# Title: Carcass utilization by tigers: implications for calculating prey requirements

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**Short title:** Carcass utilization by tigers

**ABSTRACT**

Fewer than 3,500 tigers (*Panthera tigris*) remain in the wild. Habitat loss and fragmentation, and depletion of prey are key factors contributing to their decline, prompting investigations on prey requirements needed to sustain their dwindling populations. To estimate prey requirements from consumption rates the Non-Consumed Portion of a carcass (NCP) or degree of carcass utilization is required, as depending on prey size part of the kill might not be consumed. Because NCPs for tigers have never been systematically estimated, the aim of this study was to develop a model to calculate NCPs based on prey body mass, and to determine whether the NCPs used in current tiger literature were accurate. Additionally, we applied the model to two tiger reserves to test if our results improved prey requirement estimates calculated with current NCPs. The study took place at Laohu Valley Reserve (South Africa), where four male and five female tigers were fed fresh carcasses of six ungulate species. Each prey carcass was weighed prior to feeding to tigers and once abandoned, the remains were weighed allowing the weight consumed minus the gastrointestinal contents to be calculated. We observed a strong positive relationship between prey body mass and NCP. For large prey, prey requirement estimates obtained with the NCPs yielded by our model were very similar to those obtained with the NCPs used in current tiger literature. However, differences increased for smaller prey, and for those species that comprised a high percentage of the tiger diet. In summary, we provide a model to calculate NCPs based on prey body mass, and demonstrate the importance of using specific values of NCPs in calculating prey requirements from consumption rates. These results could be useful for other large carnivores, as well as for calculating feed portions for large predators in captive settings.

**Key words:** *Panthera tigris*, large carnivores**,** prey requirements, carcass utilization, conservation, kill rates

## INTRODUCTION

Tigers (*Panthera tigris*) are endangered throughout their range (Goodrich *et al*., 2015). With habitat loss and fragmentation (Linkie *et al*., 2006), as well as depletion of prey species as some of the drivers of population decline (Karanth & Stith, 1999; Miquelle *et al*., 1999), research on tiger feeding ecology has become a priority. A viable habitat must include sufficient prey to sustain tiger populations (Karanth & Stith, 1999; Simcharoen *et al*., 2014).

Kill rates (number of prey killed per unit of time) and consumption rates (kilograms of prey consumed per unit time) are important parameters in carnivore ecology. They are necessary for assessing the impact of tigers on prey populations (Odden & Wegge, 2009; Miller *et al.*, 2013), determining tiger carrying capacity, and calculating area requirements for viable tiger populations (Miquelle *et al*., 2010; Simcharoen *et al.*, 2014). Moreover, because tiger diets differ between regions (Miquelle *et al.*, 1996; 1999; Sunquist, Karanth & Sunquist, 1999), consumption rates enable the calculation of kill rate estimates for specific prey species in areas where the latter have not been studied (Miller *et al.*, 2013).

Kill rates can be easily converted into consumption rates and *vice versa*, provided the degree of carcass utilization or Non-Consumed Portion (NCP) is known. Tigers do not usually abandon their kills until they have consumed them completely (Schaller, 1967; Kerley *et al*., 2002). However, scavenging (Yudakov & Nikolaev, 1987; Miller *et al.*, 2013), loss or spoilage due to hot and humid conditions (Sunquist & Sunquist, 2002), human disturbances (Kerley *et al.*, 2002; Wilmers *et al.*, 2003) and the inability of the predator to consume certain parts of the kill, such as long bones and horns (Schaller, 1967; Sunquist, 1981), will influence the degree of carcass utilization, and the amount of biomass killed might not equate the amount of biomass consumed. While the magnitude of the first three factors will depend on location, the ability to consume certain body parts is related to prey body mass (Schaller, 1967; Viljoen, 1993; Stander *et al*., 1997, Chakrabarti *et al*., 2016).

