# Effect of prey mass and selection on predator carrying capacity estimates

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## Abstract

The ability to determine the prey-specific biomass intake of large predators is fundamental to their conservation. In the absence of actual prey data, researchers generally use a 'unit mass' method (estimated as 3/4 adult female mass) to calculate the biomass intake of predators. However, differences in prey preference and range across geographic regions are likely to have an influence on biomass calculations. Here we investigate the influence of estimated prey mass on leopard biomass calculations, and subsequently carrying capacity estimates, in an understudied mountain population. Potential leopard feeding sites were identified using global positioning system (GPS) location clusters obtained from GPS collars. We investigated 200 potential leopard feeding sites, of which 96 where actual feeding sites. Jaw bones, horns, hooves, and other indicative bones were used to determine gender and age of prey items, which were subsequently used to calculate mass of each prey item based on previously published values. There were significant differences in the biomass values calculated using the traditional unit mass method and the calculated prey masses obtained from leopard feeding sites. However, there were no considerable differences in the carrying capacity estimates using the preferred prey species model and leopard density estimates calculated using a non-biased spatial approach, which suggests that estimating carnivore carrying capacity based on 3/4 adult female masses is a reliable method, also for the mountain population in this study.

**Key Words** biomass calculation, carnivore ecology, carrying capacity, diet, GPS, *Panthera pardus*

## Introduction

Large carnivores play an important role in regulating natural terrestrial ecosystems (Estes et al 2011). However, on small enclosed reserves, large carnivores can reduce prey populations (Bisset et al. 2012). Therefore, knowledge of carnivore numbers and carrying capacity are important for management of enclosed reserves (Fuller & Sievert 2001, Hayward et al. 2007). Predator-prey relationships serve as a foundation to determine the prey-specific biomass intake of predators which can then be used to estimate the carrying capacity of large carnivores (Hayward et al. 2007). Carrying capacities of several large carnivores (e.g., lions *Panthera leo*, leopards *Panthera pardus,* cheetahs *Acinonyx jubatus,* spotted hyenas *Crocuta crocuta,* and African wild dogs *Lycaon pictus*) have been predicted and tested for small reserves by regressing carnivore density to the abundance of their preferred prey (Hayward et al. 2007).

Although prey preference and abundance are key factors in calculating the carrying capacity of large predators, availability and range of prey species are also important factors to consider, especially across different geographic study areas. For example, leopards preferentially prey on species within the range of 10–40 kg (Hayward et al. 2006). However, in certain mountainous regions, such as the Cederberg Mountains of South Africa, leopards mostly have access to smaller species, like klipspringers (*Oreotragus oreotragus,* ± 12.5 kg) and rock hyrax (*Procavia capensis*, ± 3.2 kg) (Martins et al. 2011). These differences in the average mass of available prey likely affect biomass calculations, and subsequently carrying capacity estimates of large predators.

In this study, we collected female leopard prey remains to estimate actual age and mass of the prey species consumed. We then used these masses to calculate biomass consumed by these female leopards and thus estimate leopard carrying capacity in a mountain population. To assess the implications of using various metrics of biomass consumption, we also calculated carrying capacity based on the widely used technique of ignoring the gender and age of each prey item and simply calculating the biomass as 75% of the mass of adult females of preferred prey species, i.e. unit mass.

## Methods

### *Study Area*

The study was conducted on Welgevonden Private Game Reserve in the Waterberg Biosphere in South Africa. The reserve, which caters mainly for wildlife safaris, currently covers an area of approximately 37,500 ha at an elevation of 1200-1500 masl. Eighty percent of the reserve is mountainous with numerous deep valleys (Kilian 2003).

The reserve hosts more than 50 mammal species, including lions, leopards, cheetahs, and numerous smaller carnivores like brown hyenas (*Hyaena brunnea*), and black-backed jackals (*Canis mesomelas*). Herbivores range in size from giraffes (*Giraffa camelopardalis*), plains zebras (*Equus quagga*), and blue wildebeests (*Connochaetes taurinus*), to smaller antelope such as impala (*Aepyceros melampus*), mountain reedbucks *(Redunca fulvorufula*), and steenbok (*Raphicerus campestris*).

