

## ORIGINAL ARTICLE

# A comparison of food habits and prey preference of Amur tiger (*Panthera tigris altaica*) at three sites in the Russian Far East

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## Abstract

Prey availability is one of the principal drivers of tiger distribution and abundance. Therefore, formulating effective conservation strategies requires a clear understanding of tiger diet. We used scat analysis in combination with data on the abundance of several prey species to estimate Amur tiger diet and preference at 3 sites in the Russian Far East. We also examined the effect of pseudoreplication on estimates of tiger diet. We collected 770 scats across the 3 sites. Similar to previous studies, we found that tigers primarily preyed on medium to large ungulates, with wild boar, roe, sika and red deer collectively comprising 86.7% of total biomass consumed on average. According to Jacobs' index, tigers preferred wild boar, and avoided sika deer. Variation in preference indices derived from these scat analyses compared to indices derived from kill data appear to be due to adjustments in biomass intake when sex–age of a killed individual is known: a component missing from scat data. Pseudoreplication (multiple samples collected from a single kill site) also skewed results derived from scat analyses. Scat analysis still appears useful in providing insight into the diets of carnivores when the full spectrum of prey species needs to be identified, or when sample sizes from kill data are not sufficient. When sample sizes of kill data are large (as is now possible with GPS-collared animals), kill data adjusted by sex–age categories probably provides the most accurate estimates of prey biomass composition. Our results provide further confirmation of the centrality of medium ungulates, in particular wild boar, to Amur tiger diet, and suggest that the protection of this group of species is critical to Amur tiger conservation.

**Key words:** Amur tiger, diet, Jacobs' index, predation, Russian Far East

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## INTRODUCTION

Habitat destruction, prey depletion and poaching have all contributed to the precipitous decline in tiger [*Panthera tigris* (Linnaeus, 1758)] populations over

the past century (Nowell & Jackson 1996). Across their range, tigers prey on a wide range of species that vary greatly in size (Andheria *et al.* 2007; Miquelle *et al.* 2010a; Hayward *et al.* 2012), and with few exceptions (e.g. Rabinowitz 1989) tigers preferentially prey on large and medium-sized cervids, as well as a suids and bovids (Seidensticker 1986; Miquelle *et al.* 2010b; Hayward *et al.* 2012). Because tiger distribution and density are closely tied to that of their primary prey (Karanth *et al.* 2004; Miquelle *et al.* 2010b) and prey density is a driving force in determining home range size in female tigers (Simcharoen *et al.* 2014), and thus critical to determining area requirements for viable tiger populations (Miquelle *et al.* 2010a), understanding the primary components of tiger diet is fundamental to designing effective conservation strategies.

The Amur tiger (*Panthera tigris altaica* Timminck, 1884) is the northernmost subspecies of tiger. Fewer than 400 Amur tigers remain in northeast Asia, where they are primarily confined to the Russian Far East provinces of Primorye and Khabarovsk (Miquelle *et al.* 2007), although there are also  $\leq 20$  tigers distributed within the Changbaishan and Wandashan mountains of Northeast China. Although food habits of Amur tigers in Russia have been the focus of many studies (Abramov 1962, 1978; Zhivotchenko 1981; Kucherenko 1985; Yudakov & Nikolaev 1987; Miquelle *et al.* 1996, 2007, 2010b) most have relied on information from kills found during winter snow tracking or telemetry studies. However, reliance on kill data can overestimate the proportion of large prey in tigers' diet (Karanth & Sunquist 1995). Increasing the spatial and temporal scale of a study can also influence results by increasing the number of individuals sampled or revealing variation in prey diversity and selectivity (Kapfer *et al.* 2011). In this study we used scats collected from three sites that had different assemblages and abundances of potential prey species in Primorskii Krai, Russia to investigate seasonal variation in Amur tiger diet and tiger prey selection. Because biased results can occur when collecting multiple scats from a single predation site (a form of pseudoreplication [Hurlbert 1984]), we also attempted to assess the potential extent of this collection bias on estimates of tiger diet.

