

Re-evaluating models for estimating prey consumption by leopards

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Introduction

Assessing the diet of large, terrestrial carnivores is important for ecological research and conservation, but is difficult given the rarity and cryptic nature of these species (Nilsen *et al.*, 2012). Diet profiles are generated mostly by indirect methods such as identification of undigested prey remains (hair, bones, teeth, hooves and claws) in scats found in the environment (Klare, Kamler & Macdonald, 2011). Despite the progress in methodologies of prey recognition in scats, reliable estimation of prey biomass from scats remains challenging (Rühe, Ksinsik & Kiffner, 2008; Klare *et al.*, 2011; Rodgers & Janečka, 2013).

Although still frequently used, frequency of prey occurrence (FO) in scats introduces a bias in prey proportions by over-

Abstract

Biomass regression models and associated correction factors derived from feeding trials are essential to convert frequency of prey occurrence from scats into biomass and numbers of prey individuals consumed by carnivores. These dietary analyses form a substantial part of many research projects on predator–prey relationships and human–carnivore conflicts. So far, diet studies of leopard (*Panthera pardus*) applied the linear biomass model developed for puma (*Puma concolor*). Recent works, however, suggested that non-linear biomass models are more meaningful for estimating prey biomass and numbers, and presented a generalized model of biomass consumption for all tropical felids. This model accounted for partial consumption of prey, but did not include ecological factors limiting prey consumption by felids. Hence, using 35 feeding trials we developed a leopard specific regression equation by setting a consumption limit for leopard per prey. This new correction factor takes into account the proportion of inedible matter of prey and daily food intake. Besides refining the leopard specific biomass models, our study also showed the saturation in scat production with consumption of larger prey, which was described in recent studies. A reanalysis of prey consumption by leopards from published diet studies by using our new regression models suggests a significant decrease in estimated absolute numbers of prey individuals consumed. This finding and the higher share of larger prey in leopard diet may affect subsequent analyses using prey profiles, and may affect decisions made in biodiversity conservation and management, especially in the area of human–carnivore conflict.

representing small prey species and underestimating large prey species in the diet (Floyd, Mech & Jordan, 1978; Ackerman, Lindzey & Hemker, 1984; Klare *et al.*, 2011). This is because (1) the surface-to-volume ratio is inversely related to prey body mass and (2) small prey is often consumed completely while large-bodied species are only ingested partly by carnivores (Floyd *et al.*, 1978; Wachter *et al.*, 2012). Hence, indigestible matter is disproportionately represented in ingested smaller prey, leading to larger number of scats when feeding on small vs. large prey species (Floyd *et al.*, 1978; Ackerman *et al.*, 1984; Jethva & Jhala, 2004). To overcome this bias in estimating biomass and individuals of consumed prey from scats, several methods are proposed and have been reviewed by Ruhe *et al.* (2008) and Klare *et al.* (2011). These are usually based on

data from feeding trials in which carnivores consume prey species of different body masses and the produced scats are subsequently quantified. Two different approaches can then be used to estimate prey biomass from scats:

- (1) Dry mass of indigestible matter is related to fresh matter of the prey individual. This generates a single conversion factor for a given prey species or size class (Webbon *et al.*, 2006; R uhe *et al.*, 2008), or a linear function that can be used to convert dry mass of indigestible scat remainders to prey body mass (R uhe, Burmester & Ksinik, 2007).
- (2) Prey biomass consumed per excreted scat is related to prey body mass as expressed by linear or non-linear regressions equations, known as biomass models or correction factors (CF's; Wachter *et al.*, 2012).

Biomass models were first developed for wolf (*Canis lupus*; Floyd *et al.*, 1978) and subsequently for several felid species, e.g. puma (*Puma concolor*; Ackerman *et al.*, 1984) and cheetah (*Acinonyx jubatus*; Marker *et al.*, 2003; Wachter *et al.*, 2012), with the equation of Ackerman *et al.* (1984) still being the most widely applied in felid diet studies (e.g. Selvan *et al.*, 2013; Lyngdoh *et al.*, 2014; Santos *et al.*, 2014; Hern andez-SaintMart ın *et al.*, 2015).

As leopards (*Panthera pardus*) are known for their diverse diet, biomass models are preferred over conversion factors because they can deal with the full range of prey species and are less laborious (Ciucci, Tosoni & Boitani, 2004; Hayward *et al.*, 2006; Klare *et al.*, 2011; Shehzad *et al.*, 2012). Yet, two issues arise when applying these models. The first concerns the shape of the curve of the biomass model. Previous models assumed a linear relationship between prey biomass consumed per excreted scat (y) and prey body mass (x) (Floyd *et al.*, 1978; Ackerman *et al.*, 1984). However, Wachter *et al.* (2012) suggested that this relationship should reach an asymptote due to physiological constraints related to the amount of food intake and defecation, and applied non-linear regression models to their cheetah data. A recent study validated this non-linear relationship for biomass consumption and introduced a generalized model to calculate biomass consumption for all tropical felids based on feeding trials with lion (*Panthera leo*), leopard, jungle cat (*Felis chaus*) and domestic cat (*F. catus*) (Chakrabarti *et al.*, 2016). The second issue concerns the estimation of numbers of prey individuals consumed. Previous approaches assumed the complete consumption of prey body by simply dividing the biomass consumed (D) by the average prey body mass (x) to obtain the numbers of prey individuals consumed (E) (Floyd *et al.*, 1978; Ackerman *et al.*, 1984; Marker *et al.*, 2003). Yet, carnivores often do not consume a carcass completely (Vucetich, Vucetich & Peterson, 2012), e.g. the mean carcass utilization by cheetah and Eurasian lynx (*Lynx lynx*) during feeding trials was 69.7% and 78.0%, respectively (Marker *et al.*, 2003; R uhe *et al.*, 2007). Also, the portions of inedible matter typically depend on prey body mass (Stander *et al.*, 1997). Therefore, Wachter *et al.* (2012) developed two CF's, which account for these two biases: correction factor 1 (CF_{1w}) to determine the consumed prey biomass and

