logistic regression models for predicting Amur tiger (*Panthera tigris altaica*) small prey kill sites from large prey kill sites in the Russian Far East.

Model Description	N	K	Log Likelihood	ΔAICc	AIC Weights	Evidence Ratio – Compared to Best Model
Days	62	2	-26.56	0.00	0.284	1.000
Days + Avg distance	62	3	-25.80	0.70	0.200	0.704
Days + Radius	62	3	-26.49	2.07	0.101	0.355
Days + % Fidelity	62	3	-26.56	2.21	0.094	0.332
Hours	62	2	-27.86	2.62	0.077	0.270
Days + % Fidelity + Avg distance	62	4	-25.78	2.95	0.065	0.228
Hours + Avg distance	62	3	-27.20	3.50	0.049	0.174
Hours + % Fidelity	62	3	-27.62	4.33	0.033	0.115
Days + Radius + % Fidelity	62	4	-26.48	4.35	0.032	0.114
Hours + Radius	62	3	-27.67	4.45	0.031	0.108

CHAPTER 3: CONSERVATION IMPLICATIONS OF AMUR TIGER (*PANTHERA TIGRIS ALTAICA*) ENERGETIC REQUIREMENTS IN THE RUSSIAN FAR EAST.

Recent estimates suggest there are fewer than 3,500 wild tigers (*Panthera tigris*) remaining in the world (Walston et al. 2010). The Global Tiger Recovery Program, a collaborative effort between the 13 tiger-range countries, views increasing prey populations as a crucial component to reaching their goal of doubling wild tiger numbers by 2022 (Global Tiger Recovery Program 2010). Prey depletion is a primary threat to tiger survival not only in Russia but across Southeast Asia, where conservation efforts are challenged by some of the densest and fastest growing human populations in the world (Karanth & Stith 1999; Miquelle et al. 1999). Poaching and legal subsistence hunting have led to the empty forest syndrome (Redford 1992) throughout much of Asia where intact forests are depleted of large ungulates – including the main prey species required for persistence of viable tiger populations (Madhusudan & Karanth 2002).

The northern limit of tiger distribution is hypothesized to be constrained by densities of key prey species (Miquelle et al. 2010). Given that Amur tigers (*P. t. altaica*) exist at the lowest densities of ungulates for any known tiger subspecies (Miquelle et al. 1999), the challenge of understanding prey requirements for survival and reproduction is particularly acute for this northern subspecies. As an impoverished prey base will support only occasional reproduction (Karanth & Stith 1999), determining the threshold consumption rate for reproduction is an important conservation question. Determining if reproduction is energetically feasible in areas with ungulate populations composed of nothing larger than a 10 kg musk deer (*Mochus* spp.) for Amur tigers, or 14 kg muntjac (*Muntiacus* spp.; prey weights from Hayward et al. 2012) for Southeast Asian tiger subspecies, is another way of phrasing the same question that has implications across all tiger ranges because of the empty forest syndrome (Redford 1992). The conservation challenge for Amur tigers is then to manage ungulate harvest and poaching to achieve a necessary minimum prey density. Quantifying the energetic requirements of tigers allows scientists and managers to estimate nutritional carrying capacity (Hobbs 1989; Laundre 2005), estimate the impact of tigers on prey, and develop science-based conservation recommendations (Odden & Wegge 2009).

Most studies of wildlife energetics have relied on laboratory experiments to model the energetic costs of wild animals or attempted to validate previous research on new species (Barboza et al. 2009; Oftedal & Gittleman 1989). Few studies have attempted to estimate the energetic costs of wild carnivores and relate them to prey requirements (but see Powell 1979). Calculating prey requirements for survival and reproduction requires knowledge of energetic demands and food consumption in the wild (Ackerman et al. 1986; Aldama et al. 1991; Laundre 2005). Recent advances in Global Positioning System (GPS) collars provide an approach to obtain empirical estimates of activity and movement costs that can be combined in energetics models (Eriksen et al. 2011; Fuller & Fuller 2012). GPS collars have recently been used to estimate annual kill and consumption rates for many carnivores (Chapter 2), however, to date attempts to understand energetic requirements by combining empirical data from GPS collar data with models of energetic costs have been few.

The primary energetic activities of adult tigers are resting, traveling, eating, hunting, and the periodic energetic costs associated with reproduction and thermoregulation (Powell 1979). Time spent in different activities multiplied by the energetic costs of each activity results in an estimate of daily energy requirements (Laundre 2005; Powell et al. 1985). Reproductive female tigers experience higher energetic costs than males because of the additional costs of gestation, lactation, and then securing sufficient prey biomass for 1–4 growing young. Sunquist et al. (1999) suggested that a reproductive tigress with two large cubs needs approximately 50% more food than solitary females because of the increased energetic demands. While individual tigers may be able to exist at relatively low prey densities, population persistence requires that females acquire sufficient energy to successfully rear young to independence. Translating tiger energetic requirements into consumption rates or prey requirements can assist in defining minimum prey requirements throughout tiger range.

To aid tiger conservation efforts, we developed an energetics model to estimate prey requirements for tigers to survive and reproduce in the wild. We have two broad goals, first to estimate tiger energetic requirements and then determine the consequences of these energetic requirements in terms of predicted prey requirements in single and multi-prey communities. We developed this field-based tiger energetics model using information from the literature to estimate the energy budget of tigers, and tested the model using GPS-based, empirically derived movement rates and kill/consumption rates on Amur tigers in the Russian Far East. Although we developed the energetics model based on data from Amur tigers, we also demonstrate its application using previously collected data from Bengal tigers (*P. t. tigris*) in the Bangladesh Sundarbans (Barlow 2009). This model will allow conservationists to estimate tiger prey requirements and assess which suite of prey is likely to ensure survival and successful reproduction, information that is critical for global tiger conservation efforts.

STUDY AREA

We conducted our research in the Sikhote-Alin Mountains of the Russian Far East, focusing around the 4,000km^2 Sikhote-Alin Biosphere Zapovednik (SABZ), home to approximately 20–35 tigers (Smirnov & Miquelle 1999). SABZ was founded in 1935 and is maintained as an IUCN Class I protected area. Situated near the village of Terney, Primorski Krai (province), in the Russian Far East (Figure 2-1), SABZ is closed to the public and access is strictly limited to Zapovednik (Reserve) staff and visiting scientists. The Zapovednik has low poaching rates and no legal hunting, whereas prey populations in the Sikhote-Alin Mountains outside of protected areas are exposed to legal hunting and higher poaching rates (Miquelle et al. 2005). The Sikhote-Alin Mountains parallel the Sea of Japan coastline with elevations up to 1,600 m within SABZ, but most mountains are less than 1,200 m. The Sikhote-Alin Mountains occur in the Far Eastern temperate climatic zone and are characterized by strong seasonality with dry, cold winters (mean = -14°C, January in Terney) and warm, humid summers (mean = 15°C, July in Terney; Goodrich et al. 2001). Dominant vegetation communities in the Sikhote-Alin Mountains include oak (*Quercus mongolica*) forests along the coast and mixed conifer-deciduous forests at higher elevations including Korean pine (*Pinus koraiensis*), larch (*Larix komarovii*), birch (*Betula* spp.), and spruce (*Picea ajanensis*) – fir (*Abies nephrolepis*). The primary prey species of tigers in the Sikhote-Alin Mountains are red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), sika deer (*C. nippon*), and roe deer (*Capreolus pygargus*; Miquelle et al. 1996). Other prey species in the system that Amur tigers opportunistically prey upon in the Sikhote Alin Mountains include moose (*Alces alces*), musk deer, ghoral (*Nemorhaedus caudatus*), brown bear (*Ursus arctos*), Himalayan black bear (*U. thibetanus*), wolf (*Canis lupus*), raccoon dog (*Nyctereutes procyonoides*), badger (*Meles leucurus*), lynx (*Lynx lynx*), and domestic dog (*C. familiaris*; Miquelle et al. 1996).

METHODS

General field methods

We deployed GPS collars on adult tigers in and around the SABZ from 2009 – 2010 using Aldrich foot snares (Goodrich et al. 2001) and anaesthetized with Zoletil® (UM IACUC # AUP 043-09; Lewis & Goodrich 2009). Captured tigers were fitted with LOTEK 4400 (Newmarket, Ontario; Canada), or LOTEK and VECTRONIC (Berlin, Germany) Iridium GPS collars. We combined GPS-derived movement rates with modeled kill rates (Chapter 2) to estimate the energy budget required for wild tigers to survive and reproduce. GPS collars were programmed to obtain locations every 90 minutes, 2 hours, or 3 hours. Because of the temperate climate in our study area, we estimated energetic costs during summer and winter, where winter was defined as December 1st to April 20th (Hojnowski et al. 2012). All other estimates were considered constant throughout the year. We calculated the daily energetic demands of average male and non-reproductive female adult tigers as well as reproductive females raising 1-4 cubs and an average litter (2.4 at birth but decreases to 1.3 from 1 year until dispersal; Kerley et al. 2003).

