Estimating Amur tiger (*Panthera tigris altaica*) kill rates and potential consumption rates using global positioning system collars

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The International Union for Conservation of Nature has classified all subspecies of tigers (*Panthera tigris*) as endangered and prey depletion is recognized as a primary driver of declines. Prey depletion may be particularly important for Amur tigers (*P. t. altaica*) in the Russian Far East, living at the northern limits of their range and with the lowest prey densities of any tiger population. Unfortunately, rigorous investigations of annual prey requirements for any tiger population are lacking. We deployed global positioning system (GPS) collars on Amur tigers during 2009–2012 to study annual kill rates in the Russian Far East. We investigated 380 GPS location clusters and detected 111 kill sites. We then used logistic regression to model both the probability of a kill site at location clusters and the size of prey species at kill sites according to several spatial and temporal cluster covariates. Our top model for predicting kill sites included the duration of the cluster in hours and cluster fidelity components as covariates (overall classification success 86.3%; receiver operating characteristic score of 0.894). Application of the model to all tiger GPS data revealed that Amur tigers in this study made a kill once every 6.5 days (95% confidence interval [95% CI] 5.9–7.2 days) and consumed an estimated average of 8.9 kg of prey biomass per day (95% CI 8.8–9.0 kg/day). The success of efforts to reverse tiger declines will be at least partially determined by wildlife managers' ability to conserve large ungulates at adequate densities for recovering tiger populations.

Key words: Amur tiger, consumption rates, global positioning system (GPS) collars, kill rates, *Panthera tigris altaica*, Russian Far East, Siberian tiger, Sikhote-Alin Mountains, tiger

Fewer than 3,500 wild tigers (*Panthera tigris*) remain in the world (Walston et al. 2010) and all 6 remaining subspecies are listed as endangered by the International Union for Conservation of Nature (IUCN). 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 Initiative 2010). Primary threats to tiger persistence include habitat loss and fragmentation (Wikramanayake et al. 1998), depletion of prey species (Karanth and 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). Approximately 10% of the world's tigers inhabit the Russian Far East, where a single metapopulation represents 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 rather 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 documented a steady decline in ungulate prey populations throughout Amur tiger habitat (Miquelle et al. 2007). Hunting of large ungulates is a traditional food source for residents and is legal in

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TABLE 1.—A review of published studies focusing on annual tiger (*Panthera tigris altaica*) kill rates on prey populations in Russia (based on snow-tracking data) and Chitwan National Park, Nepal (based on very-high-frequency–telemetry data).

Study	Kills/year			Days/kill			
	Low	High	Range	Low	High	$\bar{X}$	Range
Kovalchuk (1988)	40	50	40–50	9.13	7.30	8.22	7.30–9.13
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)[a]	40	50	40–50	9.13	7.30	8.22	7.30–9.13
Seidensticker (1976)[a]	61	73	61–73	5.98	5.00	5.49	5.00–5.98
This study	50.4	61.3	50.4–61.3	7.18	5.89	6.54	5.89–7.18

[a] Study site located in Chitwan National Park, Nepal.

approximately 85% of the remaining 156,000 km^2 of tiger habitat in the Russian Far East (Miquelle et al. 1999a). Unfortunately, conflict exists between Russian hunters and tigers over a shared prey base. Because the majority of tiger habitat in Russia is unprotected, and 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 (Kerley et al. 2003; Goodrich et al. 2010), coexistence between tigers and people in the multiple-use forests of the Russian Far East is a conservation imperative (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 humans based on an estimated annual predation rate by the tiger population (Miquelle et al. 2005a). Thus, one key to minimizing conflict is the acquisition and application of reliable scientific information about annual prey requirements of Amur tigers. Unfortunately, data on kill rates and prey requirements of wild tigers are difficult to obtain, particularly during snow-free months in Amur tiger range or in tropical portions of tiger range. To date, annual kill rates by Amur tigers have been estimated by extrapolating winter kill rates from intensive snow-tracking efforts (Yudakov and Nikolaev 1987; Pikunov 1988; World Wildlife Fund 2002). Recent research has highlighted the dangers of extrapolating large carnivore kill rates collected during winter without adjusting for expected seasonal differences (Sand et al. 2008; Knopff et al. 2010; Metz et al. 2012). Advances in global positioning system (GPS) collars provide an alternative monitoring technique that enables researchers to estimate kill rates year-round (Anderson and Lindzey 2003; Knopff et al. 2009; Merrill et al. 2010). Anderson and Lindzey (2003) were the 1st to use GPS collars to estimate large felid kill rates and their approach has since been applied to a wide number of large carnivore species (e.g., Webb et al. 2008; Cavalcanti and Gese 2010; Tambling et al. 2012). Nevertheless, GPS collars have been deployed on Amur tigers only recently (Miller et al. 2011; Rozhnov et al. 2011) and have not been used to estimate tiger kill rates (Table 1).