correction factor 2 (CF_{2w}) to express the number of prey individuals consumed. Though the CF_{2w} approach accounts for partial consumption of prey, duration of single feeding trials does not span the entire time free-ranging leopards spend on their kills. Leopards have been observed to prey for up to 5 days upon a carcass and to consume on average 4.7 ± 0.3 kg of meat per day (Odden & Wegge, 2009).

So far, studies of leopard diet applied the linear regression equation developed by Ackerman *et al.* (1984) in spite of novel models by Wachter *et al.* (2012) and Chakrabarti *et al.* (2016) (Selvan *et al.*, 2013; Taghdisi *et al.*, 2013; Farhadinia, Moqanaki & Hosseini-Zavarei, 2014; Sidhu, Raman & Mudappa, 2015). However, applying potentially inaccurate methods to estimating prey consumption by leopards might be particularly problematic when assessing the extent of human-leopard conflict, e.g. when quantifying livestock depredation rates or the extent of prey overlap with human hunters (Kissui, 2008; Henschel *et al.*, 2011; Shehzad *et al.*, 2014; Athreya *et al.*, 2016). Hence, accurate estimation of prey individuals consumed by leopards is a priority topic for conservation, which could help mitigating drivers of conflict, e.g. by restoring depleted wild prey base and planning reintroduction projects for sympatric carnivores (Hayward *et al.*, 2006; Inskip & Zimmermann, 2009; Mondal *et al.*, 2012; Kabir *et al.*, 2014). Moreover, accurate estimates help evaluating the impact of leopards on prey species of conservation concern (Farhadinia *et al.*, 2014).

In this study, we (1) develop leopard specific biomass models from feeding trials to improve the existing biomass models for obtaining more realistic estimates of prey biomass and numbers consumed, and (2) apply these models to selected published leopard diet studies in order to reassess and compare these estimates.

Materials and methods

Feeding trials

We conducted 21 feeding trials with 22 captive leopards between 2012 and 2016 in eight zoos in Germany, Switzerland and Iran (Tables S1 and S2). The prey species ranged from 0.87 kg (rabbit *Oryctolagus cuniculus*) to 69.45 kg (domestic sheep *Ovis aries*) (Table S2). All feeding experiments were carried out by zoo personnel following the same protocol and setup of previous studies (Ackerman *et al.*, 1984; Wachter *et al.*, 2012). Prior to feeding, leopards were fasted for at least 48 h until no more scats from previous feedings were produced, and all scats were removed from the enclosure. During each feeding experiment, leopards were provided with one or more intact prey items of the same species of known body mass. If leopards did not feed on the prey after some time, the prey's abdominal cavity was opened. In one trial, the prey head was removed for safety concerns. The zoos provided all prey specimens and the feeding events were part of their usual feeding programme. Because of the dependence of scat production on prey body mass, food items were selected to cover the whole prey range of the leopard (Ackerman *et al.*, 1984). Large prey items were left in the enclosure for up to 2 days.

In one case, the prey was left for 65 h. Small prey items were removed earlier if the leopard showed no signs of feeding behaviour for at least 2 h. Thereafter, all prey remains were collected from the enclosure, weighed and compared with the initial prey body mass to assess carcass utilization. After fasting for another 48 h, all scats produced in the enclosure during the feeding event were collected, counted and weighed individually. The period of 48 h used for fasting and scat collection was based upon the observations by Bothma & Le Riche (1994) and was similar to other studies (Floyd *et al.*, 1978; Ackerman *et al.*, 1984). To increase sample size, we added 14 feeding trials with leopards from Chakrabarti *et al.* (2016), which followed the same procedure as Ackerman *et al.* (1984) and Wachter *et al.* (2012). The prey species ranged from 1.7 kg (chicken *Gallus* sp.) to 151 kg (water buffalo *Bubalus bubalis*) (Chakrabarti *et al.*, 2016).

Data analysis

We obtained the leopard specific correction factors, $CF1_{\text{leopard}}$ to estimate biomass and $CF2_{\text{leopard}}$ to estimate number of individuals consumed, following the method specified by Wachter *et al.* (2012).

To obtain $CF2_{\text{leopard}}$, we amended Wachter *et al.*'s (2012) method by extrapolating the number of excreted scats per leopard and prey (Q_4) from the actual consumption of a carcass (CU, %) in relation to the maximum possible carcass utilization (S_i , %) based on field observations and defined S_i as 100% consumption of prey < 5 kg, 95% of 5–25 kg prey and 70% of prey > 25 kg (Stander *et al.*, 1997). As complete consumption of large prey seems unrealistic we added another consumption limit to our $CF2_{\text{leopard}}$ model. Based on an average maximum daily food intake of 5 kg and a maximum of 5 days spent per kill (Odden & Wegge, 2009), we set the maximum consumption limit to 25 kg (5 kg per day by 5 days) of meat per prey larger than 35.7 kg (70% = 25 kg). Hence, for each feeding trial we used these consumption limits to predict the number of scats produced under natural conditions ($Q_{4,\text{new}}$): for prey > 35.7 kg $Q_{4,\text{new}} = (Q_4/CU_i) * ((25 \text{ kg}/Q_1) * 100)$; for prey < 35.7 kg $Q_{4,\text{new}} = Q_4/CU_i * S_i$. $Q_{4,\text{new}}$ was then regressed against Q_1 (body mass of the i -th prey individual consumed) and a model fitted. Finally, to test the $CF2_{\text{leopard}}$ method with the previous approach, we developed a $CF2_{\text{leopard-W}}$ model for leopard following Wachter *et al.*'s (2012) $CF2_W$ method.