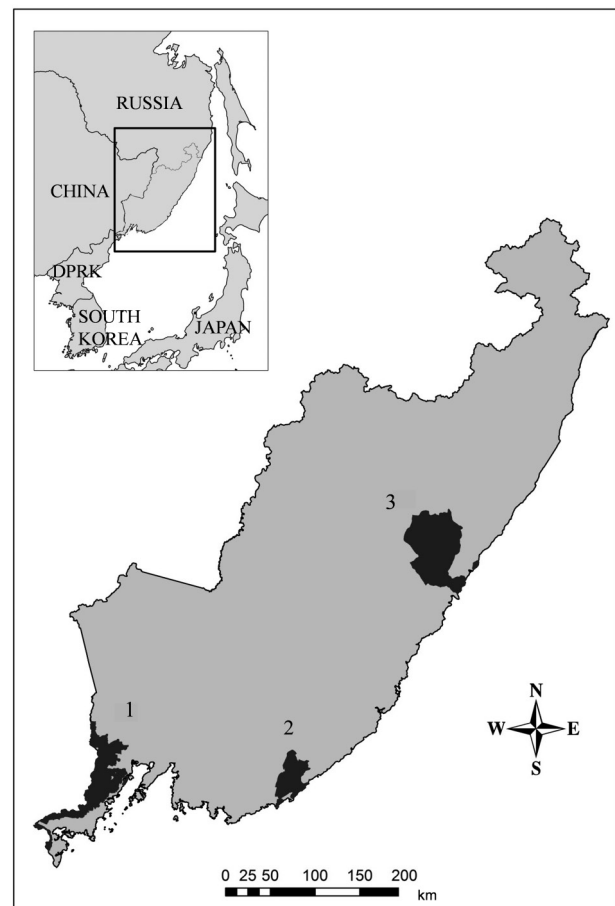
## MATERIALS AND METHODS

### Study area

Amur tiger scats were collected at 3 sites (Fig. 1): southwest Primorye (SW), Lazovskii State Nature Zapovednik (LZ) and Sikhote-Alin Biosphere Zapovednik (SABZ).

#### Southwest Primorye

Scats were collected from an area of approximately 600 km<sup>2</sup> in the northern part of the territories of the Nezinskoe hunting lease and the Leopardovy wildlife refuge. In 2012, portions of both these areas were incorporated into the Land of the Leopard National Park. This



**Figure 1** Three study sites in Primorskii Krai, Russian Far East where scats were collected for this study: (1) southwest Primorye (SW); (2) Lazovskii State Nature Zapovednik (LZ); and (3) Sikhote-Alin Biosphere Zapovednik (SABZ).

area is dominated by the eastern slopes of the Changbaishan Mountains and confined by Pervaya Rechka River in the north, Gryaznaya River in the south, Razdolnaya River in the east and the Russian–Chinese border in the west.

Dominant vegetation in SW consisted of stands of Mongolian oak (*Quercus mongolica*) and mixed conifer–deciduous forests dominated by Korean pine (*Pinus koraiensis*), black fir (*Abies holophylla*), linden (*Tilia amurensis*, *T. mandshurica*) and birch (*Betula costata*, *B. lanata*). The most common species of the ungulate complex is sika deer (*Cervus nippon* Temminck, 1838), with wild boar (*Sus scrofa* Linnaeus, 1758), Siberian roe deer (*Capreolus pygargus* Pallas, 1771) and musk deer (*Moschus moschiferus* Linnaeus, 1758) also present.

#### *Lazovskii State Nature Zapovednik*

The 1240-km<sup>2</sup> Lazovskii State Nature Zapovednik is a strictly protected reserve located along the southern portion of the Sikhote-Alin mountain range and is bordered to the east by the Sea of Japan. A dense river system runs through the area, and the vegetative community is similar to that of SW, with Mongolian oak and mixed conifer–deciduous forests. The ungulate complex is also similar to that at SW with the exception that red deer (*Cervus elaphus* Linnaeus, 1758) are also present, although they are not as common as sika deer or wild boar. Musk deer are rare and goral (*Naemorhedus caudatus* Milne-Edwards, 1867) are uncommon and limited to coastal and inland cliffs.

#### *Sikhote-Alin Biosphere Zapovednik*

The 3902-km<sup>2</sup> Sikhote-Alin Biosphere Zapovednik is bordered by the Sea of Japan to the east, and has the central crest of the Sikhote-Alin Mountains running through it parallel to the coastline. Coastal rivers are fast-running, with steep slopes leading to the central crest, while on the inland side hills are more rolling, with broader river valleys and more gentle streamflow. Near the coast the dominant plant community is Mongolian oak forests; further inland and at higher elevations forests are mixed conifer–deciduous dominated by Korean pine, larch (*Larix komarovii*), birch, aspen and other deciduous species. Five ungulate species, including red deer, roe deer, sika deer, musk deer and wild boar, occurred at SABZ. Sika deer were mainly restricted to the coastal areas, and musk deer mostly to the higher elevation/inland conifer forests. The other three species occur throughout most vegetation types.