Welgevonden is encircled by a boundary fence, but fences rarely act as barriers to leopards (Hayward et al. 2007b) and they are able to move freely between neighboring properties. The reserve is bordered by Marekele National Park on the southwestern side, private game farms on the south and east, and livestock farms on the remainder where leopards are seen as potential damage-causing animals.

### *Prey and leopard abundance*

We estimated prey abundance with annual aerial counts conducted in the dry season when wildlife is most easily detected. Welgevonden was divided into grids that were systematically inspected to improve accurate detection of prey species. Each count was conducted over a 4-day period. We estimated prey abundance by using the most recent aerial count (2010). Aerial census techniques are biased against smaller, cryptic animals, so correction factors previously applied in Kruger National Park (Owen-Smith & Mills 2008) were used to adjust counts for these species.

We followed camera trapping protocols for closed population mark recapture studies on large carnivores to estimate leopard density (Karanth & Nichols 2002). Welgevonden was divided into 57 (2.5km x 2.5km) grid cells. However, due to a shortage of camera traps we grouped 12-15 grid cells to create four survey blocks. Twelve to fifteen camera trap (Moultrie I40 digital infrared; Moultrie Feeders, Inc, Alabaster, AL) pairs operated in each survey block (12-15 grid cells) for 18-22 days, where after they were moved to the next survey block until the whole reserve were surveyed. Cameras were positioned at opposite sides of roads, chosen in such a way as to maximize leopard encounters. Due to a slow camera trap trigger speed, we baited (rotten eggs and fermented fish) each station every 5 days (Gerber et al. 2012). Our complete camera trapping period (90 days; May-July 2009) and systematic trap placement assured that we did not violate assumptions of demographic closure and that no individuals had a non-zero capture probability (Karanth & Nichols 2002; Wang & Macdonald 2009).

For comparative reasons, we used both a likelihood based spatially explicit capture recapture (SECR; Efford et al. 2009) and a non-spatial capture recapture model (software CAPTURE; Rexstadt & Burnham 1991) to estimate leopard density. For the non-spatial model we pooled data across the four survey blocks (12-15 grid cell areas) to construct a capture matrix. For the SECR models we used the complete trap layout file and indicated when camera traps were active. We fitted a heterogeneous (Mh; heterogeneity in capture probabilities) model to both the SECR (2-class finite mixture for heterogeneity in g0) and non-spatial models (with Jack-knife estimator in CAPTURE), because such a model is generally thought appropriate for large solitary carnivores (Karanth et al. 2004, Wang & Macdonald 2009). Leopard density based on abundance estimates from CAPTURE were calculated by using ½ mean-maximum-distance-moved (MMDM), where we buffered each camera station with ½ MMDM for all individuals captured more than once to estimate an effective trapping area (Karanth & Nichols 1998). The R package 'secr' (Efford 2012) was used to implement the likelihood based SECR models. SECR models do not make any assumptions with regard to the effective survey area, can incorporate movement of camera traps and generally produce less biased density estimates (Noss et al. 2012). For the SECR model we assumed a half-normal detection function and a Poisson distribution of home range centers (Efford 2004).

### *Leopard capture and collaring*

We captured leopards from May to August 2010 using soft-hold foot snares (Frank et al. 2003). Leopards were immobilized with teletamine-zolazepam (Zoletil ® 100, Virbac RSA (Pty) Ltd., Centurion, South Africa; dosage 4-5mg/kg). We weighed, measured, and examined leopards for general health, and fitted three females and one male with GPS/GSM cellular collars (Followit Tellus, Lindesberg, Sweden). The male leopard damaged and dropped his collar shortly after capture; thus, data in this paper concern only the three females. Immobilized leopards recovered in a wooden crate and were released near the capture site. We conducted the study under the University of Pretoria Animal Use and Care Committee ethics clearance protocol AO 22-06 with all its amendments and a Limpopo Province standing permit (no. S13631) for scientific institutional research. We released all collars from the leopards on completion of the study using a remote controlled drop-off function.

