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REVIEW

Body mass relationships affect the age structure of predation across carnivore–ungulate systems: a review and synthesis

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ABSTRACT

1. The size or body mass of predators relative to prey plays a key role in structuring animal communities, as the strength of predator–prey interactions is often dependent on the body mass relationship. Also, in long-lived species, a direct functional relationship exists between adult survival and population growth rate. Therefore, any cause of mortality acting on the adult segment of the population is expected to exert a strong influence on population performance.

2. Despite the large amount of literature available on carnivore–ungulate predation patterns, the relationship of predator and prey body mass with the age structure of predation has not yet been synthesised within a common framework. We review the main studies conducted during the last five decades on carnivore–ungulate predation patterns, and synthesise how the body mass relationship influences the age composition of individuals killed.

3. For each study, we compiled the predator and prey species under study, their body mass and sex, the geographical location of the study site, the methodology used, and the resulting age composition of individuals killed, at the highest available resolution. We used generalised linear mixed effects models to assess the influence of all these variables on the proportion of individuals killed consisting of juveniles.

4. The proportion of individuals killed that were juvenile in a given predator–prey system was strongly dependent on prey body mass, with a positive asymptotic relationship. The asymptote value decreased for increasing predator body mass. Also, felids and canids followed different trajectories. Male predators killed more adults than female predators, and the proportion of juveniles in their diet was lower when predators were preying on solitary ungulates, than when they were preying on species living in groups or herds.

5. Morphological and behavioural traits of predator and prey species interact to influence the age structure of predation, with possible consequences on the potential for different carnivore species to affect their prey demography.

INTRODUCTION

Body mass is one of the main constraints in the evolution of morphological and behavioural traits. It is related to patterns of displacement, such as locomotion, dispersal and

space use (Peters 1983, Jetz et al. 2004), to biological rates such as growth, metabolism, reproduction and mortality (Peters 1983, Brown et al. 2004), and to population characteristics such as density and trophic level (Jennings et al. 2001, Cohen et al. 2003). Also, body mass has been shown

to play a key role in structuring communities, so that the strength of trophic interactions in a food web can be strongly dependent on the consumer–resource size relationship (Cohen et al. 1993, Emmerson & Raffaelli 2004, Brose et al. 2006).

Ungulates, like most mammals, produce offspring that are small in relation to their adult body weight, on average weighing at birth about 10% of maternal body mass (26% in birds, 41% in reptiles, 59% in fish; Blueweiss et al. 1978). Young ungulates experience a long post-natal phase of physical and behavioural development. This suggests that juvenile and adult individuals of the same species experience very different body mass relationships with the same predator, and are subject to a different predation risk. Also, being long-lived, highly iteroparous species with long generation times (Gaillard et al. 2000, 2005), ungulates exhibit a strong functional relationship between adult survival and population growth rate (Gaillard & Yoccoz 2003). Therefore, any cause of mortality acting on the adult segment of the population is expected to exert a strong influence on population growth rate (Gaillard et al. 2000, Gaillard & Yoccoz 2003, Nilsen et al. 2009a).

Most carnivores preying on ungulates do not kill individuals of different ages and sizes at random, but rather show some degree of selectivity (Mills & Shenk 1992, Wright et al. 2006, Gervasi et al. 2012). Optimal foraging theory predicts that a predator will try to maximise its net energy gain, by choosing a prey item that corresponds to the best trade-off between energy expenditure (e.g. searching time, risk of injury, capture success) and the intake resulting from prey consumption (MacArthur & Pianka 1966). One might therefore expect that predators will preferentially prey on adults whenever they can achieve an advantageous capture rate at a low risk of being injured during hunting. They are also expected to shift to juvenile individuals when capture success on adults is too low, when injury risk is high, or if the energy intake resulting from killing an adult is lower than the total energy required to locate, subdue and consume it (Sunquist & Sunquist 1989). Moreover, as the risk of total or partial loss of a kill to scavengers and/or competitors increases with increasing handling time, juvenile individuals can often become a more advantageous prey for a predator of a given size, as they can be more fully consumed. Carcasses of adult prey must often be abandoned to competitors and scavengers at a certain stage of the potentially long handling process (Paquet 1992, Wilmers et al. 2003).

Such a link between body mass relationship, the differences in the costs and benefits of predation as a function of prey age, and the different contribution that each age class makes to population growth rate, suggests that carnivore–ungulate body mass relationship is likely to affect both the age structure of predation and the potential demographic

impact of a given carnivore on the population performance of its prey. Sinclair et al. (2003) described how predator–prey body mass relationship can determine predation risk and prey accessibility in carnivore–ungulate communities of the African savannah. Several other researchers have revealed the role of the predator–prey body mass relationship as an ecological correlate of potential predation impact (Owen-Smith & Mills 2008, Odden et al. 2010), mainly focusing on the effect of prey accessibility and selection within multi-prey assemblages. Accordingly, there is a growing body of literature that demonstrates a relationship between a predator's selectivity for adult individuals and its potential to exert top–down control on its prey species (Mills & Shenk 1992, Wright et al. 2006, Wilmers et al. 2007, Gervasi et al. 2012).

Despite the large amount of scientific work available on carnivore–ungulate predator–prey interactions (see Abram 2000 for a synthesis), and despite the importance that the age structure of predation can have on the demography of prey species, a review and synthesis of the many factors influencing the age composition of kills in carnivore–ungulate systems is not available. In fact, factors other than body mass can influence the selectivity of a predator for a specific age segment of the prey population. First, morphological and phylogenetic constraints lead different taxonomic groups of carnivores to adopt dissimilar predation strategies. Most felids, such as cougars *Puma concolor*, leopards *Panthera pardus* and Eurasian lynx *Lynx lynx*, are solitary stalking predators that try to get as close as possible to their prey before making an attack (Husseman et al. 2003, Andersen et al. 2007). As a result, they often surprise and kill their prey instantly, and their kill composition tends to be poorly correlated with the age and physical condition of their prey. On the other hand, most canids and hyaenids, such as grey wolves *Canis lupus*, spotted hyaenas *Crocuta crocuta* and African wild dogs *Lycaon pictus*, chase their prey over long distances while hunting in packs (Kruuk 1972, Sand et al. 2008). These coursing predators tend to be more selective, and tend to kill a larger proportion of more vulnerable individuals (Smith et al. 2004). Also, ungulates comprise both solitary and social species, with social units ranging from a few up to several thousand individuals. As social behaviour in ungulates has been empirically linked to variation in predation risk (Schaller 1972), prey social organisation is also expected to influence the mechanisms of age-specific predation (Owen-Smith & Mills 2008, Knopff et al. 2010). Finally, if having greater body mass plays a role in a predator's ability to subdue a higher percentage of adult prey, male predators are also expected to kill more adults than females of the same species, given the widespread sexual dimorphism in carnivores (Meiri et al. 2005).

