

ESTIMATING TIGER KILL RATES USING GPS COLLARS

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There are fewer than 5,000 wild tigers remaining in the world (Wildlife Conservation Society, 2008). The key threats to the survival of tigers in Asia include habitat loss and fragmentation in areas with some of the densest and fastest growing human populations in the world (Wikramanayake et al., 1998), over-hunting of prey (Miquelle et al. 1999), direct killing of tigers for traditional Chinese medicine (Nowell, 2000), and retaliatory killing after tiger-human conflicts (Miquelle et al., 2005). Roughly ten percent of the world's tigers inhabit the forests of the Russian Far East, as the subspecies of Siberian, or Amur tiger (*Panthera tigris altaica*). Tiger habitat in the Russian Far East consists of large contiguous blocks of forests with low human densities. The primary short-term threats to the Amur tiger are not associated with habitat loss and fragmentation, but with the depletion of prey populations throughout their range and direct poaching of individual tigers (Chapron et al., 2008). Annual ungulate surveys from 1998 to 2009 have recently documented a steady decline in prey populations throughout Amur tiger habitat (Miquelle, unpublished data). Messier (1994) suggests that predation can be strongly density dependent at the lower range of prey densities. Therefore, declines in prey populations in the Russian Far East could be due to predation by tigers and/or human hunting, leading to a conservation dilemma. Conflicts exist in these unprotected lands where both hunters and tigers rely on the same prey base. Because Amur tigers require large tracts of forest with sufficient ungulate prey and low human disturbance to survive (Kerley et al., 2002), tigers and people must find a way to co-exist in the vast unprotected, multiple-use forests of the Russian Far East. Hunters claim tigers are reducing the amount of prey, thus negatively affecting their livelihoods. Conservationists claim over-hunting is destroying the prey base of tigers.

Legal ungulate harvests by hunters in tiger habitat are reduced to account for the estimated yearly predation rate by tigers (Miquelle et al., 2005). This approach assumes that predation rate, which ultimately drives prey population dynamics, are driven by kill rates (Messier, 1994). Predation rate by different predators (tigers, humans) is a function of both the numeric response (how the density of predators changes as a function of prey density) and the functional response (kill rate of prey by predators as a function of prey density) (Holling, 1959; Messier, 1994). Given that tigers likely have a linear numeric response to increasing prey density (Miquelle et al., 1999), kill rates will likely determine tiger predation rates on prey (Messier, 1995). Therefore, accurate estimates of yearly tiger kill rates are a key component of determining appropriate harvest rates by hunters. Currently, year-round tiger kill rates are calculated by extrapolating kill rates derived from winter snow tracking data (Yudakov, Nikolaev, 1987; Pikunov, 1981). If kill rates on ungulates are lower in summer, then predation rate by tigers may be lower on ungulates than assumed in the scientific literature. Conversely, if kill rates on ungulates are higher in summer, then predation rates of tigers on ungulates may be higher and human harvest may be at an unsustainable level. Moreover, if female tigers kill more than males, adjusting harvest based on a mean kill rate (including males) may result in lower prey densities than required for reproduction.

Unfortunately, data on kill rates and requirements of Amur tigers outside the winter season are difficult to obtain. Recent advances in Global Positioning System (GPS) collar technology enable researchers to gain new insights into predator-prey dynamics (e.g. Webb et al., 2008) and help address this important aspect of tiger conservation in a scientific manner.

Low prey densities in the Russian Far East are hypothesized to limit the northern distribution of tigers in Russia (Miquelle et al., 2010). Given that Amur tigers might live near the threshold of sufficient prey densities (Miquelle et al., 1999), the conservation challenge is to not only adjust legal harvest, but to determine what are the ungulate prey thresholds needed to meet the energetic requirements for survival and reproduction of wild tigers. The greatest energetic costs are likely to be incurred by females that must provide for 1 to 4 young. Therefore, while tigers may be able to exist at lower prey densities, the distribution of reproducing females is likely to be defined by their ability to acquire sufficient energy (i.e., adequate prey densities) to successfully rear young. One approach to this problem is to estimate energetic requirements for tigers and then determine prey biomass necessary to meet these needs (Ackerman et al., 1986; Aldama et al. 1991; Laundre, 2005). Quantifying the energetic requirements of wildlife allows scientists and managers to estimate nutritional carrying capacity (Parker et al., 1984; Hobbs 1989, Laundre 2005, Robbins et al., 2007), the impact of predators on prey, and develop science-based conservation recommendations (Odden, Wegge, 2009). Calculating a threshold prey biomass necessary to sustain tigers requires knowledge of their energetic requirements and food consumption (kill rates) in the wild (Ackerman et al., 1986; Aldama et al., 1991; Laundre, 2005).

