BioOne COMPLETE

Fine-scale spatio-temporal variation in tiger Panthera tigris diet: effect of study duration and extent on estimates of tiger diet in Chitwan National Park, Nepal

Authors: Kapfer, Paul M., Streby, Henry M., Gurung, Bhim, Simcharoen, Achara, McDougal, Charles C., et al.

Source: Wildlife Biology, 17(3) : 277-285

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/10-127

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Wildl. Biol. 17: 277-285 (2011)
DOI: 10.2981/10-127
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Fine-scale spatio-temporal variation in tiger *Panthera tigris* diet: effect of study duration and extent on estimates of tiger diet in Chitwan National Park, Nepal

Paul M. Kapfer, Henry M. Streby, Bhim Gurung, Achara Simcharoen, Charles C. McDougal & James L.D. Smith

Attempts to conserve declining tiger *Panthera tigris* populations and distributions have experienced limited success. The poaching of tiger prey is a key threat to tiger persistence; a clear understanding of tiger diet is a prerequisite to conserve dwindling populations. We used unpublished data on tiger diet in combination with two previously published studies to examine fine-scale spatio-temporal changes in tiger diet relative to prey abundance in Chitwan National Park, Nepal, and aggregated data from the three studies to examine the effect that study duration and the size of the study area have on estimates of tiger diet. Our results correspond with those of previous studies: in all three studies, tiger diet was dominated by members of Cervidae; small to medium-sized prey was important in one study. Tiger diet was unrelated to prey abundance, and the aggregation of studies indicates that increasing study duration and study area size both result in increased dietary diversity in terms of prey categories consumed, and increasing study duration changed which prey species contributed most to tiger diet. Based on our results, we suggest that managers focus their efforts on minimizing the poaching of all tiger prey, and that future studies of tiger diet be of long duration and large spatial extent to improve our understanding of spatio-temporal variation in estimates of tiger diet.

Key words: Chitwan National Park, faecal analysis, Felidae, food habits, Nepal, niche breadth, Panthera tigris, tiger

Paul M. Kapfer, Conservation Biology Program, University of Minnesota, 1980 Folwell Avenue, Saint Paul, Minnesota 55108, USA - e-mail: kapf0005@umn.edu
Henry M. Streby, U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, 1980 Folwell Avenue, Saint Paul, Minnesota 55108, USA - e-mail: streb006@umn.edu
Bhim Gurung & James L.D. Smith, Department of Fisheries, Wildlife & Conservation Biology, University of Minnesota, 1980 Folwell Avenue, Saint Paul, Minnesota 55108, USA - e-mail addresses: guru0023@umn.edu (Bhim Gurung); smith017@umn.edu (James L.D. Smith)
Achara Simcharoen, Department of National Park, Wildlife and Plant Conservation, Bangkok, Thailand - e-mail: knr_hkk@hotmail.com
Charles C. McDougal, International Trust for Nature Conservation, Kathmandu, Nepal - e-mail: info@tigermountain.com

Corresponding author: Paul M. Kapfer

Received 6 December 2010, accepted 11 June 2011

Associate Editor: John W. Laundré

The largest felid in the world, the tiger *Panthera tigris,* is threatened due to habitat destruction, prey depletion and poaching (Nowell & Jackson 1996). Of these threats, the poaching of tiger prey is considered the most insidious because of its potential to not only impact tiger populations by increasing rates of human-tiger conflict, but also indirectly affect them by decreasing their prey base and presumably, depressing their reproduction (Karanth & Stith 1999). Despite considerable investment and public support, conservation efforts aimed at mitigating these threats have experienced limited success, and tiger numbers and distributions have continued to contract (Dinerstein et al. 2007). As human popula-

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

tions in tiger range states continue to grow, so too will the pressure they exert on tiger populations and habitats.

Accurate knowledge of a species' dietary habits is one of several prerequisites for effective conservation, and it is fundamental to conservation initiatives such as habitat prioritization, protection and restoration. Given ample food and refuge from human persecution, tigers are capable of surviving in almost any vegetative association (Sunquist et al. 1999); tiger range encompasses a large variety of ecosystems and tiger distribution and density are closely tied to that of its primary prey (Miquelle et al. 1999, Karanth et al. 2004). Consequently, understanding the tiger's trophic requirements is essential to predicting its response to human-mediated environmental change (Sunquist et al. 1999).

Given its importance to the conservation of the species, it is not surprising that tiger diet has received considerable attention. Studies of tiger diet have been conducted throughout much of the range of the species, including India (Karanth & Sunquist 1995, Chundawat et al. 1999, Biswas & Sankar 2002, Sankar & Johnsingh 2002, Bagchi et al. 2003, Reddy et al. 2004, Andheria et al. 2007), Nepal (Seidensticker 1976a, McDougal 1977, Sunquist 1981, Johnsingh 1992, Seidensticker & McDougal 1993, Støen & Wegge 1996, Wegge et al. 2009), Bangladesh (Khan 2004), Thailand (Rabinowitz 1989), Bhutan (Wang & MacDonald 2009) and Russia (Miquelle et al. 1996). These studies indicate that tigers generally prey upon 8-15 species, and while they occasionally consume prey weighing up to 1,000 kg, the majority of tiger diet consists of small prey (i.e. $\leq$ 20 kg; e.g. Rabinowitz 1989) and medium-sized cervids (i.e. of 50-200 kg; e.g. Karanth & Sunquist 1995).

