Computing biomass consumption from prey occurrences in scats of tropical felids

Dissertation submitted to the Saurashtra University, Rajkot in partial fulfillment of Masters Degree in Wildlife Science (2013)

By

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CERTIFICATE

This is to certify that Mr. Stotra Chakrabarti has carried out original research titled "*Computing biomass consumption from prey occurrences in scats of tropical felids*", in partial fulfilment of Master's Degree in Wildlife Science from Saurashtra University, Rajkot. The study was carried out under our supervision from December 2012 to June 2013. We hereby certify that this work has not been submitted for any other degree to any other university.

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Acknowledgements

"... I shall be telling this with a sigh,

somewhere ages and ages hence;

two roads diverged in a wood, and I,

I took the one less travelled by,

And that has made all the difference"

The road not taken

(Robert Frost, 1916)

I first read 'the road not taken' when I was in my sixth standard. There was something about the last five lines of the poem which made me think, and think to this very day. I always wanted to be a writer. My father had a deep urge to see his son pursue literature, however, things didn't quite turn up as he had desired and I went on with biology. The strongest reason why I got interested in wildlife was for my grandmother. She, through her very basic knowledge of natural history described to a very young me, how koels never made their own nests, how sparrow parents (showing a nest on our window altar) take turns to feed their ever hungry chicks and how repulsive looking caterpillars magically transformed into flying jewels. I owe a lot to her and I find it most appropriate to start my list of thanks giving from her.

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Still in search of the road not taken,

Stotra Chakrabarti

5th June 2013

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Summary

Background: A robust understanding of prey use and selection by carnivores provides crucial insights into their ecology, conservation and management. In majority of the cases, scat analysis is most effective to assess diet spectrum of carnivores, but require correction for potential biases for estimating biomass contribution of different prey items. Since small prey have higher indigestible matter per unit body mass due to higher surface area-to-volume ratio, relative frequencies of prey remains in scats do not represent their consumed biomasses. Thus, to accurately estimate the proportions of different prey consumed, it is necessary to develop relationships between biomass consumed per field collectable scat and prey weight through feeding experiments. However, no such relationship exists for felids of the Indian sub-continent. The studies on diet of big cats like lion (*Panthera leo*), tiger (*Panthera tigris*) and leopard (*Panthera pardus*) have used a similar relationship based on cougars (*Puma concolor*) by Ackerman *et al.* 1984 owing to the unavailability of any species specific relations .

Methods: A series of feeding trials were used on Asiatic lion (*Panthera leo persica*), leopard and jungle cat (*Felis chaus*) to develop prey incidence to biomass conversion equations (hereafter mentioned as biomass models or biomass equations).

Principal findings: All the models showed satiating relationships between biomass consumed per collectable scat and prey weight given by asymptotic exponential functions. However, carnivore specific models when scaled to their respective body weights did not differ significantly between each other, allowing derivation of a generalized biomass model for tropical felids. Inferences using present study models refined existing representation of diet of tropical carnivores.

Significance: Results from the present study have strong implications on feeding ecology of tropical felids. Present study refined previous understanding of biomass contribution of different prey species in large felid diet by substantially increasing proportion of medium prey consumption. Such inferences question niche separation of sympatric large felids on the basis of prey species of different sizes, where large carnivores like tiger optimizing on large prey like gaur (*Bos gaurus*) and sambar (*Rusa unicolor*), while medium felids like leopard maximizing on chital (*Axis axis*). Domestic livestock significantly reduced in carnivore diet, reducing livestock depredation rates, indicating lower human-carnivore conflict levels.

Introduction

1. Introduction

1.1. Carnivores in an ecosystem

Ecosystems are highly diverse, complex and multilayered. Such complexities are often difficult to decipher and model in a fashion proper for human understanding. Top carnivores being at the apex of trophic levels, their interactions with different layers of the food web act as useful proxies for understanding ecosystem functions (Gittleman 1996). Studies on carnivores have significantly contributed to our understanding of natural history, different intricate ecological processes and anthropogenic impacts on the entire ecosystem. Carnivores of the world are represented by 283 extant species belonging to 123 genera under 15 families (Macdonald 2010). Carnivores in the wild have always captured human psyche and historically, they were feared as predators, domesticated as pets, and intensively managed as pests. They represent qualities like strength, power, intellect and skill. Our fascination for them has been played out in stories, art, literature and government and private policies (Clark *et al.* 1999). The world today is witnessing the highest concern that we have ever shown towards the conservation of carnivores and their habitats (Mech 1996, Weber and Rabinowitz 1996). Conservation of carnivores prove to be the ultimate test of society's willingness to safeguard wildlife (Miquelle *et al.* 2005) and thus, they become important and charismatic tools in shaping conservation approaches worldwide (Dalerum *et al.* 2008).

1.2. Carnivore conservation: an Indian scenario

Increasing human domination of ecosystems caused by agricultural intensification and urban sprawls is progressively transforming them into depauperate systems (Sala *et al.* 2000). In an agrarian country like India, such ecosystem degradation becomes more intense with rapid increase in human population. Owing to the predatory and wide-ranging nature of top carnivores, they often come into conflicts with human interests resulting in their range contractions and population declines (Divyabhanusinh 2006, Treves and Karanth 2003, Karanth and Chellam 2009). At least 20% of large mammal species in India are likely to face extinction in near future, while several species have already disappeared from more than 90% of their original range (Madhusudan and Mishra 2003). An estimated population of around 40,000 wild tigers 100 years back (Pocock 1929, Mondol *et al.* 2009) has presently declined to less than 2,000 (Jhala *et al.* 2008). Indian gray wolf (*Canis lupus pallipes*) population, a top carnivore species of the open plains (semi-arid grasslands, scrublands and grazing land), has drastically declined to 2000-3000 individuals in their entire Indian range (Jhala 2000).

Many species have become rare and localized endemics (Nilgiri tahr- *Hemitragus hylocrius*, swamp deer- *Cervus duvaucelii*) while many are widely distributed but at very low densities (mouse deer- *Moschiola meminna*, four-horned antelope- *Tetracerus quadricornis*) (Karanth 2008). On the other hand, successful conservation policies have resulted in recovery of few previously endangered species (Singh and Gibson 2011, Banerjee and Jhala 2012) often leading into their population spill-over outside the formal boundaries of the Protected Areas (Karanth and DeFries 2010). Carnivore conservation in India therefore becomes a multifaceted challenge wherein, reduction in space available to carnivore species and conflict mitigation stand out to be the major concerns (Karanth and Chellam 2009, Meena *et al.* 2011). Thus, clear and robust understanding of carnivore ecology (demography, ranging patterns and resource utilization) becomes necessary in formulating viable conservation strategies.

1.3. Carnivore diet

A predator's choice of prey serves as the foremost link connecting the dynamics of species on different trophic levels. A predator's prey choice is guided by natural selection to maximize nutrient intake (Hayward and Kerley 2005) which in turn depends on its own body weight, presence of competitors, habitat, activity pattern and differential use of space. Prey selection of a predator determines spacing patterns, population growth rate and distribution of prey species. Key factors that determine carnivore habitat use are prey abundance, less disturbance, water availability and forest continuity (Banerjee 2012). The acquirement of food is a fundamental component for every predator's existence. Hence, prey selection is critical for understanding life history strategies of any carnivore (Miquelle *et al.* 1996).

1.4. Diet quantification and its problems

Estimation of carnivore diet has been done using different techniques, each subject to different biases (Mills 1992, Marker *et al.* 2003). However, carnivore diet has been most extensively characterized by quantifying undigested prey remains in scats (Korschgen 1980, Putman 1984, Kohn *et al.* 1997). But relative frequencies of prey remains in scats do not represent their consumed biomass (Floyd *et al.* 1978), leading to a biased estimation of predator's diet. This is because of differential digestibility of small and large prey. Smaller prey having higher surface area-to-volume ratio contain more indigestible matter (hair) per unit biomass compared to larger prey. Thus, when a carnivore consumes a small prey, the prey remains are more frequent in scats than in case of consumption of large prey. Hence, relative frequencies of prey remains in scats over-estimate small prey in a carnivore's diet

(Mech 1970). For accurate estimation of diet, it is imperative to correct for differential digestive ability of a predator for different sized prey (Floyd *et al.* 1978, Ackerman *et al.* 1984, Jethva and Jhala 2004). For this purpose, feeding trials have been applied widely to develop relationships that calibrate biomass consumed and number of collectable scats produced (Floyd *et al.* 1978, Ackerman *et al.* 1984, Marker *et al.* 2003, Jethva and Jhala 2004). These relationships are known as biomass models or biomass equations. Biomass models can be used to convert the relative occurrence of prey remains in scats to actual biomass consumed.

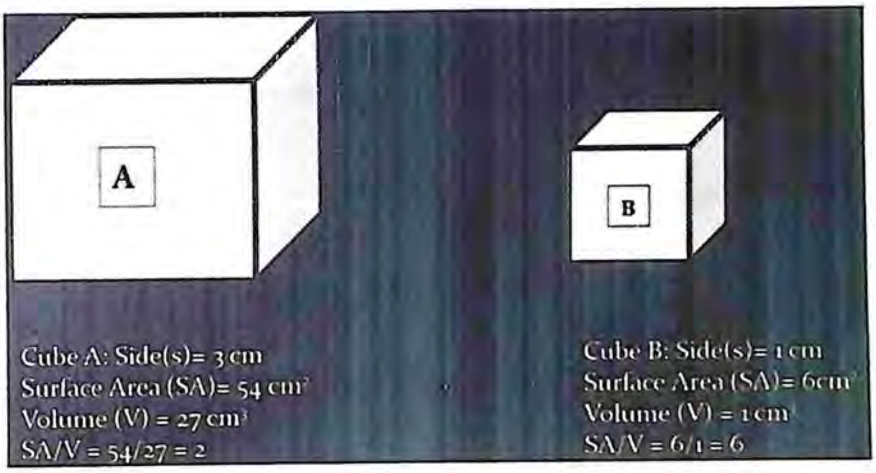


Fig. 1. Diagrammatic representation of the problem of higher surface area: volume ratio for small prey, using two different sized hypothetical cubes

Table 1. List of developed biomass models

Species	*Model*	Author	Study area
Grey wolves (*Canis lupus*)	$y = 0.02x+0.38$	Floyd *et al.* (1978)	Minnesota, USA
Cougars (*Puma concolor*)	$y = 0.035x+1.98$	Ackerman *et al.* (1984)	Utah, USA
Corrected equation for Grey wolves	$y = 0.008x+0.439$	Weaver (1993)	Utah, USA
Cheetahs (*Acinonyx jubatus*)	$y = 0.0098x+0.34$	Marker *et al.* (2003)	Namibia, South Africa
Indian wolves (*Canis lupus pallipes*)	$y = 0.0148x+0.135$	Jethva and Jhala (2004).	Gujarat, India.
Combined for wolves in tropics and temperate areas	$y = 0.0182x+0.217$	Jethva and Jhala (2004).	Gujarat, India.
Lynx (*Lynx lynx*)	$y = 1.330x+15.06$	Ruhe *et al.* (2007)	Central and East Europe
Corrected equation for cheetahs	$y=2.358\{1-exp(-0.075x)\}$	Wachter *et al.* (2012).	Namibia, South Africa

1.5. Correction of biomass models

Biomass models have been mostly developed for temperate prey-predator species (Floyd *et al.* 1978, Ackerman *et al.* 1984, Weaver 1993, Ruhe *et al.* 2007) but their applicability to tropical systems is limited (Jethva and Jhala 2004). This is because of the difference in surface area to body mass ratio and coat composition between temperate and tropical prey species. This alters the digestibility of tropical prey from their temperate counterparts (Jethva and Jhala 2004). Moreover, cougar and tropical big cats like tiger and lion differ significantly in their body weights and range of prey sizes. The prey weight range used by Ackerman *et al.* (1984) in feeding experiments on cougar may not be suitable for representing the appropriate prey range of lion and tiger (Hayward and Kerley 2005, Hayward *et al.* 2012) Thus, applying correction equations developed on a temperate predator (e.g. cougar, Ackerman *et al.* 1984) on tropical predators (e.g. lion *Panthera leo*, tiger *Panthera tigris* and leopard *Panthera pardus*) may bias the estimates of the latters' food habits.

1.6. Current research

The problems of computing biomass consumption from prey occurrences in carnivore scats took a new turn with Mech's hypothesis (1970). Late 1970's and early 80's were marked by a number of research work on this field, primarily by Floyd *et al.* (1978) (on Grey wolves *Canis lupus*) and Ackerman *et al.* (1984). However, there are very few accounts of recent development in this field.