### *Locating leopard feeding sites*

We programmed collars to record a GPS location every two hours and downloaded GPS locations via the cellular network on a daily basis. Potential predation GPS clusters were identified and mapped in ArcGIS v.9.2 (ESRI, Redlands, CA, USA) to locate possible leopard feeding sites (Valeix et al. 2011, Martins et al. 2011, Tambling et al. 2010). A GPS location from each potential predation site was used to navigate to clusters on foot and searched for prey remains for a maximum of 30 minutes. We excluded three occurrences of scavenging (all blue wildebeest), as indicated by the lack of typical signs of a leopard feeding/kill site (e.g., plucked hair, blood, drag marks, fighting circle), and two unidentified prey species from the analysis. Prey remains were photographed *in situ* and collected for later identification. We identified prey by either microscopic comparison of cuticular hair scale patterns and cross sections to reference keys (Dreyer 1966, Keogh 1979, 1983, Buys & Keogh 1984), or by macroscopic prey remains like horns and skin.

### *Estimation of age and mass of prey species*

We used two methods to estimate the biomass of prey consumed by leopards. First, we applied the widely used convention of a generalized “unit mass”, defined as ¾ of the average adult female body mass for each species (referred to as the “unit mass method” herein; e.g., Van Orsdol et al. 1985, Radloff & Du Toit 2004, Hayward & Kerley 2005, and Hayward 2006). This method was proposed to adjust biomass calculations assuming that some calves and sub-adults are also preyed upon (Schaller 1972). It is a popular technique because difficulty locating kills, species characteristics (e.g., a lack of sexual dimorphism), and the condition of prey remains make estimating the biomass consumed by carnivores difficult.

Second, we attempted to directly estimate the biomass by determining the gender and age of each prey item. We relied on hard tissue (e.g., jaw bones, horns, hooves, and other indicative bones) to determine gender and age of prey items captured by leopards. Teeth wear, replacement, and horn growth served as the most reliable indicators of age. Mean time of birth was recorded for group-birthing animals (e.g., impala, plains zebra) on the reserve and was used to assist in determining the age of juveniles. We used the mean mass of the species when suitable aging samples were absent at feeding sites. There were no abundance estimates available for smaller species i.e., red rock rabbits (*Pronolagis radensis*), banded mongooses (*Mungos mungo*), African civets (*Civettictis civetta*), and several bird species. We therefore excluded them from the carrying capacity estimates but their small size suggests they would not have increased the estimates using the actual dietary data.

The following studies were used to estimate age and mass of prey species: Roettcher & Hofmann 1970, Child 1964 (impala); Simpson 1966, Wilson 1965 (kudu *Tragelaphus strepsiceros*); Smuts 1972, 1974 (zebra); Wilson & Child 1965 ( klipspringer *Oreotragus oreotragus*); Stoltz 1977 (baboon *Papio ursinus*); Seydack 1983 (bushpig *Potamochoerus larvatus*); Norton & Fairall 1991 (mountain reedbuck); Wilson, Schmidt & Hanks 1984 (duiker *Sylvicapra grimmia*); and Skinner & Chimimba 2005(common reedbuck *Redunca arundinum*).

### *Statistical analysis*

We estimated the carrying capacity of leopards using the equation

$K = 10^{(-2.248=0.405x)}$ (Hayward et al. 2007)

where $x$ is $\log_{10}$ biomass of the prey. First, we estimated biomass as ¾ of the adult female mass of the three most preferred prey species of leopards: impala, bushbuck, and duiker (Hayward et al. 2007, Table II). Second, we calculated biomass as the mean mass of actual prey consumed by leopards on Welgevonden (Table II). We compared the resulting estimates of carrying capacity against the population estimate obtained from mark-recapture methods (L.H. Swanepoel, unpublished data).

We used chi-square tests to evaluate overall differences between prey biomass calculated directly and estimated by the unit mass method. We also used Strauss' linear index of selection ($L_i$ = *unit mass*$_i$ – *direct estimation*$_i$; Strauss 1979) to determine if the unit mass method over- or underestimated our direct calculations of the consumed biomass of each prey species. Strauss' linear index of selection gives values from -1, representing a large underestimation, to 1, representing a large overestimation of prey biomass with the unit mass method.