Although kill rate is an important ecological parameter influencing prey populations, ultimately it is consumption rate that may determine tiger reproduction rates and population dynamics (Sunquist et al. 1999). Metz et al. (2012) showed that interpretations of seasonal predation varied significantly depending on the metric used to quantify kill rates. For example, kill rates of wolves (*Canis lupus*) in Yellowstone National Park were higher in summer than in winter if looking at kill rate as the number of animals killed per unit time but lower in summer if looking at kill rate as the biomass acquired per unit time (Metz et al. 2012). However, most studies of carnivores do not actually estimate consumption rates through behavioral observation; instead, they convert kill rates to estimated consumption rates by adjusting for estimated losses to scavengers, estimated live weights of prey from literature values, edible portions of the prey species, and so on (Knopff et al. 2010; Metz et al. 2012). Conversion of kill rates (number of prey killed per unit time) to estimated consumption rates (kilograms of prey consumed per unit time) allows for comparisons between sexes and species (e.g., comparative metabolic demands) or to sites with different prey species (and sizes) available.

Here we use GPS data to estimate annual Amur tiger kill rates and potential consumption rates in the Russian Far East. 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 at clusters of locations. We then tested whether we could predict body size of ungulate prey using a 2-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 (Sand et al. 2008; Metz et al. 2011). Therefore, we converted kill rates to estimated consumption rates (kilograms per tiger per day) to understand the energetic consequences of seasonal changes in kill rates and prey sizes. Finally, we compared our GPS-based kill rates to previous estimates of tiger kill rates from snow tracking in Russia and very-high-frequency (VHF) tracking in

FIG. 1.—Our study was focused in and around the 4,000-km² Sikhote-Alin Biosphere Zapovednik, Russian Far East, from 2009 to 2012.

Nepal, as well as to other GPS-based kill-rate estimates from other large felids.

MATERIALS AND METHODS

Study area.—We conducted our research in and around the 4,000-km² Sikhote-Alin Biosphere Zapovednik (or Reserve). Founded in 1935, the Reserve is an IUCN Category I protected area near the village of Terney, Primorskii Krai (province), in the Russian Far East (Fig. 1). Access to the Reserve is strictly limited to Reserve staff and visiting scientists. Inside the Reserve, hunting is illegal and poaching is relatively low, whereas prey populations outside of the Reserve are exposed to legal hunting and high poaching rates (Miquelle et al. 2005b). Within the Reserve, the Sikhote-Alin Mountains parallel the Sea of Japan with elevations reaching 1,600 m, but most peaks are < 1,200 m. The Reserve occurs in the Far Eastern temperate climatic zone and is characterized by strong seasonality with dry, cold winters ($\bar{X} = -12.9$°C, January in Terney), moderate snowfall ($\bar{X} = 1,190$ mm snow in Terney per winter), warm and humid summers ($\bar{X} = 15$°C, July in Terney), and average annual precipitation of 760 mm (Gromyko 2010).

Dominant vegetation communities within the Reserve 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*—Vasiliev and Fliagina 2006). The key tiger prey species in the Reserve include red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), sika deer (*Cervus nippon*), and roe deer (*Capreolus pygargus*—Miquelle et al. 1996, 2010b). Amur tigers in the Reserve also opportunistically prey on moose (*Alces alces*), musk deer (*Moschus moschiferus*), ghoral (*Naemorhedus 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 (*Canis lupus familiaris*—Miquelle et al. 1996).

Predicting tiger kill and consumption rates with GPS data.—We deployed GPS collars on tigers captured in and around the Reserve from 2009 to 2012 using modified Aldrich foot snares (Goodrich et al. 2001). Tigers were anesthetized with Zoletil (Lewis and Goodrich 2009) and fitted with VECTRONIC (Berlin, Germany) or LOTEK (Newmarket, Ontario, Canada) satellite GPS collars that allowed for real-time monitoring within days or 1–2 weeks of predation sites. Capture and handling of tigers followed guidelines of the American Society of Mammalogists (Sikes et al. 2011), and protocols were approved by the University of Montana Institutional Animal Care and Use Committee (UM IACUC AUP 043-09) and the Wildlife Conservation Society Global Health unit. We combined GPS data collection with stratified sampling of potential kill sites to estimate tiger kill rates as the number of days between kills (days per kill per tiger) and in terms of potential biomass consumption rates (kilograms per tiger per day). We stratified potential kill sites for investigation according to the relative probability (i.e., high or low) that a GPS location was a kill site by adapting previously developed methods for large cats (Knopff et al. 2009). To estimate the number of kills, we used GPS location data to detect clusters of locations in close spatial and temporal proximity that represented potential kill sites (Anderson and Lindzey 2003). Previous research on mountain lions (*Puma concolor*) indicated that 95% of kill sites were correctly identified at a fix rate of 1 location/4 h (Anderson and Lindzey 2003). We programmed collars to obtain locations at intervals of 90, 180, or 360 min. After uploading GPS data, we used a Python script (Python Software Foundation, Hampton, New Hampshire) developed by Knopff et al. (2009) to identify potential kill sites as clusters of 2 or more locations within 100 m and 48 h of each other. We located kill sites by physically searching 50 m or more around each location in a cluster. During winter, we located kill sites by downloading GPS data from collars and snow tracking GPS-collared tigers to clusters in the field. During snow-free months, we relied on GPS data downloads and cluster searches to locate kill sites. We attempted to search putative kill sites for prey remains after 1–2 weeks of receiving