Marker *et al.* (2003) implemented Floyd's work for computing biomass equations for Namibian cheetahs (*Acinonyx jubatus*). The work stressed on the importance of feeding trials in formulating correction factors to negotiate differential digestive abilities of predators for different sized prey. This study also commented on the difference between '*perceived*' and '*actual*' livestock depredation rates by cheetahs and the conservation implications of accurate diet estimation methods of carnivores.

The research work by Jethva and Jhala (2004) on similar perspectives on Indian wolves (*Canis lupus pallipes*) was based on the difference in digestibility of tropical and temperate prey species. The study came out with a combined biomass equation for wolves across tropical and temperate systems by combining the results with that of Floyd *et al.* (1978). This study estimated actual biomass consumed by wolves in the feeding trials by accounting for loss of weight owing to desiccation from the presented prey carcasses.

Another study dealing with biomass consumption of lions and leopards in captivity was carried out by Mukherjee and Goyal (2004). This study was important in providing baseline information about consumption rates of the two carnivores in captivity. However, the authors acknowledged the limitation of this study in developing relationship between biomass consumed per collectable scat and prey weight of the carnivores owing to the narrow range of prey biomasses fed to them and the use of only one prey species (buffalo).

Ruhe *et al.* (2007) did feeding trials and developed an equation for estimating biomass consumption in lynx (*Lynx lynx*). The study recommended the use of correction equation as well as prey specific conversion factors while representing lynx diet.

Another study by Ruhe *et al.* (2008) did feeding trials on lynx, grey wolf and red fox (*Vulpes vulpes*) and developed prey specific conversion factors for each predator. They compared these conversion factors among the three carnivores in the study and also compared the biases associated with different laboratory techniques used in scat analysis studies of carnivores. They strongly suggested the use of predator specific biomass equations and conversion factors while representing food habits of a carnivore.

The most recent research work has been done on cheetahs by Wachter *et al.* (2012). In contrast to previous studies which developed biomass equations (through linear regression models) for different carnivores, this study used an exponential regression model where the consumed prey biomass to excrete one scat satiated at large prey sizes. This is because, as prey body weight increased, carnivores selectively consumed highly digestible flesh rather than less digestible bones and hide.

No other work has been pursued for other carnivores in the recent past and equation developed on cougar has been used for estimating food habits of lions, tigers and leopards (Table 1). Moreover, no study has developed any correction equation specific for tropical small felids.

Table 2. List of reviewed research works (1992-2013) which have used 'Ackerman's equation' (1984) to estimate food habits of big cats in the Indian sub-continent

Sl.no.	Species	Research work	Total
1.	Asiatic lion (*Panthera leo persica*)	Banerjee and Jhala(2013), Chellam(1993), Meena *et al.*(2011).	3
2.	Bengal tiger (*Panthera tigris tigris*)	Andheria *et al.*(2007), Bagchi *et al.*(2003), Bhattarai and Kindlmann(2012), Biswas and Sankar (2002), Harihar *et al.*(2007), Karanth and Sunquist(1995), Karanth and Sunquist(2000), Kumar *et al.*(2008), Kumaraguru *et al.*(2011), Kapfer *et al.*(2011), Mazumder *et al.*(2012), Mondal *et al.*(2012), Ramesh *et al.*(2009), Sankar and Johnsingh(2002), Sankar et al.(2010), Wegge *et al.*(2009).	16
3.	Leopard (*Panthera pardus fusca*)	Ahmed and Khan(2008), Andheria *et al.*(2007), Bhattarai and Kindlmann(2012), Edgaonkar and Chellam(2002), Edgaonkar(2008), Harihar *et al.*(2011), Karanth and Sunquist(1995), Karanth and Sunquist(2000), Kumar *et al.*(2008), Kumaraguru *et al.*(2011), Mazumder *et al.*(2012) Mondal *et al.*(2011,2012), Ramesh *et al.*(2009).	14

1.7. Present study

The current study seeks to develop biomass models for Asiatic lion, leopard and jungle cat. The study can be divided into two aspects;

A. Developing the equations

Use of feeding trials on lion, leopard and jungle cat to calibrate between prey biomass consumed and the number of collectable scats produced.

B. Re-characterization of food habits of the three carnivores

To re-analyze published data on food habit studies of lions and leopards using the developed equations.

1.7.1. Biological queries

A. To examine the difference between 'Ackerman's equation' (1984) (on cougar) developed on temperate prey-predator system and that of the equations developed specific for Indian large felids.

B. To examine the effect of body size on biomass equations and hence, on patterns of biomass consumption and scat production in tropical felids.

Study Site

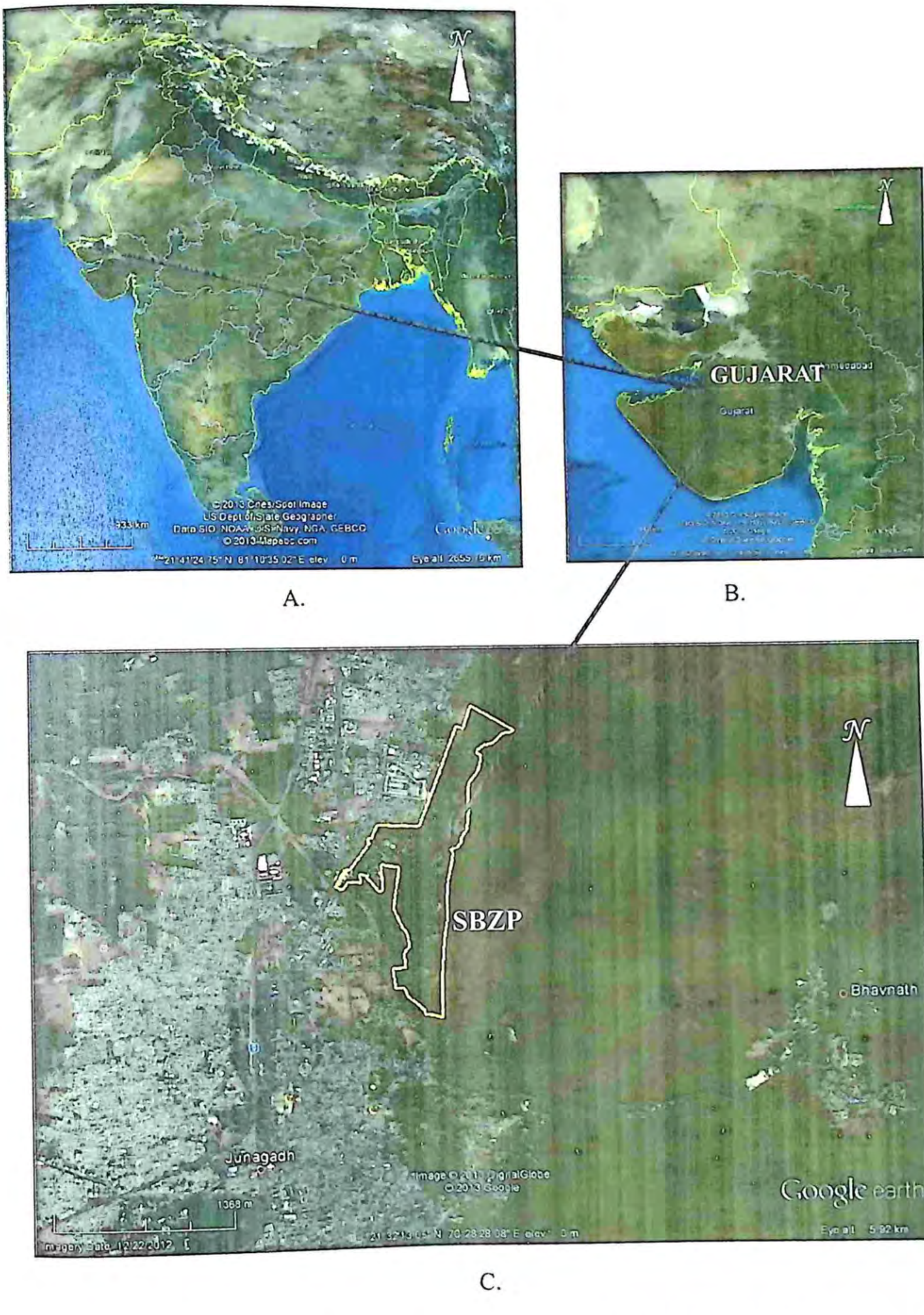
2. Study Site

The study was conducted in Sakkarbaug Zoological Park (henceforth mentioned as SBZP) in Junagadh, Gujarat. SBZP, established in 1863, is one of the oldest zoos in India. Spread over 198 Ha in the foothills of Mount Girnar, the zoo houses more than 1100 wild animals which includes 38 *spp.* of mammals, 56 *spp.* of birds and 13 *spp.* of reptiles. The zoo serves to the curiosity and educational needs of around 1.2 million visitors each year. Based on its collection of wild animals, area and number of visitors, Central Zoo Authority (CZA), India has designated SBZP as one of the 15 large and one of the 57 important zoos, out of 350 animal collections in the country.

2.1. SBZP: past and the present

Established as a personal animal collection by the then Nawab of Junagadh, the zoo was maintained by the *nawabs* from 1863 to 1947. Post Indian independence, SBZP came under the administration of the Education Department and subsequently under the supervision of the District Forest Officer, Junagadh of the Greater-Bombay state. After the reorganization of the present Gujarat state in 1960, SBZP came under the direct governance of Gujarat Forest Department.

SBZP is a 'specialist' zoo as it is the only zoo in the country set up exclusively to cater to the needs of a single state, Gujarat. SBZP runs conservation breeding programmes for Asiatic lion (*Panthera leo persica*), Chinkara (*Gazella bennettii*), Chowsingha (*Tetracerus quadricornis*), Indian wolf (*Canis lupus pallipes*) and Asiatic wild ass (*Equus hemionus*).



Map 1. Image of A. India, B. Gujarat and C. Sakkarbaug Zoological Park (SBZP) (courtesy: Google Earth, 2013

Methods

3. Methods

Ethics Statement

All permissions to carry out the research work were obtained from the Office of the Chief Wildlife Warden, Gujarat State and Ministry of Environment and Forests, Government of India under the provisions of the Wildlife (Protection) Act, 1972, Government of India and Central Zoo Authority (CZA), Government of India. Domestic livestock used in the feeding trials were bought from their owners without any coercion, euthanized and offered to the carnivores under strict supervision of veterinary officials of SBZP. Wild prey carcasses used in the trials were from road kills and natural mortalities and only entire carcasses were used. House rats offered to jungle cats were trapped from SBZP premises and once an animal was trapped it was quickly killed.

3.1. Field Methods

3.1.1 Feeding experiments

Between January 2013 and April 2013, 44 feeding trials were conducted on three lions, two leopards and two jungle cats. During the trials the concerned carnivores were kept in observation enclosures with *ad libitum* access to water. All the carnivores used in the study were wild caught individuals, excluding one captive born female lion (Table 3).

Table 3. Details of carnivore individuals used in the study

Sl.No.	Species	Sex	Individual code	Details
1.	Asiatic lion	Male	L_1	Adult, caught from Rajula range, Nageshri, Greater-Gir Landscape, 31.08.2012.
2.	Asiatic lion	Female	L_2	Adult, caught from Ransivao range, Girnar WLS, 26.05.2008.
3.	Asiatic lion	Female	L_3	Sub-adult (3 years), cub of L_2, captive born, used as a lion group with wild mother.
4.	Leopard	Male	Lp_1	Adult, caught from Bhojde, Sasan range, Sasan-Gir, 09.12.2012.
5.	Leopard	Female	Lp_2	Adult, caught from Veraval range. Sasan-Gir, 30.12.2012
6.	Jungle cat	Male	JC_1	Adult, rescued from SBZP premises, 2010
7.	Jungle cat	Male	JC_2	Adult, caught from Girnar WLS, 2010.

Procedure used by Floyd *et al.* (1978), Jethva and Jhala (2004) and Wachter *et al.* (2012) was used for conducting feeding experiments. Each feeding trial was divided into three periods: the fasting period before feeding, feeding event and fasting period after feeding.

3.1.1.1. Fasting period before feeding

Before each trial, the concerned carnivores were fasted for a minimum of 60 hours to a maximum of 120 hours (depending upon the weight of prey consumed in the preceding trial event) to clear their digestive systems. All scats were removed from their respective enclosures.