Tigers, as well as other large felids do not consume the prey's gastrointestinal contents or *digesta* (Schaller, 1967; Sunquist, 1981; Labisky & Boulay, 1998; Stahler, Smith & Guernsey, 2006; Delibes *et al.*, 2011; Vucetich, Vucetich & Peterson, 2012). This complicates the estimation of NCP, as digesta dries rapidly once exposed and it is often scavenged by other animals. Because of this and other logistical difficulties in performing feeding trials in the wild, researchers frequently rely on NCPs from previous studies (Karanth & Sunquist, 2000; Miller *et al.*, 2013; Miller *et al.*, 2014). These NCPs however are sometimes based on small sample sizes, anecdotal data, and/or from other species of predator and prey (Table 1), potentially introducing significant errors in the calculation of kill rates, and consequently in the estimation of prey requirements. Despite this risk, the accuracy of NCP estimates for tigers has never been tested, but assumed as valid instead. The aims of this study are to determine whether the degree of carcass utilization used in current tiger literature is accurate, and to analyze the potential effects of using different NCPs in calculating prey requirements from consumption rates. To achieve this, we determined the degree of carcass utilization (NCP) by tigers feeding on different prey species under controlled conditions, and developed a model to estimate the NCP based on prey body mass. To test the effect of using different NCPs on calculating prey requirements, we estimated prey requirements at two tiger reserves using our NCPs, and compared them to those prey requirements calculated with the NCPs used by other authors (Sunquist, 1981; Miller *et al*., 2013).

The bulk of tiger diet for wild populations is comprised of wild boar (*Sus scrofa*) and deer such as muntjac (*Muntiacus muntjak*), chital deer (*Axis axis*), and larger species such as sambar (*Rusa* *unicolor*) (Karanth *et al.*, 2004; Sunquist, 2010; Hayward, Jędrzejewski & Jedrzejewska, 2012). Because our study was conducted in South Africa where wild boar and deer do not naturally occur, we selected indigenous surrogate species of similar body mass and phylogeny to the prey species within tiger range for the feeding trials.

## MATERIALS AND METHODS

### *Subjects and housing*

Four male and five female South China tigers (*Panthera tigris amoyensis*) ranging from two to 10 years of age and 100 to 135 kg in mass were included in the study. The study was conducted at Laohu Valley Reserve (Free State Province, South Africa), a private facility where the charity Save China's Tigers breeds and prepares South China tigers for later reintroduction into protected areas in China. The reserve consists of approximately 33,000 ha of natural habitat with tigers confined to predator-proof fenced camps ranging from 0.4 ha to 100 ha. Three 0.4 ha camps and a 1 ha camp were used for this study. Camps enclosed natural substrate, where shelter and fresh water were provided *ad libitum*. Camps were delimited with solar powered electric wire fencing that complied with National Norms and Standards for predators in South Africa (Botha, 2005). A 1 m high mesh-wire barrier spanned the bottom of the fence to prevent access by caracals (*Caracal caracal*), black backed jackals (*Canis mesomelas*), and smaller scavengers such as members of the Herpestidae family. Pied crows (*Corvus albus*) and pale chanting goshawks (*Melierax canorus*) could not be excluded from the camps, but the potential biomass taken by birds was considered negligible since tigers guard their kills aggressively (Schaller, 1967; Sunquist, 1981). Access to the reserve was restricted to staff and no visitors were allowed near or at the tiger premises.

Research was conducted under the University of Pretoria Animal Use and Care Committee ethics clearance protocol V053-12 with all its amendments.

*Data collection*

Data were collected from February 2013 through May 2014. Tigers were fed fresh entire carcasses of free-ranging ungulates. We selected warthog (*Phacochoerus africanus*) as surrogate for wild boar, springbok (*Antidorcas marsupialis*) as surrogate for small deer, and blue wildebeest (*Connochaetes taurinus),* red hartebeest (*Alcelaphus bucelaphus)* and common eland (*Taurotragus oryx)* as surrogate for larger deer. Blesbok (*Damaliscus pygargus*) was used as surrogate for sikka deer (*Cervus nippon*), as it resembles in size the deer species of southern China where studied tigers are planned to be released (Harris, 2008).

To determine the degree of carcass utilization, the body parts (e.g. skin, long bones, horns) remaining once the tiger had abandoned the carcass were categorized as *remains*, and the contents of the prey's stomach/s, small intestine, cecum and large intestine were categorized as *digesta*. Digesta therefore referred to the luminal contents of these viscera, but not to the viscera *per se*. The combined mass (kg) of *remains* and *digesta* was defined as NCP.