## Results

Over a period of five months, we visited 200 potential feeding sites of three female leopards, 96 of which were determined to be actual leopard feeding sites. Leopards preyed

**Table I.** Prey item remains located at leopard feeding sites. The determined biomass was calculated with consideration of gender and age of the prey actually consumed. The unit mass method estimates body mass of each species as ¾ of adult female body mass.

| | | | Biomass | |
|---|---|---|---|---|
| Species | Number | % of Kills | Determined | Unit Mass |
| Impala | 18 | 20.22 | 20.42 | 15.77 |
| Kudu | 4 | 4.5 | 25 | 13.8 |
| Mountain reedbuck | 7 | 7.9 | 7.2 | 3.6 |
| Common reedbuck | 1 | 1.1 | 2.6 | 1.5 |
| Klipspringer | 11 | 12.4 | 5.6 | 3.1 |
| Zebra | 8 | 9 | 12.2 | 51.3 |
| Baboon | 18 | 20.22 | 18.7 | 6 |
| Bushpig | 2 | 2.25 | 4.8 | 2.4 |

upon a total of 14 species with the most commonly taken prey items being baboons (20.2% of all identified prey), impala (20.2%), and klipspringers (12.4%) (Table I). Duiker (n = 1) and bushbuck (n = 0), which are often considered to be preferred prey of leopards, were rarely or never consumed in this study. Smaller prey species like banded mongooses, red rock rabbits, African civets, and several bird species accounted for 3.5% of the leopard's biomass intake. Distinct age preferences were seen in some prey, like zebras, where only foals were preyed upon.

**Table II.** Minimum, maximum, and average masses of prey taken by leopards on Welgevonden represent the published values for the ages and genders of individuals found at feeding sites. The ¾ adult female masses are used in calculations of carrying capacity assuming we had no knowledge of genders and ages of taken prey. The percentage of kills estimated refers to the % of kills where age-indicative prey remains were located. Ratio refers to the ratio of juvenile to sub-adult to adult for prey species where age-indicative prey remains were located.

| Species | Minimum mass | Maximum mass | Average mass | % of kills estimated (n) | Ratio | Unit mass |
|---|---|---|---|---|---|---|
| Impala | 10 | 45 | 25.71 | 50 (9) | 4:2:3 | 31.5 |
| Kudu | 99 | 190 | 143 | 100 (4) | 0:2:2 | 123.75 |
| Mountain reedbuck | 8 | 31 | 23.5 | 43 (3) | 1:0:2 | 18.375 |
| Common reedbuck | 60 | 60 | 60 | 100 (1) | 0:0:1 | 52.5 |
| Klipspringer | 11 | 12 | 11.5 | 55 (6) | 0:0:6 | 10.125 |
| Zebra | 35 | 35 | 35 | 100 (8) | 8:0:0 | 230.625 |
| Baboon | 16 | 35.5 | 23.79 | 50 (9) | 0:1:8 | 12 |
| Bushpig | 55 | 55 | 55 | 100 (2) | 0:0:2 | 42.75 |

Chi-square analysis revealed a highly significant difference in estimated prey biomass killed between the two methods ($\chi_8^2 = 37.6$, $P < 0.0001$). The biomass of killed zebras was overestimated by the unit mass method (linear selection index: 0.391), which is caused by the exclusive predation on zebra foals by leopards on Welgevonden (Table II). Baboons (-0.127) and kudu (0.112) were the two most underestimated prey species.

We photographed 16 individual leopards which equated to a density of 4.5± 1.48 leopards /100km² (CL = 3.0–6.2) using CAPTURE which yielded an estimate of 17 leopards for Welgevonden; SECR yielded an estimate of 13 leopards for Welgevonden (density = 3.26 ± 1.42 leopards per 100km$^2$, CL = 1.44-7.36).