3.1.1.2 Feeding event

Whole carcasses of different prey species, representing the entire weight range of prey normally taken by the concerned carnivores in the wild (Sinha 1987, Chellam 1993, Karanth and Sunquist 1995, Sankar and Johnsingh 2002, Mukherjee *et al.* 2003 Andheria *et al.* 2007, Edgaonkar 2008, Meena *et al.* 2010, Harihar *et al.* 2011, Majumder *et al.* 2011, Banerjee and Jhala 2013) were accurately weighed and offered through 44 different feeding experiments. 18 trials were conducted for lions, 13 for leopards and 13 for jungle cats (Table 4, 5 and 6). Prey items weighing less than 30 kg were weighed to an accuracy of 0.002 kg, items from 30-100 kg to an accuracy of 0.2 kg and prey weights greater than 100 kg to an accuracy of 1 kg. For prey items weighing less than 3 kg, more than one carcass was offered to lions and leopards, to avoid depriving them of food. The same was done for prey items less than 100 g for jungle cats. Simulating wild conditions, the carcasses were kept in the enclosures till the carnivores stopped feeding on them. Large carcasses were kept for longer duration than smaller ones. Uneaten portions of the carcasses were removed 24 hours after the carnivores' last feeding attempt and precisely weighed to calculate consumed biomasses.

3.1.1.3. Fasting period after feeding

During this period, scats were categorized into collectable (hard, firm feces which would retain their form and most likely get collected in the field) and non-collectable (loose, viscous feces unlikely to persist long enough to be collected in the field) (Floyd *et al.* 1978, Ackerman *et al.* 1984). Collectable scats were collected in paper bags twice daily from the enclosures to prevent trampling and desiccation until further scat production stopped. The scats were then cleaned using a soft brush and weighed on an electronic scale to an accuracy of 0.002 kg. All collectable and non-collectable scats were counted and noted down.

Table 4. List of prey items offered to lions

Sl.No.	Prey type	Number of trials
1.	Adult goat (*Capra hircus*)	3
2.	Goat kid	3
3.	Adult sheep (*Ovis aries*)	2
4.	Sheep lamb	1
5.	Adult buffalo (*Bubalus bubalus*)	1
6.	Buffalo calf	2
7.	Rabbit (*Oryctolagus sp.*)	2
8.	Chicken (*Gallus sp.*)	3
9.	Nilgai (*Boselaphus tragocamelus*)	1
		Total: 18

Table 5. List of prey items offered to leopards

Sl.No.	Prey type	Number of trials
1.	Adult goat (*Capra hircus*)	1
2.	Goat kid	3
3.	Adult Sheep (*Ovis aries*)	2
4.	Sheep lamb	1
5.	Buffalo calf	2
6.	Rabbit (*Oryctolagus sp.*)	1
7.	Chicken (*Gallus sp.*)	2
8.	Chital (*Axis axis axis*)	1
		Total: 13

Table 6. List of prey items offered to jungle cats

Sl.No.	Prey type	Number of trials
1.	Pigeon (*Columba sp.*)	3
2.	Chicken (*Gallus sp.*)	2
3.	Rabbit (*Oryctolagus sp.*)	2
4.	Laboratory (white) rat (*Rattus norvegicus*)	1
5.	House rat (*Rattus rattus*)	2
6.	Goat kid (*Capra hircus*)	1
7.	Guinea pig (*Cavia sp.*)	2
		Total: 13

3.1.2. Computing moisture loss from carcasses

Weight loss from carcasses was an outcome of the synergistic effects of consumption and desiccation. To account for moisture loss from the carcasses owing to evaporation, procedure used by Jethva and Jhala (2004) was implemented to calculate actual fresh weight amounts (kg) consumed by the carnivores. Since the carcasses (during the trials) were kept in the enclosures for a minimum of 24 hours to a maximum of 120 hours (depending on the prey size offered), there were varying degrees of moisture loss from the carcasses. Three different prey types (chicken, goat and buffalo) representing the entire weight and surface area to volume ratio range of prey used in the trials, were selected. These prey types were dressed and portions of skin, bones and little meat attached to them (usually left unconsumed in the trials) were left open to the environment for periods corresponding to their consumption times during the trials. The carcasses were precisely weighed (to an accuracy of 0.002 kg) every 24 hours. Chicken carcass was allowed to lose moisture for 48 hours, goat for 72 hours and buffalo for 120 hours. Percentage weight loss was calculated.

3.2. Laboratory methods

Cleaned collectable scats were sun-dried and then oven-dried at 70°C for 24 hours (Jethva and Jhala 2004). Dried scats were then weighed on an electronic scale to an accuracy of 0.002 kg and the respective dry weights noted.

3.3. Analytical methods

3.3.1 Carcass weight loss through evaporation

Actual fresh weight amounts consumed by the carnivores in the study were calculated after correcting for loss of weight from the carcasses owing to evaporation. For this, a pooled regression analysis was done for goat and buffalo carcasses (assuming similar moisture loss between mammalian carcasses), and a separate one for chicken. Since the initial weights kept for drying in case of buffalo and goat carcasses were different, so the weights corresponding to the different time intervals were standardized by scaling them to their respective initial weights (*standardization by the maximum*). Scaled carcass weights respective to the different time intervals were regressed against time to estimate percentage moisture loss.

3.3.2. Carnivore specific biomass equations

Correction equations for lion, leopard and jungle cat were determined by regressing consumed prey mass per excreted collectable scat to the mean prey body weight. When more than one carcass was offered in the feeding experiments, the mean of the consumed mass of each carcass was used. Observation from the scatter plots (see appendix, Fig. i), residual plots (see appendix, Fig. ii and iii) and following Wachter *et al.* (2012) non-linear regression models were fitted. The non-linear exponential model represented a satiating response where biomass consumed to excrete one collectable scat reached an asymptote at higher prey sizes.

3.3.3. Comparison of the three equations

Data from trials on lion, leopard and jungle cat were combined together to compare the different correction equations across tropical felids. However, such a comparison was inappropriate as the four carnivores differed in their range of prey size classes and consumption rates and hence, the equations differed in their scales. Published literature on carnivore energetics and life history parameters suggested that prey size and consumption patterns have a strong relationship with physiological rates, hence with carnivore body size (Huggett and Widdas 1951, McNab 1980, Gittleman 1986, Earle 1987). This relationship was further strengthened when the asymptotes of the correction equations were positively correlated with their respective predator body weight (further discussed in section 4). Thus, biomass equations were scaled to their respective predator mass so as to compare scale free equation coefficients.

3.3.4. Computing digestibility indices

Digestibility indices (D) for different prey size classes of the three carnivores were determined using the underlying formula (moisture content of carnivore diet was assumed to be 70%) (Robbins 1983, Jethva and Jhala 2004) and plotted against mean fresh weight of prey.

$$D = \frac{\text{Dry weight of prey consumed} - \text{Dry weight of all collectable scat}}{\text{Dry weight of prey consumed}}$$

3.3.5. Comparison of Ackerman's (1984) and present study equations

Biomass equation based on feeding trials on cougar (Ackerman *et al.* 1984) was a linear regression model where biomass consumed per collectable scat (Y_A) increased linearly with increase in prey body weight (X_A), given by:

$Y_A = 1.98 + 0.035\, X_A$

However, the equations developed in the present study were explained through non-linear functions. Thus, comparison between the parameter estimates of Ackerman's equation and the present study equations was inappropriate. Hypothetical prey weight classes within the normal prey weight range for lions and leopards were created. Using these classes their corresponding Y (biomass consumed per collectable scat) values were calculated using Ackerman's equation and equations specific for lion and leopard (See appendix, Table i and Fig. iv). The difference between the Y values from Ackerman's equation and the present study models were plotted against their respective prey weight classes to examine the pattern of the difference in the models, if any.

3.3.6. Re-construction of carnivore diet

From recent published literature, one food habit study for lion and leopard was used and re-analysed using carnivore specific and generalized regression models. However, owing to inadequacy of food habit studies from the sub-continent, jungle cat was not included in this meta-analysis. There are a few studies on jungle cat diet in India (Mukherjee *et al.* 2004, Mazumder *et al.* 2011), however, they do not report the entire diet spectrum or the weights of individual prey species.

Biomass consumed per collectable scat (Y) values, of different prey species reported in the studies, were calculated using carnivore specific and generalized models. Proportion of biomass contribution of each prey species to a carnivore's diet was compared across different biomass models.

Since data from the feeding trials on cougar by Ackerman *et al.* (1984) was not available and neither were the standard errors associated with the parameter estimates, Ackerman's model was reconstructed using approximate x and y values from the graph (see appendix, Table ii). The re-constructed Ackerman's model did not differ significantly from the actual model (see appendix, Fig. iv); hence, standard errors of the re-constructed model were used on percentage biomass consumption values from the studies.

All analysis was done using SPSS 16.0 (SPSS Inc., Chicago, IL) and Microsoft Excel 2010 (Microsoft Corporation).

Table 7. Details of 44 feeding experiments on lion, leopard and jungle cat

Predator	Number (sex)	Prey (number)	Prey wt. (kg)	Mean prey wt. (kg)	Coll. (non-coll.) scats	Coll. scats /pred & prey	Biomass consumed (kg) /pred & prey	Biomass (kg) /coll. scat
Lion	1 (F)	Rabbit (2)	3.6	1.8	4 (0)	2.0	1.54	0.77
	1 (M)	Rabbit (2)	4.8	2.4	4 (1)	2.0	2.04	1.02
	1 (M)	Chicken (2)	5.2	2.6	4 (0)	2.0	2.61	1.31
	1 (F)	Chicken (1)	3.8	3.8	3 (1)	3.0	3.80	1.27
			4.5	4.5	2 (1)	2.0	4.45	2.23
	1 (F)	Goat kid (1)	6.6	6.6	5 (0)	5.0	5.91	1.18
			8.5	8.5	5 (0)	5.0	6.48	1.30
	1 (M)	Goat kid (1)	10.5	10.5	4 (0)	4.0	9.01	2.25
	1 (M)	Lamb (1)	10.5	10.5	4 (0)	4.0	9.54	2.39
	1 (F)	Sheep (1)	28.6	28.6	6 (1)	6.0	16.37	2.73
	1 (M)	Sheep (1)	31.0	31.0	6 (1)	6.0	19.35	3.22
	1 (F)	Goat (1)	26.9	26.9	6 (1)	6.0	14.90	2.48
	1 (M)	Goat (1)	30.1	30.1	5 (1)	5.0	16.38	3.28
			33.2	33.2	7 (1)	7.0	20.13	2.88
	1 (M)	Buffalo calf (1)	74.0	74.0	10 (0)	10.0	36.92	3.69
	2 (F,F)	Buffalo calf (1)	114.0	114.0	10 (2)	5.0	19.00	3.80
	2 (M,F)	Nilgai (1)	131.0	131.0	10 (0)	5.0	19.85	3.97
	3 (M,F,F)	Buffalo (1)	319.0	319.0	20 (3)	6.7	30.01	4.50
Leopard	1 (M)	Chicken (2)	3.4	1.7	5 (0)	2.5	1.66	0.66
			4.0	2.0	6 (1)	3.0	1.96	0.65
	1 (M)	Rabbit (1)	2.5	2.5	4 (0)	4.0	2.28	0.57
	1 (F)	Goat kid (1)	6.7	6.7	5 (1)	5.0	4.87	0.97
	1 (M)	Goat kid (1)	6.7	6.7	5 (1)	5.0	6.30	1.26
			7.5	7.5	4 (0)	4.0	6.18	1.54
	1 (M)	Sheep lamb (1)	7.8	7.8	6 (0)	6.0	6.67	1.11
	1 (F)	Goat (1)	17.3	17.3	8 (0)	10.0	10.53	1.05
	1 (F)	Sheep (1)	20.2	20.2	4 (3)	5.0	6.29	1.26
	1 (M)	Sheep (1)	27.3	27.3	8 (1)	9.0	13.49	1.50
	1 (M)	Chital (1)	30.7	30.7	8 (0)	8.0	16.54	2.07
	1 (M)	Buffalo calf (1)	44.0	44.0	9 (1)	9.0	18.91	2.10
			74.0	74.0	15 (1)	15.0	30.95	2.06
Jungle cat	2 (M)	Domestic Rat (2)	0.2	0.1	4 (0)	2.0	0.08	0.04
			0.2	0.1	5 (0)	2.5	0.11	0.04
		White Rats (2)	0.3	0.2	5 (0)	2.5	0.15	0.06
		Pigeon (1)	0.3	0.3	4 (0)	4.0	0.26	0.06
			0.3	0.3	3 (0)	3.0	0.29	0.10
			0.3	0.3	4 (0)	4.0	0.31	0.08
		Guinea Pig (1)	0.7	0.7	7 (0)	7.0	0.63	0.09
			0.8	0.8	7 (0)	7.0	0.67	0.10
		Rabbit (1)	0.8	0.8	7 (0)	7.0	0.67	0.10
			1.6	1.6	12 (0)	12.0	1.36	0.11
		Chicken (1)	2.3	2.3	5 (0)	5.0	0.63	0.13
			2.3	2.3	10 (0)	10.0	1.44	0.14
		Goat kid (1)	3.5	3.5	10 (0)	10.0	1.42	0.14

Results

4. Results

One hundred and fifteen (90%) out of one hundred and twenty eight lion scats, eighty eight (91%) out of ninety seven leopard scats and all (100%) of eighty three jungle cat scats were collectable (Table 7).