Based on these theoretical premises, we compiled a database of studies conducted during the last five decades on

carnivore predation patterns on ungulates, with the main focus on the age structure of predation. We explored how carnivore and ungulate body masses interact to determine the resulting age composition of individuals killed, and how the patterns are modulated by a set of behavioural and ecological factors, such as hunting strategy, predator sex, and prey social organisation. This resulted in the following *a priori* hypotheses:

1. Larger (heavier) carnivore species are able to kill a higher proportion of adults for a given prey species mass.
2. Larger ungulate species experience lower predation on the adult segment of the population from a carnivore species of a given mass.
3. Group hunting coursers kill a higher proportion of adult prey than solitary stalkers.
4. Male carnivores kill a higher proportion of adult prey than females.

The scope of the study was to provide a general, quantitative assessment of how morphological and behavioural traits can potentially affect the tendency of a given carnivore to focus on a specific age segment of its prey population. We provide a conceptual framework for the interpretation of the observed differences in the age composition of kills among large carnivores, and of the potential of large carnivores to exert demographical control on their prey species.

METHODS

Data set

We searched the literature for studies presenting data on the age structure of ungulate prey killed by different carnivore species, using a range of literature databases (ISI, SCOPUS; Google Scholar, JSTOR), 'snowball' sampling (using literature cited in papers already reviewed), and drawing from our own archives of publications, books and technical reports that have been collected during more than 20 years of research. Although most large carnivores also prey on smaller non-ungulate species, we did not include them in the review, as the aim of the study was to explore the specific predation patterns on ungulates. As we did not aim to assess the relative importance of ungulates in large carnivore diets, this did not affect the robustness and accuracy of the results. The studies included in the review spanned the period from 1960 (Mitchell et al. 1965) to 2010 (Knopff et al. 2010). For each study, we extracted the predator and prey species under study, their body masses, the geographical location of the study site, the study season (winter or summer), the method used [direct visual observations, tracks, very high frequency (VHF) or global positioning system (GPS) telemetry collars] and the sex of the individual predators under study (only males, only females or both sexes). Because of limitations in the available litera-

ture, we could not consider prey sex as a factor in this review, neither could we account for sex-related differences in prey body mass. Whenever available, body mass estimates were derived from the studies documenting predation, or from the same study areas. We derived most of the remaining body mass estimates from the geographically closest population listed by Silva and Downing (1995). When studies included only one sex of the focal species, we used sex-specific estimates of body mass; otherwise, we averaged male and female body mass values. A list of body mass estimates and references is provided as Appendix S1. For each predator species, we also compiled the taxonomic group (at the level of family), the prevalent hunting strategy (stalker or courser) and the grouping behaviour (solitary or group predator). We also recorded the social organisation (solitary or herd) for each ungulate species. Finally, from each study, we recorded the age composition of the individuals killed, at the highest available resolution. As most authors reported the age composition of kills only as the proportion of juveniles (<1 year old) and adults (>1 year old), we opted to use the proportion of juveniles represented in the diet as a uniform metric for all the available study cases. Such a classification was based on a biologically important difference in ungulate life-history traits between the first and the subsequent years of life. Ungulates exhibit a monotonic decreasing growth rate: they experience a fast increase of body mass during the first year of life, which rapidly decreases in subsequent years (Gaillard et al. 1997). Therefore, most ungulates, regardless of their adult size, reach between 70% and 90% of their adult body weight by the end of their first year of life (Gaillard et al. 1997, Solberg et al. 2004). Moreover, as highlighted by Gaillard et al. (2000) in a review of almost 30 ungulate species ranging from 20 to 400 kg, the age-specific mortality patterns of ungulates significantly change at the end of the first year of life; juveniles exhibit the lowest survival rates, and older age classes (yearlings and prime age adults) have broadly similar annual mortality probabilities (Gaillard et al. 2000). Therefore, when synthesising the importance of the body mass relationship on age-specific predation of ungulates, the partition between juveniles and older individuals is the most relevant and biologically meaningful. On the other hand, not all individuals older than 1 year retain the same reproductive value in ungulates, because of variation in the age of first reproduction (Gaillard et al. 2000). As small ungulates (<80 kg) usually mature as yearlings whereas larger ones often delay maturation until the age of 3–4 years (Gaillard et al. 2000), the functional relationship between yearling survival and population growth rate is stronger in smaller ungulates than in larger ones (Gaillard et al. 2005). Therefore, although there is a clear relationship, the proportion of individuals killed by each carnivore species that are juvenile should not be interpreted as a direct proxy for the

demographical impact of predation in the context of the present work. A complete evaluation of the subject would require accounting for the differences in reproductive value of the age classes older than 1 year.