location data to avoid displacing tigers from kills or losing information to decomposition or scavenging of the carcass (Sand et al. 2008; Webb et al. 2008). We searched most (88.5%) of the largest clusters ($\geq$ 24 h from 1st location in the cluster until the last) and many smaller clusters to determine which clusters contained kill sites, but also searched a subset ($n = 518$) of nonclustered GPS locations to verify that our sampling technique did not underestimate potential kill sites. We also collected data during an intensive sampling period where we searched every location (clustered and nonclustered) from an individual tiger during a 2-week period in the summer to verify presence or absence of small-prey remains. We opportunistically snow tracked 134 km between consecutive GPS locations of 2 different tigers, which ensured a near 100% kill-site recovery rate along the route, regardless of prey size.

We used multiple logistic regression (Hosmer and Lemeshow 2000) to model the presence or absence of a kill at GPS clusters. We measured 6 potential spatiotemporal predictor variables for each GPS cluster: hours: the total number of hours between the 1st and last locations in the cluster; days: the number of 24-h periods when at least 1 fix was obtained within the cluster; average distance: the average distance away from the cluster center that all points in the cluster were located; radius: the difference between the cluster center and the farthest clustered point away; multiday binary: a binary coding of days on the cluster that separated clusters into those with locations across multiple 24-h periods and those with all locations within a single 24-h period (e.g., Knopff et al. 2009); and percent fidelity: the percentage of locations over the duration of the cluster that fell within the cluster. We estimated the explanatory power of these variables using logistic regression to predict the presence (1) or absence (0) of a kill (Pr(Kill)) following:

$$Pr(Kill) = \frac{\exp^{(\beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \beta_3 * X_3 + ... \beta_8 * X_8)}}{1 + \exp^{(\beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \beta_3 * X_3 + ... \beta_8 * X_8)}}, \quad (1)$$

where β_0 is the intercept, and βs are the coefficients of the effects of the covariates, X_i, on Pr(Kill). We excluded explanatory 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 noncollinear predictor variables, fit them to the data, and assessed model support with Akaike's information criteria (AIC—Burnham and Anderson 2002). We summed AIC weights (Σw_i) from the top models to rank support among predictor variables influencing the probability a cluster contained a kill site. To correct for potential missed kills in our full cluster data set, we then used predicted values from our top model to estimate the probability of kills at clusters we were unable to field sample (Knopff et al. 2009). We conducted all analyses using Stata 11.0 (Stata Corp., College Station, Texas).

To distinguish between large- and small-bodied prey species based on GPS data, we used a 2nd multiple logistic regression analysis to model the effects of the same 6 cluster parameters on prey size (e.g., Knopff et al. 2009). For consistency within the tiger literature, we followed Chundawat et al. (1999) in using a 40-kg cut point to assign prey species into small (0) and large (1) categories. For each cluster in our full data set we then estimated the probability a cluster contained a kill (i.e., equation 1 above), and 2nd, the probability that predicted kills were small or large.

We used sensitivity and specificity curves to classify predictions from the top regression models differentiating clusters as kill sites from nonkill sites and small-prey kill sites from large-prey kill sites (Hosmer and 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 (Zimmermann et al. 2007; Webb et al. 2008; Knopff et al. 2009). A cut point that maximizes sensitivity will correctly classify most kill sites but may incorrectly classify a high proportion of nonkill sites, thereby overestimating the predicted kill rate. Conversely, a cut point that maximizes specificity will correctly classify most nonkills but may incorrectly classify many kill sites as nonkills, 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 1st model or a probable large-prey kill site in the 2nd model (Hosmer and Lemeshow 2000; Liu et al. 2005).

We estimated the kill rate as the sum of predicted kills divided by the number of days of continuous monitoring. We calculated kill-rate variance using a design-based ratio estimator with individual tigers as the sample unit (Thompson 2002; Hebblewhite et al. 2003). We estimated potential consumption rates by converting our kill-rate estimates into potential prey biomass (kg) consumed per tiger per 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 the Russian Far East have been reported for all sex and age classes (Bromley and Kucherenko 1983; Danilkin 1999). 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 elk (*Cervus elaphus*) was estimated to be 68% (Wilmers et al. 2003) and white-tailed deer (*Odocoileus virginianus*) was estimated to be about 79% (Ackerman et al. 1986). Using these estimates, we assumed 68% of a large-prey carcass was edible and 79% of a small-prey carcass was edible biomass. Tigers that are not disturbed by humans rarely leave edible portions of a carcass (Kerley et al. 2002), but Yudakov and Nikolaev (1987) estimated that 15% of each tiger kill was lost to scavengers. Because human disturbance in the backcountry of the Reserve is limited, we assumed tigers did not abandon kill sites, consumed all edible portions, and lost 15% of each prey item to scavengers. As with kill rates, we used a design-based ratio estimator to calculate variance in potential consumption rates (Thompson 2002; Hebblewhite et al. 2003).