4.1. Moisture loss estimation

4.1.1. Mammalian carcass

From the pattern observed in the scatter plot, carcass weights reduced with increasing number of days, however with a satiating trend. Biologically this implied that desiccation rates were the highest in the first few days, which reduced (owing to near-complete desiccation of carcass by then) with progressive days. A quadratic regression model was fitted:

Carcass weight after 'x' days $(Y_x) = 0.992 - 0.098x + 0.009x^2$ ($R^2 = 0.97$, $p < 0.05$) (Fig. 2)

This equation was used to re-trace the fresh weight amount (kg) of unconsumed portions of carcasses according to their respective trial durations.

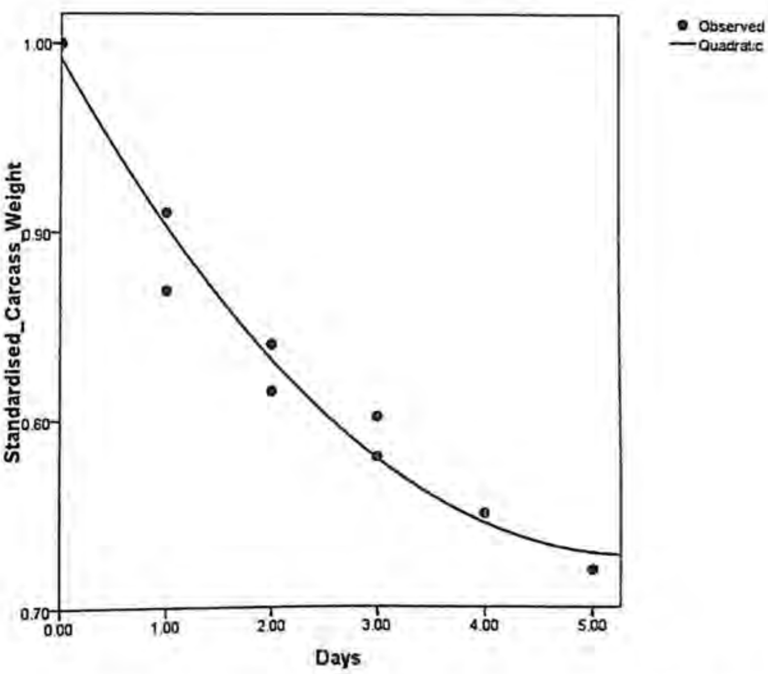


Fig. 2. Relationship between standardized carcass weight (goat and buffalo) with time (days)

Table 8. Percentage weight loss from mammalian carcasses with time

Time (days)	Percentage weight loss through desiccation
1	9.5
2	16.3
3	21.3
4	24.5
5	26

4.1.2. Chicken carcass

Loss of moisture from chicken carcass was a predator specific (jungle cat) correction need as the large carnivores in the study (lion and leopard) entirely consumed such carcasses, leaving only feathers and crop contents. A linear regression model ($Y_x = 1.005 - 0.181x$; x in days, $R^2 = 0.99$, $p < 0.05$) was used to estimate moisture loss (Fig. 3)

The chicken carcasses provided to jungle cats in the study were considerably large for them to consume in one or two feeding attempts. Percentage moisture loss was higher in chicken than mammalian carcass as portions of soft body parts like intestine and flesh (with high moisture content) were also left unconsumed. Loss of moisture from chicken accounted for 38% of weight loss in 2 days.

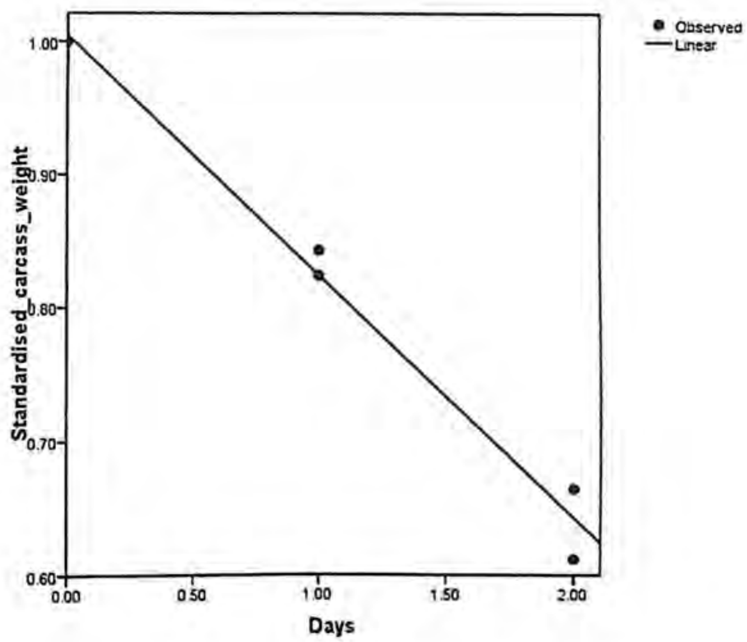


Fig. 3. Relationship between standardized carcass weight (chicken) with time (days)

4.2. Carnivore specific biomass model

Prey biomass consumed by a carnivore to produce one collectable scat (Y) increased with mean prey body mass (X) and leveled out at a certain weight of prey. However, the prey weight at which the biomass equation reached an asymptote differed between the three carnivores in the study (discussed in details in section 4.1.4.). Each of the biomass equations was described by an exponential function.

$\mathbf{Y = b_1 (1 - e^{b_2 X})}$, where b_1 represented the biomass consumed per collectable scat at the asymptote and b_2 the negative of the intrinsic slope of the equation (Wachter *et al.* 2012)

4.2.1. Model for lion

Data on biomass consumed per collectable scat and mean prey body mass from 18 feeding trials on lion (Table 7) was described by the function,

$Y = 3.674 (1 - e^{-0.079x})$, ($R^2 = 0.799$, $p < 0.05$) **(eqn. 1)**

3.674 kg being the biomass consumed per collectable scat where the curve reached an asymptote. Consumed prey mass to excrete one collectable scat reached its asymptotic upper limit at a prey body mass of approximately 60 kg.

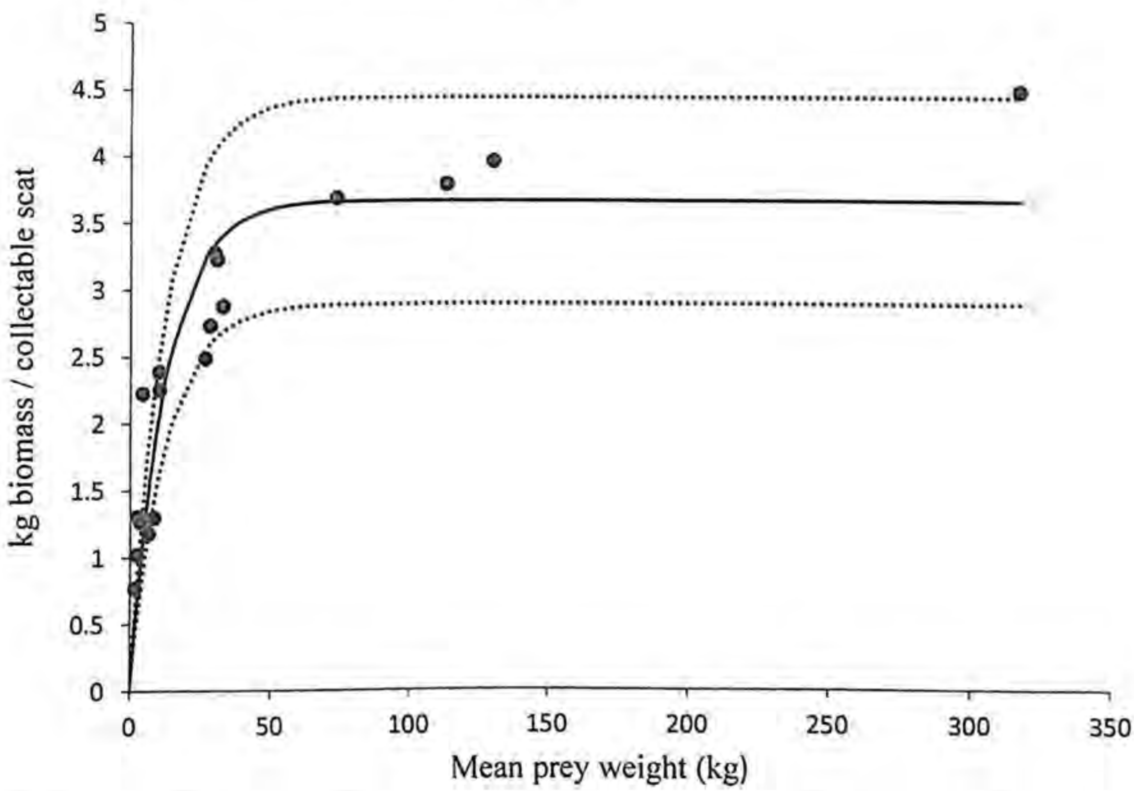


Fig. 4. Consumed prey mass (kg) to excrete one collectable scat as a function of mean prey weight (kg) for lion (broken lines represent 95% CI)

4.2.2. Model for leopard

Biomass consumed per collectable scat and mean prey body mass were related by the function,

$Y = 1.922(1 - e^{-0.123X})$, ($R^2 = 0.858$, $p < 0.05$, $n = 13$) **(eqn. 2)**

1.922 kg being the asymptotic biomass consumed per collectable scat. Consumed prey mass to excrete one collectable scat reached its asymptotic upper limit at a prey body mass of approximately 30kg.

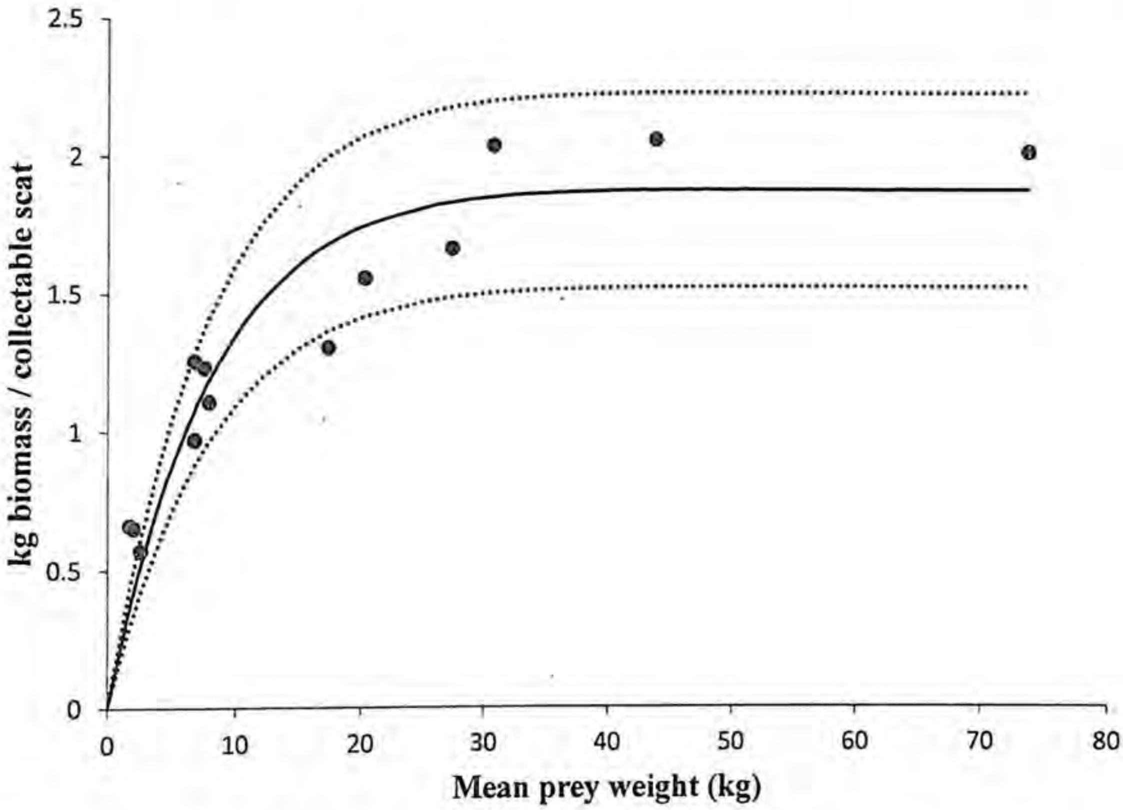


Fig. 5. Consumed prey mass (kg) to excrete one collectable scat as a function of mean prey weight (kg) for leopard (broken lines represent 95% CI)

4.2.3. Model for jungle cat

Biomass consumed per collectable scat and mean prey body mass were related by the function,

$Y = 0.125(1 - e^{-3.004X})$, ($R^2 = 0.818$, $p < 0.05$, $n = 13$) **(eqn. 3)**

0.125 kg being the asymptotic biomass consumed per collectable scat. Consumed prey mass to excrete one collectable scat reached its asymptotic upper limit at 1.3 kg of mean prey weight.