Tiger Energetics Model

We estimated the total daily energetic demands (C_{total}) of an adult tiger using equation 1 (Aldama et al. 1991; Powell 1979):

$$C_{total} = C_r+C_{tr}+C_h+C_e+C_{rep}+C_{th} \quad \text{(equation 1)}$$

which includes the costs of resting (C_r), traveling (C_{tr}), hunting (C_h), eating (C_e), reproduction (C_{rep}), and energetic costs associated with thermoregulation (C_{th}).

The first step in estimating equation 1 is to determine daily time budgets and the proportional time allocated to each activities. Daily time budgets of tigers were calculated by dividing the number of locations (at a fixed GPS fix interval/tiger) from known activities (eating and digesting at predicted and known kill sites, resting, and traveling) by the total number of received locations. We considered the remainder of a tiger's time budget to be time spent hunting and attacking prey. We considered activity budgets constant throughout the year. Missed locations were not included in time budget analyses. We assume any introduced biases from missed locations was low because of high overall fix rates (91.4%) of data used during these analyses (Frair et al. 2010).

Resting costs (C_r)

The energetic cost of resting (C_r), also called the basal metabolic rate (BMR), is the minimal rate of bodily heat production within an animals' thermo-neutral zone (Moen 1973). Pioneering work published by Rubner (1883) showed that BMR of domestic dogs was related to their body weight. Kleiber (1961) extended this analysis to birds and mammals in a laboratory and provided allometric equations to estimate BMR across all species (the famous mouse-to-elephant curve). Values of basal metabolic rate measured under laboratory conditions for the domestic cat (*Felis catus*; Kleiber 1961), the cheetah (*Acinonyx jubatus*; Taylor and Rowntree 1973), the serval (*Felis serval*; Downs et al. 1991), and the tiger (McNab 1989) closely mirror values predicted by Kleiber's equation. Although values derived from captive animals may not represent values from wild animals, few have successfully studied BMR of wild carnivores. Therefore, we used a tiger's body weight to estimate basal metabolic rate with the equation:

$$C_r = 70W^{0.75}t \text{ kcal/day (equation 2)}$$

where W represents the weight of the tiger in kilograms and t represents the daily time spent resting (Kleiber 1961). Weights were measured at time of capture and assumed constant throughout the year. For unknown tigers, we used values reported by Slaght et al. (2005) for wild adult Amur tiger males of 176.4 kg (n = 18; SE = 4.3) and wild adult females of 117.9 kg (n = 13; SE = 2.1).

Traveling costs (C_{tr})

Metabolic rates are usually thought to increase linearly with movement (Taylor et al. 1974). Under laboratory conditions, the energetic cost of traveling for cheetahs (Taylor et al. 1974) and cougars (*Puma concolor*; Corts & Lindzey 1984) were similar to those predicted using Taylor et al.'s (1970) equation. In his study of fisher (*Martes pennanti*) energetics, Powell (1979) also found the cost of traveling in this free-living, solitary carnivore to be similar to predicted by Taylor et al. (1970). The energetic cost of traveling was described by Taylor et al. (1970) using an allometric relationship between body weight and energy expended:

$$C_{tr} = (5.8W^{0.75}t)+(2.6W^{0.6}d) \quad \text{(equation 3)}$$

We used this equation to estimate the energetic cost of traveling (C_{tr}) in tigers, where W is defined above as tiger weight, t represents the daily time spent traveling, searching for prey, and territorial marking in hours, and d represents the total daily distance traveled in kilometers (Aldama et al. 1991; Taylor et al. 1970).

An accurate estimate of the distance a tiger travels during a specific period of time is critical to calculate the cost of traveling (C_{tr}). From 1970–1973, Yudakov and Nikolaev (1987) snow tracked Amur tigers 1,500 km and presented the most reliable data available in the literature on 24 hour movements. The 24-hour distance averaged 9.6 km (41 km max.) in males (n = 8) and 7 km (22 km max.) in females (n = 6; Yudakov & Nikolaev 1987). Accurate data on travel distances can be obtained during labor-intensive snow tracking efforts but year round data are difficult to obtain. Recently, advances in GPS collar technology enabled researchers to gather detailed data on tiger movements during all seasons of the year (Miller et al. 2010). We used a combination of snow tracking and GPS collar data to calculate seasonal tiger-specific movement rates. Straight-line distances between consecutive locations were calculated using Hawth's Tools (Beyer 2004) in ArcMap 9.3 (Environmental Systems Research Institute, Redlands, California, USA) and represent the minimum distance travelled between fixes. We calibrated straight-line distance traveled by a tiger during sampling intervals by comparison to real movement distances observed from snow tracking (Musiani et al. 1998; Pepin et al. 2004). To standardize distances travelled between consecutive fixes, we divided the corrected distance by the fix rate and report corrected movement rates as meters/hour for each month, seasonal averages, and total averages. To represent travel rates, or distances covered while a tiger is actually moving, we removed step lengths associated with a cluster of locations when resting or foraging. We assumed straight-line correction factors were constant for both winter and summer. Much of our snow tracking data from one tigress was gathered while she recovered from a poaching attempt. We included these data in our correction factor analysis because we are determining real distance travelled compared to straight line distances between locations and recovery behavior should not influence estimation of correction factors for actual distances traveled.

Hunting costs (C_h)

Tigers are solitary carnivores that capture prey during short attacks, resulting in a burst of energy in a short time span (C_h; Aldama et al. 1991) that results in both successful and unsuccessful attacks. Tiger hunting success estimated from snow tracking was reported as one kill for every three to five attempts (Matyushkin 1977). Yudakov and Nikolaev (1987) reported that pursuit distance averaged 200 m on unsuccessful wild boar hunts and tigers did not pursue red deer more than 100 m. Calder (1984) showed that the maximum energetic output of 32 mammal species could be estimated using the formula:

$$C_h = 78.3W^{0.84}\,t \quad \text{(equation 4)}$$

where t represents the total time, in hours, spent successfully and unsuccessfully attacking and subduing prey. Between the short pursuit distances and the rapid dispatch of prey, we assumed a very short period of time per hunting attempt, successful or unsuccessful. We calculated the total time hunting as 0.1% of each day, or 1.44 minutes spent hunting per day and the energetic costs of hunting were considered constant throughout the year.

Costs of eating (C_e)

The energetic cost of feeding and digestion, while difficult to estimate, is higher than BMR (Barboza et al. 2009). We followed Aldama et al. (1991) and Ackerman et al. (1986) who assumed the cost of eating to be equal to the cost of traveling at mean travel speed. We estimated the time spent eating and digesting as described above and applied our empirically-derived yearly movement rates to estimate the average travel speed. Using these mean travel speeds, we replaced d in equation 3 with the product of speed and time (T_s) and used an equation from Aldama et al. (1991) to estimate the energetic costs of eating:

$$C_e = ((5.8W^{0.75})+(2.6W^{0.6}T_s))t \quad \text{(equation 5)}$$

where T_s represents the average travel speed in kilometers per hour and t represents the time spent eating in hours. The energetic costs of eating were considered constant throughout the year.

Thermoregulation costs (C_{th})

The energetic costs of thermoregulation (C_{th}) by carnivores have been considered insignificant under a thermo-neutrality assumption; for Iberian lynx (*Lynx pardinus*; Aldama et al. 1991), cougars (Ackerman et al. 1986; Laundre 2005), dingos (*C. l. dingo*) and coyotes (*C. latrans*; Shield 1972). However, Mautz and Pekins (1989) estimated thermoregulation in wild-caught bobcats (*L. rufus*) under laboratory controlled conditions during mean winter temperatures resulted in a 15% metabolic increase above BMR. Given that Amur tigers live in a harsh northern climate (even though they are equipped with thick winter pelage), we felt the assumption of thermo-neutrality was unrealistic. Therefore, to account for the additional energetic demands of thermoregulation we increased energetic costs (C_{total}) during the winter season by 15%.