With few exceptions (e.g. Karanth & Sunquist 1995), most studies of tiger diet have been of limited spatio-temporal scale, potentially hindering our understanding of variation in the tiger's diet (Table 1). Stochastic events such as drought and outbreaks of disease (McDougal 1977) result in fluctuations in prey abundance and vulnerability (Schaller 1967, Johnsingh 1983, Dave & Jhala 2011); short term studies that encompass a single season or year may not detect variation in tiger diet resulting from these fluctuations. In addition, tigers exhibit intrasexual territoriality and maintain large home ranges (Sunquist 1981), and small study areas are unlikely to encompass the home ranges of more than a few tigers. In combination, the short duration and small study areas of most investigations of tiger diet may inhibit our understanding of tiger diet.

To better understand the spatio-temporal dynamics of tiger diet in relation to prey abundance and the effect of study duration and study area size (hereafter extent) on estimates of the tiger diet, we used heretofore unpublished data on tiger diet in combination with two previous studies of tiger diet conducted in Royal Chitwan National Park, Nepal (McDougal 1977, Sunquist 1981).

Methods

Study area

All three studies were conducted in Chitwan National Park, Nepal (Fig. 1), which covers an area of 932 km^2 and lies at approximately 27°30'N latitude and 84°20'E longitude in south central Nepal. More than half of the Park boundary is delimited by three rivers: the Narayani and Rapti Rivers form the northwestern boundary and the Reu River forms most of the southern boundary. Park altitude ranges from 90 m a.s.l. on the flood plains to about

Table 1. Duration (in months), study area size (in km^2), number of scats collected, tiger density (in numbers/100 km^2) and location of previously published studies of tiger diet using scat analysis for which estimates of tiger density are available. We took density estimates for India from Karanth et al. 2004 and density estimates for Thailand from Simcharoen et al. 2007.

Study	Duration	Size of study area	Number of scats	Tiger density	Location
Andheria et al. 2007	2	880[a]	381	11.97 ± 3.71	Bandipur Tiger Reserve, India
Bagchi et al. 2003	5	34	109	11.46 ± 4.20	Ranthambore National Park, India
Biswas et al. 2002	6	61	75	7.29 ± 2.54	Pench National Park, India
Johnsingh 1992	23	20	36	11.97 ± 3.71	Bandipur Tiger Reserve, India
Karanth & Sunquist 1995	36	104	490	11.50 ± 1.70	Nagarahole National Park, India
Rabinowitz 1989	22	100	38	3.98 ± 0.51	Haui Kha Khaeng Wildlife Sanctuary, Thailand

[a] Size of reserve; the study area size was not provided.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

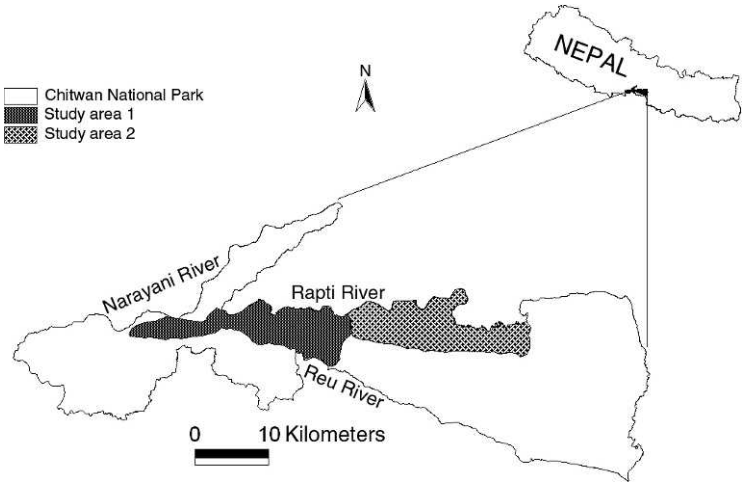


Figure 1. Location of the two study areas in Chitwan National Park, Nepal. Study area 1 encompasses locations of scats collected by McDougal (1977), and study area 2 encompasses locations of scats collected for our study and the study of Sunquist (1981).

900 m a.s.l. on the Hills. Chitwan's climate is subtropical with distinct wet and dry seasons; annual rainfall averages 250 cm with the majority occurring during June - September (Mishra 1982).

There are three main vegetative associations within the park. Sal forest, a climax moist deciduous community dominated by sal trees *Shorea robusta*, occupies approximately 73% of the park and occurs in well-drained, upland areas. On slopes and ridges at higher elevations, the near continuous coverage of sal is increasingly interrupted by occasional patches of chir pine *Pinus roxburghii*. Riverine forests dominate the banks of the rivers Rapti, Narayani and Reu and are composed of khair *Acacia catechu* and shisam *Dalbergia sissoo* trees interspersed with grasslands and dense shrubs. Riverine forest covers approximately 10% of the park. Grasslands are a prominent feature of the alluvial plains and cover 15% of the park's area. Grass species commonly found includes *Saccharum* spp., Cogon grass *Imperata cylindrical* and *Themeda* spp.