After nearly 20 years of research in the Russian Far East, the Wildlife Conservation Society (WCS) and the Siberian Tiger Project (STP) still have several unanswered questions regarding the implications of tiger-prey dynamics on tiger conservation programs.

Recently, GPS collars have been used to estimate annual kill rates for other large carnivores (Laundre, 2008; Sand et al., 2008), but no one has attempted to apply this approach to tigers, nor to understand energetic requirements by combining GPS collar data with models of energetic costs. Our research goals are to apply this new technology to better understand year-round tiger-ungulate dynamics and the energetic demands facing tigers. We initiated this research project in the fall of 2009. In this article we present our research approach and methods as well as preliminary data.

We will combine GPS collars, field work, and modeling to address 2 research questions:

1. Are there seasonal differences in the kill rates of large ungulates by tigers in the Russian Far East?
2. What are the energetic and hence, prey requirements for tigers to a) survive; and, b) reproduce?

Estimating the rate at which tigers kill prey (kills/tiger/day) with traditional VHF radiocollar technology is difficult because tigers are elusive and difficult to observe, the prey may be small and quickly consumed, and because intensive monitoring is logistically and financially difficult. While prey composition in the diet of Amur tigers in SABZ has already been published, little is known of yearly tiger kill rates (Yudakov, Nikolaev, 1987; Pikunov, 1981; Miquelle et al., 1996), especially during snow-free spring, summer and fall months (hereafter, summer). To bridge this knowledge gap, we will use GPS technology to estimate tiger kill rates and test for seasonal differences in large-ungulate kill-rates by Amur tigers.

There are two schools of thought on how summer predation rates may differ from winter predation rates on large ungulates. The first hypothesis proposes that Amur tigers may kill more ungulates in winter than summer due to a shift in diet in summer to bears and smaller mammals that are hibernating and/or not as accessible during the winter months (e.g. badgers (*Meles meles*) and raccoon dogs (*Nyctereutes procyonoides*)). Recent scat analyses in the Russian Far East has shown non-ungulate prey species are more common in tiger scat during the summer months (Kerley, unpublished data).

Alternately, Amur tigers may kill more ungulates during the summer than winter. Such an increase in kill rates might be the result of high predation rates on young ungulates (calves, fawns, and piglets). For example, Sand et al. (2008) found an increase in wolf (*Canis lupus*) predation rates in summer due to a dramatic increase in the number of calf moose (*Alces alces*) killed. We will test these alternative hypotheses through field-based tracking of GPS collared Amur tigers in the Russian Far East.

STUDY AREA

This research will be conducted in and around the Sikhote-Alin Biosphere Zapovednik (SABZ) near the village of Terney, in Primorski Krai (province), in the Russian Far East. At just under 400,000 ha, it is the largest zapovednik (reserve) in southern Russian Far East and harbors 20–35 tigers (Smirnov, Miquelle, 1999). Hunting is prohibited in the reserve, and tiger and prey densities in SABZ are higher than the surrounding multiple-use lands, where hunting of ungulates is legal and enforcement capacity is lower. The primary prey species of the tiger in SABZ include the Manchurian red deer (*Cervus elaphus*), Ussuri wild boar (*Sus scrofa*), and sika deer (*Cervus nippon*), although tigers also prey on roe deer (*Capreolus capreolus*), musk deer (*Moschus moschiferus*), Manchurian moose (*Alces alces*), goral (*Neomorphodus caudatus*), brown bear (*Ursus arctos*), Himalayan black bear (*Ursus thibetanus*), wolf, raccoon dogs, badger, lynx (*Lynx lynx*), and mink (*Mustela vison*) (Miquelle et al., 1996).