Reproductive Costs

Reproduction is among the most energetically expensive activity in mammals (Harvey 1986), and the most challenging to estimate for wild carnivores. The cost of reproduction in females is the combined costs of gestation (C_{gest}), lactation, and post-weaning costs associated with growth of cubs (C_{grow}). To estimate the daily energetic costs of nursing and post-weaning dependence on a tigress, we summed the daily energetic cost of growth, travel, and maintenance for each cub and added that to the maternal energetic requirements. The total energetic costs for a single cub (C_{cub}) were:

$$C_{cub} = C_{grow}+C_r+C_{tr}+C_e \text{ (equation 6)}$$

As both the prenatal (C_{gest}) and postnatal (C_{cub}) demands fall solely on the tigress, the estimated daily energy demands per litter were calculated and added to maternal energy requirements. Following Ackerman et al.'s (1986) cougar energetics model, we assumed that reproductive costs for adult male tigers (searching for a mate, courtship) were accounted for in their overall activity levels. As cubs are born throughout the year (Kerley et al. 2003), we could not predict the age and weight of cubs during winter, and therefore, did not estimate the costs of thermoregulation of cubs.

Pregnancy in mammals involves expending energy during fetal growth and in the development of the uterus, placenta, and mammary glands (Oftedal & Gittleman 1989). The energetic costs of gestation (C_{gest}) were estimated using the cost of fetal growth and was then increased by 27% to simulate production costs of the placenta and fetal fluids (Kaczmarski 1966). The gestation period in tigers averages 103 days (Nowell & Jackson 1996), and the birth weight of a tiger cub averages 1,255g (Oftedal & Gittleman 1989). The litter energy per metabolic body size was calculated from litter weight, assuming energy content of 0.98 kcal/g, and was multiplied by gestation length (Oftedal & Gittleman 1989). Using these parameters, we calculated the additive energetic cost of gestation using the following formula:

$$C_{gest} = ((\Delta W\ g/day*28.624\ kcal/day*0.98\ kcal/g*Litter)*103)*1.27 \quad \text{(equation 7)}$$

where ΔW was the age specific weight gain in g/day, 28.624 kcal/day is the daily energetic costs per metabolic body size in kg, 0.98 kcal/g was the average caloric content of mammals, 103 was the gestation period, in days, and multiplying the entire equation by 1.27 accounts for the additional production costs of the placenta and fetal fluids (Kaczmarski 1966; Oftedal & Gittleman 1989). We divided the birth weight of a tiger cub by the gestation period to standardize the daily weight gain (ΔW) per cub across the 103 day gestation period to be able to estimate daily costs. A recent study on the reproductive parameters of wild Amur tigers in our study area reported that mean litter size at first detection was 2.4 cubs per litter (range 1–4) but decreased to 1.3 cubs per litter from 12 months until dispersal due to cub mortality (Kerley et al. 2003). To estimate a range of energetic costs we estimated the energetic costs of 1–4cubs and an average litter of 2.4 cubs at birth and 1.3 cubs from 1 year to dispersal. We assumed a 50:50 sex ratio at birth.

After birth, development and growth of young is possible only if energy gain by the tigress exceeds the total energetic costs of the cubs (Gittleman & Oftedal 1987). Postnatal growth rate and lactation are linked by the dependence of tiger cubs on milk as the primary source of energy (Gittleman & Oftedal 1987). Lactation costs to the tigress were calculated assuming a 60% conversion efficiency of the female's metabolized energy to milk and subsequent assimilation by the cubs (Moen 1973). Following Ackerman et al. (1986) and Laundre (2005), we used the following equation to estimate the energetic cost of growth in wild tiger cubs from birth to dispersal:

$$C_{grow} = (\Delta W * 1{,}430)/e \quad \text{(equation 8)}$$

where ΔW was the age specific weight gain in kg/day, 1,430 kcal/kg wet weight was the energetic value of cougar flesh (assumed to be the same as tigers; Golley et al. 1965), and e was 60% growth efficiency during the 56 day nursing period and 100% during the post-weaning dependence period (Moen 1973). We started birth weight at 1,255 g (Oftedal & Gittleman 1989) and calculated age specific weight gain using Michaelis-Menton growth curves based on wild Amur tiger weights (Slaght et al. 2005).

As the cubs continue to grow, their energetic costs exceed that provided by milk, leading to weaning and the addition of solid meat to the diet provided by the tigress (Gittleman & Oftedal 1987). We estimated daily energy costs after weaning similarly to adults and added them to the maternal energetic requirements. Available data from tracking radio collared females with cubs suggest that females return to a den site for the first month, and there is little movement of cubs through the second month (Miquelle, pers. comm.). From 2 months to 6 months, we assumed cubs traveled 2 km during 3 hours/day, and subtracted time spent traveling from time spent resting. From 6 months to dispersal at 19 months (Kerley et al. 2003), we assumed cubs traveled with their mother, and calculated daily energetic costs of cubs based on movements and time budgets of the tigress. Finally, we added the total energetic costs of each litter to the total energetic demands of the tigress over the 19 months of conception to independence of the cubs.

Calculating Predicted Prey Requirements

Our second main research objective was to convert daily tiger energetic estimates into predicted prey requirements in both single and multi-prey communities. Therefore, we calculated the number of ungulate (and other) prey required by tigers to meet the energetic costs (C_{total}) given by equation 1 above. The primary prey species available to tigers in the SABZ are red deer, wild boar, sika deer, and roe deer (Miquelle et al. 1996). We estimated percent composition by weight in the diet of these (and other) prey species using kill-data from GPS-derived cluster searches (Appendix B). The average weights of primary prey species in and around SABZ were previously reported for all sex and age classes (Bromley & Kucherenko 1983; Danilkin 1999); we used these estimates to calculate prey requirements based on estimates of caloric demands from equation 1 (C_{total}).

The edible portion of whole mule deer (*Odocoileus hemionus*) fed to captive cougars was estimated to be about 77-79% (Ackerman et al. 1986; Hornocker 1970). Davison et al. (1978) calculated the value of white-tailed deer (*O. virginianus*) meat and organs to be 1,890 kcal/kg of wet weight. Due to a lack of information on specific caloric values for the prey species in SABZ, we assumed a similar value of 1,890 kcal/kg for all prey species.

The number of ungulates killed per day (PB_k) can be estimated using the potential biomass consumed per day, the average weight of the various prey species available, the % diet composition of each of the prey species (Appendix B) and the edible portion of each carcass. Digestibility of meat is generally high in carnivores (Grodzinski & Wunder 1975) but assimilation is reduced by the presence of hair and bones. Previous studies have estimated that 14% of the energy ingested from deer meat is lost during digestion and assimilation by cougars (Ackerman et al. 1986). As human disturbance in our study area was limited, and tigers that are not disturbed by humans rarely leave edible portions of a carcass

(Kerley et al. 2002), we assumed tigers rarely abandoned edible biomass at kill sites. To account for occasional prey abandonment, scavenging and carcass decay during summer, we followed Yudakov and Nikolaev (1987) and assumed 15% of each kill was lost. Based on these parameters, we estimated the potential biomass of ungulate prey consumed (PB_c) following Ackerman et al. (1986) as:

$$PB_c \text{ kg/day} = C_{tot} \text{ kcal} / (1{,}890 \text{ kcal/kg} \times 0.86 \times PB_u \times 0.85) \quad \text{(equation 9)}$$

where PB_u represents the proportion of diet of tigers that are ungulates. Using these parameters, we estimated the total number of a single prey species killed per day for all prey species individually, as well as in a multispecies context where the number of each different prey species was calculated in proportion by weight to the rate found in the diet of GPS collared tigers (Appendix B) with the same equation as Ackerman et al. (1986):

$$PB_k = PB_c / (M_w \times 0.79) \text{ prey/day} \quad \text{(equation 10)}$$

where M_w was the mean live weight of prey in kilograms.

Testing Predictions of the Energetics Model

We compared the predicted number of prey killed by tigers from our energetics model to empirical data (Table 3-3) to understand whether the tiger energetics model predicts collared tigers to be starving, meeting maintenance requirements, or meeting reproduction requirements. For example, if the energetics model predicts tigers require 5 kg/day/tiger and field estimates are 8 kg/day/tiger, then this suggests that tigers in the Russian Far East are meeting basic maintenance energetic requirements, on average. We also tested for seasonal differences between the empirical estimates and the energetics model. Therefore, we evaluated the sensitivity of the predicted kill rate of ungulates to estimated model parameters (weight, movement rates, activity patterns) using sensitivity analysis of equation 1 to identify the most important parameters driving tiger energetics. We increased each parameter, one at a time, by one percent to evaluate the influence each parameter had on equation 1. We averaged the percent increase of each parameter from 4 estimates (males and females during winter and summer), divided each parameter increase by the total increase from all 4 simulations, and then ranked each parameter in order of importance.