Potential medium-to-large prey of tigers found in both study areas include sambar *Cervus unicolor*, chital *Axis axis*, barking deer *Muntiacus muntjak*, hog deer *Axis porcinus* and wild boar *Sus scrofa*. Whereas the hog deer is a grassland species, sambar and barking deer are more common in riverine and sal forests (Mishra 1982). Chital and wild boar use all three habitat types. Dhungel & O'Gara (1991) estimated the relative abundance of these species in grassland and riverine forest. In grasslands, estimated hog deer density (19/km^2) was highest compared to sambar (12/km^2), chital (8/km^2), wild boar (2/km^2) and barking deer ($<$ 1/ km^2). However, in the riverine forest, chital (55/km^2) and sambar (30/km^2) abundance was relatively higher compared to other species (Dhungel & O'Gara 1991).

Scats used in McDougal (1977) were collected during 1976-1977; scats used in Sunquist (1981) were collected during 1974-1976. Hereafter, McDougal (1977) is referred to as McDougal and Sunquist (1981) as Sunquist. Scats used in McDougal and Sunquist were collected in adjacent study areas in the park. We collected scats during 1979-1980 from the same study area as Sunquist. Hence, McDougal and Sunquist overlapped temporally, and Sunquist and our study overlapped spatially.

Field methods

Methods used in all three studies were broadly comparable but not identical. Herein, we describe differences relevant to our analysis and results and refer to each study for a more complete treatment of their respective methods. All studies used scat analysis to estimate tiger diet (Putman 1984) by collecting scats opportunistically along game trails, roads and near kills during the dry season (i.e. November-May). We differentiated tiger scats from those of sympatric species by size, morphology and associated signs such as tracks or scrapes (Karanth & Sunquist 1995). Tiger and leopard *Panthera pardus* scats overlap in size and share similar morphological characteristics, which could produce spurious identifications (Farrell et al. 2000). However, misidentifications were unlikely because $>$ 90% of the scats collected were associated with tracks or scrapes, which differ in size between the two species (Cutter 2009). Furthermore, leopards in the areas where the scats were collected were

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

considered to be rare (McDougal 1988). However, we cannot rule out the possibility that some of the scats were misidentified in this study, as well as in most other studies that examined tiger diet. Scats were placed into paper or mesh bags and dried before being placed into dry storage until analysis in 2005. Upon removal from storage, scats were washed over a sieve to separate undigested remains (e.g. hair and bone fragments). We identified prey species contained in each tiger scat to the highest possible taxonomic resolution by comparing the undigested remains from each scat to a reference collection prepared from hair samples collected in the field and from captive animals. We selected several hairs from each scat haphazardly and compared them to a reference collection using macro- and microscopic characteristics including colour, length, medulla pattern, thickness and cross-section characteristics (Moore et al. 1974).

Analysis

We analyzed the contribution of each prey species to tiger diet and expressed it as percent occurrence (number of occurrences of each prey/total number of occurrences $\times$ 100) and percent biomass contribution (biomass of each prey type consumed/total biomass consumed $\times$ 100). We estimated percent occurrence to allow comparison with previous studies. However, small prey species, having proportionately more indigestible material (e.g. hair and bones) per unit weight than large prey species, produce more scats per volume consumed, resulting in overestimates of their relative contribution to tiger diet. Consequently, the percent occurrence is not an accurate indication of the contribution of a particular prey to the diet when there is a large variation in prey size (Floyd et al. 1978, Ackerman et al. 1984). To correct this overestimation, we applied the regression equation developed for cougars *Puma concolor* by Ackerman et al. (1984):

$$Y = 1.980 + 0.035X,$$

where Y is the weight of prey consumed/scat produced, and X is the live weight of the prey. This equation relates prey weight to the number of scats produced/unit weight consumed. 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. When possible, we used the estimated live weights of prey consumed by tigers in Nagarahole, India (Karanth & Sunquist 1995); otherwise, we used average prey weights (Schaller 1967, Lekagul & McNeely 1977, Nowak 1991).

Slight differences in the methods of the three studies required minor data manipulations to maintain analytical consistency. In the interest of focusing on the tiger's natural prey, McDougal excluded scats containing domestic livestock, and to be consistent, we did likewise. Consequently, we disregarded all occurrences of domestic livestock (one in our study and two in Sunquist) in tiger scats. Similarly, we discarded all scats composed entirely of vegetation. In his analysis, Sunquist failed to distinguish between chital, hogdeer and muntjak hairs, resulting in a single prey category (*Axis* spp. or *Muntiacus muntjak*). Again, for consistency, we aggregated all occurrences of chital, hogdeer and muntjak into the single prey category for all three studies. For calculations of percent biomass and mean mass of prey consumed, we took the mean weight of all three prey species combined.

