FOOD HABITS OF AMUR TIGERS IN SIKHOTE-ALIN ZAPOVEDNIK AND THE RUSSIAN FAR EAST, AND IMPLICATIONS FOR CONSERVATION

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Abstract: Diet of Amur tigers (*Panthera tigris altaica*), based on kill composition, is reported for 54 years of data in Sikhote-Alin State Zapovednik, Russia. Although relative importance changed over time, elk (*Cervus elaphus*) and wild boar (*Sus scrofa*) were consistently the two key components of the diet, together accounting for 84% of kills. Adults were predominant, but young comprised 30–36% of the kill composition. From 1992–1994 kill composition of radio-collared and non-collared tigers did not vary, but individual tigers did show variation in prey selection. Tigers killed an average 4.3 dogs and 4.2 domestic livestock per year between 1975–1994, but recent trends suggest that fewer are being killed. An inverse linear relationship exists in the percentage of the diet composed of wild boar and elk for Amur tiger, suggesting, while reduction in density of one prey species can be presumably compensated for by the other, some combination of the two at relatively high densities will provide the best chances for survival of the Amur tiger in the Russian Far East. We suggest that habitat quality is an ill-defined concept for tigers, and that there are few ecological restraints that relate to habitat quality except as they relate to habitat for key prey species. Tigers across their entire range appear to be intricately linked to ecologically similar ungulate assemblages, and therefore one of the primary goals of a tiger conservation program should be identification of and management for the key prey species.

Key words: Amur Tiger, carnivore conservation, *Cervus elaphus*, food habits, *Panthera tigris*, predation, prey, Sikhote-Alin Zapovednik, *Sus scrofa*, Russia.

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INTRODUCTION

Information on food habits is of basic importance in understanding the natural history and ecology of large carnivores. Because acquisition of food is a fundamental component of every predators' daily existence, knowledge of food selection is critical to understanding life history strategies and developing sound conservation recommendations. The Amur, or Siberian tiger (*Panthera tigris altaica*) is presently threatened with extinction. With only a handful of Amur tigers lingering in Northeast China and possibly North Korea, the Russian Far East (including Primorye and Khabarovsk Krais, or Provinces) represents the last stronghold of the subspecies. In 1985 Pikunov (1993) estimated that there were 240–250 individuals remaining in the Russian Far East. Since that time, increased poaching pressures have undoubtedly reduced population size, although the exact magnitude of this impact is unknown (Miquelle et al. 1993, Mills and Jackson 1994).

Although there exists a considerable body of information on food habits of the Amur tiger, much of the literature is available only in Russian, or has not been published. Our objectives are 5-fold: first, to present an extensive body of data on tiger food habits in Sikhote-Alin State Zapovednik covering 54 years. Secondly, we compare kill composition from this extensive period with results from an intensive, radio telemetry study of tigers in the same region from 1992–1994. Thirdly, we summarize existing data on the food habits of Amur tigers in Primorye and Khabarovsk Provinces, and compare results from Sikhote-Alin Zapovednik with other regions of the Russian Far East. Fourthly, we compare food habits of the Amur tiger with that of other subspecies, and suggest that ecologically similar ungulate complexes are linked to survival of the tiger throughout its range. Finally, we suggest that habitat quality for tigers is poorly defined, and that, in consideration of the key linkage between predator and prey assemblages, conservation plans for tigers will be most effective by managing habitat for prey species, rather than by attempting to provide quality habitat for tigers per se.

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STUDY AREA AND METHODS

Study area

Sikhote-Alin State Zapovednik (SASZ), located in northeast Primorye Krai of the Russian Far East, was gazetted in 1935, and at that time encompassed 1,000,000 ha. It's size has changed several times over the past 60 years, the most dramatic event being a severe reduction to 100,000 ha in 1951. Presently, the Zapovednik is 400,000 ha. Zapovedniks in Russia are a system of highly protected reserves: access is restricted to scientists and forest guards. Therefore, human impact on both tigers and prey species in Sikhote-Alin Zapovednik is minimal.

We report information on kills of wild and domestic animals in and adjacent to SASZ, the total region encompassing approximately 500,000 ha. Although the human population is relatively sparse outside the Zapovednik, villages are located at all corners, with the bulk of human population situated along the coast of the Sea of Japan. Terney and Plastun, the 2 largest villages, have a population of approximately 4,000 each. Small scale agriculture, including rearing of domestic animals, hunting, and trapping are important components of the local economy, and lands adjacent to the Zapovednik are heavily used for both agrarian and subsistence purposes.

The central feature of the SASZ is the Sikhote-Alin Mountains, a low range (most peaks are below 1,200 m) that parallels the coast of the Sea of Japan. Coastal drainages are relatively short; on the inland side the upper reaches of larger rivers drain into the Ussuri, and, ultimately, the Amur River.

On the coastal side of the SASZ, the dominant plant communities are oak and mixed conifer-broadleaved forests. Mongolian oak (*Quercus mongolica*) is most common near the coast, where a series of fires in the last century destroyed the original forest type. More inland, and at higher elevations on the coastal side, a mixture of deciduous and conifer forests persist, characterized by Korean pine (*Pinus koraiensis*), larch (*Larix komarovii*), birches (*Betula costata*, *B. lanata*, and others), basswood (*Tilia amurensis*), and fir (*Abies nephrolepis*). On the inland side of the Sikhote-Alin crest, boreal forests are dominant, including firs, spruce (*Picea ajanensis*), and larch.