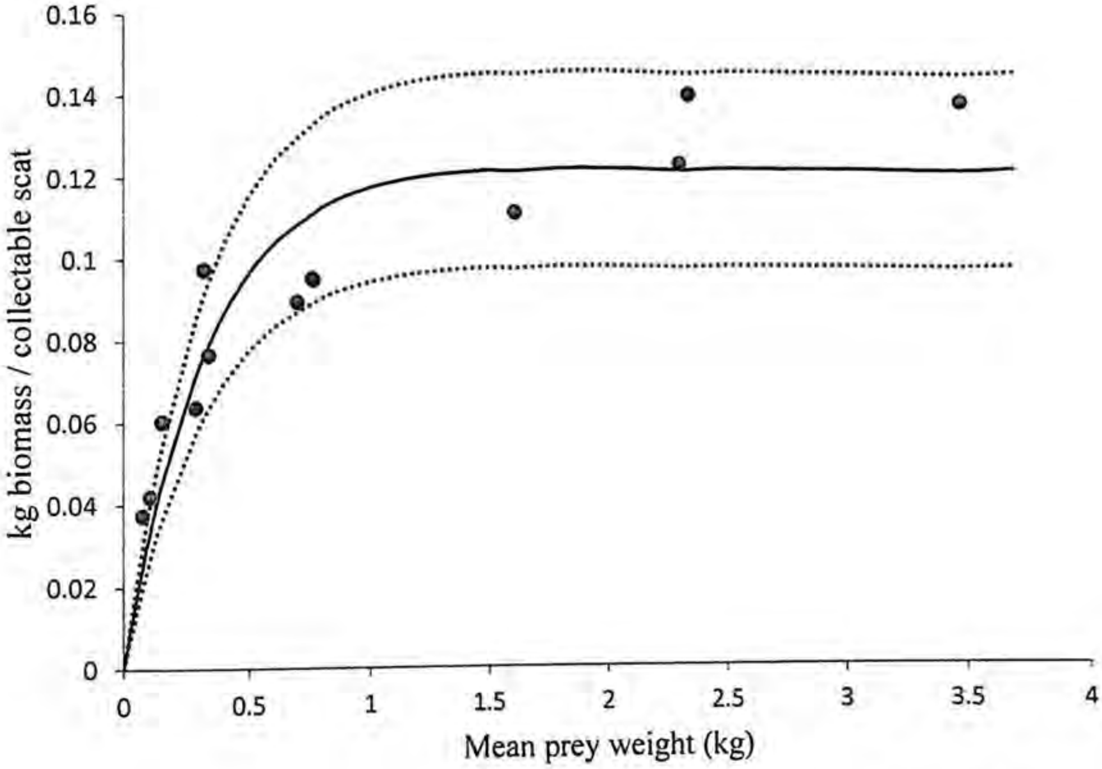


Fig. 6. Consumed prey mass (kg) to excrete one collectable scat as a function of mean prey weight (kg) for jungle cat (broken lines represent 95% CI)

4.3. Generalized biomass equation for tropical felids

The equations (eqn. 1, 2 and 3) differed in their magnitudes. However, biomass consumed to produce one collectable scat at the asymptote (b_1) of the three equations were found to have a strong positive relationship with the corresponding average carnivore body weights (w), given by a linear function:

$b_1 = 0.03w + 0.07$ ($R^2 = 0.99$, n = 3).

(Average carnivore weights were taken from Prater (1971), Mukherjee and Groves (2006) and Macdonald (2010)).

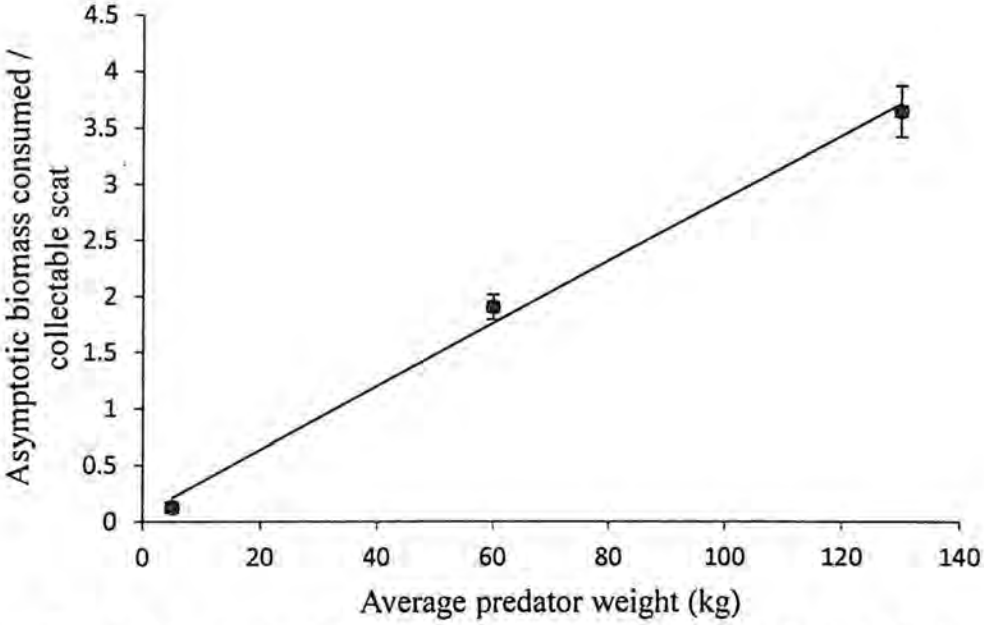


Fig. 7. Relationship between b_1 and average predator body weight (kg)

The allometric relationship clearly indicated that biomass consumption rates, hence b_1 are a function of the predator body weight. Thus, each of the biomass equations was standardized to its predator mass to bring them at scales comparable across different carnivores (Fig. 8).

The parameter estimates (b_1 and b_2) of the equations for lion, leopard and jungle cat when scaled to their average body weights did not differ significantly from each other (Table 9).

Table 9. b_1 and b_2 estimates and their corresponding 95 % CI of scaled equations for lion, leopard and jungle cat

Predator	b_1	95% CI		b_2	95% CI	
		Lower bound	Upper bound		Lower bound	Upper bound
Lion	0.028	0.025	0.032	-10.268	-14.644	-5.892
Leopard	0.032	0.028	0.036	-7.396	-10.244	-4.547
Jungle cat	0.025	0.022	0.028	-15.019	-21.264	-8.774

A pooled regression analysis was done using data from the three carnivores to create a generalized biomass model for tropical felids.

In accordance with each of the correction equation on tropical felids, the generalized model was described by a similar function where, biomass consumed to produce one collectable scat scaled to predator body mass (Y_g) increased with mean prey weight per predator mass (X_g) and leveled out at a certain ratio between prey and predator weight (Fig. 8):

$Y_g = 0.029(1 - e^{-9.909X_g})$ ($R^2 = 0.802$, $p < 0.05$, $n = 44$) **(eqn. 4)**

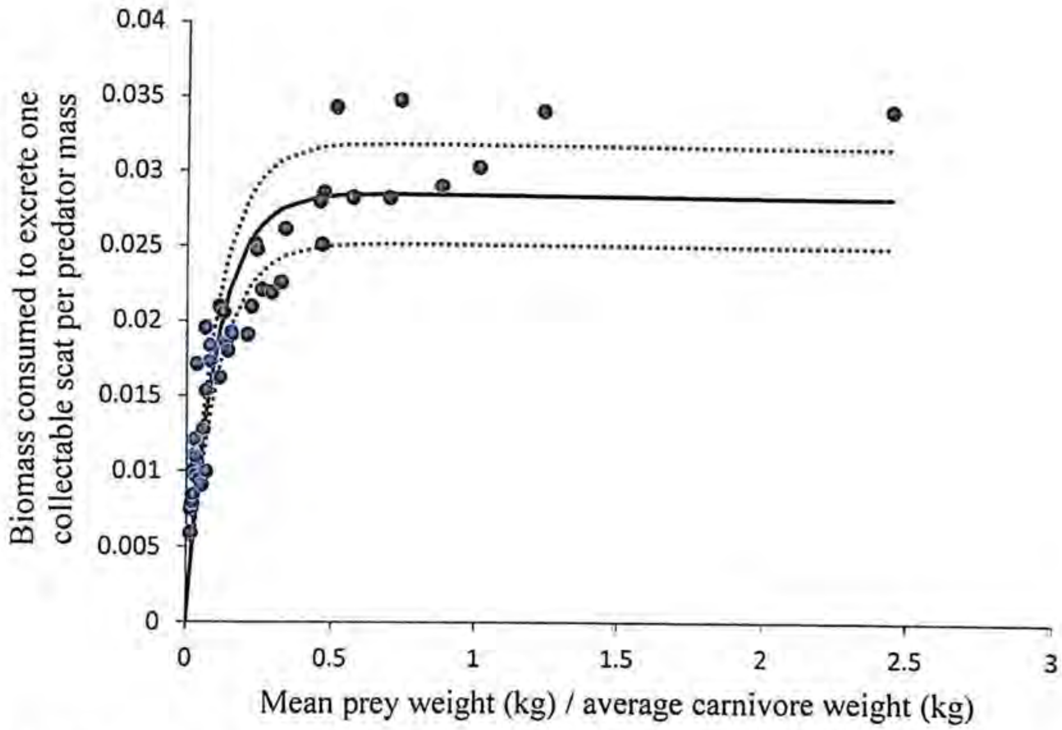


Fig. 8. Consumed prey mass (kg) to excrete one collectable scat (scaled to average predator weight) as a function of mean prey weight per predator mass for tropical felids (broken lines represent 95% CI)

4.4. Digestibility indices

Digestibility indices (D) of different prey size classes increased linearly with mean prey body weight (X_m) for all the three carnivores (Fig. 9) given by:

$D = 0.0867 X_m + 72.52$ ($R^2 = 0.59$, $p < 0.05$, $n = 18$) (lion)

$D = 0.3614 X_m + 79.06$ ($R^2 = 0.79$, $p < 0.05$, $n = 13$) (leopard)

$D = 6.65 X_m + 70.71$ ($R^2 = 0.76$, $p < 0.05$, $n = 13$) (jungle cat)

However, digestibility (as a percentage, D%) across prey weights showed a very narrow range in all the three carnivores (average: 64% - 90%).

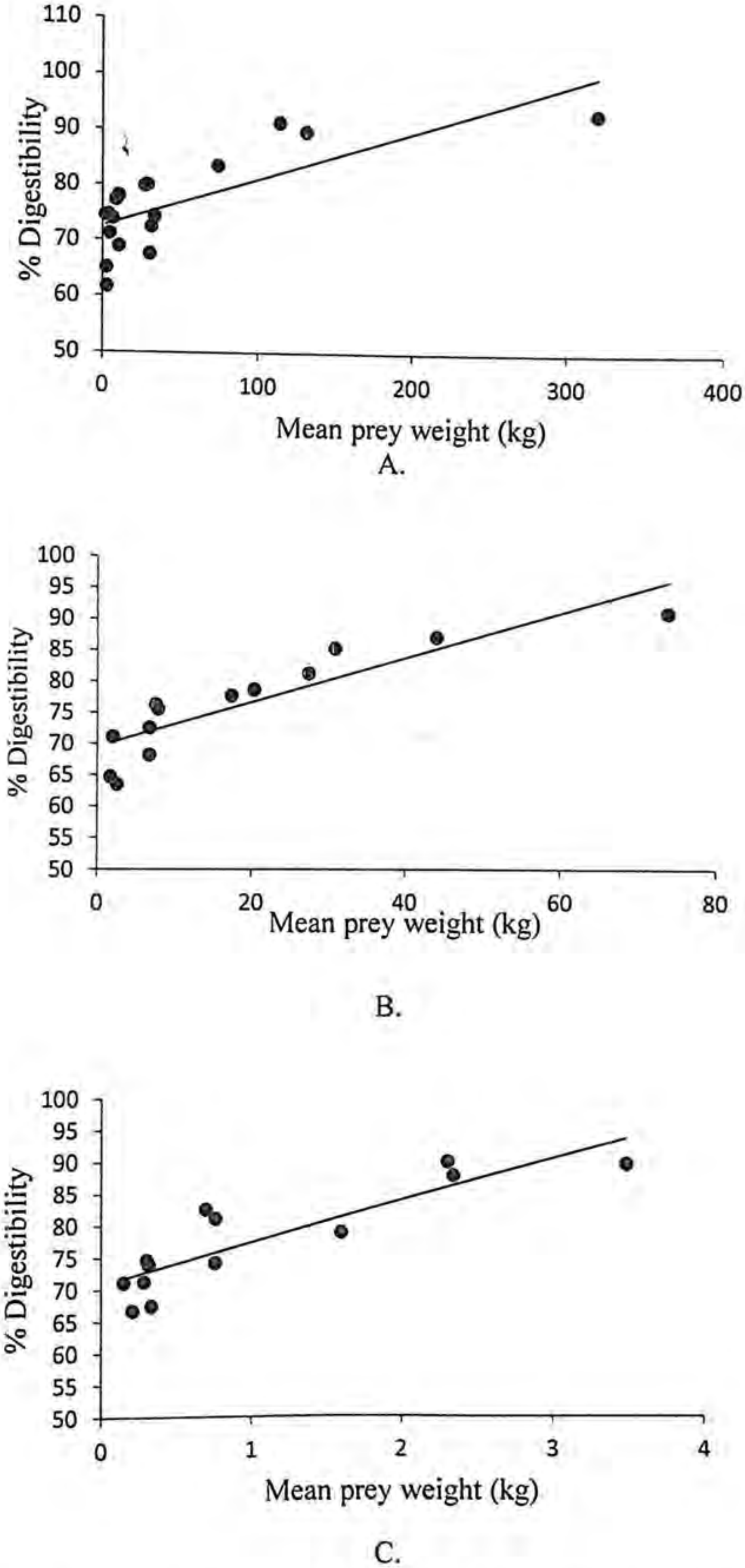


Fig. 9. Relationship between % digestibility and mean prey weight for A. lion. B. leopard and C. jungle cat

4.5. Comparison of Ackerman's (1984) and present study equations

A significant difference was found in Y values estimated using Ackerman's equation and eqn. 1 (lion specific), same was observed for values estimated by eqn. 4 (generalized model) (Fig. 10).