We used data on prey abundance collected during companion studies that were conducted in 1974, 1977 and 1980, corresponding with the time periods when the scats were collected (Seidensticker 1976b, Mishra 1982, Tamang 1982) to assess the relationship between prey abundance and tiger diet using Spearman rank correlations. We summed the density estimates for chital, hog deer and muntjak into a single category for comparison with our combined prey category. We calculated the total number of prey species consumed to determine trophic niche breadth.

To examine the effect of study duration on estimates of tiger diet, we combined our data with those of Sunquist and qualitatively compared the percent biomass contribution and maximum number of species consumed in either study to the aggregate for both studies combined. To examine the effect of study extent on estimates of tiger diet, we compared the percent biomass contribution and the number of species preyed upon from McDougal and Sunquist to their aggregate estimates. To quantify the effect of study duration and study extent on estimates of tiger diet, we compared the percent biomass contribution and number of species consumed from all three study sites to their aggregate estimates.

Results

We collected 77 scats and compared these data with those from the 123 and 55 scats collected by Mc-

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 2. Percent occurrence and 95% bootstrapped confidence intervals (in parentheses), based on 10,000 replicates, of prey in tiger diet as identified by analysis of scats in three studies (1: McDougal 1977, 2: Sunquist 1981 and 3: our study) conducted in Chitwan National Park, Nepal. See study areas in Fig. 1.

Species/Order	Study 1	Study 2	Study 3	Study 1 & 2	Study 2 & 3	Study 1, 2 & 3
Axis axis	33.3 (24.4-41.5)	-	9.5 (3.2-17.5)	-	-	-
Axis porcinus	15.5 (9.8-22.0)	-	12.7 (6.3-20.6)	-	-	-
Muntiacus muntjak	4.1 (0.8-7.3)	-	6.3 (4.8-20.6)	-	-	-
Axis spp. or *M. muntjak*	52.9 (44.8-61.8)	68.0 (56.0-80.0)	28.6 (17.5-39.7)	57.2 (49.7-64.7)	46.0 (37.2-54.9)	49.6 (43.2-55.9)
Cervus unicolor	29.3 (22.0-36.6)	22.0 (10.0-32.0)	36.5 (23.8-49.2)	27.2 (20.8-34.1)	30.1 (22.1-38.9)	29.7 (23.7-35.6)
Sus scrofa	10.6 (5.7-16.3)	4.0 (0.0-10.0)	11.1 (4.8-19.1)	8.7 (4.6-13.3)	8.0 (3.5-13.3)	9.3 (5.9-13.1)
Hystrix indica	0.8 (0.0-2.4)	-	1.6 (0.0-4.8)	0.6 (0.0-1.7)	0.9 (0.0-2.6)	0.9 (0.0-2.1)
Lepus nigricollis	0.8 (0.0-2.4)	-	-	0.6 (0.0-1.7)	-	0.4 (0.0-1.3)
Semnopithicus entellus	5.7 (1.6-9.8)	4.0 (0.0-10.0)	6.4 (0.0-12.7)	5.2 (2.3-8.7)	5.3 (1.8-9.7)	5.5 (3.0-8.5)
Viverridae	-	2.0 (0.0-6.0)	-	0.6 (0.0-1.7)	0.9 (0.0-2.65)	0.4 (0.0-1.3)
Melursus ursinus	-	-	1.6 (0.0-4.8)	-	0.9 (0.0-2.65)	0.4 (0.0-1.3)
Bos frontalis	-	-	1.6 (0.0-4.8)	-	0.9 (0.0-2.65)	0.4 (0.0-1.3)
Catopuma temmincki	-	-	3.2 (0.0-7.9)	-	1.8 (0.0-4.42)	0.9 (0.0-2.1)
Panthera pardus	-	-	1.6 (0.0-4.8)	-	0.9 (0.0-2.6)	0.4 (0.0-1.3)
Martes flavigula	-	-	3.2 (0.0-7.9)	-	1.8 (0.0-4.4)	0.9 (0.0-2.1)
Arctonyx collaris	-	-	1.6 (0.0-4.8)	-	0.9 (0.0-2.6)	0.4 (0.0-1.3)
Aves	-	-	1.6 (0.0-4.8)	-	0.9 (0.0-2.6)	0.4 (0.0-1.3)
Rodentia	-	-	1.6 (0.0-4.8)	-	0.9 (0.0-2.6)	0.4 (0.0-1.3)