Finally, following Cavalcanti and Gese (2010), we tested the relationship between the interkill time interval and the size of

TABLE 2.—Summary of data used during analyses of Amur tiger (*Panthera tigris altaica*) kill rates (days kill^{-1} tiger^{-1}) and potential consumption rates (kg consumed day^{-1} tiger^{-1}; CR) on and near Sikhote-Alin Biosphere Zapovednik, Russia, from 2009 to 2012.

Tiger indentification	Sex	No. days monitored	No. locations	Fix %	No. clusters searched	No. kills	Observed days/kill	Predicted days/kill	Observed CR	Predicted CR
Pt99	Female	420	2,988	90.4	169	47	8.94	6.77	4.79	8.62
Pt100	Male	99	1,529	96.6	48	14	7.07	5.21	7.20	11.20
Pt114	Female	311	4,644	96.4	161	50	6.22	6.76	7.63	8.64
Total	3	830	9,161	94.4	378	111				
$\bar{X}$		276.7	3,053.7	94.5	126.0	37.0	7.41	6.25	6.54	9.49
SD		163.23	1,558.54	3.52	67.67	19.97	1.389	0.899	1.534	1.488
Ratio estimator							7.48	6.54	6.14	8.93
Ratio SD							0.727	0.211	0.089	0.023

predicted kills using a 1-tailed *t*-test to test whether satiation following larger kills might influence kill rates. To evaluate the interkill interval of predicted kills, we compared the time from the 1st location in a predicted kill site to the 1st location in the following predicted kill site with the predicted size (large or small) of the kill.

RESULTS

Predicting tiger kill and consumption rates with GPS data.—From 2009 to 2012, we captured and GPS-collared 3 adult females, 2 adult males, and 1 subadult female tiger (subadults being individuals no longer associating with their mother but not yet reproducing), but we restricted analyses to 3 adults with sufficient data to estimate kill rates (Table 2). These 3 tigers were each monitored 99–420 days, with a combined total of 830 tiger-days (Table 2). We obtained 1,529–4,644 locations from each tiger, with a total of 9,161 locations and a fix success rate of 94.5% (Table 2).

As our focus was predicting kill rates and potential consumption rates of healthy adult tigers, we screened out locations when tigers were known or believed to be unhealthy (see "Discussion" for more details). Pt100 and Pt114 both lived in and around the Reserve, but Pt99 lived exclusively in unprotected, multiple-use forests. We estimated 982 unique clusters representing potential kill sites and investigated 378 clusters (range, 48–169 clusters per tiger or 36.1–41.6% of

total clusters from each tiger), resulting in 109 observed kills at clusters (range, 14–50 per tiger; Table 2). Two additional kills (both were badgers) were located at single locations during our investigation of a subset of nonclustered GPS locations ($n = 518$). Of the total observed kills, 27.9% were wild boar, 24.3% were red deer, and 23.4% were roe deer (Table 3). Among known wild boar kills, 25.8% were adults, 67.7% were juveniles and piglets, and 6.5% could not be accurately classified into an age class. Red deer kills consisted of 70.4% adults and 29.6% juveniles and calves. Among roe deer kills, 53.9% were adults, 26.9% were juveniles, and 19.2% could not be accurately classified. Juvenile ungulates comprised 18 (50.0%) of 36 observed summer large ungulate kills and 17 (51.5%) of 33 winter kills. Overall, wild ungulate species represented 90.1% of all tiger kills, with nonungulate or domestic prey comprising the remaining kills (Table 3).

Our best logistic regression model for differentiating clusters that contained tiger kills from nonkill clusters included hours at the site and percent fidelity to the site (Table 4). The top model showed that the probability a cluster contained a kill increased as a tiger spent more time at a site and as fidelity to the site increased ($P \le 0.005$; Table 5). Covariates were ranked in the following order based on summed variable importance weights (Σw_i) of the top 8 models: 1st, percent fidelity to the site $\Sigma w_i = 1.000$; 2nd, hours at the site $\Sigma w_i = 0.965$; 3rd, radius of cluster $\Sigma w_i = 0.252$; 4th, average distance from each location to the cluster center $\Sigma w_i = 0.198$; 5th, clusters that contained

TABLE 3.—Prey species located at Amur tiger (*Panthera tigris altaica*) kill sites identified at single global positioning system (GPS) locations or from logistic regression–directed cluster sampling of GPS-collared tigers in the Sikhote-Alin Mountains, Russian Far East, 2009–2012.