As with the plant communities, the faunal complex of Sikhote-Alin Zapovednik is represented by a mixture of Asian and boreal life forms. The ungulate complex is represented by 7 species, with Manchurian elk (*Cervus elaphus xanthopygus*) and Ussuri wild boar (*Sus scrofa ussuricus*) being the most common: both are found throughout SASZ. Manchurian moose (*Alces alces cameloides*) are near the southern limits of their distribution, and are sparsely distributed in the inland boreal forests. Sika deer (*Cervus nippon*), near their northern limits, are primarily confined to the coastal zone. Musk deer (*Mochus moschiferus*) are associated with the upper elevation conifer forests, and roe deer (*Capreolus capreolus bedfordi*) are confined to regions of limited snow depth. Ghoral (*Nemorhaedus caudatus*) are restricted to coastal cliffs.

Both brown bear (*Ursus arctos*) and Himalayan black bear (*Ursus thibetanus*) are common. Wolves are present but rare in and around SASZ, though the density has fluctuated over the period of study (Matyushkin 1992). Medium-sized mammals found in the Zapovednik include racoon dogs (*Nyctereutes procyonoides*), badgers (*Meles meles*), lynx (*Lynx lynx*), red fox (*Vulpes vulpes*) and six species of mustelids: yellow-throated marten (*Martes flavigula*), sable (*Martes zibellina*), ermine (*Mustela nivalis*), Siberian weasel (*Mustela sibirica*), mink (*M. vison*), and otter (*Lutra lutra*).

Tiger populations have fluctuated dramatically within SASZ (Smirnov and Miquelle, in press). Populations were decreasing throughout the Russian Far East, including the Zapovedniks, through the late 1930's and 1940's due to hunting, poaching, and capture of cubs (Matyushkin et al. 1980). Hunting of tigers was outlawed in 1956. Despite this prohibition, tigers were virtually absent in Sikhote-Alin Zapovednik between 1951 and 1966. Population density increased rapidly through the 1970's and 1980's, apparently reaching a peak in the early 1990's (Smirnov and Miquelle, in press) when poaching activity increased substantially (Miquelle et al. 1993).

Methods

Estimates of tiger diet composition in Sikhote-Alin Zapovednik are based on the relative abundance of kills located and reported by researchers and forest guards. Kills are located either by following tiger tracks in the snow (Kaplanov 1948, Abramov et al. 1978, Yudakov and Nikolaev 1987), by observing behavior of scavengers such as ravens and crows, or by chance encounters during routine patrol by forest guards. The same basic techniques for location of kills has been employed for 50 years.

The first work on food habits of tigers in Sikhote-Alin Zapovednik was conducted by Kaplanov (1948). This information is apparently included in the report by Shamikin (in Abramov, 1962) for the period 1933–1948. No information is available from 1949–1956, when tigers were mostly absent from the Zapovednik (Smirnov and Miquelle, in press). Occasional dispersers may have been present in the early 1960's, but recolonization of the Zapovednik apparently occurred in the mid-60's. Because of the scarcity of data, information from during the 1957–1969 period was combined. During 1964–1972, 1977, and 1984 Matyushkin conducted investigations of tigers in the Zapovednik (Matyushkin 1977, 1991, 1992; Matyushkin et al. 1981). From 1972 to the present, Smirnov coordinated data collection by forest guards and researchers. Therefore, beginning in 1970, when tigers were relatively abundant, a fairly consistent effort in data collection has been main-

Table 1. Diet composition of Amur tigers, based on 552 located kills, during 7 time periods between 1933 and 1994, in Sikhote-Alin State Zapovednik, Primorye Province, Russia. Numbers in parentheses refer to number of kills reported for each time period.

Prey species	Percent of total kills reported							
	1933–1948 (59)	1957–1969 (21)	1970–1974 (33)	1975–1979 (38)	1980–1984 (134)	1985–1989 (108)	1990–1994 (159)	TOTAL (552)
Wild ungulates								
Elk	22.0	71.5	78.7	73.7	41.8	62.0	59.7	54.3
Wild boar	35.6	19.0	15.2	21.1	43.3	22.2	27.0	29.5
Roe deer	3.4	0.0	6.1	0.0	9.0	4.6	8.9	6.3
Musk deer	13.6	0.0	0.0	0.0	3.0	0.9	0.6	2.5
Moose	10.2	9.5	0.0	2.6	0.0	0.0	0.6	1.8
Ghoral	0.0	0.0	0.0	0.0	0.7	2.8	0.6	0.9
Sika deer	0.0	0.0	0.0	0.0	0.7	0.0	1.3	0.5
Other								
Tiger	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.2
Bear	8.5	0.0	0.0	2.6	0.7	3.7	0.6	2.2
Wolf	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.2
Lynx	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Badger	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.2
Raccoon dog	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.2
Mink	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.2
Grouse	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
Subtotal ungulates	84.8	100.0	100.0	97.4	98.5	92.6	98.7	96.0
Subtotal other	15.2	0.0	0.0	2.6	1.5	7.4	1.3	4.0
TOTAL	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

tained (1970–1994).