Statistical analyses

Using the package *lme4* (Bates et al. 2011) in R (Anonymous 2008), we applied generalised mixed effects models with a logit link and a binomial distribution, to test for the influence of all the explanatory variables on the proportion of individuals killed, of each prey species, consisting of juveniles in carnivore–ungulate predator–prey systems. We first plotted predator and prey body mass against the dependent variable, and found a non-linear relationship. Hence, we applied a log-transformation to both variables, in order to make the relationship linear, and used the log-transformed variables for the regression analysis. From an ecological perspective, we expected the body mass of each predator relative to that of its prey, rather than the absolute predator or prey body mass, to be the main predictor of the age composition of kills. This was mathematically translated into using a ratio between predator and prey body mass, as a potentially suitable variable summarising the body mass relationship between each carnivore species and its ungulate prey species. However, the use of ratios in regression analysis has been heavily criticised (Atchley et al. 1976, Smith 1999), especially when the fundamental assumptions of independence and isometric scaling are not met. Allometric scaling occurs whenever the ratio between measures of two morphological characters is not constant for different values of the characters (West et al. 1997). Therefore, in the fundamental allometric equation:

$$Y = aX^b \text{ or } \log(Y) = \log(a) + b \log(X)$$

where X and Y are measures of the two characters and b is their scaling factor, an allometric relationship occurs whenever $b \neq 1$. When using a ratio between two allometric characters as the explanatory variable in a regression analysis, a false effect of the explanatory variable on the dependent one can emerge as a consequence of the allometric scaling, rather than because of a real causal effect (Toth et al. 1993). In such cases, the use of the two elements of the ratio as separate explanatory variables is advised to remove the risk of artificial effects (Albrecht et al. 1993); the possibility to test for possible interactions between them remains.

In our case, we needed to test whether the scaling factor between predator and prey body mass in the data set was significantly different from one, as a strong allometric relationship would have made the use of a predator–prey body mass ratio unsuitable for our analysis. To test for the allometric scaling, we first performed a linear regression analysis

between prey and predator $\log_{10}(\text{body mass})$, using the whole data set, thus testing whether the regression slope was significantly different from one. However, the slope estimate derived from this analysis was expected to be negatively biased, because we did not take into account small, non-ungulate prey species of small predators, and therefore did not cover the whole range of possible predator–prey body mass ratios. We therefore performed a linear regression analysis using only the heaviest prey of each predator species as input data (known as upper slope regression, *sensu* Blackburn et al. 1992), thus generating an unbiased estimate of the regression slope.

We included the predator taxonomic group (felid or canid/hyeanid, here referred to as canid) as an explanatory variable in the regression analysis. As all felids in the data set were stalkers and all canids were coursers and group hunters, the taxonomic group of each predator species was highly correlated with its social organisation and hunting strategy. This was not due to limitations in the reviewing process, but rather it reflected a real uneven distribution of predation strategies among the two taxonomic groups, as a result of their phylogenetic constraints (Cardillo 2011). As a consequence, our analysis did not allow us to distinguish between underlying phylogenetic and ecological causes of the observed differences between carnivore groups. Lions *Panthera leo*, for example, are felids and mostly group hunters, but were classified in the same group as other smaller felids (Eurasian lynx, leopard), which exclusively hunt alone. Unfortunately, the limited number of carnivore species for each group did not allow us to treat these factors separately at the statistical level. Consequently, we interpreted the effect of the variable ‘taxonomic group’ as the combined result of the phylogenetic history, social organisation, and hunting strategy of a given predator species on its observed predation pattern.

We used predator sex and prey social organisation (solitary or herd) as additional explanatory variables in the regression analysis. Finally, we included the type of research technique applied in each study, to test for any methodological effects on the age composition estimates. As the sample size of studies using either VHF or GPS collars was rather small when compared with observation-based studies, we were not able to test for differences related to the type of collar used, but just distinguished observation and collar-based studies. As only a minority of researchers reported separate age composition estimates for different seasons, and most of the data points were derived from annual studies, we were not able to test for seasonal variations in the age composition of individuals killed. Some predator–prey couples had several observed age composition estimates. Therefore, we fitted mixed-effect logistic regression models with individual predator–prey couples as a random effect, to account for pseudoreplication (Hurlbert 1984).

Table 1. Summary of the canid and hyaenid species included in the analysis of the main factors influencing the age composition of carnivore-killed ungulates. For each predator, the list of available ungulate prey species and the average percentage of individuals killed that are juvenile is shown, together with the number of study cases available for each predator–prey couple

Predator	Prey	Average percentage of individuals killed that are juvenile (%)	Number of studies
African wild dog <i>Lycaon pictus</i>	Common duiker <i>Sylvicapra grimmia</i>	10	1
	Impala <i>Aepyceros melampus</i>	49	3
	Kudu <i>Tragelaphus strepsiceros</i>	100	1
	Nyala <i>Tragelaphus angasii</i>	15	1
	Thomson's gazelle <i>Gazella thomsonii</i>	42	1
Coyote <i>Canis latrans</i>	Wildebeest <i>Connochaetes taurinus</i>	84	1
	Pronghorn <i>Antilocapra americana</i>	44	1
	White-tailed deer <i>Odocoileus virginianus</i>	39	1
Dhole <i>Cuon alpinus</i>	Chital <i>Axis axis</i>	43	1
	Sambar <i>Rusa unicolor</i>	82	1
Spotted hyena <i>Crocuta crocuta</i>	Eland <i>Taurotragus oryx</i>	64	1
	Gemsbok <i>Oryx gazella</i>	79	1
	Wildebeest <i>Connochaetes taurinus</i>	48	3
Grey wolf <i>Canis lupus</i>	Bison <i>Bison bison</i>	40	1
	Caribou <i>Rangifer tarandus</i>	12	1
	Dall sheep <i>Ovis dalli</i>	8	1
	Elk <i>Cervus elaphus</i>	48	3
	Moose <i>Alces alces</i>	50	9
	Mule deer <i>Odocoileus hemionus</i>	65	1
	Red deer <i>Cervus elaphus</i>	31	2
	Roe deer <i>Capreolus capreolus</i>	23	2
	White-tailed deer <i>Odocoileus virginianus</i>	35	3
	Wild boar <i>Sus scrofa</i>	51	2

We started the model selection procedure from an initial, fully parameterised model, which included also two biologically reasonable interactions: one between predator and prey body masses, and one between predator body mass and predator taxonomic group. After generating reduced models, we selected the most parsimonious one using the Akaike information criterion (AIC) of model fit (Burnham & Anderson 2002). Models with $\Delta\text{AIC} < 2$ were considered to be equally supported by the data. For each model, we also computed Akaike weights (Burnham & Anderson 2002). As the sum of all weights in a set of candidate models is equal to one, Akaike weights provide a measure of the relative support for each of the models in the subset, given the data and the model subset.