Prey species	No. kills located	% of total kills	% biomass[a]	Kills/day (SE)
Wild boar (*Sus scrofa*)	31	27.9	26.9	0.037 (0.004)
Red deer (*Cervus elaphus*)	27	24.3	43.6	0.033 (0.004)
Roe deer (*Capreolus pygargus*)	26	23.4	12.6	0.031 (0.003)
Sika deer (*Cervus nippon*)	15	13.5	12.9	0.018 (0.008)
Musk deer (*Moschus moschiferus*)	1	0.9	0.2	0.001 (0.001)
Brown bear (*Ursus arctos*)	1	0.9	1.6	0.001 (0.001)
Asiatic black bear (*U. thibetanus*)	1	0.9	0.9	0.001 (0.001)
Feral dog (*Canis lupus familiaris*)	3	2.7	0.5	0.004 (0.001)
Badger (*Meles leucurus*)	5	4.5	0.7	0.006 (0.001)
Cattle (*Bos taurus*)	1	0.9	0.2	0.001 (0.001)
Total	111	100	100	0.134 (0.009)

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

TABLE 4.—The top 8 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. Avg Dist = average distance.

Model description	n	K	Log likelihood	ΔAIC_c	AIC weights	Evidence ratio— compared to best model
Hours + % Fidelity	380	3	−140.801	0.000	0.533	1.000
Hours + Radius + % Fidelity	380	4	−140.582	1.605	0.239	0.448
Hours + % Fidelity + Avg Dist	380	4	−140.799	2.038	0.193	0.361
MDB[1] + % Fidelity	380	3	−144.347	7.091	0.015	0.029
MDB + Radius + % Fidelity	380	4	−143.527	7.494	0.013	0.024
MDB + Avg Dist + % Fidelity	380	4	−144.305	9.050	0.006	0.011
Days + % Fidelity	380	3	−147.660	13.717	0.001	0.001
Days + Radius + % Fidelity	380	4	−146.713	13.866	0.001	0.001

[a] MDB = Multiday binary: a binary coding of hours on the cluster that separated clusters into those with locations across multiple 24-h periods and those with all locations within a single 24-h period.

locations from multiple days (Multi Day Bin) $\Sigma w_i = 0.034$; and 6th, number of 24-h periods with at least 1 location at the site $\Sigma w_i = 0.001$. We used only the top model (AIC weight = 0.533) 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 distinguishing kill sites from nonkill sites fit the data well (likelihood ratio chi-square score of 177.46 [*P*-value < 0.0001], pseudo $R^2 = 0.39$, and receiver operating characteristic [ROC] score of 0.894). The maximized probability cutoff for which we considered a cluster a probable kill site was 0.23, which corresponded to an overall classification success of 86.3%.

The number of hours at a site was the only predictive variable in our top model for discriminating small prey from large prey ($P \leq 0.005$; Table 6). Our top model suggested that the probability a kill was a large-prey item increased with increasing hours spent at the site (Table 5). Despite a low AIC weight, we chose to use only the top model (AIC weight = 0.232), instead of multimodel inference, because model averaging would have included collinear variables. Considering summed variable importance weights (Σw_i) of the top 10 models, covariates were ranked in the following order: 1st, hours spent at the site $\Sigma w_i = 0.681$; 2nd, radius of cluster $\Sigma w_i = 0.308$; 3rd, days at the site $\Sigma w_i = 0.275$; 4th, percent fidelity to the site $\Sigma w_i = 0.243$; and 5th, average distance from each location to the cluster center $\Sigma w_i = 0.165$. Our top model for predicting small-prey from large-prey kill sites fit the data well (likelihood ratio chi-square score of 27.39 [*P*-value < 0.0001], pseudo $R^2 = 0.20$, and ROC score of 0.801). The optimal probability cutoff for which we considered a cluster a large-prey kill site was 0.72, which corresponds to an overall classification success of 71.2%.

Our logistic regression model predicted slightly higher kill rates than those estimated from only those kills observed in the field, mostly due to 8 kills predicted by the model that were not investigated during field sampling. The average kill rate estimated only on the basis of observed kills was 1 kill every 7.48 days (95% confidence interval [95% *CI*] 5.27–9.69 days; ratio-estimator *SE* = 0.51), or 0.13 kills/day (95% *CI* 0.094–0.173 kills/day; *SE* = 0.009), resulting in an average of 48.8 kills/year (95% *CI* 34.4–63.3 kills/year; *SE* = 3.36). Predicted kill rates from our top logistic regression model were slightly higher—an average of 1 kill every 6.54 days (95% *CI* 5.89–7.18 days; *SE* = 0.149), or 0.153 kills tiger^{-1} day^{-1} (95% *CI* 0.138–0.168 kills tiger^{-1} day^{-1}; *SE* = 0.0035). Using these predicted kill rates, the annual kill rate was 55.8 prey killed tiger^{-1} year^{-1} (95% *CI* 50.4–61.3 prey killed tiger^{-1} year^{-1}; *SE* = 1.28). Using these predicted kill-rate estimates and known composition of sizes and proportions of observed kills, the potential consumption rate from our top logistic regression model was 8.93 kg day^{-1} tiger^{-1} (95% *CI* 8.83–9.03 kg day^{-1} tiger^{-1}; *SE* = 0.023), or an average of 3,260.6 kg year^{-1} tiger^{-1} (95% *CI* 3,224.7–3,296.5 kg year^{-1} tiger^{-1}; *SE* = 8.35). The observed potential consumption rates from all monitored tigers averaged 6.14 kg day^{-1} tiger^{-1} (95% *CI* 5.76–6.52 kg day^{-1} tiger^{-1}; *SE* = 0.09), with total biomass consumed composed of 26.9% boar, 43.6% red deer, 12.9% sika deer, 12.6% roe deer, and 4.0% of all other prey items (Table 3).