Dougal and Sunquist, respectively. We excluded 15 scats which contained grass, leaves, domestic livestock or unidentifiable animal remains from further analyses. Tigers preyed upon a minimum of eight, five and 16 species during McDougal, Sunquist and our study, respectively. Cervids constituted the primary prey of tigers for all three studies with $>$ 65% percent occurrence (Table 2). In our study, tigers preyed primarily on sambar, differing from studies McDougal and Sunquist in which the combined prey category of chital, hog deer and muntjak formed the bulk of tiger diet. The discrepancy in primary prey among studies differed in terms of biomass contribution (Fig. 2); sambar contributed the largest percent biomass for McDougal and for our study and nearly so for the study by Sunquist. However, when we increased study duration (aggregating data from Sunquist and our study), sambar contributed the most biomass to tiger diet, replacing the combined prey category of *Axis* spp. or *Muntiacus muntjak*. For all other species, increasing study duration or extent resulted in estimated biomass contributions between those estimated for each study singly, but did not change their order of importance (see Fig. 2). Mean mass of prey consumed was 55.3 kg for McDougal, 50.2 kg for Sunquist and 36.7 kg for our study. Mean mass of prey consumed when we extended the study duration was 41.1 kg, was 53.8 kg when the extent was increased, and was 47.4 kg when duration and extent were increased.

Composition of tiger diet was unrelated to the

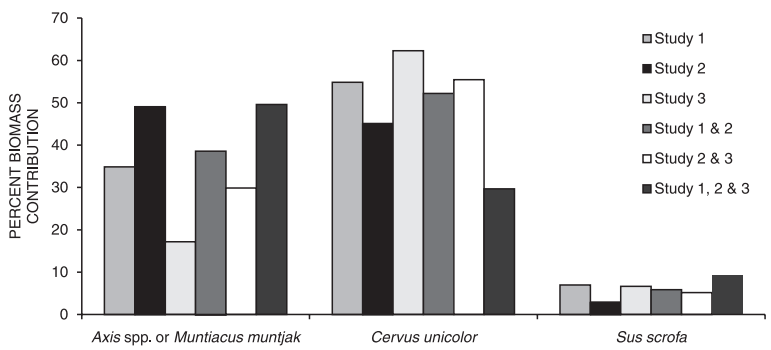


Figure 2. Percent biomass contribution of the primary prey of tigers from three studies conducted in Chitwan National Park, Nepal. Study areas 1 and 2 are shown in Figure 1. Study 1 & 2, Study 2 & 3 and Study 1, 2 & 3 refer to the combinations of all scats collected from respective studies to estimate percent biomass contribution.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

density of prey ($\rho = -0.10$, $df = 10$, $P = 0.74$). Tigers preyed upon a total of 18 species (15 prey categories) across the three studies (see Table 2). Tiger diet was more varied during our study (N = 13 prey categories) than during the studies of McDougal (N = 6) or Sunquist (N = 5). Increasing the study duration (i.e. aggregating data from Sunquist and our study) resulted in the identification of one more prey category (belonging to Viverridae) consumed by tigers than in our study alone, and 10 more than in the Sunquist study. Increasing the size of the study area (aggregating data from McDougal and Sunquist) resulted in the identification of one more prey category (belonging to Viverridae) than in McDougal alone and two more than in Sunquist. Increasing study duration and study area size (aggregating data from all three studies) increased the number of prey categories by nine, 10 and two, for McDougal, Sunquist and our study, respectively.

Discussion

Composition of tiger diet for Sunquist and McDougal, which overlapped in time but not in space, were broadly similar. Overlapping confidence intervals indicate that, while there were slight differences in the percent occurrence of primary prey items among the two studies (i.e. sites), the differences were largely indistinguishable. Two species were unique to McDougal, whereas one species was unique to Sunquist; regardless, none of the species unique to either study contributed substantially to tiger diet (see Table 2).

Conversely, the composition of tiger diet for Sunquist and our study, which overlapped in space but not in time, differed dramatically, with sambar contributing far more, and the prey category containing chital, hog deer and muntjak contributing far less to tiger diet during the our study (see Table 2), to the extent that sambar became the largest contributor, in terms of biomass, to tiger diet (see Fig. 2). If tigers in Chitwan were non-selective predators, we would expect that an increase in the consumption of sambar was the result of either increased sambar abundance or decreased abundance of the other three species. However, studies of tiger prey selection from other tiger populations indicate that tigers are selective predators (Karanth & Sunquist 1995, Bagchi et al. 2003, Wegge et al. 2009), and the results of our rank correlation analysis support the conclusion that tigers are actively selecting certain prey types. Although our analysis did not incorporate prey selectively, the heavy reliance on sambar by Chitwan tigers is consistent with and provides further support for the finding that tigers actively select prey weighing > 176 kg (Karanth & Sunquist 1995).

Increasing study duration and study area size changed the relative contribution of prey species to tiger diet. Combining the results of Sunquist with McDougal and our study increased the percent biomass contribution of sambar while decreasing the percent biomass contribution of the prey category combining chital, hog and barking deer, with the end result that sambar, rather than the combined prey category, contributed more biomass to tiger diet in Chitwan; all other changes to prey biomass contributions were nominal and did not change their relative rank importance in tiger diet. Previous analyses have suggested that the percent occurrence of prey items tends to stabilize between 50 and 60 scats (Biswas & Sankar 2002, Bagchi et al. 2003), so a possible explanation for the observed differences is that only by combining the 50 scats from Sunquist with the 62 scats from our study were we able to get an accurate estimate of tiger diet. If this is the case, results from studies using fewer or similar numbers of scats to estimate tiger diet should be viewed more sceptically.