To assess the amount of variation explained by the fixed and random parts of the models, we followed a two-step process: first, we estimated the intraclass correlation ρ , to evaluate the proportion of the total residual variation that could be attributed to individual predator–prey couples (Rodríguez & Elo 2003, Skrondal & Rabe-Hesketh 2004); then, we estimated the squared correlation index (R^2) between the fitted and observed values, without the effect of random factors.

RESULTS

Data collection

The final data set comprised 159 predator–prey couples, derived from 47 publications on carnivore–ungulate predation patterns, based on a total of 12 carnivore and 37 ungulate species. A summary of the derived data set is provided in Tables 1 and 2, with descriptive statistics on the average age composition of kills for each predator–prey couple. The complete data set is available in Appendix S2.

Carnivore–ungulate predator–prey studies were almost exclusively located in four main geographical regions: North America, Sub-Saharan Africa, Europe, and the Indian sub-continent (Fig. 1). As shown in Fig. 1, these areas are not representative of all the regions where predator–prey interactions between large carnivores and ungulates occur. In particular, the review of carnivore–ungulate literature from the South American continent, which hosts charismatic species such as the jaguar *Panthera onca* and the puma *Puma concolor*, did not provide any quantitative assessment of predation patterns, apart from some information about

Table 2. Summary of the felid species included in the analysis of the main factors influencing the age composition of carnivore-killed ungulates. For each predator, the list of available ungulate prey species and the average percentage of individuals killed that are juvenile is shown, together with the number of study cases available for each predator–prey couple

Predator	Prey	Average percentage of individuals killed that are juvenile (%)	Number of studies
Bobcat <i>Lynx rufus</i>	Pronghorn <i>Antilocapra americana</i>	100	1
	White-tailed deer <i>Odocoileus virginianus</i>	85	1
Cheetah <i>Acinonyx jubatus</i>	Common duiker <i>Sylvicapra grimmia</i>	16	1
	Impala <i>Aepyceros melampus</i>	39	5
	Kudu <i>Tragelaphus strepsiceros</i>	100	3
	Nyala <i>Tragelaphus angasii</i>	28	1
	Reedbuck <i>Redunca arundinum</i>	19	1
	Springbok <i>Antidorcas marsupialis</i>	20	1
	Steenbok <i>Raphicerus campestris</i>	6	1
	Thomson's gazelle <i>Gazella thomsonii</i>	54	1
	Bighorn <i>Ovis canadensis</i>	44	1
Cougar <i>Puma concolor</i>	Elk <i>Cervus elaphus</i>	43	5
	Guanaco <i>Lama guanicoe</i>	58	1
	Moose <i>Alces alces</i>	88	1
	Mule deer <i>Odocoileus hemionus</i>	31	7
	White-tailed deer <i>Odocoileus virginianus</i>	35	1
	Chamois <i>Rupicapra rupicapra</i>	39	3
Eurasian lynx <i>Lynx lynx</i>	Red deer <i>Cervus elaphus</i>	70	2
	Roe deer <i>Capreolus capreolus</i>	31	6
	Bushbuck <i>Tragelaphus scriptus</i>	30	2
Leopard <i>Panthera pardus</i>	Chital <i>Axis axis</i>	23	3
	Common duiker <i>Sylvicapra grimmia</i>	14	2
	Impala <i>Aepyceros melampus</i>	26	3
	Kudu <i>Tragelaphus strepsiceros</i>	55	2
	Springbok <i>Antidorcas marsupialis</i>	10	1
	Steenbok <i>Raphicerus campestris</i>	5	2
	Thomson's gazelle <i>Gazella thomsonii</i>	8	1
	Warthog <i>Phacochoerus aethiopicus</i>	76	3
	Wildebeest <i>Connochaetes taurinus</i>	88	1
	Zebra <i>Equus zebra</i>	93	2
	Buffalo <i>Syncerus caffer</i>	25	3
	Bushbuck <i>Tragelaphus scriptus</i>	8	1
	Elan <i>Taurotragus oryx</i>	19	2
	Gemsbok <i>Oryx gazella</i>	27	1
	Giraffe <i>Giraffa camelopardalis</i>	41	3
	Hartebeest <i>Alcelaphus buselaphus</i>	4	1
Lion <i>Panthera leo</i>	Impala <i>Aepyceros melampus</i>	30	4
	Kob <i>Kobus kob</i>	5	1
	Kongoni <i>Alcelaphus busephalus</i>	14	3
	Kudu <i>Tragelaphus strepsiceros</i>	13	2
	Nyala <i>Tragelaphus angasii</i>	3	1
	Springbok <i>Antidorcas marsupialis</i>	24	2
	Warthog <i>Phacochoerus aethiopicus</i>	19	4
	Wildebeest <i>Connochaetes taurinus</i>	19	8
	Zebra <i>Equus zebra</i>	49	8
	Chital <i>Axis axis</i>	20	2
	Gaur <i>Bos gaurus</i>	59	1
	Red deer <i>Cervus elaphus</i>	20	1
	Rhino <i>Rhinoceros unicornis</i>	100	1
	Sambar <i>Rusa unicolor</i>	18	1
	Wild boar <i>Sus scrofa</i>	26	1
Tiger <i>Panthera tigris</i>			