METHODS

Tigers have been safely captured and collared by researchers in SABZ since 1992 by placing Aldrich foot snares on tiger-marked trees, game trails, and kills (Goodrich et al., 2001). All captured adult tigers will be fitted with GPS collars using UHF communication or Iridium GPS collars. GPS collars offer two-way communication that enable researchers to upload new schedule files and download data, and Iridium collars enable data transmission via satellite phone networks. Our goals are to deploy up to 8 GPS collars on adult tigers in the SABZ. While a sample size of ≤ 8 may be low, this will be the first study addressing year-round tiger kill rates using GPS collars, and our research will address an important issue currently being debated in the scientific and conservation community. We will combine GPS data collection with traditional snow tracking in the winter and summer tracking to investigate potential kill sites and movement patterns. We will combine these GPS data with previously (Miquelle et al., 1996; Miquelle et al., 1999; Kerley et al., 2002) and concurrently collected VHF data to validate GPS estimated tiger kill.

We will use a combination of GPS data analysis and field work to estimate tiger kill rates as the number of prey killed by a tiger per unit time (# prey/tiger/day). We will track GPS collared tigers in the field and locate kills using traditional ground-based field methods during winter (snow tracking) combined with uploading GPS data from collars. During summer, we will depend on GPS data uploads and cluster searches to locate kill sites. We will locate kills by searching GPS clusters until we are able to determine if the site contains a carcass or other tiger sign. We will search putative kill sites using conventional field tracking methods for prey remains within 1–2 weeks, to avoid missing kills due to scavenging or decomposition (Sand et al., 2008; Webb et al., 2008). We will sample a subset of non-clustered GPS locations (i.e., putative movement locations) to verify our sampling technique is not underestimating potential kill sites. We will also collect data during several intensive sampling periods when every location will be searched during a two week period to verify small prey presence or absence.

Once we have uploaded GPS data, we will adopt the methods of Webb et al. (2008) to process GPS locations using the program SaTScan (Boston, Massachusetts, USA; Kulldorff et al., 2005) to identify location clusters or potential kill-sites. This program, originally developed to identify spatial cluster of disease outbreaks, identifies clusters of locations statistically unique from baseline distribution or movement patterns (Kulldorff et al., 2005; Webb et al., 2008). A cluster will be defined spatially and temporally as two or more locations within 100 m and 48 hours of each other. Previous research on wolves found that a fix-rate of 1 location/2 hours was sufficient to locate 90 percent of large ungulate kills (e.g., elk and moose) (Webb et al., 2008), whereas 95 percent of mountain lion predation was confirmed at a fix-rate of 1 location/4 hours (Anderson, Lindzey, 2003). We will use a fix-rate of 1 location/3 hours to locate tiger kills, and adjust sampling to a burst sampling scheme with an alternating schedule of 3 weeks at 3 hours and 1 week of 1 hour data to ensure we are not missing smaller kills such as fawns and piglets during summer.

We will statistically test our hypotheses using the empirical kill-rate estimates from field sampling intervals using repeated measures ANOVA on individual tigers, and treatment effects of SEX (and reproductive status, e.g. females with and without young, and age of young) and SEASON (Zar, 1998). We will also test our hypothesis using logistic regression of factors influ-

encing empirical and predicted kill sites. Following recent studies on large carnivores, we will use known kills from GPS and snow track searches to develop a logistic regression model to estimate kills at clusters we were unable to field sample to increase our sample size of kills (Anderson, Lindzey, 2003; Webb et al., 2008; Knopff et al., 2009). Anderson and Lindzey (2003) found the most important factor in estimating the probability that a cluster contained a cougar kill site was

$$\text{Pr}(\text{Жертва}) = \frac{\exp(\beta_0 + \beta_1 * \text{Сезон} + \beta_2 * \text{Пол} + \beta_3 * X_3 + \dots \beta_4 * X_4)}{1 + \exp(\beta_0 + \beta_1 * \text{Сезон} + \beta_2 * \text{Пол} + \beta_3 * X_3 + \dots \beta_4 * X_4)} \quad (1)$$

the number of nights a cougar spent within a cluster. Knopff et al. (2009) used logistic regression models in combination with field efforts to successfully predict >95 percent of cougar kills over 8 kg. By explicitly integrating our hypothesis (season, sex) into a logistic regression model predicting the presence or absence of a kill, we will test for whether different seasons and sexes have different kill rates using the following model:

We will use equation 1 to test our hypothesis; for example, if $\beta_1 = 0$, then kill rates are statistically identical between winter and summer.