**Table III.** Abundance and biomass data (based on actual kills and ¾ adult female body mass) from Welgevonden. While all actual prey items were used in our refined calculations of the carrying capacity, only those significantly preferred prey species with asterisks (*) were used in estimations of carrying capacity using the traditional method.

| Species | Abundance estimate | Owen-Smith & Mills (2008) correction factors | Biomass based on body mass of actual prey individuals (kg km$^{-2}$) | Biomass based on ¾ adult female body mass (kg km$^{-2}$) |
|---|---:|---:|---:|---:|
| Baboon | 828 | 1.2 | 52.5 | 24.8 |
| Bushpig | 129 | 3 | 0 | 15.5 |
| Common duiker | 3 | 1 | 0 | 0.1 * |
| Impala | 1105 | 1.7 | 75.8 | 60.2 * |
| Klipspringer | 16 | 1 | 0.5 | 0.4 |
| Kudu | 275 | 1.8 | 105 | 99.1 |
| Reedbuck, common | 159 | 3 | 25.4 | 16.2 |
| Reedbuck, mountain | 45 | 3 | 2.8 | 2.7 |
| Zebra, plains | 728 | 1.2 | 68 | 339.9 |

Using the preferred prey species model (Hayward et al. 2007) of leopard carrying capacity and calculating biomass as ¾ adult female body mass yielded an estimate of 11 leopards (3.1 per 100 km$^2$; Table III), which is six below the CAPTURE estimate of 17 and two below the SECR estimate of 13. Calculating carrying capacity based on the calculated biomass of the actual prey consumed (i.e., accounting for all species consumed as well as the age and gender of each individual) yielded an estimate of carrying capacity of 22.

## Discussion

Our leopard density estimates concur with various other studies where likelihood based SECR models estimated lower densities than boundary strip methods (e.g. ½ MMDM methods; Obbard et al. 2010, Noss et al. 2012). Boundary strip methods using ½ MMDM seem to overestimate density because they underestimate the effective trap area which subsequently results in an overestimation of density (Soisolo & Cavalcanti 2006, Obbard et al. 2010). The use of SECR models have subsequently been advocated (Obbard et al. 2010, Noss et al. 2012) since they do not rely on geographic closure (Effort 2004). They can also account for relevant heterogeneity in capture probabilities and home ranges (Obbard et al. 2012) and include additional sources of uncertainty in the variance around estimated densities compared to boundary strip methods (Obbard et al. 2010). The more reliable leopard densities derived from the SECR models were similar to estimates by Gusset & Burgener (2005; 3.2/100km$^2$) for leopards in the Waterberg, however, it was considerably higher than the 1.9/100km$^2$ estimated by Grimbeek (1992). Such a difference in densities from historical studies (e.g. Grimbeek 1992) can be due to increases in prey availability associated with growth in game farms and game reserves in the Waterberg (De Klerk 2003). However, we acknowledge that such differences can also arise due to different methodologies used by the different studies (e.g. density estimates derived from track counts, capture-recapture and from radio-tracking data).

Taking into consideration only the species for which population estimates were available, female leopards on Welgevonden consumed prey species ranging in size from 8-190 kg (Table II). There were obvious differences in the estimated mass of several prey species when using the unit mass method and direct estimation. For example, since the leopards in this study mostly preyed upon adult baboons rather than sub-adults (Jooste et al. in press), we estimated an average mass of nearly 24 kg, compared to 12 kg as specified by the unit mass method. The leopards in this study preyed commonly on baboons (Table I), and these estimated mass differences (which lead to underestimates of biomass intake in the unit mass method) affected estimated carrying capacity estimates. The same holds for kudu where we estimated an average of 143 kg compared to the previously used 123.75 kg.