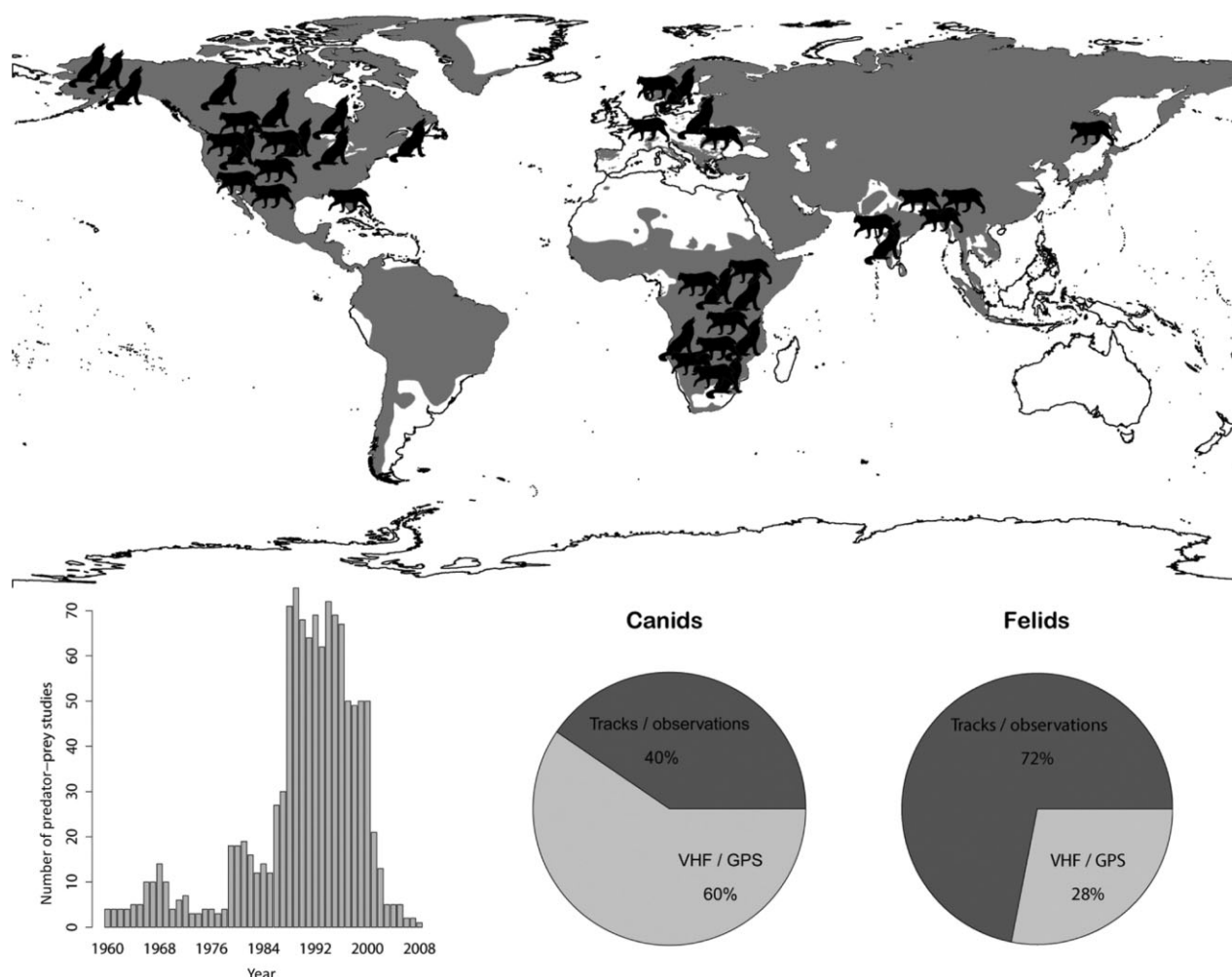


Fig. 1. Spatio-temporal distribution of research projects included in the review, showing research effort on carnivore–ungulate predation patterns between 1960 and 2010 (bar chart). Grey zones on the world map represent intersections between large carnivore and ungulate distributions. Dog and cat symbols indicate canid-based and felid-based projects. The pie chart shows the percentage of studies included in the review based on very high frequency (VHF) or global positioning system (GPS) collars and on tracking or observation, for canids and felids separately.

prey selection (Iriarte et al. 1990, Mazzolli 1997, Garla et al. 2001). Also Russia and the other former republics of the Soviet Union, home to species such as tigers *Panthera tigris*, grey wolves *Canis lupus* and snow leopards *Uncia uncia*, were almost absent from the English-based scientific literature.

Such uneven distribution of knowledge is also reflected at the level of species: among canids, grey wolves dominate, as 58% of all canid studies refer to this species. Among felids, lions have a similar status, accounting for 38% of all the publications reviewed; if we add predator–prey studies on leopards to this figure, the two species comprise 57% of all reviewed predator–prey research projects on felids.

Differences between felid-based and canid-based studies also emerged when comparing the methods applied. The

majority of predation data on canids (60% of studies) was based on capturing and collaring of individual animals, followed by intensive VHF or GPS monitoring. Studies on felids were instead mostly (72%) based either on direct observation of predation events or on ground or aerial tracking.

A plot of the temporal trend in the number of active carnivore–ungulate research projects by year (see Fig. 1) revealed a strong increase in research effort on this subject around the end of the 1990s: the number of active research projects quickly increased from about 20 to more than 70. Such effort remained constant for a decade, until 2000, when it rapidly dropped to less than 10 projects per year in the last 10 years. While the low numbers reported for the last years may be caused by the delay between data collec-

Model	Model description	Deviance	AIC	Δ AIC	AIC weight
1	Log(predator body mass) + Log(prebody mass) + Felid/canid + Prey Social. Org. + predator sex	779.08	795.08	0	0.5
2	Log(predator body mass) + Log(prebody mass) + Felid/canid + Prey Social. Org. + Predator sex + Method	778.98	796.98	1.89	0.19
3	Log(predator body mass) * Log(prebody mass) + Felid/canid + Prey Social. Org. + Predator sex + Method	778.08	798.08	2.99	0.11
4	Log(predator body mass) + Log(prebody mass) + Prey Social. Org. + Predator sex	784.18	798.18	3.09	0.11
5	Log(predator body mass) * Felid/canid + Log(prebody mass) + Prey Social. Org. + Predator sex + Method	776.62	798.62	3.53	0.09
6	Log(predator body mass) + Log(prebody mass) + Felid/canid + Predator sex	791.69	805.69	10.60	0.00
7	Log(predator body mass) + Log(prebody mass) + Felid/canid + Prey Social. Org.	811.13	823.13	28.04	0.00
8	Log(predator body mass) + Felid/canid + Prey Social. Org. + Predator sex	810.50	824.50	29.41	0.00
9	Log(prebody mass) + Felid/canid + Prey Social. Org. + Predator sex	817.37	831.37	36.28	0.00

Table 3. Results of model selection procedures for the analysis of the main factors influencing the age composition of ungulates killed by carnivores. The variables tested were carnivore body mass, ungulate body mass, carnivore type (canid or felid), ungulate social organization (solitary or herd), carnivore sex, and study method (collared-based methods or indirect methods). The dependent variable was the proportion of individual ungulates killed by each carnivore species that were juvenile

tion and scientific publication of the results, such a remarkable decrease (–85%) probably also reflects a reduced effort in investigating carnivore–ungulate predation patterns.