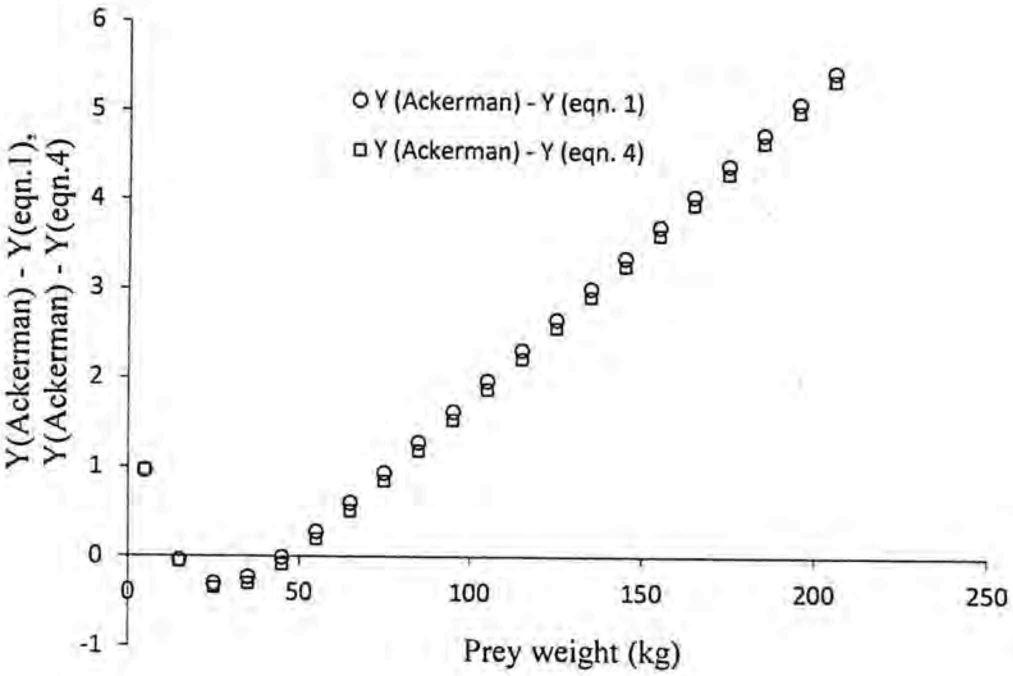


Fig. 10. Differences between Y values for the three models plotted against prey weight (kg). Also, given alongside is the legend of the graph

The difference between Y values gradually reduced from positive to negative and after a certain prey weight range increased in the positive direction infinitely. Thus, Ackerman's equation overestimated small prey consumption in lions owing to a positive intercept, underestimated medium sized prey (just below 50 kg) and overestimated higher prey size classes. A similar trend was observed in case of leopards.

4.6. Re-construction of carnivore diet

4.6.1. Lion

Eqn. 1 and 4 were used to derive percentage biomass consumption of lion prey reported in Banerjee *et al.* (2013). The data used was from the eastern part of the Gir forests. Percentage biomass consumption of each prey species were compared between former and present approaches (Fig. 11).

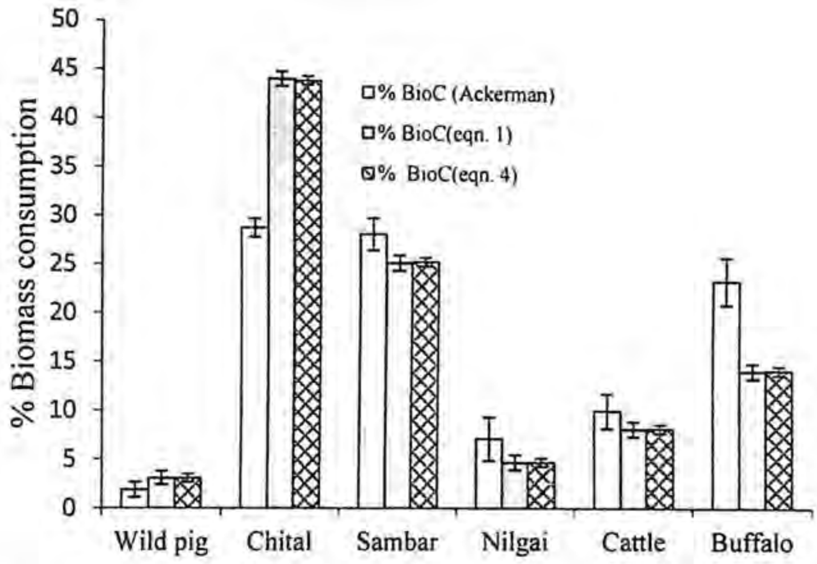


Fig. 11. Comparison between percentage prey biomass consumption of lion in eastern Gir forests using Ackerman's equation (Banerjee *et al.* 2013) and using present study models. Error bars represent standard errors.

The results showed a similar trend as observed from Fig. 10. Chital (*Axis axis*) biomass consumption increased significantly and consumption of large prey like buffalo reduced. There was no significant difference of percentage biomass consumption of lion prey between eqn. 1 and 4.

4.6.2. Leopard

Eqn. 2 and 4 were used to derive percentage biomass consumption of leopard prey reported in Mondal *et al.* (2013). The data used was from Sariska Tiger Reserve. Percentage biomass consumption of each prey species were compared between former and present approaches (Fig. 12).

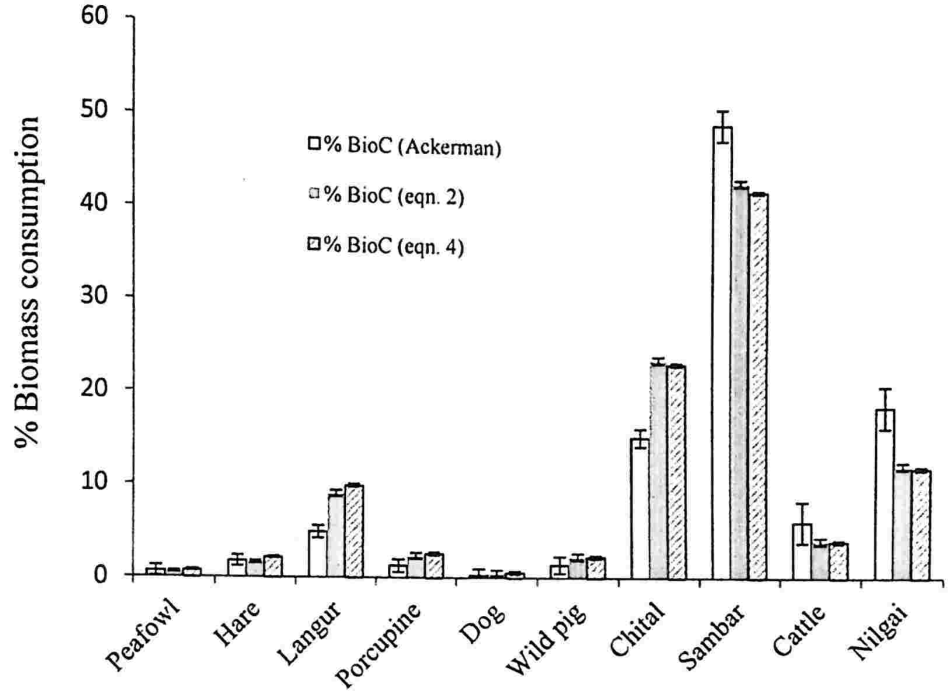


Fig. 12. Comparison between percentage prey biomass consumption of leopard in Sariska Tiger Reserve using Ackerman's equation (Mondal *et al.* 2011) and using present study models. Error bars represent standard errors.

Percentage biomass consumption from common langur (*Semnopithecus entellus*) and chital increased significantly, whereas reduced in significant proportion from large prey like sambar (*Rusa unicolor*) and nilgai (*Boselaphus tragocamelus*) in leopard diet. Again, no significant difference was found from results of leopard specific (eqn. 2) and generalized model (eqn. 4).

4.6.3. Tiger

Since there was no significant difference between results obtained using carnivore specific equations and the generalized model, the latter was used to re-characterize tiger diet from published literature. A study from Pench Tiger Reserve by Biswas and Sankar (2002) was chosen and data was re-analysed using eqn. 4. Average body weight of tiger was taken from Schaller (1967) Percentage biomass consumption of each prey species were compared between former and present approach (Fig. 13).

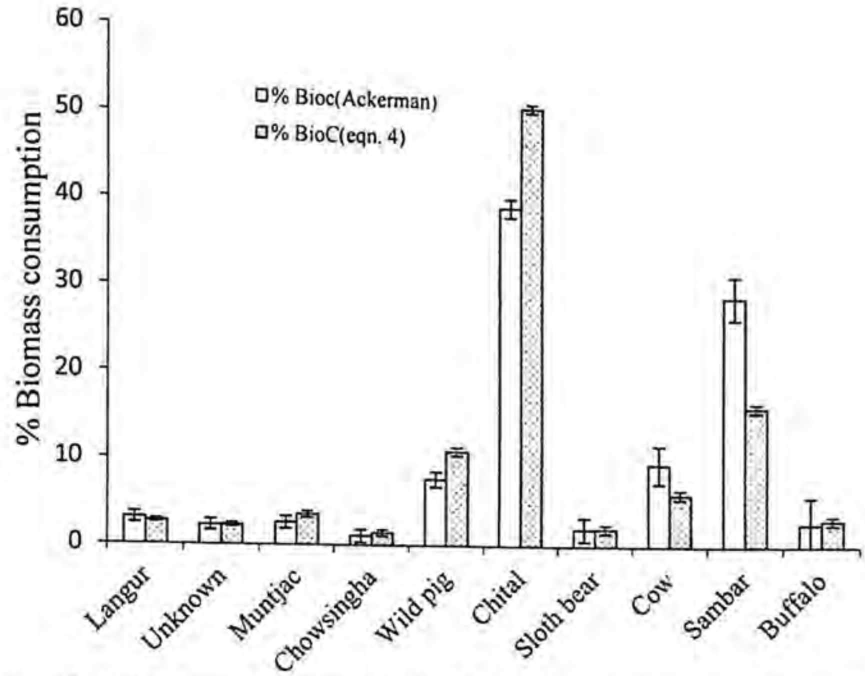


Fig. 13. Comparison between percentage prey biomass consumption of lion in Pench Tiger Reserve using Ackerman's equation (Biswas and Sankar 2002) and using present study models. Error bars represent standard errors.

A trend similar to that in lion and leopard was observed, wherein proportion of medium prey size classes like wild pig (*Sus scrofa*) and chital significantly increased and large prey like sambar and domestic livestock reduced in tiger diet.

Discussion

5. Discussion

This study in agreement with Wachter et al. (2012) demonstrates the need of using a wide prey weight range for proper development of biomass models for carnivores. When prey sizes above the preferred weight range of a carnivore are included in feeding experiments, they enhance the accuracy of the biomass models by generating more information on intrinsic physiology of that carnivore. Number of collectable scats produced by a carnivore from a certain prey weight class is a function of the ratio of digestible-to-indigestible matter in consumed biomass and proportion of utilized carcass.