From 1992–1994, eleven tigers were captured and outfitted with radio-collars. During this period, in addition to locating kills by the traditional methods, kills were located based on movement patterns of radio-collared tigers. Monitored animals that remained in one area for more than 1 day were suspected of having made a kill, and the area was investigated after tigers left the site. Data reported for radio-collared tigers covers the period from January 1992 through November 1994.

Information on radio-collared animals may be a less biased indication of food habits because collection of kills was not dependent on travel routes of researchers or forest guards (e.g., easy travel routes along river bottoms may favor discovery of kills representing prey species which select such habitats) or may have different biases. Therefore, we compare species and age composition of kills by radio-collared and non-collared tigers during the period 1992–1994 to assess potential differences in the two methods.

The 25-year period with consistent effort at data collection, 1970–1994, was divided into 5-year blocks. In combination with the two earlier periods (1933–1948 and 1957–1969), we assessed variation in food habits of tigers over all 7 time periods using a chi-square analysis. We examined cell chi-square values to assess the importance of specific periods on the total chi-square value and then tested the importance of specific periods by hypothesizing a non-significant total chi-square when key time periods were deleted (Zar 1984).

The sex and age composition of prey killed by tigers for the period 1992–1994 was analyzed and compared to fragmentary information from earlier periods. Where information was available, we classified all kills as adult, yearlings, and young of the year, based on tooth eruption patterns (Bubenik 1982, Bromley 1964). Seasonal variation in composition of prey was also analyzed.

Because kill composition may be a poor indicator of relative importance of prey species (Karanth and Sunquist 1995), we estimated percentage biomass contribution of each prey species to the diet of tigers by multiplying number of kills by weight, specific for species, sex, and age. Weights of animals were

Table 2. Sex and age composition of Manchurian elk and Ussuri wild boar kills made by Amur tigers in Sikhote-Alin State Zapovednik, 1992–1994. Kills were separated into three age classes: adults (>2 years), yearlings (between 12 and 24 months), and young (<12 months). For each species the percentage of kills in each age class, and sex ratio (males:females) is presented.

Age	Manchurian elk				Ussuri wild boar			
	% of total		Sex ratio		% of total		Sex ratio	
	n	%	n	M:F	n	%	n	M:F
Adults	33	51.6	29	1:2.2	18	60	18	1:1.0
Yearlings	8	12.5	7	1:0.8	3	10	1	
Young	23	35.9	11	1:1.7	9	30	5	1:4.0
TOTAL	64	100.0	47	1:1.8	30	100.0	24	1:1.2

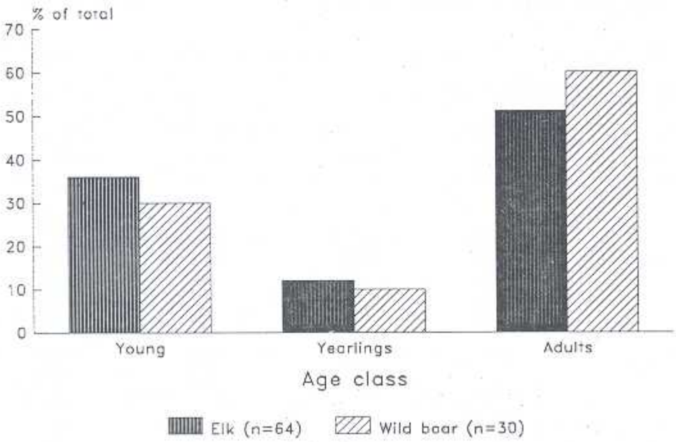

Fig. 1. Age composition of Manchurian elk and Ussuri wild boar kills made by Amur tigers in Sikhote-Alin State Zapovednik, Primorye, Russia between 1992–1994.

Fig. 2. Comparison of relative importance of prey species, based on numbers killed and biomass contributed to the diet, for Amur tigers in Sikhote-Alin State Zapovednik, Primorye, Russia, 1992–1994.

based on data provided by Bromley and Kucherenko (1983), Bromley (1964), and Krevosheyev (1984). We assumed that the same percentage of each kill was consumed from all species and sex-age classes (Hornocker 1970, Ackerman et al. 1986), and therefore simply used total weight of animals as a relative comparison.

We compared the information in Sikhote-Alin to 5 other food habit studies of Amur tigers where at least 50 kills were reported. The relationship between relative abundance of wild boar and elk in the diet was assessed with a regression analysis.

Information on kills of domestic animals comes from 2 sources. Official reports are made to the regional government by people seeking compensation for livestock killed by tigers. Because not all people file claims, additional information came through discussions with local farmers and livestock owners. Information on predation on dogs is mostly derived from anecdotal reports of hunters who lost dogs while in the forest. We included only those reports where kills were made within 30 km of Zapovednik boundaries. The source of information and the types of biases associated with collection of domestic and wild kills makes the data incomparable, so the data sets are presented separately.

Chi-square tests are used to assess variations in kill composition. Where biases could occur due to small expected frequencies, log-likelihood ratios are used. All means are reported with ±95% confidence intervals.