Allometric scaling

Data exploration revealed no relevant collinearity among any of the explanatory variables. Variance inflation factors were <2 for all the variables, and all Spearman's correlation indexes between pairs of variables were <0.6 . Therefore, we included all the terms described earlier in the most parameterised model. Based on the whole data set, an allometric relationship between predator and prey body mass was evident ($\beta = 0.286$; $P < 0.001$). A weaker allometric scaling was present when conducting upper slope regression based on the heaviest prey species observed to be eaten by each predator species. However, this approach also revealed an allometric relationship, as the slope was significantly different from one ($\beta = 0.721$; $P < 0.001$). Hence predator and prey body masses violated the fundamental assumption of isometric scaling for the use of their ratio as an explanatory variable in the regression analysis. For subsequent analyses we included predator and prey body mass as separate variables, and tested for a possible statistical interaction between them.

Regression analysis

In the best supported model (based on its AIC value; model 1 in Table 3), the proportion of animals killed that were

juvenile was a function of carnivore and ungulate body mass, carnivore taxonomic group (canid or felid), ungulate social organisation (solitary or group living) and carnivore sex. This model had an Akaike's weight w_i of 0.50 and explained 51% of the total variation in the age composition of kills in our data set (45% through the fixed part and 6% through the random part; see Fig. 2). Models including two-way interactions were significantly less supported by the data.

The structure of the most supported model illustrates the effect of the predator–prey body mass relationship on the age structure of kills (Fig. 3). In general, bigger predators were able to kill a higher proportion of adults, but this proportion decreased with increasing values of the prey body mass up to an asymptotic value. Also, the shape of the resulting curve was different for different carnivore types: in felids there was a sharp increase in the proportion of individuals killed that were juvenile with increasing prey body mass (Fig. 3a). In canids, this pattern was much less pronounced, and the asymptotic percentage of individuals killed that were juvenile was only about 50–60% (Fig. 3b). Lions were an exception to this general pattern. Other smaller felids living in the same ecosystem, such as cheetahs *Acinonyx jubatus* and leopards, kill progressively fewer adults than lions do when preying on bigger ungulates. Lions are able to kill between 60% and 80% adults, regardless of their prey body mass (see Fig. 4).

Estimates from the most supported model also showed that carnivores had a lower proportion of juveniles in their

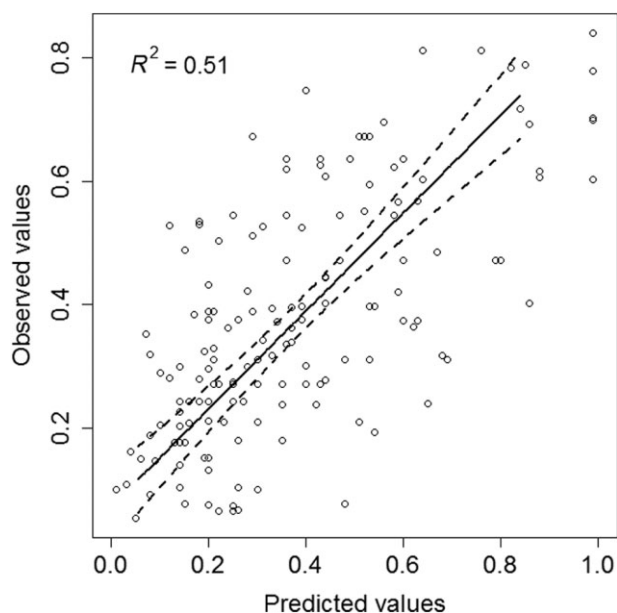


Fig. 2. Relationship between the observed and predicted proportions of individuals killed by carnivore species that were juvenile ungulates (<1 year old), in all reviewed carnivore–ungulate predator–prey couples. Predictions are derived from the most supported regression model (model 1 in Table 3).

diet when they were preying on solitary ungulates than when they were preying on species of the same mass living in herds ($\alpha = -0.676$; $P < 0.001$). Finally, for a given predator and prey body mass, male predators relied to a lesser

extent on juveniles than female predators ($\alpha = 0.285$; $P < 0.001$). The structure of the most supported model (model 1 in Table 3), with estimates of all regression coefficients, is provided in Table 4.

DISCUSSION

The importance of the body mass relationship in structuring trophic linkages within ecosystems is a well-established concept in ecology (Cohen et al. 1993). The occurrence and extent of predator–prey interactions are strongly determined by the mass of a given predator relative to that of its potential prey (Brose et al. 2006), and in ungulates, this has direct consequences for the proportion of annual mortality caused by predation in species of different body mass (Sinclair et al. 2003, Owen-Smith & Mills 2008).

Our results show that the patterns of age-specific predation by carnivores on ungulates are also strongly influenced by the effect of the body mass relationship, and that coupling them with a set of socio-behavioural traits explains a relevant portion of the variation in the age of ungulates killed by carnivores. In accordance with the expectations resulting from optimal foraging theory (MacArthur & Pianka 1966), carnivores focused more on juveniles as the relative mass of their prey increased, up to an asymptotic level, after which the age composition of kills did not show further changes. Such an asymptotic pattern, consistently evident across bio-geographical regions, taxonomic groups, and hunting strategies, suggests that a prey body mass