Similar to other studies of tiger diet (Karanth & Sunquist 1995, Miquelle et al. 1996, Biswas & Sankar 2002), tigers in Chitwan preyed heavily on medium- to large-sized large cervids. It remains unclear why the average weight of tiger prey was lower and the diversity of tiger diet higher during our study than during McDougal or Sunquist. It has been suggested that tigers include more species, as well as smaller species, in their diet when their primary prey (cervids) are unavailable (Sunquist et al. 1999, Reddy et al. 2004). However, owing to enhanced protection, cervid populations were most abundant during our study (Mishra 1982) suggesting that this was not the case. We speculate that the reason that a greater diversity and smaller mean size of prey items occurred during our study happened because we sampled a different segment of the tiger population. Although our scats were collected in the same study area as Sunquist, they were collected during activities geared towards understanding the role of juvenile dispersal in structuring the population (Smith 1993), and consequently, may have been more prone to collecting scats of juveniles and dispersers than

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

were Sunquist and McDougal, which focused on resident, breeding adults during their studies. If this is the case, it suggests that diet may vary by tiger age classes, and future studies should attempt to determine age-specific dietary habits.

Differences among studies in the number of prey species consumed suggest that studies of short duration and limited spatial extent may fail to identify rare prey items (i.e. those constituting $< 5\%$ diet biomass) in the diet of tigers. Whereas it is intuitively appealing to assume that common prey is important, the converse assumption, that rare prey are unimportant, is injudicious as rarity does not imply a relative value for prey categories. For example, in our study, prey categories that individually contributed $< 5\%$ of diet biomass, collectively contributed $> 20\%$ of the biomass consumed by tigers. Rather than being unimportant, prey that is only rarely consumed may prove vital during periods when more commonly consumed prey are unavailable (Schaller 1967).

Similarly, despite the tiger's apparent selection of medium to large prey (Karanth & Sunquist 1995, Biswas & Sankar 2002), one should not discount the importance of small prey to supplement tiger diet. During periods when larger prey are unavailable, perhaps due to disease outbreaks (McDougal 1977), seasonal changes in prey behaviour (Schaller 1967) or peaks in poaching pressure, small prey may provide sufficient sustenance to allow tiger persistence. However, we caution that, whereas small prey may collectively contribute substantially to tiger diet, it remains questionable whether, in the absence of larger prey items, small prey would be sufficient to support tiger reproduction (Sunquist et al. 1999). Modeling of cougar energetics suggests that raising young to independence requires $> 250\%$ more food than required by an adult female without young (Laundré 2005). Given that cougars and tigers have similar litter sizes and lengths of young dependency (Sunquist & Sunquist 2002), it seems highly unlikely that a tigress could raise cubs solely on small prey.

Scats used for all three studies were collected during the dry season, limiting our analysis to the annual, rather than seasonal, dynamics of tiger diet. However, it is likely that seasonal fluctuations in prey abundance and vulnerability resulting from birth pulses, rutting behaviour and migration may result in seasonal variation in tiger diet (Schaller 1967, Sunquist 1981). If possible, future research should aim to document seasonal variation in tiger diet. Of particular interest would be tiger diet during the wet season, a period when prey may be more diffuse due to the widespread availability of water, and which consequently may be a difficult period for tigers.

Our analysis provided anecdotal evidence of pseudoreplication (Hurlbert 1984). Studies of tiger diet are primarily conducted incidental to other research projects. Consequently, scats are normally collected opportunistically (i.e. haphazardly), rather than by randomized sampling design. Scats collected opportunistically, incidental to other activities (e.g. while walking transects or investigating a kill), are unlikely to be independent, and may result in biased estimates of the relative importance of certain prey (Marucco et al. 2008). This bias was evident in our study when two scats were identified as containing hairs of the Asiatic golden cat *Pardofelis temminckii* which were considered extremely rare in the park during our study. Upon closer scrutiny, we realized that both scats had been collected on the same day within a short distance of one another, likely representing the predation of a single golden cat. Presumably, a single tiger had killed a golden cat, and then defecated several times along that same game trail. In this case, the non-independence of the scats did not have a large effect on estimates of tiger diet; however, it is easy to envision a scenario in which the non-independence of scats would result in significant bias. For example, if a tiger kills a large animal such as a gaur, it typically remains with the kill for several days, alternately feeding, resting and defecating. A single kill as large as a gaur *Bos gaurus* will result in numerous tiger scats. If all the scats from that gaur kill are collected, the importance of gaur to tiger diet is likely to be overestimated while the importance of all other prey items will be underestimated. Future research on tiger diet should attempt to minimize these potential biases by adopting a sampling framework that is statistical, rather than haphazard. To accomplish this, researchers could use molecular methods to identify the individual tigers responsible for each scat and sample accordingly (Prugh et al. 2008). Use of this method has the added advantage of allowing researchers to investigate intersexual (Pilgrim et al. 2005) and individual variation in diet (Prugh et al. 2008). However, we acknowledge the difficulty of collecting viable genetic material given the climate in most of tiger range. Alternatively, researchers could minimize the potential issue of pseudoreplication by randomizing the placement of sampling transects.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Acknowledgements - funding for our study was provided by the Undergraduate Research Opportunity Program through the University of Minnesota, USA.