All analyses were carried out in R statistical software (R Development Core Team, 2012). The regression analyses were done using the package 'nlme' (Pinheiro *et al.*, 2012) with the function 'nls' (nonlinear least squares) for fitting the linear and non-linear regression models (Tables S2 and S3). Final models were chosen considering Akaike Information Criterion (Burnham & Anderson, 2002), residual sum of squares (RSS) and R^2 (Table S4).

Recalculation of diet studies

We retrieved all published articles that applied the CF's of Ackerman *et al.* (1984) or Wachter *et al.* (2012) to leopard

scat data by searching the Web of Science by Thomson Reuters. Because Chakrabarti *et al.*'s (2016) generalized biomass model for tropical felids was published only recently, no study had applied their correction factor to date. We excluded all studies lacking prey body mass (x) and frequency of prey occurrence in scats (FO). This selection resulted in eight peer-reviewed articles – seven applying Ackerman *et al.*'s conventional method (CF_A) and one applying Wachter *et al.*'s non-linear models for tropical felids ($CF1_{W-trop}$ and $CF2_{W-trop}$) – for which we recalculated relative biomass D (%) and relative number of prey individuals E (%) consumed (Khorozyan & Malkhasyan, 2002; Henschel, Abernethy & White, 2005; Andheria, Karanth & Kumar, 2007; Ramesh *et al.*, 2009; Wang & Macdonald, 2009; Taghdisi *et al.*, 2013; Sidhu *et al.*, 2015; Ghoddousi *et al.*, 2016). As absolute values of D (kg) and E (n) were not always reported, recalculation of these values was limited to two studies (Khorozyan & Malkhasyan, 2002; Ghoddousi *et al.*, 2016). Based on data from these eight studies, we compared prey biomass and numbers estimated using CF_A or $CF1_{W-trop}$ and $CF2_{W-trop}$ vs. our $CF1_{\text{leopard}}$ and $CF2_{\text{leopard}}$ models. Furthermore, we compared $CF2_{\text{leopard}}$ to $CF2_{\text{leopard-W}}$ by recalculating the same case studies.

As the regression equations ($CF1_{\text{leopard}}$, $CF2_{\text{leopard}}$, and $CF2_{\text{leopard-W}}$) were solved for each prey species (i), we estimated the biomass ($D_i = n_i * CF1_i$) and the numbers ($E_i = n_i / CF2_i$) of prey consumed, where n_i is the number of scats containing the i -th prey species. Prey body mass was taken from the corresponding studies. Wilcoxon signed-rank test was run to test for differences between the new and published estimates of D and E . Estimates of all seven studies applying CF_A were pooled for the analysis.

Results

Feeding trials

Each leopard consumed on average (\pm SE) 5.02 ± 0.78 kg ($N = 21$ trials) and 87 scats were collected in total. With the inclusion of 14 leopard feeding trials from India (Chakrabarti *et al.*, 2016), 28.57% ($N = 10$ of 35 trials) of prey used in trials fell within the prey mass range of 10–40 kg preferred by leopards and 88.57% ($N = 31$ trials) fell within the accessible (preferred and killed relative to abundance) prey mass range of 1–45 kg (Clements *et al.*, 2014).

Leopard specific correction factors

All leopard specific biomass models ($CF1_{\text{leopard}}$, $CF2_{\text{leopard}}$, and $CF2_{\text{leopard-W}}$) followed a non-linear pattern. The relationship between prey mass and biomass consumed per scat produced ($CF1_{\text{leopard}}$) was best described by the Michaelis-Menten model (Fig. 1a; Table S4). In $CF1_{\text{leopard}} = 2.242x/(4.976 + x)$ (SE: $a = 0.227$, $b = 1.701$; $R^2 = 0.54$; $P < 0.001$), the consumed prey biomass per excreted scat reached an asymptote at approximately 65 kg of prey body mass with ca. 2 kg of prey consumed per scat. The relationship between prey mass and number of scats produced per prey individual consumed ($CF2_{\text{leopard}}$) was best described by a 3-parameter asymptotic exponential function