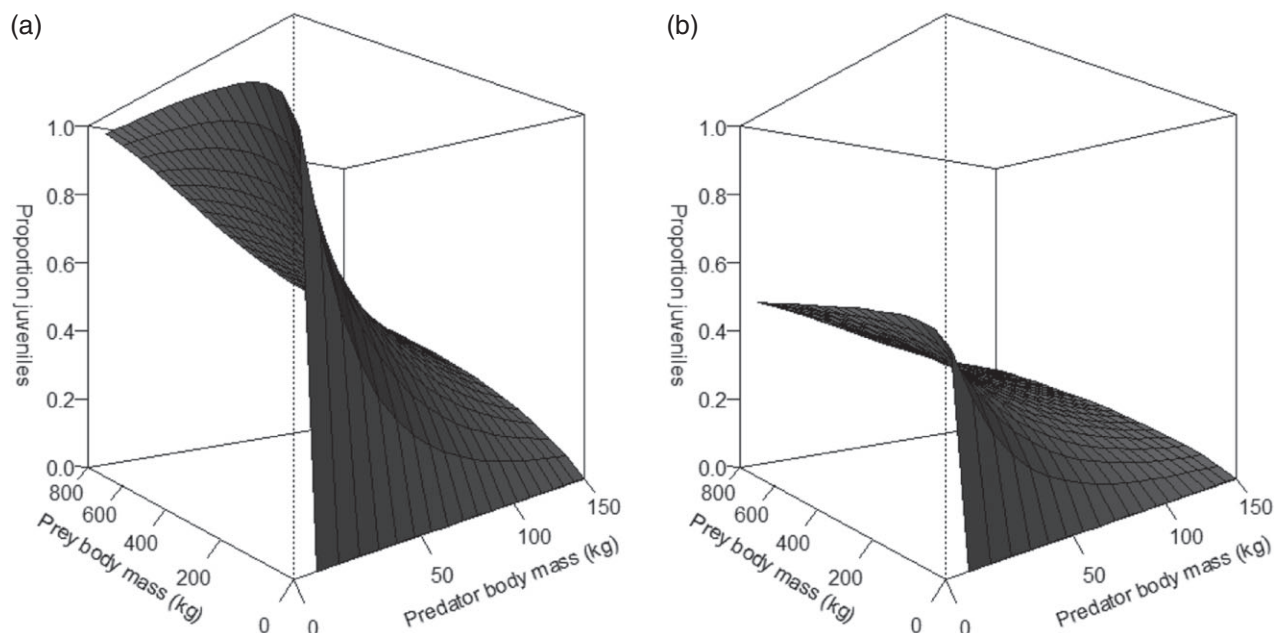


Fig. 3. Differential relationship between prey body mass and the proportion of individuals killed that were juvenile ungulates (<1 year old), considering those killed by felids (a) and by canids (b) of different body mass, as predicted by the most supported regression model (model 1 in Table 3).

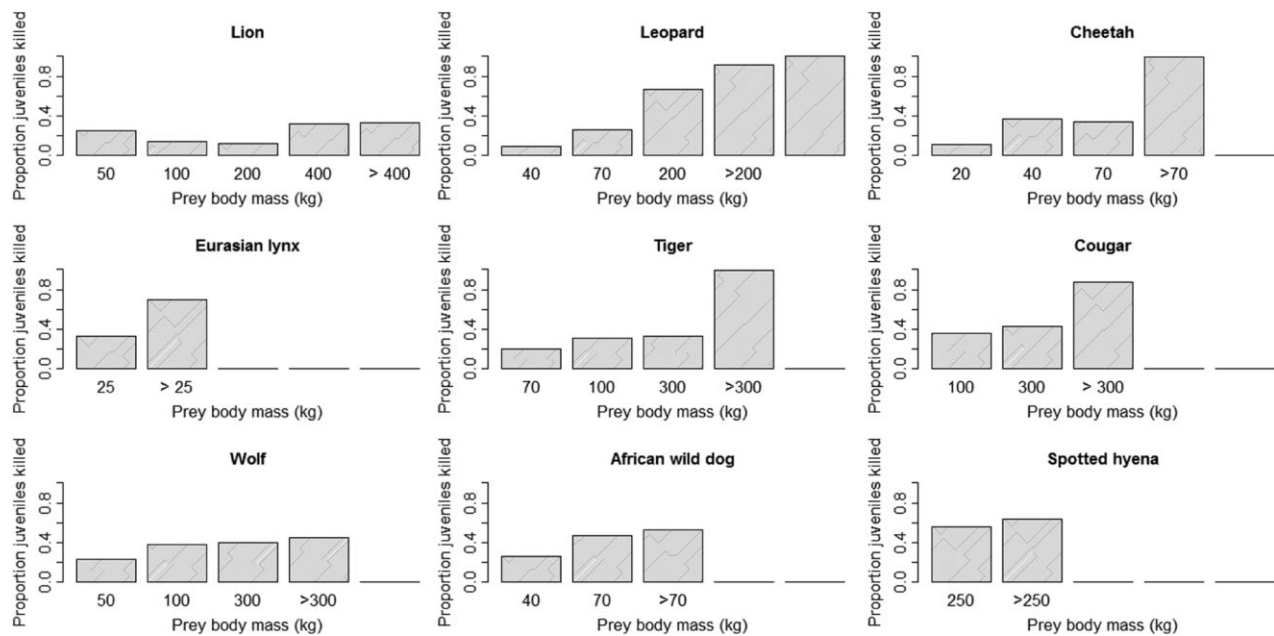


Fig. 4. Proportion of individual ungulates killed by carnivores within different prey body mass ranges that were juvenile (<1 year old). Range classes include all prey species with an adult body weight equal or lower than the category label (i.e. the 50 kg class includes all prey species with an adult body weight equal to or lower than 50 kg).

threshold exists for each carnivore, beyond which predation on adults can be too risky or not cost-effective, so that shifting to juvenile prey items becomes to a large extent the best, if not the only available option.

In addition to the combined effects of predator and prey body mass, the age composition of individuals killed was also influenced by the set of behavioural, ecological and phylogenetic constraints defining the different types of carnivores. As shown in Figs. 3 and 4, felids exhibited a steeper increase than canids in the proportion of individuals killed that were juvenile, for increasing values of prey body mass. The only exception to this pattern was represented by lions,

which did not exhibit any relevant increase in the proportion of individuals killed that were juvenile, for increasing values of their prey body mass (Fig. 4). Lions and leopards, for example, have similar body mass relationships with buffalo *Syncerus caffer* and kudu *Tragelaphus strepsiceros*, respectively, being about four times smaller than their prey. They also adopt a similar hunting strategy (ambush) and share a common phylogenetic history, but differ in that lions hunt in groups whereas leopards are solitary predators. As a result, 77% of lion-killed buffalos are adults, whereas only 34% of leopard-killed kudus are (Radloff & DuToit 2004). While the limitations imposed by sample size and by the statistical correlation of explanatory variables did not allow us to explain these differences analytically, the observed patterns strongly suggest that group hunting is the one factor enhancing a predator's ability to kill adults, irrespective of its phylogenetic history. As group hunting is directly linked to hunting success (McNulty et al. 2011), to a reduction of prey handling time (Fryxell et al. 2007) and to an increased ability to kill large prey and protect them from competitors and scavengers (Caraco & Wolf 1975, Hayward & Kerley 2005, Hayward et al. 2006), it seems reasonable to conclude that the observed difference in the age composition of kills made by solitary and social predators can be attributed to the combination of enhanced hunting efficiency, reduced time of prey consumption and lower risk of carcass loss. Also, group hunters are likely to be more motivated to attack larger adult ungulates, given the need to