RESULTS

From 2009 to 2010, we captured and collared two adult males, two adult females, and one sub-adult female (Appendix C). One radio collar failed immediately and no data were received from the adult female tigress (Pt94). The remaining four tigers were each monitored from 36 to 481 days, with a combined total of 661 days from all tigers (Table 3-3). During this time, we obtained between 205 and 3,433 locations from each tiger, with a total of 5,775 locations out of 6,317 attempts for an overall fix rate of 91.4% (Table 3-3). We used these data to predict both annual kill rates and consumption rates for individual tigers (Table 3-3).

Daily Amur tiger time budgets were calculated from GPS location data. Overall, 31.1% of tiger locations were at predicted kill sites, 30.7% were single locations while traveling, and 38.1% of the locations were at clusters of locations formed while resting (Table 3-1). Therefore, in an average day our tigers spent 7.5 hours (95% CI 7.2–7.8) at kill sites, 7.4 hours (95% CI 7.1–7.7) traveling, 9.1 hours (95% CI 8.8–9.5) resting, and the remaining 1.44 minutes were attributed to time spent hunting and attacking prey (Table 3-1).

Resting costs (C_r)

Using equation 2, average adult male Amur tigers consume 3,388.2 kcal/day (19.2 kcal/kg of tiger), or 141.2 kcal/hour, and adult female Amur tigers consume 2,504.6 kcal/day (21.2 kcal/kg), or 104.4 kcal/hour, while resting at BMR. Using the estimated time spent resting from our time budget analyses (Table 3-1), we calculated the daily caloric costs of time spent resting for each individual tiger and overall averages for male and female tigers (Tables 3-4, 3-5).

Traveling costs (C_{tr})

We snow tracked Pt100 for a total of 81.1 km between 49 pairs of consecutive locations. The average correction factor for all 49 pairs of locations at a 90 minute fix rate was 1.412 (SD = 0.2188). We snow tracked Pt99 for a total of 52.5 km between 41 pairs of consecutive locations. The average correction factor for all 41 pairs of locations at a three hour fix interval was 1.513 (SD = 0.2866). We were unable to snow track between any locations at the 2 hour fix interval, so to calibrate these location data with an actual distance travelled correction factor we took a weighted average of the 90-minute and 3-hour correction factors to estimate a 1.446 correction factor for 2 hour fix intervals. Correction factors were applied to travel distances while not localized at a cluster and standardized to m/hr (Table 3-2). During summer, male tigers averaged 1,168.8 m/hr (95% CI 1,086.0–1,251.6; SE 42.1) and female tigers averaged 828.0 m/hr (95% CI 780.6–875.4; SE 24.1). Distances travelled during winter dropped to 998.2 m/hr (95% CI 903.5–1,092.9; SE 48.1) for male tigers ($P = 0.0076$) and 564.0 m/hr (95% CI 490.9–637.1; SE 37.1) for female tigers ($P < 0.001$).

Combining seasonal movement rates with time budgets, adult male Amur tigers spent 6.5 hours traveling/day (95% CI 6.1–7.0) and moved 7.6 km/day (95% CI 6.6–8.7) in summer and 6.5 km/day (95% CI 5.5–7.6) in winter. Adult female non-reproducing Amur tigers spent 7.9 hours traveling/day (95% CI 7.6–8.3) and averaged 6.6 km/day (95% CI 5.9–7.3) in summer and 4.5 km/day (95% CI 3.7–5.3) in winter. Mean travel speed was estimated to be 1.169 km/hour (95% CI 1.086–1.251) for male tigers and 0.828 km/hour (95% CI 0.780–0.875) for non-reproducing female tigers during summer and 0.998 km/hour (95% CI 0.903–1.093) for males and 0.564 km/hour (95% CI 0.490–0.637) for non-reproducing female tigers during winter (Table 3-2). In every instance, tigers traveled less during winter than summer.

The annual mean daily energetic costs of traveling (C_{tr}) were estimated seasonally to be 2,273.6 kcal (95% CI 2,087–2,465) for adult male tigers (12.9 kcal/kg of tiger) and 1,948.0 kcal (95% CI 1,835–2,062) for adult non-reproducing females (16.5 kcal/kg) during summer (Table 3-4), and 2,209.1 kcal (95% CI 2,022–2,401) for adult males (12.5 kcal/kg) and 1852.6 kcal (95% CI 1,736–1,972) for adult non-reproducing females (15.7 kcal/kg) during winter (Table 3-5).

Costs of eating (C_e) and hunting (C_h)

The annual mean daily energetic costs of time spent eating and digesting (C_e) were considered constant throughout the year and averaged 2,576.7 kcal/day (95% CI 2,389.0–2,767.8) for adult male tigers (14.6 kcal/kg) and 1,807.7 kcal/day (95% CI 1,701.2–1,915.7) for adult non-reproducing females (15.3 kcal/kg; Tables 3-4, 3-5). The annual mean daily energetic costs of hunting and attacking prey (C_h) were considered constant throughout the year and averaged 144.9 kcal/day for male Amur tigers (0.82 kcal/kg) and 103.3 kcal/day for females (0.88 kcal/kg; Tables 3-4, 3-5).

Thermoregulation costs (C_{th})

The energetic demands of thermoregulation (C_{th}) were added to mean daily energetic estimates during the winter season (December 1 – April 20) to generate overall daily averages of energetic demands. Increasing energetic demands by 15% results in an increase of 951.0 kcal/day (95% CI 884.3–1,019.1) for an average weight adult male (5.4 kcal/kg) and 699.1 kcal/day (95% CI 659.4–739.4) for an average weight non-reproducing adult female (5.9 kcal/kg; Table 3-5).

Total energetic costs (C_{total})

The energetic costs of resting, traveling, eating, and hunting results in an overall daily estimate (C_{total}) of 6,404.7 kcal/day (95% CI 5,959.3–6,857.8) for adult male tigers (36.3 kcal/kg) and 4,756.3 kcal/day (95% CI 4,495.8–5,020.0) for adult non-reproducing females (40.3 kcal/kg) during summer (Table 3-4). The additional energetic costs of thermoregulation results in overall daily averages of 7,291.2 kcal/day (95% CI 6,779.3–7,812.8) for adult males (41.3 kcal/kg) and 5,360.0 kcal/day (95% CI 5,055.7–5,669.1) for adult non-reproducing female tigers (45.5 kcal/kg) during the winter (Table 3-5).

Reproductive Costs

During reproduction (gestation, lactation, and dependence until dispersal), the overall energetic costs to a female raising an average sized litter to dispersal are 10,016.6 kcal/day (95% CI 9,739.2–10,297.8) but a female successfully raising a litter of four cubs to independence must obtain an average of 15,355.1 kcal/day (95% CI 15,077.6–15,636.3; Table 3-6). The additional energetic costs of just gestation on a reproductive tigress averaged 1,031.7 kcal/day for producing an average size litter and 1,719.5 kcal/day for a litter of 4 cubs (Table 3-6). The energetic demands associated with lactation required a female with an average sized litter to obtain an additional 3,352.2 kcal/day, whereas a female with four cubs is required to obtain an additional 5,587.0 kcal/day to meet these lactation demands (Table 3-6). From post-weaning to six months of age, the daily costs of growth and some minor travel require a tigress with an average litter to obtain an additional 4,602.2 kcal/day and a female with four cubs to obtain an additional 7,670.3 kcal/day (Table 3-6). From six months until dispersal, energetic costs increase to an average of 6,406.2 kcal/day for an average litter and to an average of 13,943.6 kcal/day for a litter of four cubs (Table 3-6).

Calculating Predicted Prey Requirements

Using these daily caloric requirements, during summer, an average adult male Amur tiger would need to consume a minimum of 4.6 kg of meat/day (95% CI 4.3–5.0) and an average non-reproductive female would need to consume a minimum of 3.4 kg of meat/day (95% CI 3.3–3.6). During winter, these estimates increase to 5.3 kg/day for males (95% CI 4.9–5.7) and 3.8 kg/day for non-reproducing females (95% CI 3.6–4.1). From pregnancy to successful dispersal, a tigress with an average litter needs to obtain an average of 7.3 kg/day (95% CI 7.1–7.5) and a female successfully raising 4 cubs to dispersal needs to average 11.1 kg/day (95% CI 10.9–11.3) during the entire 651 day reproductive period.

Converting these daily consumption estimates to yearly estimates of biomass results in an average of 1,782.5 kg/year for an average male Amur tiger, 1,318.2 kg/year for an average lone female tigress, 2,646.3 kg/year for a female raising an average litter, and 4,056.6 kg/year for a female successfully raising a litter of 4 cubs.