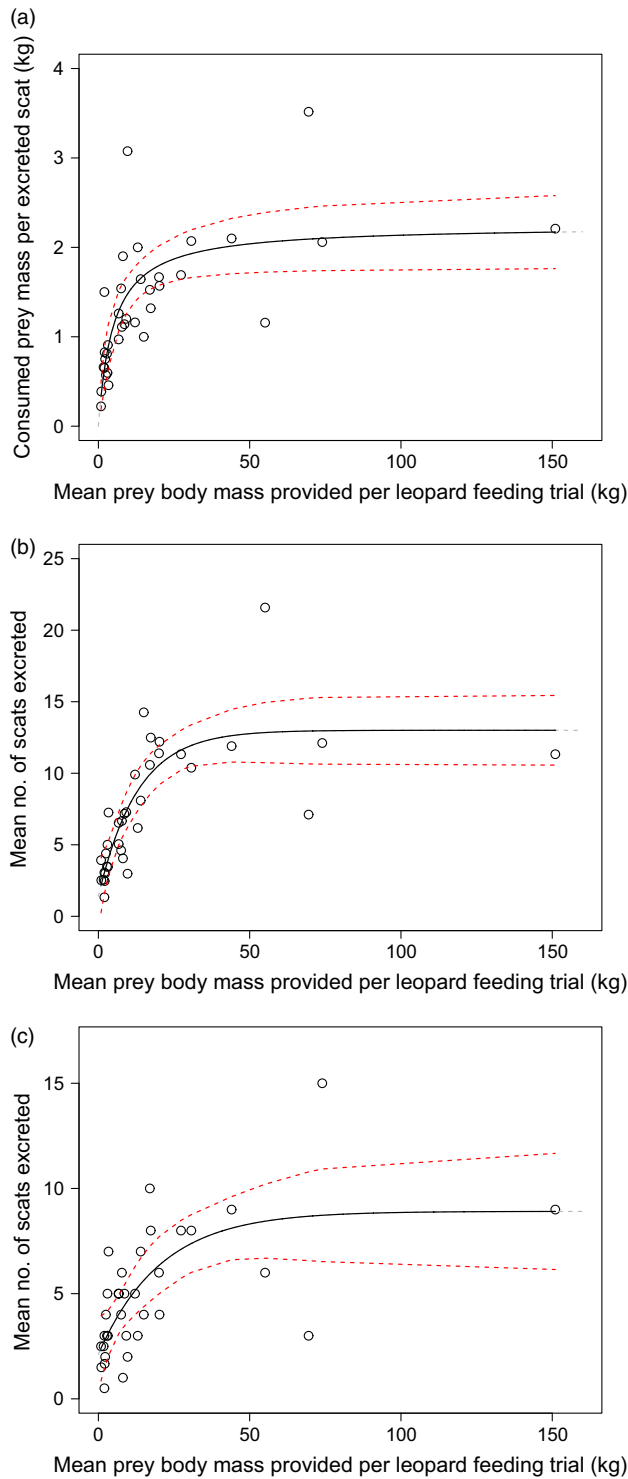


Figure 1 Leopard specific biomass regression models (solid line) showing the relationship between (a) the prey biomass consumed per excreted scat and the mean prey body mass, best described by a Michaelis-Menten function $CF1_{leopard} = 2.242x/(4.976 + x)$; (b) the mean number of collectable scats excreted per prey consumed ($Q4_{new}$), based on edible carcass proportions (Stander *et al.*, 1997) and a consumption limit of 25 kg of meat for prey larger than 35.7 kg, and the mean prey body mass, best described by a 3-parameter asymptotic exponential function $CF2_{leopard} = 13.004 - 11.601exp^{-0.078x}$; (c) the mean number of collectable scats excreted per prey consumed ($Q4$) and the mean prey body mass, following Wachter *et al.*'s (2012) method, best described by a 3-parameter asymptotic exponential function $CF2_{leopard-W} = 8.912 - 6.792exp^{-0.049x}$. Uncertainty of parameters is shown as the 95% confidence intervals (CI; broken line) for each biomass model. [Colour figure can be viewed at wileyonlinelibrary.com]

(Fig. 1b; Table S5). In $CF2_{leopard} = 13.004 - 11.601exp^{-0.078x}$ (SE: $a = 1.195, b = 1.417, c = 0.024; R^2 = 0.68; P < 0.001$) an asymptote was reached at approximately 50 kg of prey body mass with 12–13 scats excreted. $CF2_{leopard-W}$ was also best represented by a 3-parameter asymptotic exponential function $CF2_{leopard-W} = 8.912 - 6.792exp^{-0.049x}$ (SE: $a = 1.369, b = 1.400, c = 0.026; R^2 = 0.46; P < 0.001$) (Fig. 1c; Table S5). The relationship between the leopard specific $CF1_{leopard}$, $CF2_{leopard}$ and $CF2_{leopard-W}$ to other biomass models is shown in Fig. 2a,b, respectively.

Recalculations of leopard diet

Recalculation of biomass consumption from the eight selected studies with the leopard specific $CF1_{leopard}$ resulted in no significant change in estimates of relative biomass consumed D (%) compared to CF_A ($Z = -1.368, P > 0.05$; Fig. 3a–g) and $CF1_{W-trop}$ ($Z = -0.153, P > 0.05$; Fig. 3h). Relative prey numbers consumed E (%) obtained by $CF2_{leopard}$ changed significantly in either direction compared to CF_A estimates ($Z = -2.383, P < 0.05$; Fig. 3a–g) but were non-significant between $CF2_{leopard}$ and $CF2_{W-trop}$ ($Z = -0.357, P > 0.05$; Fig. 3h) and $CF2_{leopard-W}$ ($Z = -0.144, P < 0.05$) (Table S6a–h). Estimates of absolute prey biomass consumed D (kg) showed no difference with $CF1_{W-trop}$ ($Z = -1.682, P > 0.05$; Fig. 4b). However, absolute prey numbers consumed E (n) were significantly lower when applying $CF2_{leopard}$ compared to $CF2_{W-trop}$ ($Z = -2.803, P < 0.01$; Fig. 4b) and resulted in significantly smaller numbers of prey individuals consumed E (n) when compared to $CF2_{leopard-W}$ ($Z = -7.274, P < 0.001$; Table S6a–h). Absolute estimates of prey biomass and numbers of prey individuals consumed were not compared with Khorozyan & Malkhasyan (2002) due to small sample size ($N = 6$) but Fig. 4a shows a decrease in estimates of both D (kg) and E (n) by using $CF1_{leopard}$ and $CF2_{leopard}$ compared to CF_A , respectively.