Next, we will combine estimates of tiger kill and movement rates with a tiger energetic model to test if tigers are obtaining adequate energy for survival and reproduction, as well as their potential prey requirements (e.g., Ackerman et al., 1986). Comparing the estimates derived from GPS data to the estimates derived from the energetic model will help managers and conservationists determine if their tiger populations are meeting their energetic demands for survival and reproduction. Since an impoverished prey base will support only occasional reproduction (Karanth, Stith, 1999), determining the threshold consumption rate for reproduction is an important question. Determining if reproduction is energetically feasible in areas with ungulate populations composed of nothing larger than a muntjac (*Muntiacus* spp.) or musk deer is another way of phrasing the same question that has implications for all tiger subspecies. The total energetic cost (C_{total}) for any mammal in a given time period can be expressed as the sum of the energetic expenditure caused by different activities plus the cost of thermoregulation (C_{th}) (Powell, 1979). The primary energetic activities of adult tigers are resting (C_r), locomotion (C_l), hunting (C_h), eating (C_e) and energetic costs associated with reproduction (C_{rep}). Time spent in different activities multiplied by the energetic costs of each activity results in an estimate of daily energy requirements (Powell, 1979; Gustafson, 1984; Powell et al., 1985; Ackerman et al., 1986; Aldama et al., 1991; Laundre, 2005). Therefore, the total daily energetic demands on a tiger can be represented as:

$$C_{\text{total}} = C_r + C_l + C_h + C_e + C_{\text{rep}} + C_{\text{th}} \quad (2)$$

Most energetic studies have relied on formulas or values derived from laboratory experiments and either attempted to use these values for modeling energetic costs of wild animals or attempted to validate previous studies on new species. Few studies have attempted to estimate the energetic costs of different activities of free-ranging carnivores under field conditions. Because of the recent decline in prey populations in the Russian Far East, it is imperative that we have accurate estimates of tiger energetic needs and their resulting prey requirements. We will develop an energetic model using information from the western and Russian literature to estimate the energy budget of tigers and test this model using the empirically derived kill and movement rates. We will then use this model to estimate tiger food requirements when preying on their primary prey species. If the model does not validate well, we will refine the energetic model using formal sensitivity analysis of model parameters to identify the most important driver of energetic rate.

We will calculate the number of ungulate prey required for tigers to meet the energetic costs given by equation 2 above. The primary prey species available to tigers in the SABZ are red deer, wild boar, sika deer, and roe deer. We will estimate percent composition in the diet of these (and other) prey species using kill data. The average weight of prey species in SABZ has been reported as 224 and 149 kg for adult male and female red deer, 193 and 92 kg for adult male and female wild boar, 106 and 74 kg for adult male and female sika deer, and 40 and 35 kg for adult male and female roe deer, respectively (from Miquelle et al., 1996). The edible portion of whole deer carcasses fed to captive cougars was estimated to be 77 percent by Hornocker (1970) and

79 percent by Ackerman et al. (1986). Because red deer, wild boar, and sika deer are all larger than white-tailed deer (*Odocoileus virginianus*), and larger prey species will have proportionally more biomass per surface area, we will use the higher estimate and assume that 79 percent of a tiger prey carcass is edible. Tigers that are not disturbed by humans are very efficient consumers and rarely leave edible portions of a carcass (Kerley et al., 2002). Since human disturbance in the backcountry of the zapovednik is extremely limited, we will estimate the proportion of available food biomass consumed by tigers at each site, assuming that tigers are responsible for consuming all portions. We will use the estimated weights of ungulate prey species reported above to calculate prey requirements based on energetic requirements. Although the exact body composition of any animal varies throughout the year in relation to food availability and habitat quality, some generalizations can be made regarding the average composition of an animal. Davison et al. (1978) calculated the value of white-tailed deer 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 will also assume a value of 1,890 kcal/kg.