Other potential prey common to all 3 sites include carnivores such as brown bears (*Ursus arctos* Linnaeus, 1758), Himalayan black bears (*Ursus thibetanus* Cuvier, 1823), Amur badgers (*Meles leucurus* Hodgson, 1847), mustelids such as sables (*Martes zibellina* Linnaeus, 1758), yellow-throated martens (*Martes flavigula* Boddaert, 1785), Siberian weasels (*Mustela sibirica* Pallas, 1773) and raccoon dogs (*Nyctereutes procyonoides* Gray, 1834).

#### **Field methods**

We collected scats opportunistically along game trails and roads where tigers commonly deposit scats (Sunquist 1981; Karanth & Sunquist 1995), and while snow-tracking individual tigers (Yudakov & Nikolaev 1987). We also collected scats near kills that were found either by snow-tracking tigers or radio-tracking individuals, and in LZ during scat surveys to estimate tiger abundance using scent-matching dogs (Kerley & Salkina 2007). We differentiated tiger scats from those of sympatric species by size, morphology, and associated sign such as tracks and scrapes (Karanth & Sunquist 1995). Scats were wrapped in aluminum foil or placed in plastic bags, and stored in freezers until analyzed. We collected scats for 6 years at LZ (2001–2006), 5 years at SW (2008–2012) and seven years at SABZ (2007–2013), and used the total at each site to estimate the percent occurrence of each species by site.

We estimated relative prey abundance from annual winter track surveys conducted at each of the 3 sites, in which standard survey routes were traversed after sufficient snow and all fresh tracks were recorded by species (Stephens *et al.* 2006).

#### *Scat analysis*

For analyses, scats were washed through a strainer to separate undigested remains (e.g. hair, bones, hooves and teeth) from other fecal material. We then selected several hairs (preferably complete guard hairs) from three portions of each scat (to increase the chances of identifying multiple species from a single scat) and identified them to the highest possible taxonomic resolution by comparing hair and other undigested remains from each scat to a reference collection using macro and microscopic characteristics such as hair color, length, thickness and medullary configuration (Teerink 1991; Rozhnov *et al.* 2011). We recorded the presence of a species in any one scat as a single occurrence.

Scat remains that could not be identified to species based on coarse examination of bone, hooves, teeth or

hair macrostructure (i.e. hair type, thickness, color and shape), as was the case for most cervids, were examined further using a compound microscope to examine the shape and thickness of hair medulla (magnified 10 $\times$ ) and hair cuticle patterns (magnification 10 $\times$  and 40 $\times$ ). To compare hair cuticle patterns, hairs were washed in 96% ethyl alcohol, placed on glass slides with a thin layer of nail polish and removed with tweezers when the nail polish was dry, resulting in an imprint of the cuticle that was viewed under a microscope. Most scat containing cervid hair collected from SW and SABZ could be identified to species using this method but scats from LZ were collected and analyzed prior to development of this capacity, and, hence, are reported to genus only.

### Statistical analysis

We estimated the contribution of each prey species to tiger diet as percent frequency occurrence and biomass contribution. We used the regression equation developed for cougars (*Puma concolor* Linnaeus, 1771) by Ackerman *et al.* (1984) to estimate biomass contribution to the diet:

$$Y = 1.98 + 0.035X$$

where  $Y$  is the weight of prey consumed/scat produced and  $X$  is the live weight of the prey, to relate the number of scats containing a prey species to the prey's biomass. We calculated  $Y$  for each species and multiplied it by the number of occurrences of the species to estimate the relative biomass of each prey type consumed. We used the estimated live weights of prey consumed by tigers in the Russian Far East (Bromley & Kucherenko 1983; Danilkin 1999; Prikhodko 2003). We then estimated percent biomass contribution (biomass of each prey type consumed/total biomass consumed  $\times$  100). We estimated 95% bootstrapped confidence intervals of percent biomass contributions based on 10 000 replicates with replacement in program R (Version 3.0.2). Results of percent occurrence and percent biomass of species in the diet were statistically insignificant, so we report only data on percent biomass in the diet.