For herbivores, body mass is directly correlated with digesta load both across and within species (Parra, 1978; Demment, 1982; Weckerly, 2010). Although this relationship has been calculated for certain African ungulates (Demment & Van Soest, 1985), we calculated a regression equation specific to the prey species used in this study to increase accuracy of measurements, and avoid possible errors due to species specific differences. We therefore used two datasets: Dataset A, to determine the relationship between digesta weight and prey body mass, and Dataset B to assess the relationship between prey body mass and NCP.

Dataset A was comprised of 29 fresh carcasses, which included 8 springbok, 7 blesbok, 7 hartebeest, and 7 warthogs. Within two hours of being killed each whole carcass was weighed and the abdominal cavity opened to remove the gastrointestinal tract (excluding the esophagus). Digesta was manually removed from the tract, and the tract placed back in the carcass, where the combined weight was measured again. The difference in weight before and after digesta was removed corresponded to the weight of digesta.

Dataset B was comprised of 43 fresh carcasses, which included 11 springbok, 11 blesbok, 10 large antelopes, and 11 warthogs. Whole carcasses were weighed and fed to the tigers as their only source of food during the course of the study. Once a tiger was observed to have abandoned the carcass (generally within one to five days), remains were collected and weighed.

*Data analyses*

Following Demment & Van Soest (1985), we log-transformed Dataset A to normalize the data (Kolmogorov-Smirnov normality tests: $p = 0.665$ for log (digesta), $p = 0.338$ for log (live weight)) and performed a linear regression (stepwise method: Zar, 1999) to establish the relationship between prey weight and digesta weight (i.e. Equation 1). Then, we applied Equation 1 to Dataset B to estimate digesta weight in each prey carcass according to its body weight.

Dataset B was also log-transformed (Kolmogorov-Smirnov normality tests: $p = 0.474$ for log (NCP), $p = 0.616$ for log (live weight)), and a linear regression (stepwise method) was performed to establish the relationship between prey body weight and NCP, resulting in Equation 2.

*Test of the equation in two tiger reserves*

We estimated prey requirements at two tiger reserves, Chitwan National Park (Nepal) and Sikhote-Alin Biosphere Zapovednik (Russian Far East). Tiger diet differed between the two reserves offering a broad test for our NCP equation.

To estimate prey requirements, we assumed that a tiger consumed an average of 6 kg/day (Schaller, 1967; Sunquist, 1981). Based on this and diet composition (Table 3), we calculated prey requirements for the entire tiger population at both sites using the NCPs derived from Equation 2. Then, we repeated the calculations using the NCPs published by Sunquist (1981) and Miller *et al.* (2013) to estimate prey requirements in Chitwan and Sikhote Alin, respectively. Sunquist (1981) estimated an NCP of 30 % based on data of tigers feeding on wild prey, while Miller *et al.* (2013) used NCPs from other carnivore studies: 32 % NCP for prey larger than 40 kg (based on carcass utilization by wolves feeding on elk; Wilmers *et al*., 2003), and 21 % for prey smaller than 40 kg (based on captive cougars feeding on white-tail deer: Ackerman *et al*., 1986).

All statistical tests were performed with SPSS software (IBM Corp, 2011), and statistical significance set at 0.05.

**RESULTS**

Digesta, expressed as a percentage of body weight, increased with body size in Dataset A (Table 2). Likewise, the proportion of NCP in Dataset B also increased with prey size, ranging from an average of 20.9 % in the springbok (min= 18.6%, max= 25.1 %), to 29.8 % in the larger antelopes (min= 28.9 %, max= 35.1 %).

In Dataset B, tigers consumed all the edible parts of each carcass. Digesta was found at all (100 %) feeding sites. Viscera however, including the gastrointestinal tract were never present and presumed to be consumed. Legs (or parts thereof), and horns of all antelopes were also present at all feeding sites. We documented presence of maxilla (or whole skull), mandible (usually separated from the skull), vertebrae, ribcage, pelvis, scapulae, hide and/or plucked hair at most feeding sites. Complete articulated skeleton and skull were always present at feeding sites of prey weighing >100 kg but seldom documented for springbok, where only loose vertebrae and ribs were usually found along the horns and leg bones.