To meet these energetic demands under a single prey scenario, an average male tiger would need to kill and consume 15.8 wild boar/year (95% CI 14.7–17.0), 12.1 red deer/year (95% CI 11.3–13.0), 60.5 roe deer/year (95% CI 56.3–64.8), 25.1 sika deer/year (95% CI

23.4–26.9), or 187.0 musk deer/year (95% CI 174.0–200.3; Table 3-7). An average non-reproductive tigress would need to consume 11.7 wild boar/year (95% CI 11.1–12.4), 9.0 red deer/year (95% CI 8.5–9.5), 44.7 roe deer/year (95% CI 42.3–47.3), 18.6 sika deer/year (95% CI 17.5–19.6), or 138.3 musk deer/year (95% CI 130.6–146.1; Table 3-7). A reproductive tigress raising 4 cubs to dependence under a single prey scenario would need to average 36.0 wild boar/year (95% CI 35.4–36.7), 27.5 red deer/year (95% CI 27.0–28.0), 137.7 roe deer/year (95% CI 135.2–140.2), 57.1 sika deer/year (95% CI 56.1–58.2), or 425.6 musk deer/year (95% CI 417.9–433.4; Table 3-7).

To meet the average daily energetic estimates under a multiple prey scenario, where each prey species is taken in proportion to its biomass contribution from our Chapter 2 estimates, an average male tiger would need to consume 6.1 wild boar/year (95% CI 5.6–6.5), 4.5 red deer/year (95% CI 4.2–4.8), 8.3 roe deer/year (95% CI 7.7–8.9), and 5.8 other prey/year (95% CI 5.4–6.2), or 24.6 total prey/year (95% CI 22.9–26.4; Table 3-8). Under this multiple prey scenario, an average non-reproductive tigress would need to consume 4.5 wild boar/year (95% CI 4.2–4.7), 3.3 red deer/year (95% CI 3.1–3.5), 6.1 roe deer/year (95% CI 5.8–6.5), and 4.3 other prey/year (95% CI 4.0–4.5), or 18.2 total prey/year (95% CI 17.2–19.2; Table 3-8). A reproductive tigress raising 4 cubs to dependence under a multiple prey scenario would need to consume 13.8 wild boar/year (95% CI 13.6–14.1), 10.2 red deer/year (95% CI 10.0–10.4), 18.9 roe deer/year (95% CI 18.5–19.2), and 13.2 other prey/year (95% CI 13.0–13.4), or 56.0 total prey/year (95% CI 55.0–57.1; Table 3-8).

Testing Predictions of the Energetics Model

For all sexes and seasons, energetic requirements (C_{total}) were most sensitive to variation in tiger weights (41% of the variation), followed by time spent eating (22%), time spent traveling (18%), and time spent resting (11%). The last three parameters (travel speed, distance traveled per day, and time spent hunting) only accounted for 8% of the total variation in total energetic requirements.

DISCUSSION

Predictions of prey consumption by tigers from our energetics model are slightly lower than most tiger consumption estimates derived from field-based methods, but very similar to other carnivore energetics models. Comparison to other felid energetics research requires standardization of caloric estimates into kcal/kg of predator. Our estimates of 38.2 kcal/kg of male tiger and 42.3 kcal/kg of female tiger are similar to Aldama et al.'s (1991) estimates of 30 kcal/kg of male Iberian lynx and 29 kcal/kg of females. This is only true, however, if we follow Aldama et al. (1991) in assuming Amur tigers live in thermo-neutrality within their environment and remove the additional 5.4 kcal/kg for males and 5.9 kcal/kg for females attributed to the energetic costs of thermoregulation. Laundre's (2005) reports of 59.2 kcal/kg of male cougar and 59.6 kcal/kg of female cougar were much higher, however, than both our estimates and those of Aldama et al. (1991). We attribute these higher energetic estimates to Laundre's (2005) VHF-based daily travel estimates of 17.0 km/day for adult males and 14.4 km/day for adult females. In comparison, in another study, Beier et al. (1995) reported average diel travel distances of adult cougars to be 6.4 km and speed to be 0.8 km/hour, values similar to our estimates of 6.6 km/day and 0.9 km/hour for adult Amur tigers. However, our sensitivity analysis revealed that overall energetic costs are affected least by movement speeds and distances, opposing our interpretation that differences between Laundre (2005) and Aldama et al. (1991) were driven by movement rate differences.

Despite the similarity to other modeled carnivore energetic requirements, our modeled prey requirements (Tables 3-4, 3-5) are lower than field estimates of tiger consumption rates (Table 3-3). This is expected because our energetics model is built to predict the energetic needs of a sustenance diet. Any prey consumed above these requirements can be used to fuel reserves during high demand times, such as lactation, or times of prolonged hunting failures. Indeed, our empirical estimates of 7.5 kg/day for an adult non-reproductive tiger (Table 3-3) were higher than the estimates of 4.9 kg/day for an adult male and 3.6 kg/day for an adult female from our energetics model (Tables 3-7, 3-8). In fact, tiger consumption rate estimates from our energetics model are the lowest reported estimates (Appendix E). Similarly, cougar consumption rate estimates from energetic studies of 3.4–4.3 kg/day and 2.2–2.7 kg/day (Ackerman et al. 1986) or 1.9 kg/day and 1.5 kg/day (Laundre 2005) for adult males and females, respectively, are much lower than recently published empirical estimates (that were not corrected for edible biomass) of 12.9 kg/day for adult males and 6.6 kg/day for adult females (Knopff et al. 2010). For wolves, Peterson and Ciucci (2003) used energetics modeling to estimate a consumption rate of 3.25 kg/day for a 35kg adult wolf, but empirical estimates from Hebblewhite et al. (2003) averaged 5.4 kg/day and averaging seasonal results from Metz et al. (2012) produces an estimate of 6.8 kg/day. Clearly, comparison of tiger, cougar, or wolf consumption rate estimates from energetics modeling reveals they are consistently roughly half of empirical estimates using GPS collars, regardless of size of species being investigated.

The consistent discrepancies between empirical observations and energetic modeling raise a series of questions. For example, are the models failing to accurately estimate energy demands or are carnivores killing more than they need to survive? One of the ecological factors that might result in higher empirical than modeled consumption rates is the high variance in successful predation from the tiger's perspective. The standard deviation of our empirically-derived consumption rates was over 2 kg/day, suggesting that on many days our field observed consumption rates were very close to the energetic minimum, or even below the starvation threshold. Therefore, an ecological reason why empirical consumption rates are higher than energetic estimates is because carnivores strive to always have more food than might cause starvation, or a negative energy deficit. Sunquist (2010) suggested a tiger will consume 15–18 kg/day until the carcass is fully consumed and the tiger goes in search of another and Vucetich et al. (2012) found that high variance in wolf consumption rates leads wolves to exhibit partial prey consumption to ensure that their consumption rates are usually higher than a starvation threshold.

There were other energetic costs potentially facing wild tigers that we were unable to incorporate, also potentially underestimating true energetic requirements. For instance, one tigress was seriously injured from a poaching attempt and spent several weeks recuperating. We observed lower kill rates during this recovery period and not only would an injury like this negatively affect her ability to successfully hunt, there are likely additional energetic costs of healing. Additionally, Robbins (2001) suggested that the costs of traveling in snow for ungulates increased curvilinearly with increasing snow depth and snow density. We were unable to account for additional costs of travel in snow because of a lack of empirical data for carnivores. Although we recognize this as a potential bias leading to biased low estimates of consumption rates, we have observed tigers actively traveling in creeks and on packed game trails in winter, behaviors that would minimize the energetic costs of traveling in deep snow. Regardless, high variance in consumption rates and additional costs of traveling in snow would all tend to increase empirical consumption rates, emphasizing the need for ungulate conservation measures even more.

Regardless of these potential ecological reasons for our energetic model underestimating field-based consumption rates, our annual estimates of 4,989.5 kcal/day for an average Amur tigress are very similar to an estimate of 4,934 kcal energy intake/day from an average Amur tigress in Omaha's Henry Doorly Zoo (C. Dikeman, personal communication). This valuable comparison to a captive Amur tiger leads us to believe the energetics model is providing a valuable approach to estimate true energetic requirements. Despite the differences between empirical and modeled consumption rates, the critical conservation question is how to use these biomass estimates derived from energetic modeling. Until these discrepancies are resolved, the conservative approach is to rely on the field-based observations for conservation measures focusing on prey requirements for tigers, but to use energetic modeling to provide estimates for the additional costs of reproduction which are almost impossible to estimate in the wild.