5.1. Trial observations

Carnivores consumed the viscera and highly digestible parts (flesh) from the carcasses at the beginning of their feeding bout. Small carcasses were entirely eaten up with few bony remnants and feathers left unconsumed. Proportional utilization of carcasses decreased with increasing weight of prey (see appendix, Fig. v). From large carcasses carnivores consumed the choicest parts, leaving much of indigestible matter (hair, bones, skull, hooves and hide) and considerable proportion of muscle mass untouched. The duration of feeding on a carcass by the carnivores during the trials, reflected wild conditions where small carcasses were consumed within a day or two, whereas large carcasses through prolonged durations. The number of days the carnivores fed on a carcass in the trials also mimicked natural conditions where, for a certain carcass weight the number of feeding attempts of a carnivore had an upper limit based on biomass scavenged by other carnivores and rate of carcass decay.

The number of non-collectable scats did not differ significantly between lion and leopard (lion: 10%, leopard: 9%), whereas in jungle cats non-collectable scats were not observed. This might indicate that jungle cats were more efficient in re-absorption of water in their guts.

5.2. Moisture loss from carcasses

Moisture loss from unconsumed parts of carcasses accounted for a significant (26% for mammalian carcasses in 5 days, 38% for chicken carcasses in 2 days) (Section 4.1.1. and 4.1.2.) overestimation of consumption by the carnivores. Thus, if not accounted for, weight loss through desiccation could lead to biased results in computation of actual biomass consumption of carnivores.

5.3. Biomass models

The biomass models developed indicated a saturating response of biomass consumed per collectable scat with different prey size classes, given by an exponential function. Biologically this implied that with increasing prey weight, utilization of carcass reduced and preferential consumption of digestible material (flesh) over hair, bones and hide increased. The results showed that percentage utilization of carcass was higher for small prey compared to larger prey, with utilization levelling out after a certain prey weight (given by logarithmic functions) (see appendix, Fig. v). This indicated an upper ceiling on consumption by carnivores given a finite number of feeding days. Also, owing to selective feeding on highly digestible parts, digestibility of large prey classes were higher. Thus, the result of more scats for relative biomass consumption from smaller prey was a function of surface area-to-volume ratio, percentage carcass utilization and digestibility. However, the satiating response of biomass consumed per collectable scat to prey weight can only be reached at high prey sizes where selective feeding, lower carcass utilization and higher digestibility act synergistically. Previous studies (Floyd *et al.* 1978, Ackerman *et al.* 1984, Weaver 1993, Marker *et al.* 2003, Jethva and Jhala 2004, Ruhe *et al.* 2007) reported linear biomass models possibly because of providing a limited range of prey weights.

5.4. Comparison between former and present approach

Results strongly suggest that the former approach of diet estimation, using Ackerman's equation (1984) significantly overestimated consumption of large prey sizes like sambar and domestic livestock and underestimated medium prey sizes like chital in diet of big cats of the Indian sub-continent. This was essentially because, Ackerman's equation suggested a linear response between biomass consumed per collectable scat and prey weight, where biomass consumed to excrete one collectable scat increased infinitely with increase in prey body weight. However, a more biologically meaningful calibration technique (satiating response) between biomass consumed and collectable scats used in the present study depicted a different scenario (Fig. 14). Proportion of medium prey sizes increased in carnivore diet with significant reduction in large prey (domestic livestock) consumption. These results have strong conservation implication for large carnivores in a country like India with ever increasing man-carnivore conflict on 'perceived' livestock depredation rates.

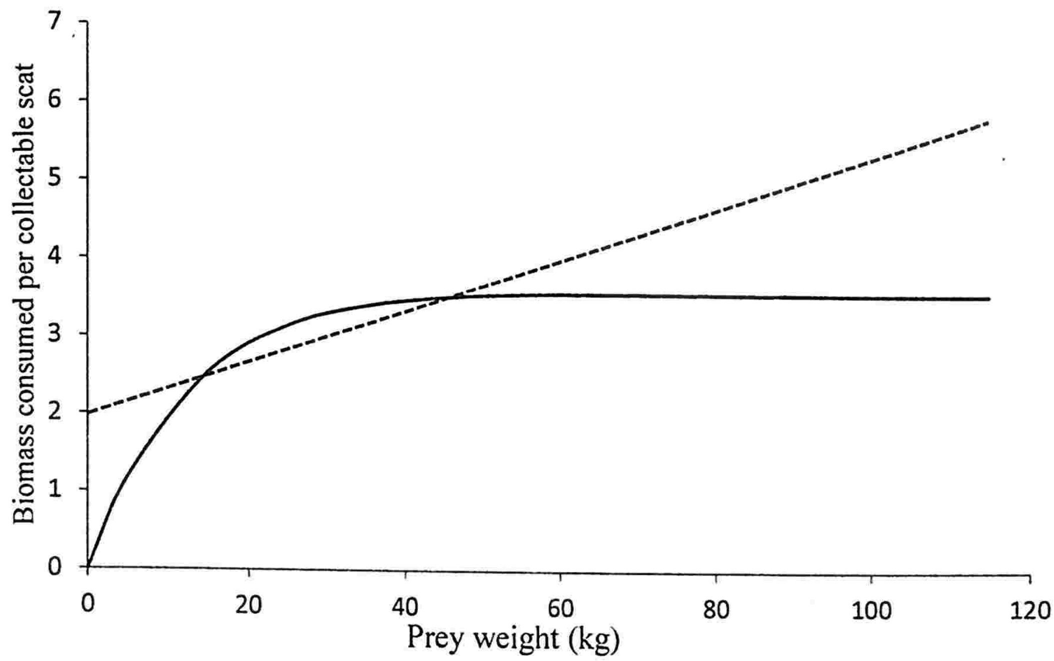


Fig. 14. Comparison of Ackerman's model (linear) and lion specific model (satiating) using a hypothetical dataset

5.5. Generalized equation for tropical felids

The present study comprised of three different tropical felids which represented a wide range of carnivore body size. However, estimates of the parameters of the three equations scaled to their corresponding predator weights, which indicated a strong allometric relation of biomass consumption and prey size class. Thus, biomass consumption and prey weight range of predators were a function of their individual body weight. Also, when the three equations were scaled to their respective carnivore body weights, no significant difference was found between them. A generalized equation representing a wide range of tropical felid body weight was established. From the generalized model it was evident that, for tropical predators, biomass consumed to excrete one collectable scat satiated at prey weight approximately half the carnivore's body weight (Fig. 8). The generalized equation differed with that of Ackerman's equation in the same proportion as did the lion and leopard specific equations. The generalized model had no significant difference with the carnivore specific equations and thus, could be used on tropical felids where no feeding trials have been done to calibrate biomass consumption and scat produced.

5.6. Re-construction of carnivore diet

Re-analyses of published literature on diet of tropical big cats, using equations developed in the current study, showed significant difference between proportions of consumed prey biomass from what postulated earlier. Medium sized prey like chital contributed more to large carnivore diet than large prey like sambar, nilgai and domestic livestock. Thus, our hitherto understanding of dietary segregation of large sympatric felids on the basis of their consumption of prey species of different body sizes (where large carnivores maximized on large prey) might not be the case. Current study models showed that chital constituted the major portion of consumed biomass of tiger and leopard making chital the most important prey species of Indian large felids. Thus, chital owing to its high availability and pan-country presence is the key to carnivore conservation in India. Present study models also refined our understanding of human-carnivore conflict, where, significant reduction of domestic livestock in carnivore diet lowered actual conflict levels.

Synthesis

6. Synthesis

1. Results showed that more biomass was consumed per collectable scat for larger prey in comparison to smaller prey eaten by the carnivores, which satiated after a certain prey weight. This reflected the higher surface area-to-volume ratio and utilization of small prey, higher digestibility of large prey and upper consumption limit of carnivores from carcasses.

2. Three relationships between biomass consumed per collectable scat (Y) and prey weight (X) were computed for lion (a), leopard (b) and jungle cat (c):

a. $Y = 3.674\ (1 - e^{-0.079X})$

b. $Y = 1.922(1 - e^{-0.123X})$

c. $Y = 0.125(1 - e^{-3.004X})$

3. Equation developed for small tropical felid (jungle cat) would help in better understanding of the intricacies of small carnivore guilds by better representation of their diets.

4. A generalized correction equation was developed for all tropical felids where biomass consumed to produce one collectable scat scaled to predator body mass (Y_g) increased with mean prey weight per predator mass (X_g) and satiated after a certain prey to predator weight ratio, given by:

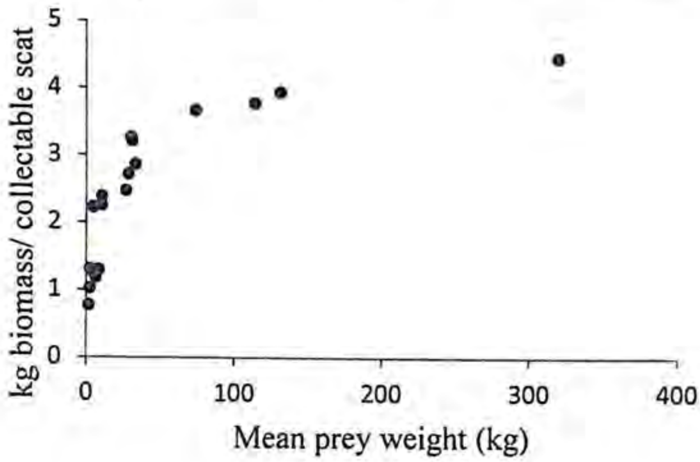
$$Y_g = 0.029(1- e^{-9.909X_g})$$

5. Equations specific for lion and leopard significantly differed from Ackerman's equation.

6. Re-characterization of Indian large felid diet using current study models substantially refined our previous understanding of biomass contribution of different prey by increasing proportion of medium prey consumption. Domestic livestock significantly reduced in carnivore diet, reducing conflict levels.

Appendix

7. Appendix



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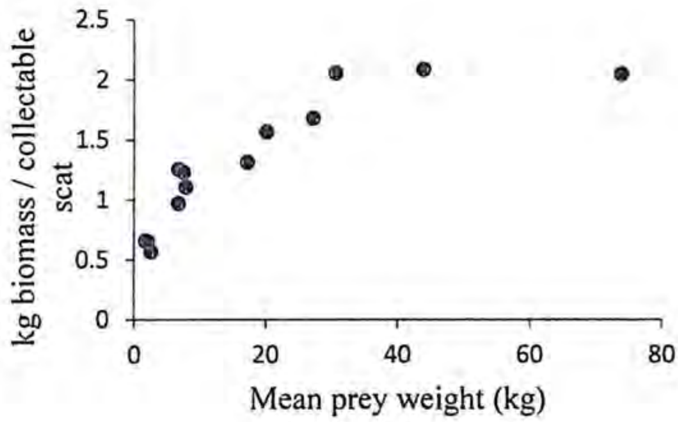
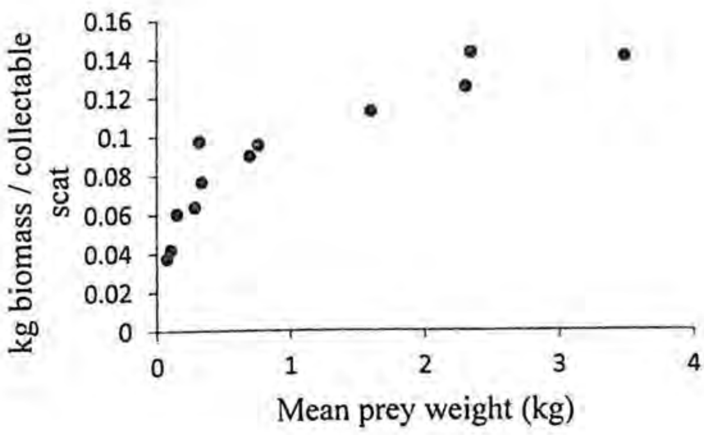
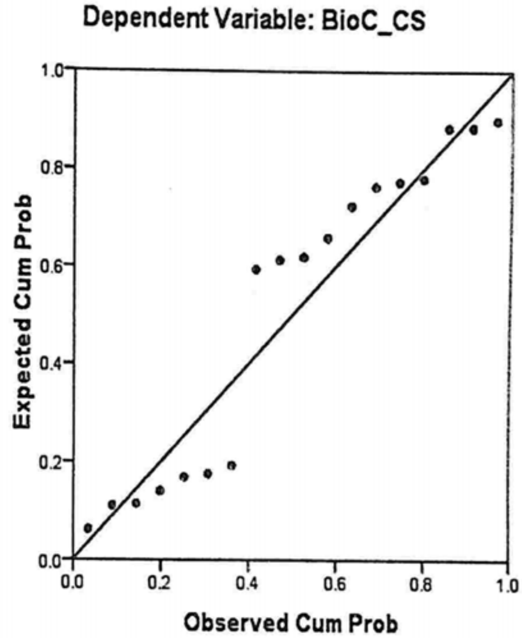


B.