*Estimation of prey digesta*

The regression analysis of whole body weight (kg) and fresh digesta (kg) in Dataset A showed a strong positive relationship ($r^2 = 0.94$, n = 29) (Fig. 1), resulting in Equation 1:

$$\log Y_1 = 1.154*\log X_1 - 1.102$$

where $Y_1$ is the weight of the digesta in kg, and $X_1$ represents prey's body weight (kg) (SE constant term = 0.098, $p < 0.01$; SE $\log X_2$ coefficient = 0.054, $p < 0.01$). This relationship held true across prey species and for ruminants and non-ruminants. Equation 1 was used to estimate digesta load for the feeding trials in Dataset B.

*Estimation of NCP of a carcass*

Regression analysis in Dataset B showed a strong positive relationship (corrected $r^2 = 0.92$, n= 43) between prey body weight and NCP (Fig. 2), with tigers consuming progressively less of a carcass as prey body mass increased. Equation 2 yielded:

$$\log Y_2 = 1.228*\log X_2 - 1.030$$

where $Y_2$ is the NCP in kg and $X_2$ the live weight of prey (kg) (SE constant term = 0.047, $p < 0.01$; SE $\log X_2 = 0.026$, $p < 0.01$). As with Equation 1, this relationship was maintained across species, both for ruminant and non-ruminants.

*Estimated prey requirements in Chitwan N.P. and Sikhote-Alin Biosphere Zapovednik*

Table 3 shows the NCPs calculated from Equation 2, and those used by Sunquist (1981) and Miller *et al*. (2013). Differences were subtle for species over 100 kg, but increased as prey size decreased, exceeding 10% in the case of hog deer, muntjac and roe deer. When estimating annual prey requirements for the entire tiger population at both reserves, the largest differences when using our NCPs and those used by Sunquist (1981) and Miller *et al*. (2013) were observed for prey species between 20 and 50 kg (e.g. 54 hog deer in Chitwan), while differences were negligible for prey species over 100 kg (e.g. less than three animals for sambar and red deer).

## DISCUSSION

As reported in tiger (Schaller, 1965, 1967; Sankhala, 1977; Sunquist, 1981) and other carnivore studies (e.g. cougars, Hornocker, 1970; bobcats, Labisky & Boulay, 1998; ocelots, Delibes *et al.*, 2011; wolves, Stahler *et al.*, 2006, Vucetich *et al.*, 2012), prey digesta (but not the viscera) was found at every feeding site, suggesting that tigers manage to separate the gastrointestinal contents and consume the tissues. In addition to the digesta, bones, horns (when applicable), plucked hair, and hide scraps and hooves in larger antelopes were the only remains after the tiger had abandoned the carcass; all the edible parts were completely consumed. Studies in free-ranging tigers also report that unless disturbed, tigers will usually eat all available meat from a carcass (Schaller, 1967; Kerley *et al.*, 2002), suggesting that tiger feeding behavior was not altered by the captive environment in our study.

Warthog carcasses were utilized by tigers in the same proportion as that for antelopes. The volume of the large intestine in non-ruminants is similar to that of the reticulo-rumen in ruminants (Parra, 1978), explaining the similar relationship between prey body weight and digesta for ruminants (antelopes) and non-ruminants (warthogs) in this and other studies (Van Soest, 1994). Given the phylogenetic proximity of warthogs and wild boars we assume similar degree of carcass utilization of the latter by free-ranging tigers. To our knowledge, carcass utilization has not been estimated for wild boar or other suids. Since wild boar generally represent a large proportion of tiger diet (e.g. Hayward *et al.*, 2012), these results are important for tiger conservation.

Our estimated NCPs agreed with published NCP estimates for prey >100 kg (Sunquist, 1981; Miller *et al*., 2013). This was particularly surprising for the NCPs used by Miller *et al*. (2013), as they used an NCP that had been estimated for wild wolves feeding on elk (Wilmers *et al*., 2003) when prey weighed over 40 kg. This “wolf NCP” and our empirically calculated “tiger NCPs” varied by less than 2 % for large prey, suggesting that NCPs may be consistent across many large carnivores, despite differences in social behavior (e.g. solitary feeding in tigers versus group feeding in wolves), and/or morphology (e.g. differences in skull and jaw size between the two species). However, our data revealed that small differences in NCPs can yield large differences in prey requirement estimates when the prey species under consideration represents a large proportion of tiger diet. This is clearly illustrated with wild boar. Wild boar represents 9% of tiger diet in Chitwan. The difference in yearly prey requirement estimates when using 30% NCP (Sunquist, 1981) and when using 24.4 % NCP (i.e. estimated from Equation 1) was six wild boars per year. At Sikhote-Alin however, where wild boar comprises 27.9% of tiger diet, yearly prey estimates when using 32% NCP (Miller *et al*., 2013) and when using 25% NCP (i.e.