The additional cost of reproduction requires females to obtain sufficient resources for her maintenance diet as well as for the growth of the cubs to dispersal. Sunquist (1999) suggested that a tigress with 2 large cubs needs 50% more biomass to feed her growing cubs. However, as cubs approaching dispersal age are nearly the same size as their mother, we feel Sunquist's (1999) estimate of only a 50% increase in biomass for 2 large cubs underestimates the energetic demands and prey acquisition requirements facing female tigers. For example, for comparison to Sunquist (1999), during the final 6 months prior to dispersal, our energetics model predicts a tigress with 2 large cubs (1 male, 1 female) needs to obtain an average of 154% more biomass/day than a solitary tigress. During the 651 day conception to dispersal period, energetic demands on a tigress raising a single cub are 54% higher than a non-reproductive adult tigress, an average litter requires 101% more biomass/day, and a tigress with 4 cubs needs 208% more biomass/day during this time. Similarly, Laundre (2005) reported over the 18 month pregnancy to dispersal period, a female cougar raising an average litter (2.6 kittens) needs to obtain an average of 160% more biomass/day. To meet the demands of obtaining more biomass/day required for reproduction, it is safe to assume the search time of a tigress would increase as they ranged further to find more prey (O'Donoghue et al. 1998).

The movement rates we estimated to parameterize our energetics models are amongst the first GPS-based movement rates of tigers in the literature, and support some previously proposed hypotheses about tiger spatial ecology. Sandell (1989) suggested that the home ranges of solitary female felids are correlated to the prey biomass available whereas male home ranges are influenced by the distribution of reproductive females. Therefore, the increased travel distances we observed in males could also be a result of reproductive behavior as males patrol their territories for receptive females and to defend against intruding males. Goodrich et al. (2010) showed that male Amur tiger home ranges are largely exclusive and often overlapped 1–5 sympatric females. An exclusive home range benefits male tigers by maintaining exclusive access to reproductive females and reduced risk of infanticide by other males (Goodrich et al. 2010). While previous authors have reported higher seasonal daily estimates for males (9.6 km/day) compared to females (7.0 km/day; Yudakov & Nikolaev 1987) and others have speculated that male tigers travel more than females (Sunquist 1981), our GPS data provides the first annual test of this hypothesis, supporting the notion that larger home ranges come with higher associated movement costs. We found that while male tigers spent an average of 1.4 fewer hours/day traveling, they travelled an average of 2 km further per day than female tigers in winter and 1 km further in summer. To maintain these large exclusive territories and the resources within them, male tigers would need to continuously patrol and scent mark the area within its borders (Protas et al. 2010, Yudakov & Nikolaev 1987), leading to increased movement rates and time spent traveling.

In addition to reproductive behavior potentially influencing movement patterns, our empirical movement rates suggest there may also be seasonal differences influencing movements. Each of our collared tigers traveled greater distances in the summer than in winter (Table 3-2). Laundre (2005) posits that decreased movement rates during the winter could be caused by snow conditions often result in concentrated prey populations, but observations of migrations by red deer in our study area do not suggest concentrations of prey in winter, or changes in relative densities between summer and winter in tiger home ranges (Hojnowski et al. 2012). Metz et al. (2012) reported high seasonal variation in kill rates of wolves in Yellowstone's Northern Range driven by changes in the availability and vulnerability of prey. Specifically, they observed a spike in neonate prey during summer, a finding that would increase search time (and movement rates) while reducing handling time during summer. Combining daily movement rates of a tigress with three cubs reported by Rozhnov et al. (2011) with a correction factor for 20 minute data estimated from our empirical estimate described above results in a summer movement rate estimate of 16.1 km/day, a winter estimate of 4.2 km/day, and an overall movement rate estimate of 5.2 km/day, or 659.6 m/hour. These daily movement rate estimates represent overall estimates, do not remove distances traveled while localized on a cluster, and are comparable to the estimates we present in Appendix F. Not only do Rozhonv et al.'s (2011) estimates support our suggestion about seasonal differences in movement rates, they also support our thoughts on reproductive tigers ranging further to find enough prey to support a growing litter.

As an example of the application of our energetics model to other tiger range countries, we applied our model to the Bengal tigers inhabiting the mangrove forests of the Bangladesh Sundarbans. Barlow (2009) deployed GPS collars on two adult female tigers (average weight 76.67kg) from 2004–2006. Combining overall daily movement rates estimated from 30 minute location data (including locations while on a cluster) with a correction factor estimated from our empirical estimates described above resulted in a daily movement rate average of 4.1 km/day (Barlow 2009), higher than our overall observed Amur tiger movement rates (Appendix F). Applying our empirical Amur tiger time budgets to Barlow's (2009) daily movement estimates results in an average travel speed of 513.6 meters/hour, higher than both the 352 meters/hour for an average Amur tiger (Appendix F) and the 210 meters/hour reported for Bengal tigers in Nagarahole, India (Karanth & Sunquist 2000). Combining these data with the time budget of an average tigress results in an estimate of 3,314.2 kcal/day, or 2.4 kg/day for a tigress in the Sundarbans. We believe there are several factors potentially influencing the reduced energetic requirements of tigers in the Sundarbans. The two female tigers captured in Bangladesh were 40 kg smaller than an average female Amur tiger thus reducing energetic requirements as all energetic costs are a function of weight. Also, tigers outside of Russia are not exposed to the energetic demands of thermoregulation. We used these preliminary energetic requirements to examine prey requirements of Bengal tigers in the Sundarbans. Khan (2004) used scat analysis to investigate prey selection by tigers in the Sundarbans and determined that spotted deer (*C. axis*) were 80.1% of the diet and wild boar were 10.6% of relative biomass consumed. Other, smaller species, such as the rhesus macaque (*Macaca mulatta*) and lesser adjutant (*Leptoptilos javanicus*), were occasionally consumed and represent the remaining 9.7% consumed biomass. Applying the daily energetic estimates of Bengal tigers in the Sundarbans with these consumption estimates results in a mixed-species prey requirement of 18.9 spotted deer/year, 3.7 wild boar/year, and 23.3 other prey/year, or 45.9 total prey/year. If we apply these data to a single prey scenario, similar to above, a tigress in the Sundarbans would need to consume 23.6 spotted deer/year, 34.6 wild boar/year, or 277.1 macaque or adjutant/year. Despite some of the assumptions made in applying our energetics model to the Sundarbans, this simple application illustrates the potential utility of our model to understanding tiger energetics, and emphasizes that large bodied ungulate prey are critically important to tigers (Hayward et al. 2012).

The potential resonance of our single small ungulate prey (musk deer/muntjac) scenario in the conservation world is important to consider. If a tigress with 4 cubs was able to kill over one musk deer/day, and only killed 20% of the population (roughly sustainable from a musk deer perspective), that would require over 2,100 musk deer per female home range. Given that mean musk deer density throughout SABZ is approximately 1/km^2 (Stephens et al. 2006) and average female home ranges have been reported to be 390 km^2 (Goodrich et al. 2010) this scenario is clearly unrealistic in the Russian Far East. Therefore, it is extremely unlikely that wild Amur tigers could survive, let alone reproduce with only small ungulate prey available in the Russian Far East. This emphasizes the conservation importance of maintaining the large, preferred ungulate prey species for tigers. Further, if true biomass acquisition requirements are closer to our field –observed estimates than our energetics modeling, this scenario becomes even more impractical. The conservation implications of this scenario clearly stress the importance of focusing conservation efforts on improving large-bodied prey populations as a means of meeting the goals of the Global Tiger Recovery Program.

CONSERVATION IMPLICATIONS

The three primary threats associated with conservation of tigers are habitat loss, poaching, and prey depletion. Other researchers have debated the relative importance of each (Chapron et al. 2008), but regardless, in order to meet the Global Tiger Recovery Program's goals of doubling wild tiger numbers by 2022, maintaining adequate prey resources is crucial. In many areas throughout Asia, tigers are decreasing or extirpated because of a lack of prey in areas with adequate potential habitat. Therefore, there is a need to define minimum prey numbers needed for survival and reproduction. Our energetics modeling shows a highly reproductive tigress will need 2–3 times more biomass than a solitary tigress. This aligns with a recent definition of habitat quality that emphasizes adequate ungulate prey as the primary determinant of "high quality" habitat for tigers (Miquelle et al. 1996; Mitchell & Hebblewhite 2012; Mosser et al. 2009).

Our tiger energetics model is the first step towards calculating the prey thresholds required for tiger survival and reproduction. Calculating the energetic demands facing tigers is an important step, but using our model to guide ungulate management to calculate minimum prey thresholds needed for tiger reproduction requires future work building on our energetics model. Hayward et al. (2012) argued that tigers should select for prey species that yield a weight ratio of tiger to prey of 1:1.1. In the Russian Far East, prey items that meet this criterion would be wild boar, red deer, and potentially sika deer. Availability and abundance estimates of these preferred prey populations are also needed to estimate the prey thresholds required for survival and reproduction. Unfortunately, rigorous estimates of prey availability are lacking throughout much of tiger range. Finally, encounter rates of preferred prey species are critical in determining prey selectivity and must be included in any estimate of prey thresholds (Huggard 1993).