For all three study sites we discarded all scats composed entirely of vegetation or vegetation mixed with tiger hair, which we assumed represented tigers ingesting their own hair during grooming. However, we assumed that tigers ate other tigers if a scat was composed of tiger hair and other tiger remains such as claws or flesh with tiger hair attached, and "tiger" was reported as an occurrence. Because cervids were not distinguished to

species in the LZ dataset, we performed two separate analyses of tiger diet. For our first analysis, we removed all scats containing an unknown deer species and analyzed deer species-specific contributions to tiger diet at each site. The results from this analysis were used in all subsequent analyses. However, we also conducted a second analysis wherein we aggregated all occurrences of red, roe and sika deer into a single category for all three sites. For calculations of percent biomass contribution when deer species were aggregated, we used the mean weight of all three species.

Availability and vulnerability to predation likely varies by season (Petruenko *et al.* 2015); for example, bears in hibernation are generally not available to predation during winter, and vulnerability of ungulate species likely varies by season as well, with snow cover being a key factor. Following Hojnowski *et al.* (2012) we defined two seasons based on general snow fall patterns, winter (November to April) and summer (May to October), and compared prey composition across sites for these two seasons.

We estimated the preference of tigers using Jacobs' index (Jacobs 1974). This index ranges in values from +1 (strongly preferred) to -1 (strongly avoided). We calculated the mean and standard error of Jacobs' index values for winter (November to April) tiger diet across years for each site. We restricted our analyses of preference to four species: wild boar, sika deer, roe deer and red deer during winter because we lacked data on the relative abundance of these species in the summer and other species for the entire year.

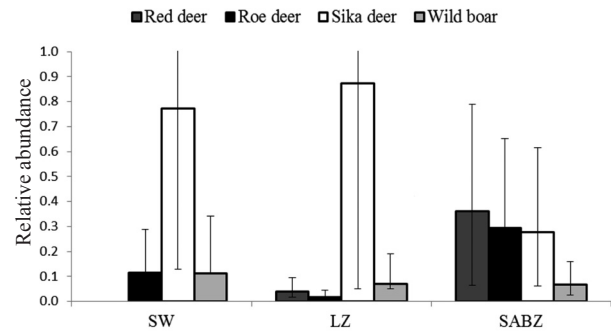
To reduce potential bias of collecting multiple scats from a single predation event, we collected only one scat within 200 m of a kill at SW and SABZ. To estimate the potential effect of pseudoreplication (collecting multiple scats from a single kill site) we collected all scats encountered in LZ and compared estimates of the percent biomass contribution from all scats combined to estimates when a single scat was used from each kill site.

## RESULTS

We collected 770 tiger scats across the three sites: 483 in LZ, 152 in SW and 135 in SABZ. Of these, 25 were composed entirely of grass or other vegetation, or contained unidentifiable prey remains, and were excluded from further analyses. We identified a total of 777 prey items in the remaining 745 scats.

Across the three sites, the relative abundance of four ungulate prey species (red deer, wild boar, sika deer and roe deer) differed (Fig. 2). Sika deer was the predominant species at SW and LZ, with all other species being relatively rare, while in SABZ sika deer were relatively rare (occurring only along the coast), with more equal representation of the other three species.

We identified a total of 14 species in tiger scats across the three sites, with 10–11 species at each site (Table 1). Wild boar contributed the largest percentage of prey biomass to tiger diets at all three sites. In SW, where sika deer were by far the most abundant species, they were superseded only by wild boar in the diet. In SABZ, there was no significant difference in the percentage biomass contributed to the diet of tigers by the three deer species even though sika deer were least common. At LZ, sika



**Figure 2** Relative abundance of wild boar, sika, red and roe deer as estimated by winter track counts in southwest Primorye (SW), Lazovskii State Nature Zapovednik (LZ) and Sikhote-Alin Biosphere Zapovednik (SABZ) study sites in the Russian Far East. Error bars represent  $\pm 1$  standard error.