obtained from Equation 2) differed in almost 28 wild boars per year. Wild boar weight were similar at both reserves (67.5 kg at Chitwan and 75 kg at Sikhote-Alin), so it was the NCP used by Sunquist (1981) and Miller *et al.* (2013) and the ones we obtained with our equation. Yet, prey requirement estimates varied from six to 28 boars per year. This example highlights the importance of using NCPs that are calculated for a specific prey size, as a small difference in NCP can yield a large error in estimated prey requirements.

For medium-sized prey (25-75 kg) our NCPs differed from those used by Sunquist (1981) and Miller *et al*. (2013) at both study sites, being these differences higher as prey body size decreased. Consequently, differences between prey requirement estimates calculated with our NCPs and with the NCPs used by other authors were larger for smaller prey. For this reason, in reserves where tigers prey predominately on small species (20-50 kg) (e.g. Panna Tiger Reserve, India: Chundawat, Gogate, & Johnsingh, 1999), or in areas where heavy poaching of larger species would force tigers to feed on smaller prey (Sunquist *et al*., 1999) our equation will provide increased accuracy compared to current NCP values. Our findings may also have applications in small reserves, where more accurate estimates of prey abundance are essential to estimate carrying capacity for tigers (Miquelle *et al.*, 2010; Simcharoen *et al.*, 2014).

The applications of our results have some limitations. Firstly, our equation provides reliable NCP estimates for prey with a body mass ranging from 24 to 293 kg. Although we used species of similar size to those preferred by tigers (i.e. medium to large-sized prey: Seidensticker & McDougal, 1993; Hayward *et al.*, 2012), tigers take prey as large as adult gaur (*Bos gaurus*, 825kg, Smith *et al*., 2008) (Karanth & Sunquist, 1995), and as small as hares (e.g. *Lepus capensis*, 4.5 kg, Wilson, 1993) (Johnsingh, 1983; Fàbregas, Fosgate & Koheler, 2015). The validity of our equation should be tested when used on species outside this weight range.

Secondly, scavenging (Yudakov & Nikolaev, 1987; Miller *et al.*, 2013; Moleón *et al.*, 2015), hot and humid conditions that contribute to spoilage (Sunquist & Sunquist, 2002), and disturbances by other tigers, other carnivores, or humans (Kerley *et al.*, 2002) may alter consumption. Our NCPs were estimated under controlled conditions (i.e. free of scavengers, human disturbance and competitors), in a dry climate, and where high temperatures are restricted to around midday. The above factors must be considered when estimating the degree of carcass utilization in the field, especially in tropical humid areas.

In summary, our NCP estimates increase accuracy over other studies in calculating tiger prey requirements where species under 100 kg are the dominant prey, particularly for small reserves where accurate prey requirement estimates are essential for reserve management. Our findings also apply to wild boar, for which the degree of carcass utilization has not been previously estimated. Additionally, in the absence of empirical values for other carnivore species, our equation may have wider application in the conservation and management of other large carnivores, given that NCPs were very similar for at least some predator species. Lastly, these findings may also be applicable to zoological parks, wildlife rehabilitation facilities or sanctuaries in establishing feeding regimes for large predators to prevent obesity, a common problem in captive carnivores (Clauss *et al*., 2010).