RESULTS

Information on food habits of tigers in Sikhote-Alin Zapovednik is based on reports of 552 kills of wild and 197 domestic animals over 54 years (Tables 1, 5). With the exception of years 1949–1956, a continuous record of kills observed by forest guards and biologists has been maintained. During the mid-sixties (1964–1966), when there were no resident tigers in the Zapovednik (Smirnov 1986), no kills were found. For the 25-year period beginning in 1970, an average 18.40±6.92 kills (non-domestic) were found each year, but yearly records vary dramatically from 3 (1971 and 1973) to 76 (1984). Using the yearly average estimate of tigers in the Zapovednik for 1966–1991 (Smirnov and Miquelle, in press), there is a significant but poor relationship between number of tigers and number of kills reported each year (r^2=0.34, F=12.7, p=0.001).

We looked for biases in the data collection method in two ways. First, we compared species composition of kills made by radio-collared and non-collared tigers between 1992–1994 to assess differences dependent on the method of finding kills. We found no significant differences in species composition of the kills of non-collared and collared tigers (χ^2=2.34, p>0.05). Therefore, this information is combined for the 5-year period 1990–1994.

Secondly, we compared age distribution of elk and wild boar kills for the periods 1970–1990 and 1992–1994. The age composition of elk killed between 1992–1994 was not significantly different than that of earlier periods (χ^2=8.0, p> 0.05), although young were more poorly represented in the earlier period. In contrast, there was a significant difference in age composition of wild boar between earlier periods and 1992–1994 (χ^2=14.7, p<0.05). This difference is largely due to the very large number of yearlings reported killed in earlier periods. Although we cannot assess if the difference is due to changes in the age composition of the boar population, we believe that forest guards may have mistakenly identified adult female wild boar as young males (the canine, or tusk, is similar in size, and is often used as a diagnostic trait). To avoid this potential bias in sex and age distribution, we report only for the years 1992–1994.

Large ungulates are the primary component of the diet of tigers in SASZ (Table 1). Ungulates comprised over 96% of the total number of kills, and of that, 84% was wild boar and elk. Roe deer were third in importance, but contributed only 6.1%

of the total kill composition. Except for the earlier periods of study (1933–1948 and 1957–1969), musk deer and moose were minor components of the diet. Ghoral and sika deer, both rare in the Zapovednik, were minor items in the kill composition.

Of the non-ungulate species, only bear kills were consistently found throughout the study period, although the frequency was low. In all cases, tigers appeared to have eaten the bear carcasses. Reports of predation on other predators were rare. Only one instance of tiger predation on wolves was reported. Kills of smaller animals were rarely found.

Because elk and wild boar were the only consistently important components of the diet, we combined all other species and used 3 food categories to assess variation in kill composition over 7 time periods. Significant differences were found when all 7 periods were included in a 3x7 contingency table (χ^2=71.8, *df*=12, $p<0.001$). Period 1 (1933–1948) and Period 5 (1980–1984) contributed disproportionately large percentages to the total chi-square value. For further testing, the period 1957–1969 was deleted because small expected frequencies would create biases in the analysis. The null hypothesis that 2 periods (1933–1948 and 1980–1984) were significantly different from the other 4 is supported by the fact that the chi-square value with these 2 periods deleted is insignificant (χ^2=7.8, *df*=6, p=0.25), while, when only one or the other of these 2 periods is deleted, significant chi-square values remain (for 5 periods 1970–1994, χ^2=28.7, *df*=8, $p<0.001$, and for 5 periods including 1933–1948 and deleting 1980–1984, (χ^2=51.7, *df*=8, $p<0.001$).

The outstanding difference between 1933–1948, 1980–1984, and the other 5 periods is the high percentage of wild boar in the diet (greater than 35%) and the small percentage of elk (less than 45%) (Table 1). In all other periods, elk kills contributed 60% or more to total kill count. Age composition of elk and boar kills was similar: adults made up the majority of kills (52–60%), yearlings were relatively rare (10–12%), and young of the year represented 30–36% (Table 2, Fig. 1). Adult cow elk were 2.2 times more commonly killed than bulls, while male and female wild boar were equally represented in the kill composition (Table 2). Age distribution of elk and wild boar kills were similar (Fig. 1).

Diet composition varied very little whether estimates were based on body weight or number of kills for the period 1992–1994 (Fig. 2). Because weights of boar and elk are roughly similar, and age distribution of kills was similar, estimates of biomass contribution to the diet vary little from estimates based strictly on numbers of individuals.

Information from 5 radio-collared tigers was sufficient to assess individual variation in kill composition. Individual tigers showed noticeable variations in kill composition (Fig. 3). Elk were the most important component of the diet of all 4 tigresses, but for the young adult male, more wild boar kills were reported than elk kills. Differences were not only due to differences in relative abundance of prey species: female F8 and male M2 maintained virtually identical home ranges, but selected prey differentially. Differences in prey selection may reflect age and hunting ability of tigers. While sample sizes are too small to permit statistical comparisons, 2 of 3 young tigresses (F1 and F8) appeared to rely more on species other than elk and wild boar, primarily roe and sika deer, which are smaller and perhaps easier to handle for relatively young and inexperienced tigers. Such an interpretation is only weakly supported by estimates of average weight of kills (Table 3). Average kill weight of young females F1 and F8 were lightest, but variation was great, and there were no significant differences among any of the 5 tigers analyzed (Table 3).

Table 3. Average weight of kills (and 95% confidence intervals) made by radio-collared Amur tigers in Sikhote-Alin State Zapovednik, 1992–1994.