References

Ackerman, B.B., Lindzey, F.G. & Hemker, T.P. 1984: Cougar food habits in southern Utah. - Journal of Wildlife Management 48: 147-155.

Andheria, A.P., Karanth, K.U. & Kumar, N.S. 2007: Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. - Journal of Zoology 273: 169-175.

Bagchi, S., Goyal, S.P. & Sankar, K. 2003: Prey abundance and prey selection by tigers *Panthera tigris* in a semi-arid, dry deciduous forest in western India. - Journal of Zoology 260: 285-290.

Biswas, S. & Sankar, K. 2002: Prey abundance and food habit of tigers *Panthera tigris tigris* in Pench National Park, Madhya Pradesh, India. - Journal of Zoology 256: 411-420.

Chundawat, R.S., Gogate, N. & Johnsingh, A.J.T. 1999: Tigers in Panna: preliminary results from an Indian tropical dry forest. - In: Seidensticker, J., Christie, S. & Jackson, P. (Eds.); Riding the tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, UK, pp. 123-129.

Cutter, P.G. 2009: Identifying Effective Approaches for Landscape scale Conservation Planning and Monitoring in Southeast Asia. - PhD dissertation, University of Minnesota, Saint Paul, Minnesota, USA, 182 pp.

Dave, C. & Jhala, Y. 2011: Is competition with livestock detrimental for native wild ungulates? A case study of chital (*Axis axis*) in Gir Forest, India. - Journal of Tropical Ecology 27: 239-247.

Dhungel, S.K. & O'Gara, B.W. 1991: Ecology of the hog deer in Royal Chitwan National Park, Nepal. - Wildlife Monographs 119: 40 pp.

Dinerstein, E., Loucks, C., Wikramanayake, E., Ginsberg, J., Sanderson, E., Seidensticker, J., Forrest, J., Bryja, G., Heydlauff, A., Klezendorf, S., Leimgruber, P., Mills, J., O'Brien, T.G., Shrestha, M., Simons, R. & Songer, M. 2007: The fate of wild tigers. - Bioscience 57: 508-514.

Farrell, L.E., Roman, J. & Sunquist, M. 2000: Dietary separation of sympatric carnivores identified by molecular analysis of scats. - Molecular Ecology 9: 1583-1590.

Floyd, T.J., Mech, L.D. & Jordan, P.J. 1978: Relating wolf scat contents to prey consumed. - Journal of Wildlife Management 42: 528-532.

Hurlbert, S.H. 1984: Pseudoreplication and the design of ecological field experiments. - Ecological Monographs 54: 187-211.

Johnsingh, A.J.T. 1983: Large mammalian prey-predators in Bandipur. - Journal of the Bombay Natural History Society 80: 1-49.

Johnsingh, A.J.T. 1992: Prey selection in three large sympatric carnivores in Bandipur. - Mammalia 56: 517-526.

Karanth, K.U., Kumar, N.S., Nichols, J.D., Link, W.A. & Hines, J.E. 2004: Tigers and their prey: Predicting carnivore densities from prey abundance. - Proceedings of the National Academy of Sciences 101: 4854-4858.

Karanth, K.U. & Stith, B.M. 1999: Prey depletion as a critical determinant of tiger population viability. - In: Seidensticker, J., Christie, S. & Jackson, P. (Eds.); Riding the tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, UK, pp. 100-114.

Karanth, K.U. & Sunquist, M.E. 1995: Prey selection by tiger, leopard and dhole in tropical forests. - Journal of Animal Ecology 64: 439-450.

Khan, M.M.H. 2004: Ecology and conservation of the Bengal tiger in the Sundarbans mangrove forest of Bangladesh. - PhD dissertation, Cambridge University, Cambridge, UK, 296 pp.

Laundré, J.W. 2005: Puma energetics: a recalculation. - Journal of Wildlife Management 69: 723-732.

Lekagul, B. & McNeely, J.A. 1977: Mammals of Thailand. - Association for the Conservation of Wildlife, Bangkok, Thailand, 758 pp.

Marucco, F., Pletscher, D.H. & Boitani, L. 2008: Accuracy of scat sampling for carnivore diet analysis: wolves in the Alps as a case study. - Journal of Mammalogy 89: 665-673.

McDougal, C. 1977: The face of the tiger. - Rivington Books, London, UK, 180 pp.

McDougal, C. 1988: Leopard and tiger interactions at Royal Chitwan National Park, Nepal. - Journal of the Bombay Natural History Society 85: 609-610.

Miquelle, D.G., Smirnov, E.N., Merrill, T.W., Myslenkov, A.E., Quigley, H.G., Hornocker, M.G. & Schleyer, B. 1999: Hierarchical spatial analysis of Amur tiger relationships to habitat and prey. - In: Seidensticker, J., Christie, S. & Jackson, P. (Eds.); Riding the tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, UK, pp. 71-99.