**Table 1** Percent biomass contribution of prey species to Amur tiger diet as determined by scat analysis at 3 sites in Primorskii Krai, Russian Far East

Prey species	SW	LZ	SABZ
Wild ungulates			
Sika deer	24.99 (17.64–28.42)	15.49 (12.00–18.99)	9.86 (5.72–14.63)
Roe deer	6.87 (3.78–9.28)	1.75 (0.70–2.80)	12.80 (8.92–16.95)
Red deer	—	4.72 (2.36–7.47)	14.12 (8.01–21.02)
Deer species combined	43.95 (36.04–51.31)	55.69 (51.08–60.29)	46.46 (37.26–53.93)
Wild boar	45.18 (45.57–64.24)	32.66 (28.47–37.05)	36.10 (33.93–53.32)
Musk deer	0.64 (0.00–1.38)	—	0.45 (0.00–1.43)
Long-tailed goral	—	0.55 (0.00–1.30)	—
Other wild prey			
Amur tiger	—	0.19 (0.00–0.58)	1.47 (0.00–3.20)
Bear spp.	4.21 (0.73–7.28)	7.12 (4.56–9.97)	12.80 (5.67–17.01)
Raccoon dog	—	0.55 (0.18–1.01)	1.36 (0.30–2.44)
European badger	1.37 (0.24–2.36)	1.94 (1.20–2.77)	0.99 (0.00–1.84)
European otter	—	—	0.37 (0.00–1.29)
Mustela spp.	0.76 (0.00–1.54)	—	—
Domestic species			
Dog	0.35 (0.00–0.92)	0.60 (0.12–1.20)	—
Cow	0.68 (0.00–1.76)	0.69 (0.00–1.61)	—

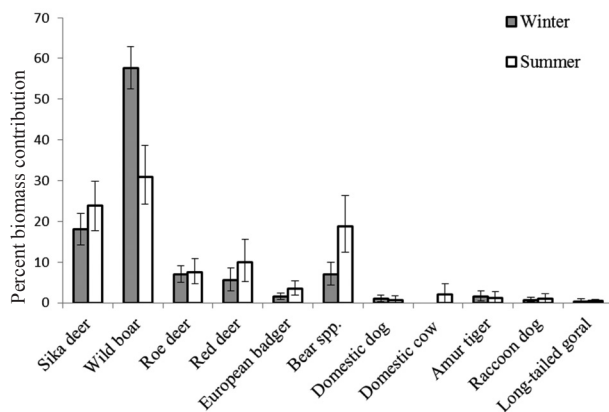
Parentheses contain bootstrapped, with replacement, 95% confidence intervals based on 10 000 replicates. Three deer species (sika deer, roe deer and red deer) were combined into a single category for comparison purposes because some scats at Lazovskii State Nature Zapovednik (LZ) were classified as unknown deer species. SABZ, Sikhote-Alin Biosphere Zapovednik; SW, southwest Primorye. Dashes indicate lack of detection of a prey species contribution to tiger diet in a given area.

deer were the second most important prey species after wild boar.

Jacobs' index values ( $\bar{x} \pm \text{SEM}$ ) for tiger prey preference during the winter indicated that tigers preferred wild boar and avoided sika deer across the three sites (Table 2). At SW, index value confidence intervals for wild boar overlapped zero. However, when we eliminated the year 2011, during which only 11 scats were collected and which had an index value that differed from the other years by  $>1.75$ , the index indicated wild boar were also preferred at SW. Therefore, we assumed that we collected too few scats to adequately estimate tiger diet in 2011 at SW, resulting in a spurious index score for that year, and, consequently, removed that year at SW from subsequent analyses.

Across all sites, tiger diet varied seasonally (Fig. 3), with tigers consuming more bear and less wild boar biomass during the snow-free months. Diet varied within sites too (see Appendix I). Other differences in percent biomass contribution to tiger diet did not differ significantly among the snow-free and snow-covered periods.

Retaining pseudoreplicates (Hurlbert 1984) in the LZ dataset overestimated the importance of the combined deer category relative to wild boar, and changed the ordering of which species contributed most to the total biomass in the diet (Fig. 4). The majority of pseudoreplicates were for deer species, and, therefore, removal of the pseudoreplicates reduced the percent biomass of the combined deer category, and increased the percent biomass of wild boar, to the extent that wild boar replaced the deer category as the largest contributor to tiger diet.



**Figure 3** Seasonal relative biomass contribution to Amur tiger diet by prey species across 3 study sites in the Russian Far East.