Tiger			Weight of kills (kg)		
Name	Age (years)	Sex	n	$\bar{x}$	95% CI
F8	2–4	female	17	77.5	26.1
F1	1.5–4	female	10	84.1	47.8
F6	>5	female	14	89.5	29.9
F3	2–4	female	8	151.7	38.9
M2	2–4	mele	14	92.3	33.2

Table 4. Seasonal distribution of kills made by tigers in Sikhote-Alin State Zapovednik, 1992–1994.

Season	n	Percentage of total kills found			
		Manchurian elk	Wild boar	Other	Total
Winter	53	47.2	41.5	11.3	100
Spring	25	72.0	16.0	12.0	100
Summer	20	60.0	5.0	35.0	100
Fall	16	62.5	31.2	6.2	100
TOTAL	114	57.0	28.1	14.9	100

There was significant seasonal variation in kill composition for the period 1992–1994 (G=17.9, $p<0.05$) (Table 4). Elk were the most common component of the kill composition in all seasons, but in summer, a greater variety of species were taken: 35% of all kills were other than elk and boar. In winter, boar were more heavily preyed upon than in other seasons.

Dogs were the most commonly reported domestic animal killed by tigers in and adjacent to SASZ between 1957 and 1994 (Table 5). Except for two time periods, dogs comprised 50% or more of the domestic kills. Killing of domestic livestock, primarily cows and horses, make up nearly all the remainder of domestic animals reported killed by tigers (Table 5). Since 1975, when the tiger population had recovered substantially, an annual average of 4.35±2.1 dogs and 4.25±1.68 livestock were reported killed by tigers in the vicinity of SASZ. There have been dramatic changes in the number of livestock depredations reported over time (Fig. 4). Kills of livestock and all domestic animals peaked between 1980 and 1984, and remained at relatively high levels until 1989. The number of kills has dropped since 1990. Of the 73 located kills made by radio-collared tigers

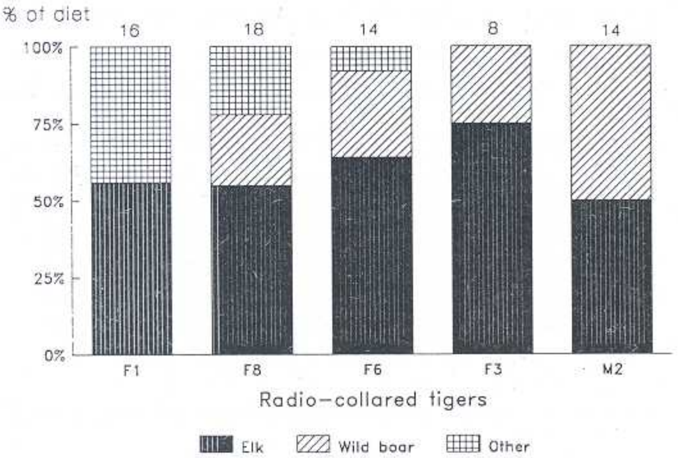

Fig. 3. Comparison of kill composition for 5 radio-collared Amur tigers (4 females and 1 male) in Sikhote-Alin State Zapovednik, Primorye, Russia, 1992–1994. Numbers above figure represent sample sizes for each tiger.

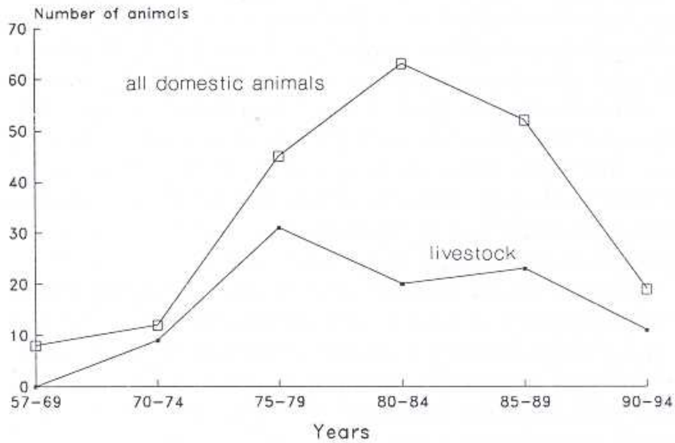

Fig. 4. Number of domestic animals killed by Amur tigers in and around Sikhote-Alin State Zapovednik, Primorye, Russia, for 6 time periods between 1957 and 1994. Differences between "livestock" and "all domestic animals" largely reflect the number of dogs being killed by tigers.

between 1992–1994, 5 (6.8%) were domestic animals.

Results of kill composition data collected in Sikhote-Alin show a similar pattern to information collected in other parts of the Amur tiger's range in Russian Far East (Table 6). Ungulates make up 85% or more of the kills found. Elk and wild boar are the two dominant ungulates in the diet in every study, together contributing 57–85% of the kill composition. Using the data from 7 time periods in Sikhote-Alin, and the other 5 sources in Table 7, a clear inverse linear relationship exists between percentage of elk and boar in the diet of Amur tigers (Fig. 5).