Miquelle, D.G., Smirnov, E.N., Quigley, H.G., Hornocker, M.G., Nikolaev, I.G. & Matyushkin, E.N. 1996: Food habits of Amur tigers in Silkhote-Alin Zapovednik and Russian Far East, and implications for conservation. - Journal of Wildlife Research 1: 138-147.

Mishra, H.R. 1982: Balancing human needs and conservation in Nepal's Royal Chitwan Park. - Ambio 11: 246-251.

Moore, T.D., Spence, L.E. & Dugnolle, C.E. 1974: Identification of the dorsal guard hairs of some mammals of Wyoming. - Wyoming Game and Fish Department, Wyoming, USA, 177 pp.

Nowak, R.M. 1991: Walker's mammals of the World. Vol. II. - Johns Hopkins University Press, Baltimore, Maryland, USA, 1084 pp.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Nowell, K. & Jackson, P. 1996: Wild cats: status, survey, and conservation action plan. - IUCN/SSC Cat Specialist Group, Gland, Switzerland, 406 pp.

Pilgrim, K.L., McKelvey, K.S., Riddle, A.E. & Schwartz, M.K. 2005: Felid sex identification based on noninvasive genetic samples. - Molecular Ecology Notes 5: 60-61.

Prugh, L.R., Arthus, S.M. & Ritland, C.E. 2008: Use of faecal genotyping to determine individual diet. - Wildlife Biology 14(3): 318-330.

Putman, R.J. 1984: Facts from faeces. - Mammalian Review 14: 79-97.

Rabinowitz, A. 1989: The density and behavior of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary, Thailand. - Natural History Bulletin of the Siam Society 37: 235-251.

Reddy, H.S., Srinivasulu, C. & Thulsi, K. 2004: Prey selection by the Indian tiger *Panthera tigris tigris* in Nagarjunasagar Srisailam Tiger Reserve, India. - Mammalian Biology 69: 384-391.

Sankar, K. & Johnsingh, A.J.T. 2002: Food habits of Tiger *Panthera tigris* and Leopard *Panthera pardus* in Sariska Tiger Reserve, Rajasthan, India, as shown by scat analysis. - Mammalia 66: 285-289.

Schaller, G.B. 1967: The deer and the tiger: a study of wildlife in India. - University of Chicago Press, Chicago, Illinois, USA, 384 pp.

Seidensticker, J. 1976a: On the ecological separation between tigers and leopards. - Biotropica 8: 225-234.

Seidensticker, J. 1976b: Ungulate populations in Chitawan Valley, Nepal. - Biological Conservation 10: 183-210.

Seidensticker, J. & McDougal, C. 1993: Tiger predatory behaviour, ecology and conservation. - In: Dunstone, N. & Gorman, M.L. (Eds.); Mammals as predators: proceedings of a symposium of the Zoological Society of London, no. 65. Zoological Society of London, London, UK, pp. 105-125.

Simcharoen, S., Pattanavibool, A., Karanth, K.U., Nichols, J.D. & Kumar, N. S. 2007: How many tigers are there in Huai Kha Khaeng Wildlife Sanctuary, Thailand? An estimate using photographic capture-recapture sampling. - Oryx 41: 447-453.

Smith, J.L.D. 1993: The role of dispersal in structuring the Chitwan tiger population. - Behaviour 124: 165-195.

Støen, O.G. & Wegge, P. 1996: Prey selection and prey removal by tiger *Panthera tigris* in lowland Nepal. - Mammalia 60: 363-373.

Sunquist, M.E. 1981: The social organization of tigers *Panthera tigris* in Royal Chitawan National Park, Nepal. - Smithsonian Contributions to Zoology, no. 336. Smithsonian Institution Press, Washington, D.C., USA, 98 pp.

Sunquist, M., Karanth, K.U. & Sunquist, F. 1999: Ecology, behaviour and resilience of the tiger and its conservation needs. - In: Seidensticker, J., Christie, S. & Jackson, P. (Eds.); Riding the tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, UK, pp. 5-18.

Sunquist, M. & Sunquist, F. 2002: Wild cats of the world. - University of Chicago Press, Chicago, Illinois, USA, 452 pp.

Tamang, K.M. 1982: The status of the tiger (*Panthera tigris*) and its impact on principal prey populations in Royal Chitwan National Park, Nepal. - PhD dissertation, Michigan State University, Michigan, USA, 123 pp.

Wang, S.W. & MacDonald, D.W. 2009: Feeding habits and niche partitioning in a predator guild composed of tigers, leopards and dholes in a temperate ecosystem in central Bhutan. - Journal of Zoology 277: 275-283.

Wegge, P., Odden, M., Pokharel, C.P. & Storaas, T. 2009: Predator-prey relationships and responses of ungulates and their predators to the establishment of protected areas: a case study of tiger, leopards and their prey in Bardia National Park, Nepal. - Biological Conservation 142: 189-202.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use