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**Table 1**. A review of published literature reporting estimates of consumed portion to calculate kill rates (animals killed/unit of time) from consumption rates (kg of biomass consumed/unit of time) or *vice versa* in large carnivores.

| | **Follows/ Based on** | **Regime** | **Species estimated for** | **Species used for** | **Sample size** | **Consumed portion estimates** | **Prey species*** |
|---|---|---|---|---|---|---|---|
| Schaller 1965 | Own | Wild | Tiger | Tiger | ** | 60%-70% | ** |
| Schaller 1967 | Own | Wild | Tiger | Tiger | 1 | 73% | Chital |
| Sunquist 1981 | Own | Wild | Tiger | Tiger | ** | 70% | ** |
| Miller *et al.* 2013 | Ackerman *et al.* 1986 | Captive | Cougar | Tiger | ** | 79% | White- tailed deer |
| | Wilmers *et al.* 2003 | Wild | Wolf | Tiger | 14 | 68% | Elk |
| Miller *et al.* 2014 | Ackerman *et al.* 1986 | Captive | Cougar | Tiger | ** | 79% | White-tailed deer |
| | Wilmers *et al.* 2003 | Wild | Wolf | Tiger | 14 | 68% | Elk |
| Rapson & Bernard 2007 | Viljoen 1993 | Wild | Lion | Lion | >100 | <50kg = 80%<br>50-150kg= 75%<br>151-250kg=70%<br>250-500kg=65% | Several |
| Vucetich *et al.* 2012 | Own | Wild | Wolf | Wolf | 14 | 70% | Moose |
| Viljoen 1993 | Ledger 1968, von La Chevallerie 1970 | Wild | Meat industry | Lion | >100 | <50kg = 80%<br>50-150kg= 75%<br>151-250kg=70%<br>250-500kg=65% | Several |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Stander 1992 | Mills 1990 | Wild | Spotted hyena | Lion | ** | <5kg = 100%<br>5-80kg = 90%<br>> 80kg = 67 % | ** |
| Hornocker 1970 | Own | Captive | Cougar | Cougar | 3 | 70% | Mule deer |
| Ackerman *et al* 1986 | Ackerman 1982 | Captive | Cougar | Cougar | ** | 79% | White-tailed deer |
| Odden & Wegge 2009 | Stander *et al.* 1997 | Wild | Leopard | Leopard | ** | <5kg = 100%,<br>5-25kg = 95%,<br>> 25kg = 70 % | ** |
| Stander *et al*. 1997 | Own | Wild | Leopard | Leopard | ** | <5kg = 100%,<br>5-25kg = 95%,<br>> 25kg = 70 % | ** |
| Wilmers *et al.* 2003 | Own | Wild | Wolf | Wolf | 14 | 68% | Elk |
| Metz *et al.* 2012 | Wilmers *et al.* 2003 | Wild | Wolf | Wolf | 14 | 68% | Elk |
| Fuller *et al*. 1995 | Own | Wild | Wild dog | Wild dogs | ** | 60% | Several |

*Cougar (*Puma concolor*), wolf (*Canis lupus*), lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), wild dog (*Lycaon pictus*), chital (*Axis axis*), white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*).

**Not reported in the study.

**Table 2.** Carcass utilization of prey species fed to captive tigers. Data are expressed as mean ± standard error. NCP stands for Non-Consumable Portion of a prey carcass.

| **Prey species** | **n** | **Body mass (kg)** | **Remains (kg)** | **Digesta** (kg)** | **Digesta** (%)** | **NCP (remains + digesta) (kg)** | **NCP (remains + digesta) (%)** |
|---|---|---|---|---|---|---|---|
| Springbok | 11 | 31.2±1.3 | 2.7±0.3 | 3.9±0.2 | 12.3±0.2 | 6.6±0.5 | 20.9±0.8 |
| Warthog | 11 | 50.7±2.3 | 3.6±0.4 | 7.4±0.4 | 14.5±0.2 | 10.9±0.7 | 21.4±0.6 |
| Blesbok | 11 | 66.2±4.1 | 7.1±0.7 | 10.2±0.7 | 15.2±0.2 | 17.2±1.4 | 25.8±0.9 |
| Large antelope* | 10 | 165.2±16.5 | 21.3±3.5 | 28.0±3.0 | 16.9±0.1 | 49.2±6.4 | 29.3±0.8 |

* Blue wildebeest (*Connochaetes taurinus*), red hartebeest (*Alcelaphus bucelaphus*), common eland (*Taurotragus oryx*).