DISCUSSION

The quantity of reported kills varied considerably among years, and although there was a significant relationship between tiger numbers and number of kills found, the relationship was weak. Other factors likely also had an impact on number of kills reported, including incentive of forest guards, and distribution of kills. For instance, in the heavy snow winters of 76–77 and 83–84, ungulates concentrated in valleys and many kills were located along trails routed along river bottoms (Matyushkin 1992). Despite these sources of variation, methods of locating and reporting kills have been consistent, so that most biases have remained constant. Therefore, although numbers of kills found has varied, differences over time in composition of kill data likely reflect real changes in prey composition of the tiger diet within SASZ.

The one exception to constancy in methodology is the results of the earliest period (1933–1948). Apparently, these results reflect samples from both kills and excrement (Matyushkin 1992) confounding meaningful comparisons since variation in methodology may explain observed variation in diet composition.

Manchurian elk and Ussuri wild boar made up the majority of the diet of tigers in Sikhote-Alin Zapovednik over the entire 54 years of study. However, their relative importance varied over time, apparently in relationship to changes in density (Matyushkin 1992). This relationship will be investigated in future studies.

Significant differences existed in age composition of kills between the older data set (1970–1990) and recent information (1992–1994) for wild boar and a trend in that direction for elk. In fact, as with many studies of large carnivores based on kill composition, predation on young animals and smaller species is probably underrepresented in both periods. Age composition is probably most skewed in summer when tigers spend relatively little time at kill sites of neonates, and it was more difficult to locate kill sites even if a kill was suspected. With large ungulates, tigers typically spent 2–4 days at a kill site (Yudadov and Nikolaev 1987, Miquelle et al., unpubl.), increasing the probability of detecting a kill using radiotelemetry locations. However, in summer tigers spent little time at kill sites of young — occasionally only a few hours; such locations are difficult to differentiate from resting sites. In winter, tracks in snow and ravens provided ready clues to the location of kills, while in summer ravens appeared less adept at locating kills, and tracks were scarce.

For the same study area for the period 1964–1984 (data collected during 7 winters) Matyushkin (1992) reported a ratio in kill composition of elk males:females + young as 1:1.75. For 1992–1994, that ratio is 1:2.6, suggesting a higher use of bulls in the earlier period. However, Matyushkin (1992) emphasized that young were taken in greater percentage than they occurred in the population. Sex and age composition of elk kills in Lazovsky Zapovednik (in southern Primorye Krai), are similar to the present study: 50% of kills were adults (51.6% in SASZ) with an adult male:female sex ratio of 1:2.75 (compared to 1:2.2 in SASZ) (Zhivotchenko 1981). In Lazovsky 50% of elk kills were calves, compared to 36% in Sikhote-Alin. Zhivotchenko

(1981) did not report yearlings separately, and they were apparently included as adults. Sex and age composition of wild boar kills in Lazovsky differs from this study: in SASZ the sex ratio of adult wild boar was equal, in Lazovsky it was 1:4, favoring females, a value that more likely reflects the ratio in the population. Young boar comprised 82% of the boars killed in Lazovsky: in Sikhote-Alin only 30% of the boar killed were young. Both samples were relatively small (n=30 and 27) and differences may only reflect sampling variation.

Seasonal variation in prey selection of tigers in Lazovsky was also similar to Sikhote-Alin. Although sample sizes are small for each study, both demonstrated that wild boar were more commonly taken in fall and winter than spring and summer, and elk were more important in spring and summer. In Lazovsky, however, tigers also depend heavily on sika deer, which are much more common. Since Sikhote-Alin Zapovednik lies near the northern limit of sika deer range, they are sparsely distributed, and represent a small percentage of available prey to tigers.

Tigers will kill other carnivores, but it is not clear if competition is a driving factor. Schaller (1967) noted that tigers will kill sloth bears (*Melursus ursinus*), and McDougal (1988) reported 5 leopards were found killed by tigers in a period of 21 months in Nepal. All food habit studies of Amur tigers report bears as a component of the diet (Table 6): tigers in Sikhote-Alin killed both brown and Himalayan black bears. Of 6 cases reported in Sikhote-Alin Zapovednik, 3 were Himalayan and 3 were brown bears. Adult brown bears in this region can weigh over 300 kg (unpubl. data), will often appropriate kills from tigers, and have been reported to kill young tigers (Heptner and Sludski 1972, Kucherenko 1985). Such animals are immune from attack by tigers in summer, but tigers will kill brown bears in their dens in winter (Bromley 1965, Kaplanov 1948).

There is circumstantial evidence that tigers will eliminate wolves from regions through direct competition. Observations of tigers killing wolves are rare: only one record exists for Sikhote-Alin (Table 1), and one for Lazovsky Zapovednik (Matyushkin et al. 1980). Nonetheless, the fact that tigers frequently kill dogs suggests that they may also readily kill wolves. Matyushkin et al. (1980) reported that wolf distribution shifted after 1966 when tigers recolonized Sikhote-Alin Zapovednik, and around Lazovsky, wolves became common around 1926 when tigers were practically eliminated (Zhivotchenko 1977). When the tiger population rebounded, the wolf population again decreased.