Discussion

Our leopard specific biomass models support previous findings that the relationships between prey body mass, biomass consumption and scat production follow an asymptotic curve

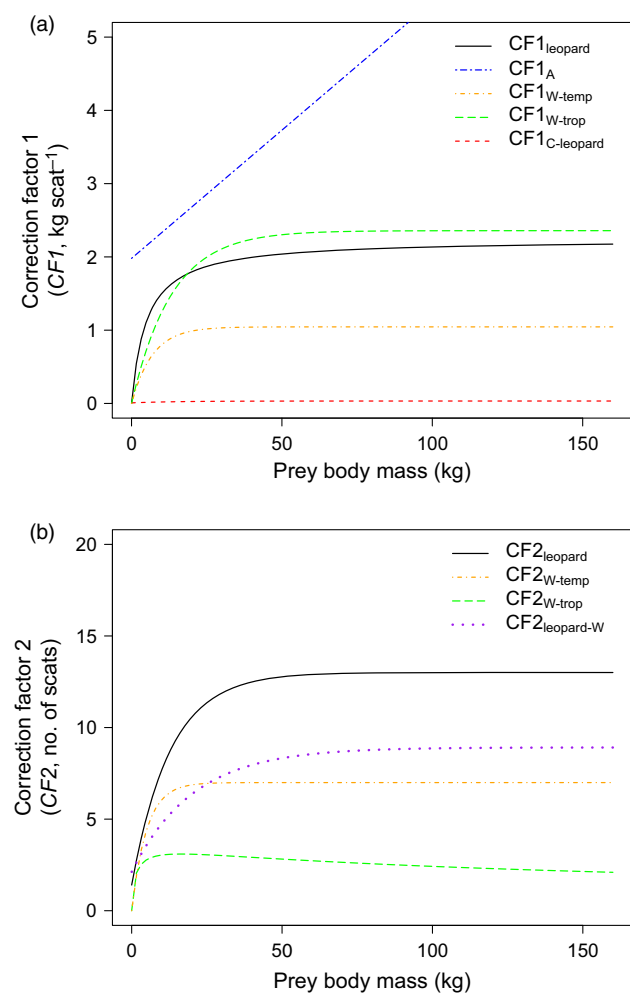


Figure 2 Comparison of different biomass regression models used in scat analyses of felids: (a) the relationship between our CF1_{leopard} (leopard), CF_A (puma; Ackerman *et al.*, 1984), CF1_{W-trop} (cheetah and tropical felids), CF1_{W-temp} (lynx and temperate felids; Wachter *et al.*, 2012), and CF1_{C-leopard} (Indian leopards, body mass of leopard is set to 65 kg; Chakrabarti *et al.*, 2016) to estimate prey biomass consumed by carnivores; (b) the relationship between CF2_{leopard} (leopard), CF2_{leopard-W} (leopard; following Wachter *et al.*'s (2012) method), CF2_{W-trop} (cheetah and tropical felids) and CF2_{W-temp} (lynx and temperate felids; Wachter *et al.*, 2012) to estimate number of prey individuals consumed by carnivores. [Colour figure can be viewed at wileyonlinelibrary.com]

(Wachter *et al.*, 2012; Chakrabarti *et al.*, 2016) in contrast with earlier models stating a linear relationship (Ackerman *et al.*, 1984; Marker *et al.*, 2003). Although Wachter *et al.* (2012) considered partial consumption of prey as an important factor in estimating prey numbers consumed, other factors such as daily food intake or limitations of in-situ experiments were not considered. Particularly, estimation of prey numbers consumed using CF2 is sensitive to carcass utilization. Considering the proportion of inedible matter of prey at different body mass ranges (Stander *et al.*, 1997), an average maximum daily

consumption limit of 5 kg and a maximum of 5 days spent feeding on prey (Odden & Wegge, 2009), we developed a biomass model (CF2_{leopard}) which potentially reflects numbers of prey individuals consumed from leopard scat data more realistically. However, estimates from biomass models should be seen as a mean within a certain predicted range. This range is e.g. given by the uncertainty of model parameters and dependent on the mean prey body mass used in solving the CF's. For the latter, $\frac{3}{4}$ of female body mass is usually used to account for variation in prey body mass within a species (Jooste *et al.*, 2013). Also, when estimating absolute numbers the application of correction factors is meaningful only if scats were sampled on a regular basis (Wachter *et al.*, 2012).

In comparison with previous linear and non-linear models, our new leopard specific models produced similar estimates of relative prey biomass consumed, but significantly different estimates of relative numbers of prey individuals consumed. Further, the new leopard-specific models confirmed significant differences in absolute biomass consumed (Fig. 4, left column) and estimated lower absolute numbers of prey individuals consumed for prey over 0.5 kg (Fig. 4, right column).