** Digesta values obtained using Equation 1.

**Table 3.** Estimated annual prey requirements for the entire tiger population at Chitwan N.P. (Nepal) and Sikhote-Alin Biosphere Zapovednik (Russian Far East). Prey requirements were calculated using the NCP (i.e. Non-Consumable Portion of a prey carcass) according to Sunquist (1981), Miller *et al.* (2013), and this study (figures represent mean values ± standard error). The entire population at both reserves was estimated to be 23 tigers, as reported in Smith (1978) for Chitwan N.P., and in Smirnov and Miquelle (1999) for Sikhote-Alin. We assumed that a tiger consumes 6 kg/day (Schaller, 1967; Sunquist 1981).

| | Prey species [a] | Diet composition (%)[b] | Prey body mass (kg) [c] | NCP (%) | | Estimated prey requirements for the entire tiger population (prey animal/year) | |
|---|---|---|---|---|---|---|---|
| | | | | Sunquist 1981 | This study | Sunquist 1981 | This study |
| Chitwan National Park | Sambar | 32 | 144.6 | 30 | 29.0 ± 7.6 | 159.1 | 156.8 ± 17 |
| | Wild boar | 9 | 67.5 | 30 | 24.4 ± 5.8 | 95.0 | 88.8 ± 6.9 |
| | Chital deer | 36 | 45.8 | 30 | 22.3 ± 5.1 | 566.2 | 510.1 ± 33.6 |
| | Hog deer | 16 | 27 | 30 | 19.8 ± 4.2 | 426.4 | 372.2 ± 19.5 |
| | Muntjac | 5 | 15 | 30 | 17.3 ± 3.3* | 239.9 | 203.0 ± 8.1* |
| | Others (small) | 3 | 6 | 30 | 14.4 ± 2.3* | 359.8 | 294.2 ± 7.9* |
| | | | | Miller *et al* 2013 | This study | Miller *et al* 2013 | This study |
| Sikhote-Alin Zapovednik | Red deer | 24.3 | 187.5 | 32 | 30.3 ± 8.4 | 96.0 | 93.7 ± 11.5 |
| | Wild boar | 27.9 | 75 | 32 | 25.0 ± 6.1 | 275.6 | 249.8 ± 20.5 |
| | Sikka deer | 13.5 | 62.3 | 32 | 23.9 ± 5.7 | 160.6 | 143.5 ± 10.8 |
| | Roe deer | 23.4 | 44.3 | 32 | 22.1 ± 5.0 | 391.7 | 341.9 ± 22.0 |
| | Others (large) | 2.7 | 140.8 | 32 | 28.8 ± 7.6 | 14.2 | 13.6 ± 1.5 |
| | Others (small) | 8.1 | 20 | 21 | 18.4 ± 3.7 | 258.2 | 250 ± 11.4 |

[*] Prey weight considerably out of the range used to calculate the NCP equation in this study (i.e. 24-293 kg).

[a] Sambar (*Rusa unicolor*), wild boar (*Sus scrofa*), chital (*Axis axis*), hog deer (*Axis porcinus*), muntjac (*Muntiacus muntjak*), red deer (*Cervus elaphus*), sikka deer (*Cervus nippon*), roe deer (*Capreolus capreolus*).

[b] Based on Seidensticker & McDougal (1993) for Chitwan, and on Miller *et al.* (2013) for Sikhote-Alin Biosphere Zapovednik.

[c] Estimated prey body mass as reported in Sunquist (1981) for Chitwan N.P. and Heptner, Nasimovich, & Bannikov (1988) for Sikhote-Alin Biosphere Zapovednik. We used three-quarters of the mean adult female body mass of prey species to account for calves and sub-adults eaten (Hayward *et al.*, 2012).