Limited sample size restricted our ability to conduct a rigorous comparison of summer versus winter kill rates. We found both predicted consumption rates (7.89 kg day^{-1} tiger^{-1} in summer versus 10.3 kg day^{-1} tiger^{-1} in winter) and kill rates (7.4 days kill^{-1} tiger^{-1} in summer versus 5.7 days kill^{-1} tiger^{-1} in winter) were lower during summer months. Additionally, we observed an increase in large-bodied prey killed during the

TABLE 5.—Beta coefficients from the top multiple logistic regression models used to predict Amur tiger (*Panthera tigris altaica*) kill sites from nonkill sites at clusters of locations, and to 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_0)	−7.03	1.128	< 0.0005	−0.91	0.410	0.027
Hours	0.08	0.010	< 0.0005	0.03	0.009	< 0.0005
% fidelity	4.49	1.054	< 0.0005			

TABLE 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. Avg Dist = average distance.

Model description	n	K	Log likelihood	ΔAIC_c	AIC weights	Evidence ratio— compared to best model
Hours	111	2	−55.491	0.000	0.232	1.000
Hours + Radius	111	3	−54.814	0.758	0.159	0.684
Days	111	2	−56.233	1.485	0.111	0.476
Hours + % Fidelity	111	3	−55.262	1.656	0.102	0.437
Hours + Avg Dist	111	3	−55.432	1.996	0.086	0.369
Days + Radius	111	3	−55.474	2.078	0.082	0.354
Hours + Radius + % Fidelity	111	4	−54.613	2.509	0.066	0.285
Days + Avg Dist	111	3	−56.124	3.379	0.043	0.185
Days + % Fidelity	111	3	−56.219	3.570	0.039	0.168
Hours + % Fidelity + Avg Dist	111	4	−55.210	3.705	0.036	0.157

winter months (64.2% of kills in summer versus 75% in winter).

Finally, we found the average interkill interval after predicted kills of small prey (5.75 days; $SE = 0.58$) was shorter than the interkill interval after predicted kills of large prey (8.12 days; $SE = 0.58$; 1-tailed t-test; $P = 0.002$), suggesting that kill rates may be influenced by satiation or handling time of prey.

DISCUSSION

The annual tiger kill rates and potential consumption rates predicted from our top logistic regression model (6.54 days/kill and 8.93 kg/day for adult tigers) are relatively high compared to most estimates from other published studies in Russia and Chitwan National Park, Nepal (Table 1). Only 1 previous study in the Russian Far East reported a lower kill-rate estimate (days/kill) than ours (Zhivotchenko 1979). In radiotelemetry 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- to 10-month-old dependent cubs made a kill every 5–6 days (Table 1; Seidensticker 1976). Kill-rate estimates based on snow tracking in Russia ranged widely from 3.86 to 10.14 days/kill, but the overall average, 6.2 days/kill (95% *CI* 4.0–8.5 days/kill; $SE = 0.91$; Table 1) was very close to our estimate. Potential annual tiger consumption rates in and around the Reserve (8.93 kg/day) were slightly higher than consumption rate estimates in both Chitwan National Park, Nepal (males 6–7 kg/day and females 5–6 kg/day [Sunquist 1981]) and Kanha National Park, India (5–7 kg day^{-1} tiger^{-1} [Schaller 1967]). Previous estimates of potential consumption rates based on snow tracking in the Russian Far East (5–15 kg day^{-1} tiger^{-1} [Pikunov 1988] and 7.2 kg/day [Yudakov and Nikolaev 1987]) resulted in overlapping estimates with our GPS-based estimates. Potential consumption rate estimates of captive tigers (males 6 kg/day and females 3–4 kg/day) were lower than our estimates from the field (Yudin 1990).

Our estimates are higher 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, because missing kills is unlikely when individuals were tracked continuously over extended periods. However, sample sizes from such intensive tracking tend to be low (e.g., 21 kills for Yudakov and Nikolaev [1987]), potentially reducing accuracy, and it is possible to push tigers from kills while tracking, causing them to eat less from each kill and to kill more frequently (Kerley et al. 2002). This may partially explain some of the previously published higher kill-rate estimates associated with snow tracking. Our intensive field sampling, guided by stratifying sampling of GPS location clusters, still occasionally missed kill sites predicted from the logistic regression model at clusters we failed to prioritize for field investigation, thereby underestimating kill rates using observed kills alone. We were, however, able to estimate our success rates for finding kills and hence correct our empirical kill-rate estimates. We also may have missed kills of small body size (2 badgers detected at single GPS locations), although such kills are of negligible consequence in terms of potential biomass consumption (Bacon et al. 2011). We believe our combination of GPS cluster searching and snow tracking should provide high kill-site detection rates and with the larger sample sizes possible with this approach, should result in more accurate estimates of both kill rates and potential consumption rates.