Reports of livestock depredation, and killings of dogs, have to a large extent reflected the density of tigers in the Zapovednik and surrounding areas. Because of biases in the data, no attempt has been made to numerically calculate contribution of domestic animals to the diet of tigers in SASZ, but it is clear that livestock predation is relatively rare, and that domestic animals make up only a minor portion of the diet of tigers in this region. Nearly 7% of kills made by radio-collared animals were domestic animals, but our record of domestic animal kills probably represent nearly 100% of actual occurrences, while our record of wild animal kills is only a small percentage. Because of the small human population surrounding the SASZ, most of the incidences of tiger predation on domestic livestock are probably recorded. Rates of predation are low largely because of the relatively few numbers of livestock, and the grazing system employed. Many villagers own one or a few milk cows, and these animals return to their barn every evening, reducing the chances of predation by tiger. Even in more remote, larger farms, in many cases animals are put in barns nightly, and people are assigned to watch herds during the day.

Throughout Primorye Province the situation is more severe (Matyushkin et al. 1980). The increase of the tiger population through the 1960's and 70's was concurrent with a decrease in ungulate populations due to overhunting, with the result that predation on domestic animals increased substantially. From 1920–1960 only 162 reports of tiger predation on domestic animals occurred province-wide; from 1961–1965 100 attacks were reported; and from 1966–1970 386 attacks were reported. Predation is apparently more common to the south, where economic development is more intensive, and human and domestic animals densities are higher.

It is not entirely clear why predation on domestic animals near the SASZ has decreased in the recent past. This may partly reflect less interest in stock raising, but predation on dogs also appears to have decreased. The drop may reflect that shooting

Table 5. Tiger depredation on domestic animals in vicinity of Sikhote-Alin Zapovednik, Primorye Krai, Russia, during 7 time periods between 1933 and 1994. Sample sizes for each period in parentheses.

Species	Percent of total kills reported							
	1933–1948 (0)	1957–1969 (8)	1970–1974 (12)	1975–1979 (45)	1980–1984 (63)	1985–1989 (52)	1990–1994 (17)	TOTAL
Dog	0.0	100.0	25.0	31.1	57.1	55.8	41.0	49.2
Cow	0.0	0.0	66.7	44.4	14.3	17.3	24.0	25.4
Horse	0.0	0.0	8.3	22.2	15.9	19.2	35.0	18.8
Pig	0.0	0.0	0.0	2.2	1.6	5.8	0.0	2.5
Sheep	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.5
Chicken	0.0	0.0	0.0	0.0	11.1	0.0	0.0	3.5
TOTAL	0.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

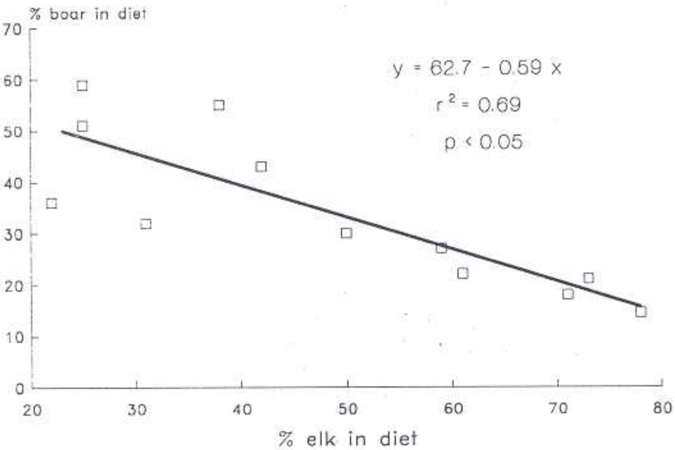

Fig. 5. The relationship between number of Ussuri wild boar and Manchurian elk in kill composition of Amur tigers in Russian Far East, based on 7 time periods of study in Sikhote-Alin State Zapovednik, and 5 other studies in Primorye and Khabarovsk Krais (see Table 6).

of depredating tigers has become more common, eliminating the individuals who habitually kill livestock or reside near settlements. Farmers who suffer repeated loses to predation have probably always killed tigers. However, with recent privatization of farms, individual farmers carry the burden of depredation directly. We suspect that killing of depredating tigers has increased. One radio-collared tiger is responsible for the death of at least 2 calves and one colt, and her life has been threatened by more than one farmer. Compensation only partly alleviates the loss, and state-determined rates for compensation have left farmers dissatisfied.

MANAGEMENT IMPLICATIONS

As noted by Matyushkin et al. (1980) and Matyushkin (1992), it is widely believed that welfare of the Amur tiger population is dependent on wild boar. Because boar overwinter survival is closely linked to mast crops, and because the primary mast-producing tree is the Korean pine, large-scale harvesting of this commercially valuable tree could be a potential threat to tiger survival. Matyushkin (1992) and the data presented here indicate that the importance of wild boar has likely been exaggerated. Figure 5 demonstrates that tigers often rely on elk more than boar, but that either species can provide the bulk of the diet. Forestry management practices could favor one prey over the other, potentially without any serious detriment. Nonetheless, these two prey species should be maintained in any forest complex that is being managed for Amur tigers. Each prey species responds to environmental changes differently, and the impact of fluctuations in either prey species can be dampened if the other prey also exists in sufficient abundance. In this scenario, the large-scale selective harvesting of pine is still seen to be a threat to tiger survival.