We found the standard method of using ¾ of the adult female body mass to estimate the biomass eaten by large carnivores underestimated the leopard carrying capacity at Welgevonden when using the CAPTURE estimate (11 vs. 17); however, it was within closer range to the more reliable SECR estimate (11 vs. 13). There are two possible reasons for this slight underestimation. First, the average masses of almost all prey species taken by leopards in this study were underestimated by the unit mass method except for plains zebra, which was overestimated. The most underestimated mass were those of kudu, baboon, and mountain reedbuck, all because mostly adults were taken. Conversely, all plains zebras preyed upon were foals, which resulted in an overestimation of biomass from the unit mass method. Predation on zebras mainly occurred after the onset of the first summer rains, which may have forced plains zebras into the mountains where juveniles were especially susceptible to predation. Given intraspecific differences in the mass of prey species, we recognize that calculations of prey biomass based on studies done in other areas may lead to biases in our Strauss' index values. Second, basing calculations of density on the biomass of species preferentially taken by leopards elsewhere (bushbuck, common duiker, and impala) as suggested by Hayward et al. (2007) seems to create a bias in the estimate because of differences in prey taken. Prey abundance estimates from Welgevonden suggest that common duiker and bushbuck are present in negligible densities; thus leopards can't prey on them. Therefore, such estimates underestimate the biomass available to support leopards and thus the estimated carrying capacity. However, when using the SECR leopard density estimate, the preferred prey species model proved reliable. An alternative explanation for the underestimation by the model is that leopards may be above the reserve's carrying capacity, especially if leopards are hunting livestock on adjacent farmland and using Welgevonden as a refuge, allowing a higher population to be sustained with reduced food availability on site. However, we didn't locate any livestock remains at leopard feeding sites in this study. It is also important to note that using GPS clusters to locate leopard kills are biased towards bigger prey items and could explain why the unit mass method estimation was closer to the SECR estimate than when using the actual biomass (11-13 vs 22-13). However, this bias seems to be less pronounced for leopards than other large carnivores (Martins et al. 2011)

Our study demonstrates that two important variables in biomass computation, namely prey selection and prey mass, can influence carnivore carrying capacity predictions. While Hayward et al. (2007) successfully predicted a range of carnivore carrying capacities across South Africa, and although not apparent in our study, we suggest that for leopards at least some local populations might be over- or underestimated using the generalized unit mass rather than site specific kill information, especially when prey species absent from the specific study area are included in the carrying capacity model. Leopard feeding ecology has been biased towards the more mesic parts of South Africa, with few studies in mountainous areas. However, the recent advances in GPS telemetry systems will undoubtedly improve dietary studies for data poor areas, which will greatly improve biomass computations and predictions for carnivore carrying capacity. However, taking into consideration the advances of spatially explicit density prediction methods (Noss et al. 2012), we recognize that predator carrying capacity can reliably be predicted using the preferred prey species model, even in a mountain population.

Although our study contributes firsthand knowledge to large carnivore predation and carrying capacity prediction, we acknowledge some shortcomings of our study. First, the model predicts carrying capacity and not population size; thus, to test the predictive success of the model, we need several years of data. In addition, we make the assumption that the current leopard population estimate is accurate. Using a non-spatial approach such as CAPTURE could have overestimated the population size (Noss et al. 2012). We also did not take gender or other covariates into consideration in the SECR or CAPTURE models, which could have underestimated leopard density and abundance (Gray & Prum 2011).

Second, we only have a sample size of three females which may result in a biased record of prey selection in the population as a whole. If this bias leads to underestimating prey biomass (because leopards are size-constrained predators and females are smaller than males), our carrying capacity predictions may be too high. Conversely, if larger males can prey upon a wider range of species, our estimates may have underestimated biomass available and therefore carrying capacity. Third, the annual aerial counts could have undercounted the small, cryptic prey species which leopards do eat on Welgevonden (e.g., klipspringer), which could lead to an underestimation of carrying capacity estimates. Although correction factors (Owen-Smith & Mills 2008) were applied to adjust prey counts, differences in vegetation types in Kruger National Park and our study area could have caused potential biases. Fourth, we were unable to collect data year round (late winter – midsummer) and prey selection is likely to change (e.g., zebra foals are obviously only seasonally available). Finally, the body masses we used were obtained from studies of savanna prey species, which may be different than body masses of these species in more nutrient-deficient, mountainous areas. Nevertheless, we still show that biomass computation can vary greatly from the unit mass method and should be taken into account in estimating predator carrying capacities, especially for understudied areas or populations.

## Management Implications

Estimating carrying capacities using the unit mass method may be the best information available in some cases (particularly where no information about the actual diet is available). Using data on the actual diet of large predators, as we have done here, is time consuming and logistically difficult, and did not improve carrying capacity estimates. It is possible that inclusion of more study animals over several seasons would potentially eliminate the discrepancy between methods in predator abundance estimates and therefore general consensus needs to be reached regarding sampling intensity. Where detailed annual information on the diet of predators is unavailable, the coarser unit mass method is likely to continue to yield viable estimates of carrying capacity.

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