Variation in the body sizes of prey killed also could contribute to discrepancies between kill-rate estimates and potential 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. Similarly, seasonal differences in wolf kill rates have been driven by increases in juvenile kills during summer (Sand et al. 2008). We also found that tigers killing smaller prey items made kills more often, as might be expected if tigers are trying to maintain some minimum consumption rate. These differences in kill rates, in which a segment of a prey population is being targeted (e.g. adults versus juveniles), will no doubt impact prey population dynamics differently. Similar to Metz et al. (2012), our results indicate that tigers are preying on more juvenile ungulates and smaller, nonungulate prey during summer. The increase in predicted consumption rates we observed in winter corresponds well with the theory that biomass acquisition should be greater in the winter due to the
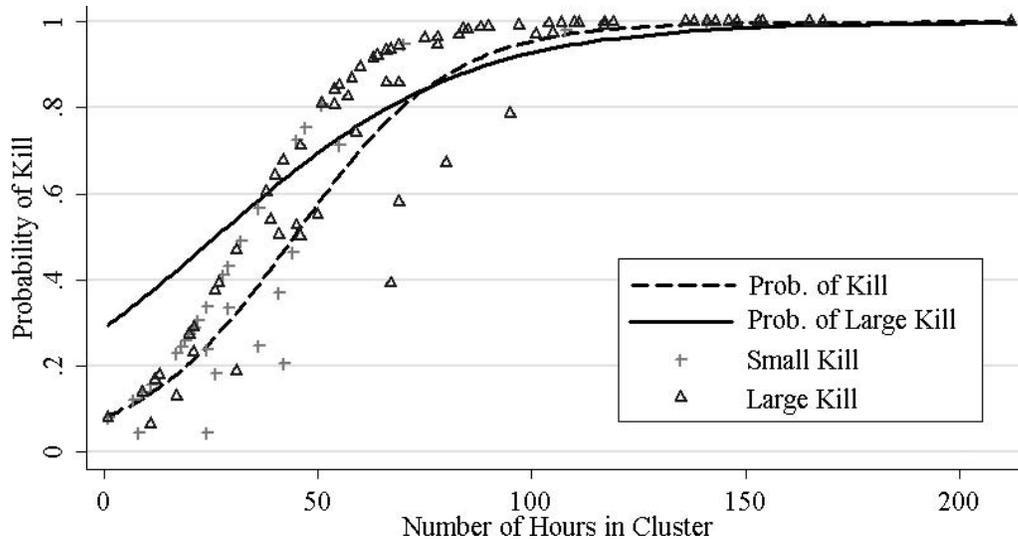
Fig. 2.—Predicted probability of Amur tiger (*Panthera tigris altaica*) kill sites as a function of hours on a cluster (dashed line) and then predicting large kills (> 40 kg) versus small kills as a function of number of hours on a cluster (solid line). The individual markers represent the predicted probability a cluster contains a kill site at confirmed small- and large-prey kill sites from investigated clusters in the Russian Far East, from 2009 to 2012.

additional energetic requirements from thermoregulatory demands (Mautz and Pekins 1989).

Our diet composition results differed slightly from previous research on Amur tigers, which showed red deer and wild boar comprised 63–92% of all kills from 6 sites across tiger range in Russia (Miquelle et al. 2010b). In contrast, only 52.3% of our confirmed kills were red deer or wild boar, and only 48.8% of predicted kills were classified as large prey. These differences could arise from a number of reasons, not only our limited sample size of tigers. First, much previous research was based in and around the Reserve, an area known for harboring healthy red deer and wild boar populations, whereas much of our data come from 1 tiger living outside protected areas, where roe deer were more abundant. For example, kills made by Pt99 represented 42.3% of our total prey sample and were all located outside of protected areas. Only 48.9% of Pt99's kills were large-bodied prey, whereas 81.3% of kills by other tigers were large-bodied. Second, methodologically, our year-round GPS methods are more likely to locate small-prey kill sites (i.e., roe deer) compared to the very-high-frequency radiotelemetry techniques used by Miquelle et al. (2010b) and because most previous work occurred during winter when many small-prey species are hibernating. Finally, recent declines in red deer and wild boar populations in our study area due to increased poaching rates outside protected areas (i.e., up 50% in the last decade [Miquelle et al. 2010a]), could have caused significant diet shifts. Our estimates of tiger kill rates and potential consumption rates are comparable to those of previous studies and the 1st rigorous year-round estimates for tigers derived from GPS collars in the scientific literature. A larger sample of Amur tigers, both inside and outside of protected areas, would improve the precision of our estimates.