As displayed with data from the Sundarbans, our tiger energetics model is adjustable for tiger populations throughout their range. Currently, many countries in Southeast Asia are attempting to conserve or re-establish viable tiger populations in the face of the densest and rapidly growing human populations. Using our energetics model, knowledge of the proportion of each prey species in tigers' diet, and estimated prey abundance will help determine if sufficient prey, their associated density, and overall area requirements exist to support tiger survival and reproduction. It is unrealistic to believe tigers can survive and successfully reproduce in landscapes suffering from the empty forest syndrome or that a tigress with 4 cubs could obtain the 425 musk deer needed per year under our single prey scenario. The conservation implications of this research will facilitate conservation efforts on protecting preferred prey populations as a key component of tiger conservation.

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Table 3-1. Number of locations from each Amur tiger (*Panthera tigris altaica*) in the Russian Far East, from 2009–2011, during different activities (at predicted kill sites, resting, and traveling) used to calculate average daily energy/time budgets and number of missed fix attempts. These energy/time budgets were considered constant throughout the year.

Tiger ID	At kill site		Resting		Traveling		Missed Fixes[1]		Total locations
	#	%	#	%	#	%	#	%	
Pt90	67	14.0	203	42.5	207	43.4	55	10.3	477
Pt97	44	21.4	87	42.4	74	36.1	70	25.5	205
Pt99 [2]	948	31.7	1,057	35.3	983	32.9	317	9.6	2,988
Pt100	600	36.1	686	41.3	374	22.5	60	3.5	1,660
Avg ♂	667	31.2	889	41.6	581	27.1	115	5.1	2,137
Avg ♀	992	31.0	1,144	35.8	1,057	33.1	387	10.8	3,193
Total	1,659	31.1	2,033	38.1	1,638	30.7	502	8.6	5,330

[1] Missed fix attempts were not included in time budgets analyses.

[2] Two months of winter location data were removed from this analysis while Pt99 recovered from a poaching attempt.

Table 3-2. Summary of corrected movement rates (meters/hour) from 4 Amur tigers (*Panthera tigris altaica*) by season in the Russian Far East, 2009–2011. Values represent the corrected distance between consecutive locations not associated with localized movements at a cluster.

Tiger ID	Winter	Summer	Total
Pt90	949.5	1,121.6	1,075.1
Pt97	636.7	665.0	656.8
Pt99 [1]	558.0	837.3	774.7
Pt100	1,010.5	1,207.0	1,100.2
Avg ♂	998.2	1,168.8	1,091.7
Avg ♀	564.0	828.0	767.7
Total	798.5	929.0	888.3

[1] Two months of winter location data were removed from this analysis while Pt99 recovered from a poaching attempt.

Table 3-3. Summary of collared Amur tigers (*Panthera tigris altaica*) in Russian Far East study area, 2009 – 2011, including length of monitoring period, GPS locations acquired, number of clusters searched, and number of kills located.

Tiger ID	Sex	Days Monitored	Good Locations	Fix %	Clusters Searched	Kills	Predicted Kill Rate (days/kill)	Predicted Consumption Rate (kg/day)
Pt90	Male	45	477	89.7	6	1	15	4.14
Pt97	Female	36	205	74.5	4	2	NA	NA
Pt99 [1]	Female	481	3,433	90.6	194	50	7.92	7.84
Pt100	Male	99	1,660	96.5	48	14	8.25	7.54
Total	4	661	5,775	91.4	252	67	8.29	7.50
Mean		165.3	1,443.8	87.8	63.0	16.8	10.39	6.51
SD		212.33	1,468.90	9.38	89.66	22.94	3.994	2.053

[1] Two months excluded from analyses while Pt99 recovered from a poaching attempt. However, snow tracking data were used during this time to generate the 3 hour correction factor.

Table 3-4. Energetic costs (kcal/day) of each activity during summer (April 21 – November 30, 2009 – 2011) for each Amur tiger (*Panthera tigris altaica*) in the Russian Far East given tiger-specific body weight, movement rates, and activity budgets estimated from GPS collars, as well as average male and female costs from averaged weights, movement rates, and time budgets.

Tiger ID	Sex	Age	Weight (kg)	BMR	Traveling	Eating	Hunting	Total	kcal/kg
Pt90	M	10yo Adult	200	1,584.3	3,942.3	1,266.2	161.0	6,953.8	34.8
Pt97	F	2yo Subadult	100	939.4	1,826.4	1,084.2	89.9	3,940.0	39.4
Pt99	F	6–8yo Adult	130	953.3	2,081.9	1,984.8	112.1	5,132.2	39.5
Pt100	M	4yo Adult	193	1,497.9	2,023.0	3,188.7	156.3	6,865.9	35.6
Avg ♂	M	Adult	176.4	1,409.5	2,273.6	2,576.7	144.9	6,404.7	36.3
Avg ♀	F	Adult	117.9	897.3	1,948.0	1,807.7	103.3	4,756.3	40.3

Table 3-5. Energetic costs (kcal/day) of each activity during winter (December 1 – April 20, 2009 – 2011) for each Amur tiger (*Panthera tigris altaica*) in the Russian Far East given tiger-specific body weight, movement rates, and activity budgets estimated from GPS collars, as well as average male and female costs from averaged weights, movement rates, and time budgets.

Tiger ID	Sex	Age	Weight (kg)	BMR	Traveling	Eating	Hunting	Thermoregulation	Total	kcal/kg
Pt90	M	10yo Adult	200	1,584.3	3,830.3	1,266.2	161.0	1,026.3	7,868.1	39.3
Pt97	F	2yo Subadult	100	939.4	1,816.3	1,084.2	89.9	589.5	4,519.3	45.2
Pt99	F	6–8yo Adult	130	953.3	1,975.6	1,984.8	112.1	753.9	5,779.7	44.5
Pt100	M	4yo Adult	193	1,497.9	1,958.0	3,188.7	156.3	1,020.1	7,821.0	40.5
Avg ♂	M	Adult	176.4	1,409.5	2,209.1	2,576.7	144.9	951.0	7,291.2	41.3
Avg ♀	F	Adult	117.9	897.3	1,852.6	1,807.7	103.3	699.1	5,360.0	45.5

Table 3-6. Reproductive costs (kcal/day) for Amur tigers (*Panthera tigris altaica*) including gestation, lactation, and weaning to dispersal at 19 months, Russian Far East, 2009 – 2011. Caloric value for each event is reported for a non-reproductive tigress, a tigress successfully raising a single male or female cub to independence, a tigress with 2–4 cubs (assuming a 50:50 sex ratio), and a tigress with an average litter.

Tiger	Gestation (103 days)	Lactation (56 days)	Weaning to 6 months (96 days)	6 months to dispersal (396 days)	Total (651 day average)	% of Non-reproducing ♀
Non-repro. ♀	NA	NA	NA	NA	4,989.5	100
♀ + 1 male cub	429.9	1,247.7	1,825.7	3,551.8	7,594.6	152.2
♀ + 1 female cub	429.9	1,545.8	2,009.4	3,420.0	7,567.2	151.7
♀ + 2 cubs	859.7	2,793.5	3,835.1	6,971.8	10,172.3	203.9
♀ + 3 cubs	1,289.6	4,190.3	5,752.7	10,457.7	12,763.7	255.8
♀ + 4 cubs	1,719.5	5,587.0	7,670.3	13,943.6	15,355.1	307.7
♀ + average litter [1]	1,031.7	3,352.2	4,602.2	6,406.2	10,016.6	200.8

[1] An average litter assumes a 50:50 sex ratio and is considered to be 2.4 cubs at birth and 1.3 cubs from 1 year until dispersal at 19 months (Kerley et al. 2003).

Table 3-7. Converting Amur tiger (*Panthera tigris altaica*) caloric demands into prey requirements under a single prey species scenario in the Russian Far East, 2009 – 2011.