In concurrence with studies on other tiger subspecies (Schaller 1967, Kruuk 1986, Sunquist and Sunquist 1989, Seidensticker and McDougal 1993, Karanth and Sunquist 1995), our data suggest that Amur tigers specialize on medium to large-sized ungulates. Despite the large geographic range of subspecies, tigers appear to be associated with very similar sets of ungulates across their entire range. (Table 7): 3 size classes of cervids (except medium-size deer missing from Java and Sumatra) and wild pigs are present throughout tiger range. In all places except Russia, a large bovid is or was present. What is of interest here is not the percentages that each species contributes to the diet of tigers, which varies from site to site based on availability and relative density, but that the complex of species is relatively similar among all sites. Seidensticker (1986) has suggested that

Table 6. Summary of kill composition data for Amur tiger in the Russian Far East, 1933–1994. Domestic animals except dogs are excluded. Data presented by area, with years of study. Sample sizes are in parentheses.

Species	Primorye[a] 1957–1959 (40)	Primorye[b] 1958–1987 (690)	Lazovksy Zapovednik[c] 1973–1979 (336)	Central Sikhote Alin[d] 1970–1973 (64)	Khabarovsk northern Primorye[e] no data (131)	Sikhote Alin Zapovednik[f] 1933–1994 (552)
Elk	50.0	37.1	31.0	25.0	25.0	54.3
Wild boar	30.0	54.8	31.8	59.4	51.0	29.5
Roe deer	2.5	2.0	5.3	6.3	5.0	6.3
Sika deer	5.0	0.1	18.2	0.0	0.0	0.5
Musk deer	2.5	2.0	0.0	3.1	4.0	2.5
Moose	2.5	0.1	0.0	0.0	3.0	1.8
Ghoral	0.0	0.0	2.9	0.0	0.0	0.9
Bear	5.0	7.3	1.5	3.1	6.0	2.2
Other	2.5	0.3	9.0	3.1	6.0	1.8
TOTAL	100.0	103.7[g]	100.0	100.0	100.0	100.0

[a] Abramov 1962; [b] Abramov et al. 1978; [c] Zhivotenko 1981; [d] Yudakov and Nikolaev 1987; [e] Kucherenko 1985; [f] this study, [g] as reported in article.

Table 7. Summary of ungulate assemblages in tiger range (after Seidensticker 1986).

Type	Chitwan Nepal[a]	Khana India[b]	Nagarahole India[c]	Sunderbans Bangladesh[d]	Huai Kha Kha-eng Thailand[e]	Java[f]	Sumatra[g]	Sikhote-Alin Russia[h]	Lazovsky Russia
Large deer									
Alces alces								present	
Cervus elaphus								present	present
C. unicolor	present	present	present		present		present		
C. duvauceli		present		formerly					
C. schomburghi					formerly				
C. timorensis						present			
Medium sized deer									
C. nippon								present	present
Capreolus capreolus								present	present
Axis axis	present	present	present	present	rare				
A. porcinus	present			formerly					
C. eldi					formerly				
Small deer									
Muntiacus spp.	present	present	present	present	present	present	present		
Moschus moschiferus								present	present
Wild pigs									
Sus scrofa	present	present	present	present	present	present	present	present	present
S. verracosus						present			
S. barbatus							present		
Large Bovids									
Bos gaurus	present	present	present		present	present			
Bos javanicus					present		present		
Babulus babulis				formerly	present				

[a] Sunquist 1981; [b] Schaller 1967; [c] Karanth 1993; [d] Heindrichs 1975; [e] Seidensticker 1986; [f] Rabinowitz 1989; [g] present study; [h] Zhivotchenko 1981.

tiger distribution in South Asia is linked to an ungulate assemblage whose essential component is large cervids. We suggest that this relationship extends into the Russian Far East, and that in some regions suids may be a more important component than has been acknowledged to date.

Despite major differences in habitat structure and composition, tigers thrive in areas where this full complex of cervids and suids is preserved. The management implications of this comparison are clear: conservation of tigers is linked to an ungulate assemblage that may vary in species composition but is comprised of species which are ecologically similar. Although tigers exist in some regions where such a complex presently does not exist (Rabinowitz 1989), the original ecosystem included such a complex, and survival of the tiger without it's primary food base is in question. In Java, Seidensticker and Suyono (1976) correlated the demise of the tiger population with the loss of the ungulate complex. In Russia, the northern limits of tiger distribution are closely linked to the northern limit of elk and wild boar (Kucherenko 1985).

Given that tigers are capable of thriving in the temperate forests of the Russian Far East as well as the jungles of Sumatra, efforts to conserve this species need not focus on habitat analyses except as they relate directly to prey species. Although there has been considerable discussion about habitat quality and critical components of habitats for tigers (Schaller 1967, Sunquist 1981, Sunquist and Sunquist 1989, Rabinowitz 1993), we argue that tigers have few ecologically constraints that relate to specific habitat requirements. For instance, it has been suggested that hunting cover is an important component of tiger habitat (Sunquist and Sunquist 1989). However, tigers successfully hunt elk and boar in the coastal forests of Sikhote-Alin Zapovednik where the only stalking cover in winter is the widely spaced trunks of oak trees. We suggest that efforts should be focused on protecting large units of forested land where management of ungulates is considered a priority, and where human-induced mortality of the tiger population can be controlled. In many areas, management for ungulates can be compatible with other human uses, and thus, tiger conservation need not directly conflict with economic realities. However, it is critical that on lands managed for multiple uses, strict control be maintained on hunting and hunters to retain high densities of critical prey species and to reduce poaching of tigers.

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