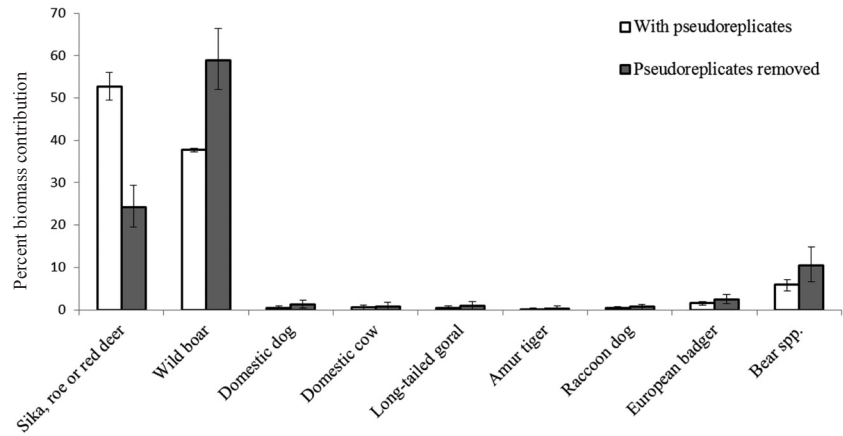
## DISCUSSION

Our results mirror those of previous studies of tiger diet throughout their range by revealing that the majority of tiger diet consists of medium to large ungulates (Karanth & Sunquist 1995; Miquelle *et al.* 1996; Biswas & Sankar 2002; Kapfer *et al.* 2011). Moreover, this study supports the findings of Miquelle *et al.* (2010b), who found that four ungulate species (red, roe and sika deer, and wild boar) were the principle prey species for tigers in the Russian Far East. In the present study, these four species collectively constituted 89–97% of biomass consumed (Table 1). However, our results differed from Miquelle *et al.* (1996) at SABZ in that wild boar contributed more to tiger diet, and red deer less. Our results in LZ also differ from Zhivotchenko's (1981) analysis from the 1970s, when red deer were the second most important prey item. These differences are likely the result of several factors. In LZ, it is clear that red deer abundance has declined dramatically since the 1970s, and, therefore, the lack of red deer in the diet of tigers in LZ is largely due to that decline. For a period that overlaps our study period in SABZ, and based on kill data, Miller *et al.* (2013) report that red deer comprised a much greater proportion of the biomass intake (43.6%) than is revealed from our scat data (14.12%). This difference is partially attributable to the fact that biomass intake estimated from kill data is adjusted by the sex–age class of the kill, something that is unknown from scat analyses. Many wild boar killed by tigers are subadults and piglets (67.7% of kills reported by Miller *et al.* [2013]), while over 70% of the red deer kills were adults (Miller *et al.* 2013). Hence, the relative contribution of wild

**Table 2** Jacobs' index scores and associated confidence intervals measuring tiger preference or avoidance for 4 ungulate species at 3 sites in Primorskii Krai, Russian Far East

Species	Jacobs' index	95% confidence intervals
Wild boar	0.790	0.618 to 0.962
Red deer	-0.326	-0.791 to 0.139
Sika deer	-0.698	-0.917 to -0.268
Roe deer	-0.368	-1.000 to 0.275

Scores represent comparison of proportionate consumption of prey relative to their abundance. Tiger diet calculated from scats and relative prey abundance calculated from winter track counts. Positive scores that do not overlap zero indicate preference for a prey species whereas negative scores indicate avoidance.



**Figure 4** Effect of pseudoreplicates on estimates of the percent biomass contribution of prey species to tiger diet at Lazovskii State Nature Zapovednik, Russian Far East.

boars to the diet of tigers will be adjusted downward when the body size of the kill is taken into account.

Usually, it is assumed that, with a larger sample size, scat data better capture the rare and smaller prey items. However, with a few exceptions, the list of prey and relative importance of prey species from Miller *et al.* (2013) and our analyses are very similar.

Seasonal differences in the dietary patterns of carnivores have been documented before (Koehler & Hornocker 1989; Joshi *et al.* 1997; Hovens & Tungalakutja 2005), and in this study we document seasonal variation in tiger diet (Fig. 3). Although not directly comparable because they divided their data into four seasons, our results roughly corroborate those of Miquelle *et al.* (1996), who found a general increase in red deer consumption and a decline in wild boar consumption in summer. In the present study, wild boar contributed significantly less to tiger diet and red deer contributed more during the snow-free months, although this difference was not significant (Fig. 3). In addition, bears constituted a significantly higher proportion of tiger diet in the summer, and while not significant, badgers increased in the diet of tigers during the snow-free period as well. The increased predation on bears and badgers is likely due to their increased availability following emergence from hibernation and the increased vulnerability of their young, although tigers do prey on adult bears and there is evidence that tigers will prey on bear while they are denning as well (Seryodkin *et al.* 2003). Amur tiger predation of bears is not a new phenomenon (Miquelle *et al.* 1999, 2005; Seryodkin *et al.* 2003), but our results, in addition to identifying seasonality in tiger predation

of bears, also suggests that bears constitute a relatively large portion of tiger diet, particularly during the snow-free period. This runs counter to previous assertions that the risk of injury was too high for tigers to regularly predate bears (Miquelle *et al.* 2010). While bear may remain a relatively minor component of tiger diet relative to ungulates on an annual basis, our study suggests they constitute a seasonally important prey item for tigers.