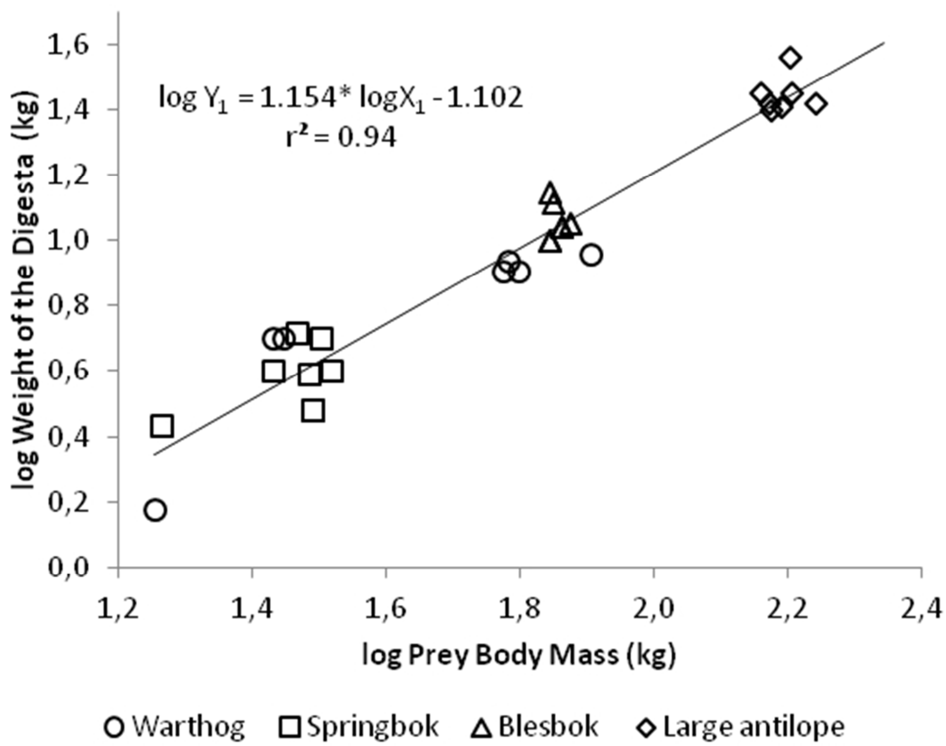


**Figure 1.** Linear regression model between log of prey body mass (kg) and log of prey gastrointestinal contents or digesta (kg) in Dataset A (n=29).
154x122mm (96 x 96 DPI)

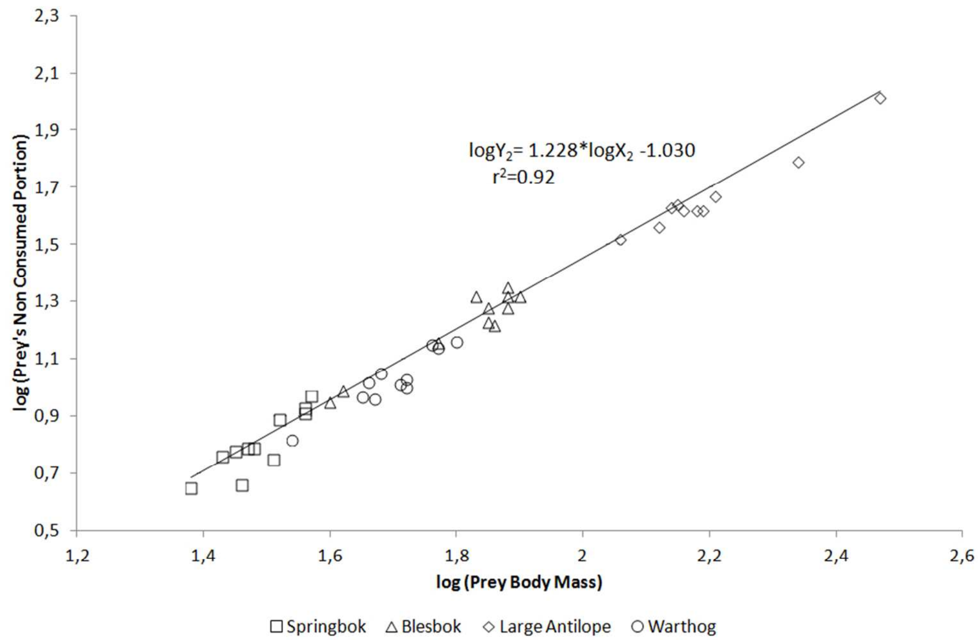


**Figure 2**. Linear regression model between log of prey body mass (kg) and log of Non-Consumed Portion (NCP) of prey carcasses (kg) in Dataset B (n=43).
259x169mm (96 x 96 DPI)

Image to be used in the on-line version of the table of contents
412x350mm (180 x 180 DPI)