We found the number of hours present and high fidelity to a site were the most important factors in determining if a GPS cluster contained a kill site (Figs. 2 and 3). Similarly, both Anderson and Lindzey (2003) and Knopff et al. (2009) found the number of nights and the amount time, respectively, to best predict mountain lion kills at GPS clusters. Webb et al. (2008) found that the 2 most important variables used to distinguish wolf kills were the number of days spent within 100 m of a cluster and the number of GPS locations (i.e., hours) within 100 m of the cluster center. 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 found the total number of hours spent at a cluster to be the most important factor in determining if a cluster contained a large prey. Although we were unable to predict 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. Such a technique also might be 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 limited sample size of collared tigers. To restrict our analyses to data from healthy adult tigers, we excluded data from these analyses to avoid concerns related to disease, injury, subadults traveling with their mother, and small data sets related to collar malfunctions. The 3 tigers we used were therefore quite representative of the adult tiger population. Regardless of small sample size, our study is among the 1st and most successful studies of tiger predator–prey relationships with GPS collars in the wild. For example, in a dissertation by Barlow (2009), information from 2 GPS-collared tigers provided important gains in our understanding of tiger predation. The only other published study, also from the Russian Far East, used data from
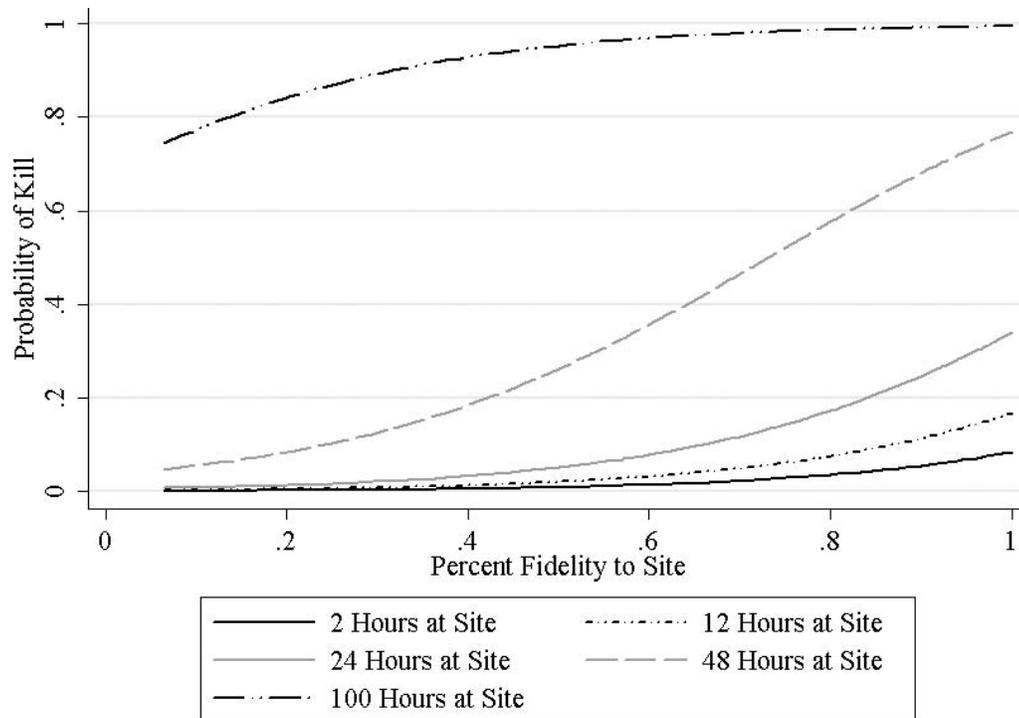
FIG. 3.—Predicted probability of Amur tiger (*Panthera tigris altaica*) kill sites as a function of percent fidelity to site at multiple temporal scales in the Russian Far East, from 2009 to 2012.

only 1 GPS-collared adult female tiger (Rozhnov et al. 2011). This work on GPS-based predator–prey relationships complements some of the pioneering work on tiger predation by Sunquist (1981) and Seidensticker (1976) that provided the 1st published kill rates focusing on 1 tigress each. More broadly, even the most comprehensive demographic study of Amur tigers in the wild (Kerley et al. 2003) used data from 8 adult female tigers and 7 cubs. Clearly, one of the challenges facing all empirical tiger ecological studies is the challenge of small sample sizes, and yet, the original studies and our GPS-based efforts provide convergent insights into tiger predation ecology that will help conservation. More data are still needed to better differentiate potential consumption rates of sex–age classes of tigers and seasonality of kill and consumption rates, but our study clearly demonstrates the utility of using GPS technology to understand tiger predator–prey requirements in the field.

Hunters are key stakeholders in tiger conservation, with more than 60,000 registered hunters on multiple-use lands in the Russian Far East. Managers of private wildlife management concessions are largely 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 annual kill rates of Amur tigers may be slightly higher than previously reported estimates based on extrapolated winter estimates. Therefore, extrapolating historic snow-tracking–based kill-rate estimates over the entire year may lead to an underestimate of annual harvest of ungulates by tigers and a subsequent overestimate of the surplus available for human harvest. If annual harvest of ungulates by tigers is estimated conservatively, sustainable hunting continues, and yet prey populations continue to decline, poaching is the likely culprit. 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 1), GPS collars may provide a crucial tool to better understand prey requirements to conserve tiger populations across the species' range.

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