As top predator with extensive distribution and diverse diet, the leopards' feeding ecology received substantial attention in the scientific literature (Hayward *et al.*, 2006; Balme *et al.*, 2014). These studies defined the leopard as an opportunistic ambush hunter that prefers preying upon ungulates within 10–40 kg of body mass within an accessible prey mass range of 1–45 kg (Hayward *et al.*, 2006; Clements *et al.*, 2014). A majority of these diet studies were based on scat analyses (e.g. Karanth & Sunquist, 1995; Andheria *et al.*, 2007; Mondal *et al.*, 2012), some of which used only frequency of occurrence, thus substantially underestimating the contribution of large prey and overestimating small prey (Ott, Kerley & Boshoff, 2007; Shehzad *et al.*, 2014; Chattha *et al.*, 2015). Multiple studies attempted to correct for size-dependent digestibility of prey using the puma specific linear biomass model of Ackerman *et al.* (1984) (e.g. Selvan *et al.*, 2013; Taghdisi *et al.*, 2013; Farhadinia *et al.*, 2014). Here, we show that these leopard prey studies underestimated the relative share of medium and larger prey individuals in the diet despite the overestimation of absolute prey numbers consumed (Fig. 3a–g). Only Ghoddousi *et al.* (2016) had applied non-linear biomass models in diet calculations.

Beyond prey body mass and feeding ecology of predators, several ecological parameters are likely to affect the shape of biomass models. As carcass utilization is important when estimating prey numbers with the CF2_W model, we advocate for the use of more realistic prey consumption rates in biomass models. In this study, we considered maximum prey intake and revisitations to kills based on field observations. However, some uncertainties remain such as the possible effect of prey lost to kleptoparasites and the overall prey abundance on carcass utilization by leopards (Bailey, 1993; Iyengar, 2008; Rühle *et al.*, 2008; Stein, Bourquin & McNutt, 2015). Also, carcass utilization may be lower in human dominated areas than in undisturbed settings, e.g. due to humans chasing leopards away from kill sites or responding to livestock depredation by removing the carcass (Treves & Naughton-Treves, 1999). Therefore, we recommend that field researchers measure daily

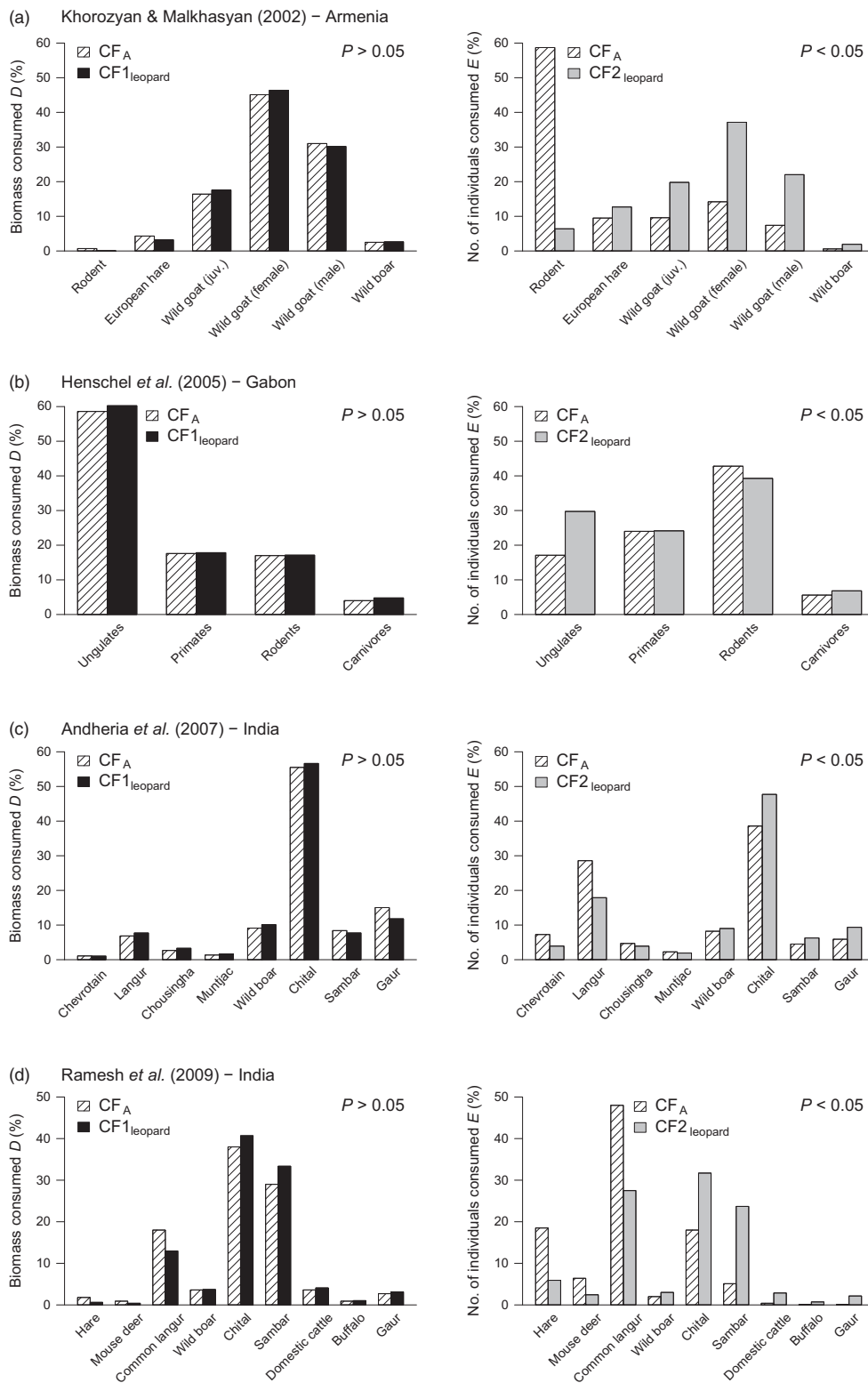


Figure 3 A comparison of relative biomass consumed D (%) and relative number of individuals consumed E (%) from selected studies based on CF_A (Khorozyan & Malkhasyan, 2002; Henschel *et al.*, 2005; Andheria *et al.*, 2007; Ramesh *et al.*, 2009; Wang & Macdonald, 2009; Taghdisi *et al.*, 2013; Sidhu *et al.*, 2015) and $CF_{1\text{leopard}}$ (Ghoddousi *et al.*, 2016) with corresponding estimates calculated using $CF_{1\text{leopard}}$ and $CF_{2\text{leopard}}$ models, respectively.