Tiger	Kcal/day	Kg/day	Boar/year	Red deer/year	Roe deer/year	Sika deer/year	Musk deer/year
Avg ♂	6,747.2	4.9	15.8	12.1	60.5	25.1	187.0
Avg ♀	4,989.5	3.6	11.7	9.0	44.7	18.6	138.3
♀ + 1 male cub	7,594.6	5.5	17.8	13.6	68.1	28.3	210.5
♀ + 1 female cub	7,567.2	5.5	17.8	13.6	67.8	28.2	209.8
♀ + 2 cubs	10,172.3	7.4	23.9	18.2	91.2	37.4	282.0
♀ + 3 cubs	12,763.7	9.2	30.0	22.9	114.4	47.5	353.8
♀ + 4 cubs	15,355.1	11.1	36.0	27.5	137.7	57.1	425.6
♀ + average litter [1]	10,016.6	7.3	23.5	18.0	89.8	37.3	277.6

[1] An average litter assumes a 50:50 sex ratio and is considered to be 2.4 cubs at birth and 1.3 cubs from 1 year until dispersal at 19 months (Kerley et al. 2003).

Table 3-8. Converting Amur tiger (*Panthera tigris altaica*) caloric demands into prey requirements under a multiple prey species scenario in the Russian Far East, 2009 – 2011. Proportions of each species in the diet are based on empirical biomass acquisition estimates from Chapter 2.

Tiger	Kcal/day	Kg/day	Boar/year (38.3%)	Red deer/year (37.0%)	Roe deer/year (13.7%)	Other prey/year[1] (11.0%)	Total/year
Avg ♂	6,747.2	4.9	6.1	4.5	8.3	5.8	24.6
Avg ♀	4,989.5	3.6	4.5	3.3	6.1	4.3	18.2
♀ + 1 male cub	7,594.6	5.5	6.8	5.0	9.3	6.5	27.7
♀ + 1 female cub	7,567.2	5.5	6.8	5.0	9.3	6.5	27.6
♀ + 2 cubs	10,172.3	7.4	9.1	6.8	12.5	8.7	37.1
♀ + 3 cubs	12,763.7	9.2	11.5	8.5	15.7	11.0	46.6
♀ + 4 cubs	15,355.1	11.1	13.8	10.2	18.9	13.2	56.0
♀ + average litter[2]	10,016.6	7.3	9.0	6.6	12.3	8.6	36.6

[1] Other prey refers to the combined estimates from sika deer (*Cervus nippon*), musk deer (*Mochus moschiferus*), brown bear (*Ursus arctos*), Himalayan black bear (*U. thibetanus*), badger (*Meles leucurus*), domestic dog (*Canis familiaris*), and cattle (*Bos Taurus*).

[2] An average litter assumes a 50:50 sex ratio and is considered to be 2.4 cubs at birth and 1.3 cubs from 1 year until dispersal at 19 months (Kerley et al. 2003).

Appendix A. Summary of recent felid literature using Global Positioning System (GPS) cluster sampling for various aspects of predation research.

Publication	Species	N	Clusters searched	Kills
Anderson and Lindzey 2003	Cougar (*Puma concolor*)	11	94	61
Knopff et al. 2010	Cougar	42	3700	1509
Ruth et al. 2010	Cougar	10	196	142
White et al. 2011	Cougar	18	436	345
Tambling et al. 2010	Lions (*Panthera leo*)	5	1447	234
Tambling et al. 2012	Lions	5	1447	236
Cavalcanti and Gese 2010	Jaguar (*P. onca*)	10	950	438
Martins et al. 2011	Leopards (*P. pardus*)	10	101	53
Gronberg 2011	Snow leopard (*P. uncia*)	7	141	89
Ersson 2011	Lynx (*Lynx lynx*)	3	69	50
This Study	Amur tiger (*P. tigris*)	3	225	62

Appendix B. Summary of prey species (by sex and age class) located at Amur tiger (*Panthera tigris altaica*) kill sites identified from logistic-regression directed cluster sampling of GPS-collared tigers in the Sikhote-Alin Mountains, Russian Far East, 2009–2011.

Prey Spp.	Wild Boar					Red Deer					Roe Deer				Sika Deer	Musk Deer	Brown Bear	Black Bear	Badger	Dog	Cow[1]
Sex/Age Class	Ad ♂	Ad ♀	Sub Ad	Calf	Unk ♂[2]	Ad ♂	Ad ♀	Ad Unk[3]	Sub Ad	Calf	Ad ♂	Ad Unk	Unk Unk[4]	Sub Ad	Ad ♂	Ad ♂	Ad ♀	Ad ♀	Ad	Ad	Ad
Weight (kg)	193	92	70	50	131.5	224	149	186.5	100	45	39.9	37.3	35.9	34.5	105.7	12.24	140.42	81.5	10	12	10
Pt90													1								
Pt99[5]	2	2	1	6		1	5	2	1	2	6	3	4	3			1	1	4	3	
Pt100	1	3	2		1	1				1	1			1	1	1					1
Summer	2	1	1	2	1	1	5	1	1	2	4	3	1	2			1	1	4	3	1
Winter	1	4	2	4		1	0	1		1	3	0	4	2	1	1					
Total	3	5	3	6	1	2	5	2	1	3	7	3	5	4	1	1	1	1	4	3	1

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[1] An estimated 10kg of meat was consumed before the carcass was abandoned.

[2] Weights of prey in an unknown age class are the averaged weights of all age classes of the same sex.

[3] Weights of prey of an unknown sex are the averaged weights of all sexes of the same age class.

[4] Weights of prey from an unknown sex and age class are the averaged weights of all sexes and age classes.

[5] Two months of winter location data were removed from this analysis while Pt99 recovered from a poaching attempt.

Appendix C. Summary of all Amur tigers (*Panthera tigris altaica*) in our study, including length of monitoring period, GPS locations acquired, number of clusters searched, and number of kills located.

Tiger ID	Sex	Days Monitored	Locations	Fix %	Clusters Searched	Kills
Pt94	Female	0	0	0	0	0
Pt90	Male	81	893	92.0	19	4
Pt97	Female	36	205	74.5	4	2
Pt99	Female	481	3433	90.6	194	50
Pt100	Male	99	1660	96.5	48	14
Total	5	697	6191	92.9	265	70
Mean		139.4	1215.4	70.8	53	14
SD		194.84	1388.06	40.41	81.04	20.83

Appendix D. Cut-points for multiple logistic regression models predicting 1) Amur tiger (*Panthera tigris altaica*) kill sites from non-kill sites and 2) Amur tiger small prey kill sites from large prey kill sites.

	Pr (Kill, No Kill)			Pr (Large kill, small kill)		
Cut-point	Classification Success	Sensitivity	Specificity	Classification Success	Sensitivity	Specificity
0.15	84.89	80.65	86.5	69.35	96.97	37.93
0.25	84.89	80.65	86.5	69.35	96.97	37.93
0.3	84.89	79.03	87.12	69.35	96.97	37.93
0.35	85.33	79.03	87.73	88.71	87.88	89.66
0.4	87.11	77.42	90.8	88.71	87.88	89.66
0.45	87.11	77.42	90.8	88.71	87.88	89.66
0.451413 [1]	86.67	75.81	90.8			
0.5	86.67	75.81	90.8	88.71	87.88	89.66
0.55	88.0	74.19	93.25	88.71	87.88	89.66
0.6	86.67	69.35	93.25	88.71	87.88	89.66
0.638915 [2]				70.97	51.52	93.1
0.65	85.33	64.52	93.25	70.97	51.52	93.1

[1] Cut-point from sensitivity-specificity sum maximization in the kill-no kill model.

[2] Cut-point from sensitivity-specificity sum maximization in the small vs. large kill model.

Appendix E. Summary of literature estimating consumption rates (kg/day) of tigers (*Panthera tigris*) using various methods. All estimates are for solitary, adult tigers unless otherwise noted.

Author	Year	Study Site	Methods	Consumption rates
Novikov	1962	Russian Far East	Snow tracking	8 kg/day
Schaller	1967	Kanha NP, India	Observational	5–7 kg/day
Sunquist	1981	Chitwan, Nepal	VHF telemetry	♂ – 6–7 kg/day
				♀ – 5–6 kg/day
Pikunov	1988	Russian Far East	Snow tracking	5–15 kg/day
This study	2012	Russian Far East	GPS cluster sampling	7.5 kg/day
This study	2012	Russian Far East	Energetic modeling	♂ – 4.9 kg/day
				♀ – 3.6 kg/day

Appendix F. Summary of total hourly corrected movement distances (meters/hour) from 4 Amur tigers (*Panthera tigris altaica*) by season in the Russian Far East, 2009–2011. Values represent the average corrected distance between any consecutive locations, regardless of activity.

Tiger ID	Winter	Summer	Total
Pt90	512.1	575.0	559.2
Pt97	249.1	323.8	297.3
Pt99 [1]	187.5	402.4	334.7
Pt100	260.2	481.7	330.3
Total	243.7	434.2	352.0

[1] Two months of winter location data were removed from this analysis while Pt99 recovered from a poaching attempt.