Scats used in dietary analyses are rarely sampled randomly, which can bias estimates of the relative contribution of prey categories (Marucco *et al.* 2008). When scats are not statistically independent, they represent pseudoreplicates, and may impair our ability to understand the relative contribution of prey species to tiger diet by inflating Type I error rates (Hurlbert 1984). Whereas the correction factor employed in this analysis (Ackerman *et al.* 1984) accounts for biases produced by the fact that smaller prey have proportionately more indigestible fur and bones and, thereby, produce more scats per unit volume consumed, it does not correct for differences in the detectability of scats. Because tigers spend more time feeding on larger prey items than on smaller ones, the distribution of scats from larger prey are likely to be more clumped in space. Hence, multiple scats from large prey are more likely to be collected than are those from smaller prey. Furthermore, because tigers are less likely to consume the entirety of larger prey and their remains are more conspicuous (i.e. have a higher detectability), scats associated with those kills are more likely to be discovered. Consequently, multiple scats from large prey are more likely to be collected unless appropriate sampling protocols are implemented. In this study the inclusion of pseudoreplicates changed the

relative importance of the 2 primary prey components of tiger diet in LZ (Fig. 4). Removal of pseudoreplicates decreased the biomass contribution of all deer combined by nearly 30% (from 52% to 24%) and increased the contribution of boar by more than 20% (from 38% to 59%), but did not significantly impact the relative contribution of other prey categories. This is similar to the results of a study examining wolf (*Canis lupus* Linnaeus, 1758) diet in the Western Alps, wherein elimination of the biases associated with pseudoreplication significantly altered the proportion of some prey species' contribution to wolf diet (Marucco *et al.* 2008). Because some analyses of carnivore diet based on scat collection do not account for potential pseudoreplication they may have incorrectly ranked the relative importance of prey items, suggesting caution should be used in interpreting these data, or in focusing management actions on only the top-most preferred prey species. Managers should prioritize conservation not only of the single most preferred, but all top tier prey species to ensure an adequate prey base will exist.

Deer kill sites were more commonly encountered than boar kill sites, resulting in a dramatically different interpretation of the data when this pseudoreplication was accounted for, but the reason for this difference is unclear. Petruenko *et al.* (2015) report relatively minor variations in models describing kill sites of wild boar and deer species in SABZ, but larger differences may exist in LZ. If, as reported by Miller *et al.* (2013) in SABZ, younger wild boar are a greater percentage of kills per species than deer in LZ, then tigers would spend less time at wild boar kills (they being smaller in size, on average), and, therefore, the probability of collecting multiple scats at a wild boar kill would be lower. Regardless of the mechanism, our results clearly indicate the need for caution when interpreting food habit results based on scat analyses when pseudoreplication is not accounted for.

Our analysis of tiger prey selection indicated that tigers preferred wild boar, across all sites, and avoided sika deer, and exhibited a neutral preference for roe and red deer (Table 2). These results differ from previous analyses of Amur tiger prey preferences in SABZ, which indicated that red deer were preferred and roe deer avoided (Miquelle *et al.* 2010b). A recent meta-analysis (Hayward *et al.* 2012) across tiger range based on both kill data and scats also demonstrated a preference for red deer and sambar (*Cervus unicolor*), an ecological equivalent of red deer. As suggested above, one import-

ant difference in these results is the inability of scat data to adjust for sex–age categories of prey being taken. Kill data collected from GPS-collared tigers in SABZ revealed important differences in sex–age classes selected from the red deer and wild boar populations, resulting in a much larger proportion of the biomass being represented by red deer: a fact that would not be noticeable based on scat analyses or strict counts of numbers of kills not adjusted for sex–age classes. These results suggest that while scat analyses are useful in revealing rare and smaller prey items, they may not provide a good estimate of the relative contribution of biomass to the diets of large carnivores. When sample sizes of kill data are large (as is now possible with GPS-collared animals), kill data adjusted by sex–age categories probably provides the most accurate estimates of prey biomass composition.