Much of the energy contained in prey is lost through incomplete use of carcass, as well as passage of undigested energy in fecal matter and urine (Ackerman et al., 1986). Digestibility of meat is generally high in carnivores (Grodzinski, Wunder, 1975) but assimilation is reduced from the presence of hair and bones. Previous studies have estimated that 86 percent of the energy ingested from deer meat remains after digestion and assimilation by cougars (Ackerman et al., 1986), bobcats (Golley et al., 1965), badgers (Jense, 1968), fishers (Davison et al., 1978), red fox (Litvaitis, Mautz, 1976) and coyotes (Litvaitis, Mautz, 1980). We propose to use this value in our estimates of energy remaining from ungulate meat after digestion and assimilation.

Based on these parameters, we propose to estimate the potential biomass of ungulate prey consumed (PB_c) with the same equation as Ackerman et al. (1986),

$$PB_c \text{ kg/day} = C_{tot} \text{ kcal} / (1,890 \text{ kcal/kg} \times 0.86 \times PB_u) \quad (3)$$

The value PB_u represents the proportion of diet of tigers that are ungulates, estimated by Miquelle et al. (1996) to be 98.7 percent during winter. We propose to use the data collected from GPS collars to estimate the proportion of prey in tiger diet that is ungulate. 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 percent diet composition of each of the main prey species (i.e., red deer, sika deer, wild boar, roe deer) and the edible portion of each carcass. Using these parameters, we propose to estimate the total number of prey killed per day with the same equation as Ackerman et al. (1986),

$$PB_k = PB_c / (M_w \times 0.79) \text{ prey/day}, \quad (4)$$

where M_w is the mean live weight of prey in kilograms. We propose to calculate the hypothetical kill rate needed to meet energetic requirements (equation 4) for all prey species individually, and compare these results to actual data based on observations of GPS collared tigers above. This application of the energetic model, in combination with the empirical kill rates, will help test for thresholds in prey availability that may limit tiger reproduction and adult survival.

RESULTS

We captured a sub-adult tigress in early November 2009 and fitted her with a GPS collar. This two-year old female was assessed to be in good physical condition. Unfortunately, this tigress died in early December from natural causes after only five weeks of monitoring. We were able to locate the carcass deep in the backcountry of the study area, conduct a brief necropsy, and retrieve the collar. From November 7 to December 11, 2009, we received 203 locations from this tigress out of 272 attempts, for a 74.6 percent success rate. During the five weeks we monitored her movements, this tigress traveled an average of 587.3 meters every three hours, nearly 4.7 km/day and covered an area far larger than would be expected from an adult tigress with an established territory (Figure). The movements and age of this tigress suggested she was dispersing from her mother's home range. We processed this location data to look for potential kill sites using the methods described above and created 26 individual clusters (Figure). Each cluster will

be searched to determine if a kill was made at the site. These methods will be repeated with each subsequent tiger we capture over the next several years to determine year-round kill rates and energetic requirements.

CONCLUSION

Hunters are key stakeholders in tiger conservation in all remaining tiger habitat in the Russian Far East except for protected areas. Hunting is an important recreational and subsistence tradition in Russia, as evidenced by the fact that there are over 60,000 registered hunters in the Russian Far East who hunt in tiger habitat. Wildlife management organizations are responsible for managing hunting, controlling poaching, and conducting surveys of game species on leased hunting territories encompassing about 85 percent of Amur tiger habitat. We are hopeful that our results will assist in assessing the true impact of tigers on prey populations, and improve estimates of legal harvest that must incorporate off-take by tigers as well. Appropriate harvest regimes of ungulates are particularly important now, when results of the Amur Tiger Monitoring Program have indicated a downturn in red deer, roe deer, and even tiger numbers. Rigorous data on the impact of tigers on prey numbers, and the prey requirements needed for viable tiger populations, are needed to guide policy decisions.

The tiger energetic model we develop will be applicable to tiger populations throughout their range. Currently, many countries in South East Asia are attempting to conserve or re-establish tiger populations in the face of some of the densest and fastest growing human populations in the world. If the proportion of each prey species in the diet of tigers and the estimated prey population sizes are known, the energetic model can help determine if sufficient prey populations are present to support tiger survival and reproduction without causing detrimental effects to the prey populations. We are hopeful that such evaluations will assist in convincing local authorities that conservation of tigers will be largely dependent on protecting ungulate populations from overharvest by humans.