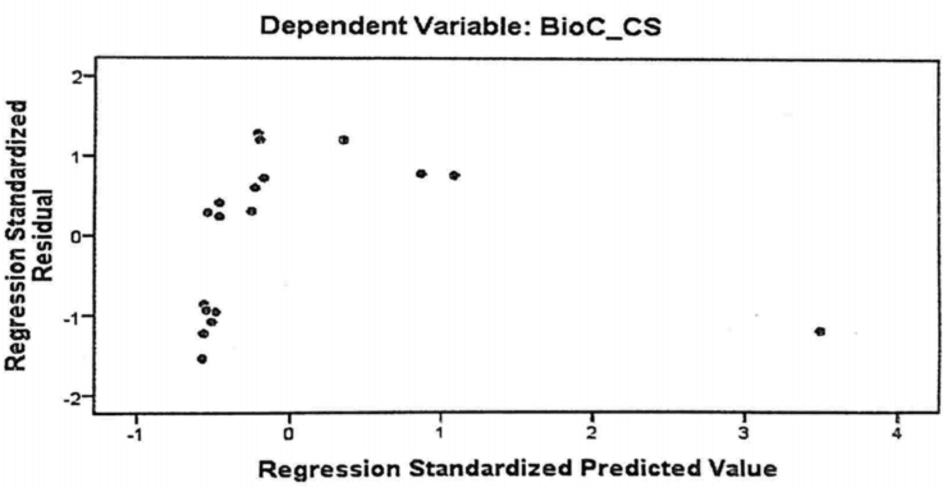


C.

Fig. i. Scatter plots between biomass consumed per collectable scat and mean prey weight for A. lion B. leopard and C. jungle cat

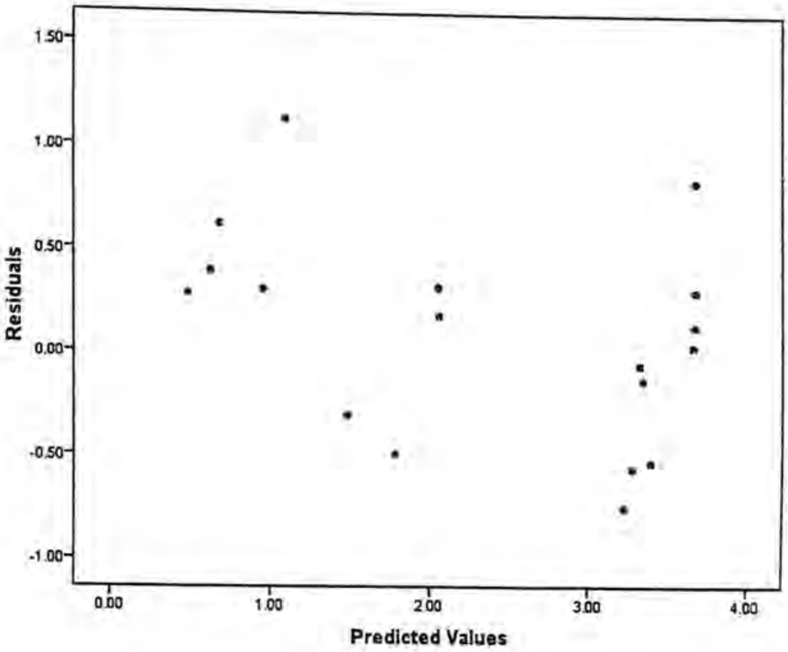


A.



B.

Fig. ii. Residual plots of linear model fitted to data from feeding trials on lion showing a strong trend, re-inforcing non-linear relationship between biomass consumed per collectable scat and mean prey weight. Similar trends were obtained when linear models were fitted to Y and X values obtained from feeding trials on leopard and jungle cat.



A.

One-Sample Kolmogorov-Smirnov Test

		Residuals
N		18
Normal Parameters[a]	Mean	.0925
	Std. Deviation	.50117
Most Extreme Differences	Absolute	.109
	Positive	.109
	Negative	-.091
Kolmogorov-Smirnov Z		.461
Asymp. Sig. (2-tailed)		.983

Test distribution is Normal

B.

Fig. iii. A. Scatter plot between residual and predicted values after fitting exponential model to lion data

B. One sample K-S test showing normal distribution of residuals from exponential model on lion data

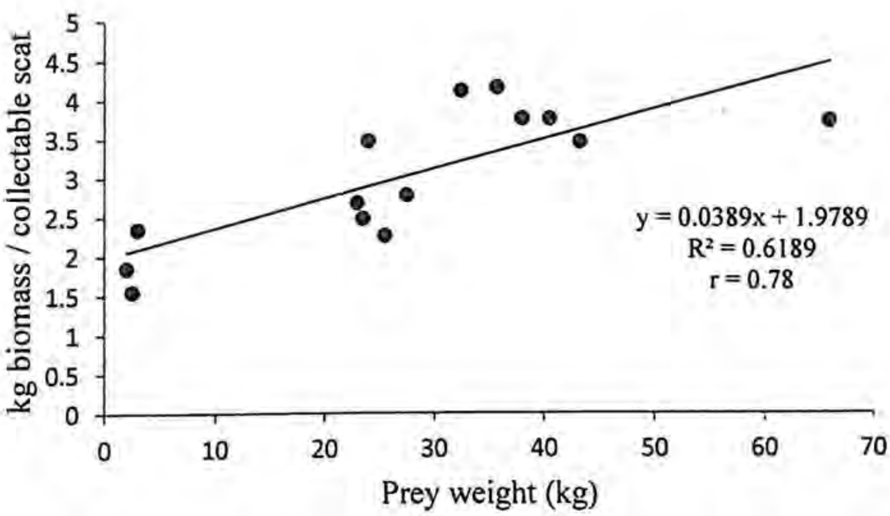
Similar trends were obtained from leopard and jungle cat data

Table i. Hypothetical dataset for lion and leopard used in section 4.6. Y(A) denote Y values using Ackerman's equation

Prey wt (kg)	Prey wt/pred wt	Y (A)	Y (eqn. 1)	Y (eqn. 4)	Y (A) - Y (eqn. 1)	Y (A) - Y (eqn. 4)	Y (eqn.2)	Y (A)-Y (eqn.2)
5	0.04	2.16	1.20	1.19	0.96	0.96	0.88	1.27
15	0.12	2.51	2.55	2.57	-0.05	-0.06	1.62	0.89
25	0.19	2.86	3.16	3.21	-0.31	-0.35	1.83	1.02
35	0.27	3.21	3.44	3.51	-0.24	-0.30	1.90	1.31
45	0.35	3.56	3.57	3.65	-0.01	-0.09	1.91	1.64
55	0.42	3.91	3.63	3.71	0.28	0.19	1.92	1.99
65	0.50	4.26	3.65	3.74	0.60	0.51	1.92	2.33
75	0.58	4.61	3.66	3.76	0.94	0.85	1.92	2.68
85	0.65	4.96	3.67	3.76	1.29	1.19	1.92	3.03
95	0.73	5.31	3.67	3.77	1.63	1.54	1.92	3.38
105	0.81	5.66	3.67	3.77	1.98	1.89	1.92	3.73
115	0.88	6.01	3.67	3.77	2.33	2.24	1.92	4.08
125	0.96	6.36	3.67	3.77	2.68	2.59	1.92	4.43
135	1.04	6.71	3.67	3.77	3.03	2.94	1.92	4.78
145	1.12	7.06	3.67	3.77	3.38	3.29	1.92	5.13
155	1.19	7.41	3.67	3.77	3.73	3.64	1.92	5.48
165	1.27	7.76	3.67	3.77	4.08	3.99	1.92	5.83
175	1.35	8.11	3.67	3.77	4.43	4.34	1.92	6.18
185	1.42	8.46	3.67	3.77	4.78	4.69	1.92	6.53
195	1.50	8.81	3.67	3.77	5.13	5.04	1.92	6.88
205	1.58	9.16	3.67	3.77	5.48	5.39	1.92	7.23

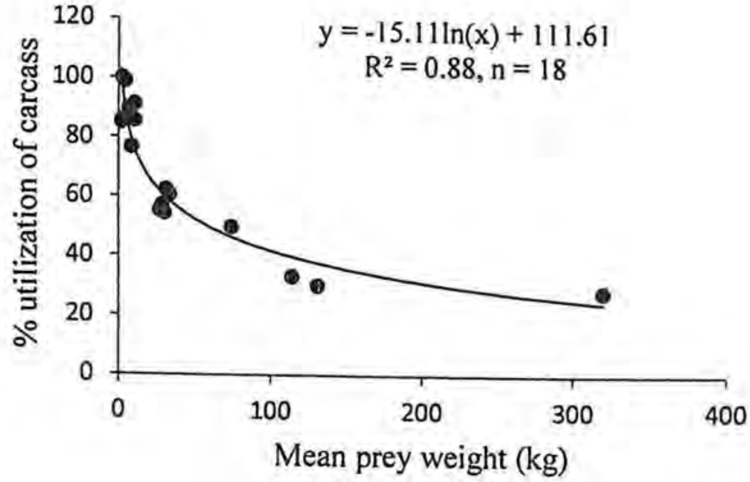
Table ii. Re-constructed Ackerman's dataset

Prey weight (kg)	kg biomass/collectable scat
2	1.85
2.5	1.55
3	2.35
23	2.7
23.5	2.5
24	3.5
25.5	2.28
27.5	2.8
32.5	4.15
35.75	4.2
38	3.8
40.5	3.8
43.25	3.5
66	3.78

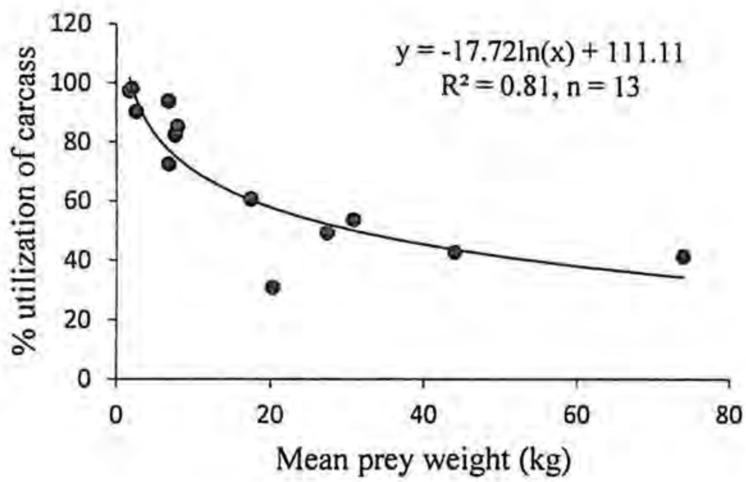


Actual Ackerman eqn. was y = 0.035x + 1.98, (r = 0.77, n= 15)

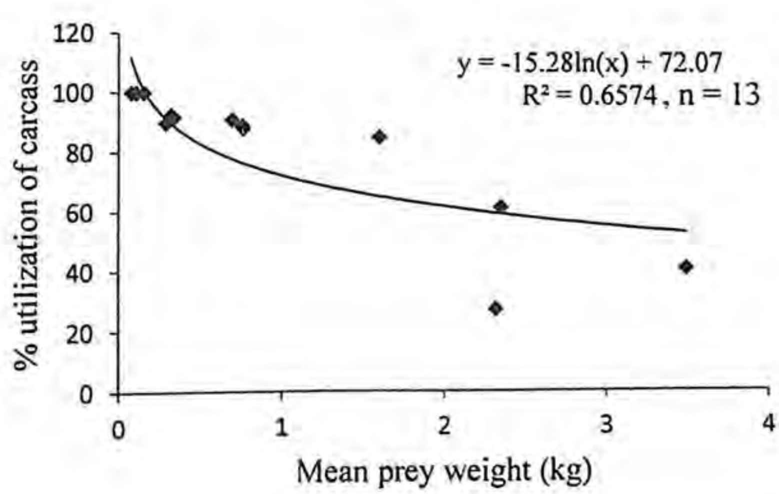
Fig. iv. Re-constructed Ackerman's model. Also given along with is the legend for the graph and the actual Ackerman model



A.



B.



C.

Fig.v. Relationship between % utilization of carcass and prey weight (kg) for A. lion, B. leopard and C. jungle cat. Also given are the corresponding equations and R^2 values in legends.

Plate 1. Field collectable and non-collectable scat of lion

Plate 2. Collection of scat from lion enclosure

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