## ACKNOWLEDGMENTS

We thank the Save the Tiger Fund (a joint project of the National Fish and Wildlife Foundation and the Exxon Mobile Corporation), the Liz Claiborne and Art Ortenburg Foundation, the United States Fish and Wildlife Service Tiger Rhino Conservation Fund, the Disney Wildlife Fund, ALTA, the Robertson Foundation, the Starr Foundation, the Wildlife Conservation Society and the Zoological Society of London for financial support to conduct this work. We thank A. A. Laptev and A. I. Myslenkov of Lazovskii State Nature Zapovednik, A. A. Astafiev and Y. Pimenov of Sikhote-Alin Biosphere Zapovednik, and A. Borodin of the Land of Leopard National Park for logistical and administrative support. We thank M. E. Borisenko, A. Bezrukov, V. Kolesnikov, I. Nikolaev, B. Schleyer, N. Rybin, A. Rybin, A. Kostyria, I. Seryodkin, V. Melnikov, A. Saphonov, V. Schukin, V. Storozhuk and E. Gizhko for assistance with data collection, and Paul Kapfer for assistance with data analyses.

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**Cite this article as:**

Kerley LL, Mukhacheva AS, Matyukhina DS, Salmanova E, Salkina GP, Miquelle DG (2015). A comparison of food habits and prey preference of Amur tiger (*Panthera tigris altaica*) at three sites in the Russian Far East. *Integrative Zoology* **10**, 354–64.

**Appendix I** Seasonal variation in percent biomass contribution of prey species to tiger diet at 3 sites in Primorskii Krai, Russian Far East

Prey species	SW		LZ		SABZ	
	Winter	Summer	Winter	Summer	Winter	Summer
<b>Wild ungulates</b>						
Sika deer	25.09 (18.12–32.06)	53.55 (35.70–71.39)	12.91 (8.22–18.19)	24.19 (16.12–33.26)	15.19 (7.92–23.77)	7.37 (1.84–14.74)
Roe deer	8.31 (4.89–12.22)	7.51 (0.00–17.52)	0.41 (0.00–1.23)	5.65 (2.12–9.89)	18.93 (12.04–25.93)	10.48 (3.88–16.79)
Red deer	—	—	6.47 (1.85–11.09)	6.35 (1.59–12.69)	13.72 (4.16–24.95)	21.75 (8.70–37.70)
Wild boar	58.60 (49.47–67.74)	11.69 (0.00–27.28)	62.80 (55.11–70.49)	36.31 (26.41–46.22)	42.05 (30.28–53.35)	30.57 (18.10–44.25)
Musk deer	0.37 (0.00–1.10)	1.87 (0.00–5.62)	—	—	0.76 (0.00–2.08)	—
Long-tailed goral	—	—	0.57 (0.00–1.71)	—	—	—
<b>Other wild prey</b>						
Amur tiger	2.81 (0.70–5.62)	3.60 (0.00–10.79)	—	1.02 (0.00–3.05)	2.66 (0.00–6.65)	—
Bear spp.	3.11 (0.00–7.25)	10.61 (0.00–26.53)	11.34 (6.11–17.44)	16.48 (7.49–26.96)	3.93 (0.00–9.81)	26.83 (13.69–41.07)
Raccoon dog	—	—	1.12 (0.28–2.25)	0.48 (0.00–1.45)	0.95 (0.00–2.53)	2.11 (0.00–5.30)
European badger	0.34 (0.00–1.01)	6.89 (1.72–13.77)	2.55 (1.13–4.24)	3.89 (1.46–6.80)	1.15 (0.00–3.18)	0.89 (0.00–2.66)
European otter	—	—	—	—	0.67 (0.00–2.00)	—
Mustela spp.	0.94 (0.00–2.19)	—	—	—	—	—
<b>Domestic species</b>						
Dog	0.44 (0.00–1.31)	—	1.83 (0.37–3.67)	1.26 (0.00–3.15)	—	—
Cow	—	4.28 (0.00–12.84)	—	2.42 (0.00–6.04)	—	—

Seasons were classified as winter or summer based on whether the snow cover was typical. Bootstrapped confidence intervals (95%) based on 10 000 replicates are in parentheses. LZ, Lazovskii State Nature Zapovednik; SABZ, Sikhote-Alin Biosphere Zapovednik; SW, southwest Primorye. Dashes indicate lack of detection of a prey species contribution to tiger diet in a given area.