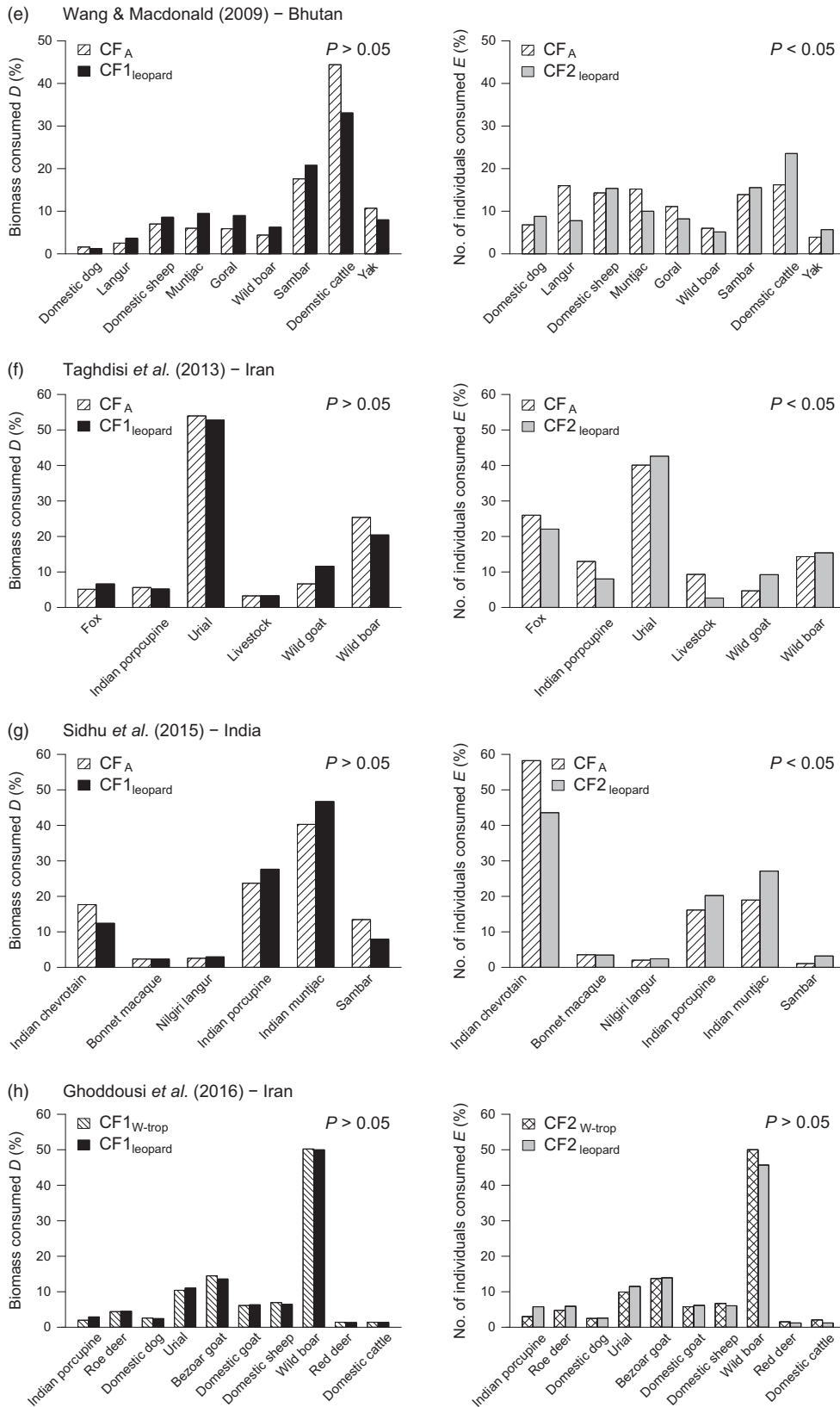


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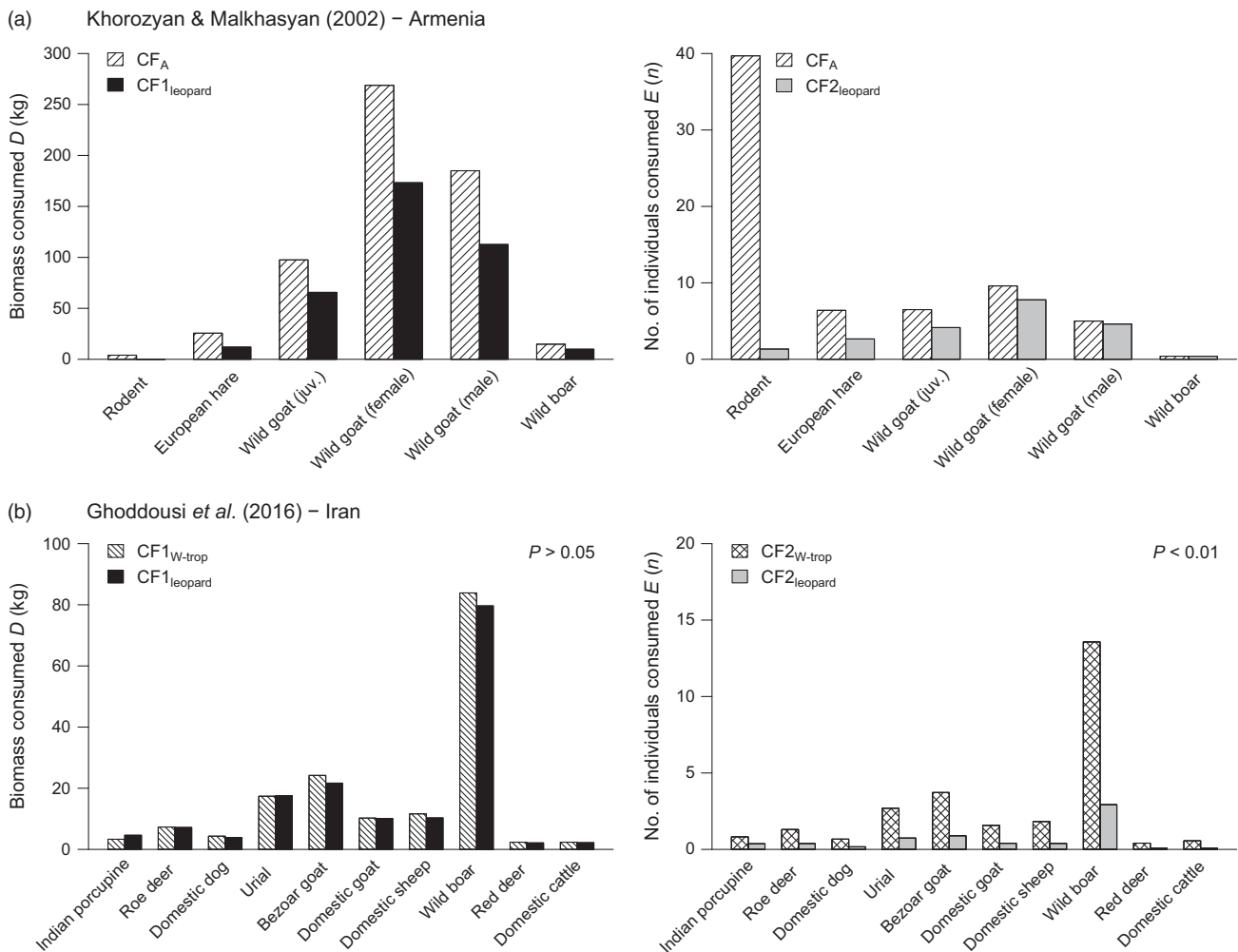


Figure 4 A comparison of absolute biomass D (kg) and absolute numbers of individuals E (n) consumed derived from CF_A (Khorozyan & Malkhasyan, 2002) and CF₂_{W-trop} (Ghoddousi *et al.*, 2016) with corresponding estimates calculated using CF₁_{leopard} and CF₂_{leopard} models, respectively. No P -values are given in graph (a) as no test was conducted due to small sample size.

food intake, carcass revisitation rates and carcass utilization under different management regimes and predator guilds and potentially incorporate new findings from techniques like Global Positioning Systems (GPS) into prey biomass estimations (Pitman, Swanepoel & Ramsay, 2012).

Since our recalculation of leopard studies shows a higher contribution of heavier prey in relative numbers compared to linear models (Fig. 3a–g), we anticipate that the application of CF₂_{leopard} may shift the preferred prey body mass range of leopard upwards (Hayward *et al.*, 2006). Moreover, our new model suggests that absolute numbers of prey individuals consumed were significantly overestimated in earlier studies (Fig. 4b). Hence, a reassessment of previous studies on leopard diet potentially affects decisions in species conservation and management. Therefore, we argue that our models can be useful in areas with high human-leopard conflicts where more accurate estimation of depredation losses is a high priority (e.g. Shehzad *et al.*, 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Names and locations of zoos in which leopard feeding trials were conducted.

Table S2. Details of feeding trials with leopards in the zoos of Germany, Switzerland and Iran between 2012 and 2016.

Table S3. Models selected to describe data in this study. Model equations were taken from Crawley (2007), Bolker (2008) and Logan (2010).

Table S4. Fitted regression models describing the relationships between $CF1_{\text{leopard}}$ (y) and prey body mass (x) sorted by ascending AIC value.

Table S5. Fitted regression models describing the relationships between $CF2_{\text{leopard}}/CF2_{\text{leopard-W}}$ (y) and prey body mass (x) sorted by ascending AIC value.

Table S6. Recalculation of selected leopard dietary studies (Khorozyan & Malkhasyan, 2002; Henschel *et al.*, 2005; Andheria *et al.*, 2007; Ramesh *et al.*, 2009; Wang & Macdonald, 2009; Taghdisi *et al.*, 2013; Sidhu *et al.*, 2015; Ghoddousi *et al.*, 2016) showing the actual and relative prey biomass consumed (D) and numbers of prey individuals consumed (E) estimated using $CF1_{\text{leopard}}$, $CF2_{\text{leopard}}$ and $CF2_{\text{leopard-W}}$ accordingly. Prey body mass and frequency of prey occurrence (FO) were taken from the corresponding studies.