Table 4. Parameter estimates for the best supported model (model 1 in Table 3). For each factor variable, regression coefficient values refer to the level reported in brackets. Significant values are highlighted in bold

Factor	Coefficient	SE	P
Intercept*	0.923	0.789	0.242
Log(predator body mass)	−3.464	0.468	<0.001
Log(preay body mass)	2.085	0.312	<0.001
Carnivore type (felid)	0.715	0.308	0.020
Prey social organisation (solitary)	−0.676	0.189	<0.001
Predator sex (female)	0.285	0.072	<0.001
Predator sex (male)	−0.159	0.086	0.054

*The intercept value refers to the combination of all baseline levels in factorial variables (carnivore type: canid; prey social organisation: herd; predator sex: both).

share the prey among several individuals after the hunt is successfully completed (Packer & Ruttan 1988, Scheel & Packer 1991).

We recognise that animal populations have a more complex age structure than the simple juvenile/adult classification that we were forced to use because of the resolution of the available data, and some of the differences we found in the age structure of predation between canids and felids should be interpreted with this in mind. Ungulates older than 1 year include yearlings, prime-age and senescent individuals, which exhibit different patterns of reproduction and natural mortality, and which contribute to a very different extent to the demographic performance of the population (Gaillard et al. 2000, 2005). While canids have shown the ability to kill a higher proportion of adult individuals than felids (Fig. 4), they are also expected to be more selective towards the weakest and least experienced individuals (yearlings and senescent individuals), as a consequence of their coursing predation strategy (Kruuk 1972, Smith et al. 2004, Sand et al. 2008). Predation by canids is therefore traditionally considered to be at least partially compensatory to the other natural causes of mortality in ungulates (Vucetich et al. 2005). Instead, predation by ambush predators such as felids exhibits a poor correlation with the age and physical condition of the prey, and such predation can remove each year a higher proportion of prime-age individuals in good physical condition, which would otherwise have survived and contributed to recruitment. Predation by felids is therefore expected to be less compensatory to natural mortality than predation by canids (Husseman et al. 2003, Andersen et al. 2007).

The type of social organisation in ungulates also emerged as a relevant factor affecting the relative age composition of kills. The effect of prey social organisation was rather strong, and resulted in on average 10–15% lower percentage points of juveniles killed in solitary species than in social species. Such an outcome certainly deserves further investigation. The evolution of social behaviour in ungulates is thought to be driven by the need to reduce vulnerability to predation by increasing the overall vigilance and diluting risk (Schaller 1972, Hebbelwhite & Pletscher 2002). Our results suggest that living in herds not only reduces the overall risk of being killed by a predator, but also contributes to shifting it onto the segment of the population (juveniles) which retains the lowest demographical elasticity (Gaillard & Yoccoz 2003). While this result does not prove that social organisation can directly affect the overall impact of predation on population growth rate, it demonstrates that at least one of the conditions for such a mechanism exists.

Our data also support the hypothesis that male carnivores are more likely to kill adult individuals than females of the same species. Such a result might be intuitive if we con-

sider that male carnivores are simply bigger predators than females, experiencing a different body mass relationship with their prey. The direct link between the energetic budget of carnivores and the intensity of their predation (Carbone et al. 1999) predicts that male carnivores also exhibit higher kill rates than females, with the exception of females with dependent young (Laundré et al. 2006, Nilsen et al. 2009b). This suggests that male and female carnivores intrinsically have a different potential demographic impact on their prey species: males usually exhibit both a higher intensity of predation and a lower tendency to rely on juveniles, the age class with the weakest functional relationship with population growth rate.

Even though we did not aim to link explicitly body mass with the strength of top–down regulation, our results do suggest that the body mass of a predator relative to that of its prey can play a role in defining its potential ability to control prey demography, as it strongly determines whether predation pressure will be mainly directed at juveniles or at adult individuals. However, formally linking the predator–prey body mass relationship, the age structure of predation, and the extent of top–down control on prey populations will require a more comprehensive approach. First, it should be noted that a higher selectivity of predation for adult individuals often corresponds to a reduced kill rate, as an effect of the greater amount of food provided by adults, so that the overall predation pressure by any given carnivore results from the combined effect of two components of predation, namely its intensity and selectivity. Second, the susceptibility of a prey species to top–down control by predation is not only a function of the type of predation pattern, but also depends on the specific life-history traits of the prey species. Ecological theory (Gaillard et al. 2005) and several empirical tests (Gaillard et al. 2000, Nilsen et al. 2009a) show that the demography of slow-living ungulate species (those with long generation time, low fecundity and high adult survival) is more sensitive to variation in adult survival than the demography of fast-living species. Large ungulates, therefore, are on the one hand expected to suffer reduced predation on the adult segment of the population than smaller ungulates, as an effect of their larger body size, but on the other hand, their population performance is predicted to be more sensitive to such predation pressure than that of smaller species, as a consequence of their slower life cycle. The interdependency of all these factors creates a set of complex dynamics that cannot be disentangled by the results of our study, but which definitely deserve attention, in an effort to explain the differential impact that different predator species have on different prey species.

In conclusion, while traditional studies of predation impact (Messier 1994, Laundré et al. 2006) have often been focused on the numerical relationships between predator and prey densities, we suggest that the main factors shown

here to be important (predator and prey body mass, predator sex, predation strategy, prey social organisation) should be taken into account when exploring the potential impact of a given predator on its prey species. Our results suggest that different types of predators intrinsically have dissimilar potential top–down impacts. Future research is needed to assess how the patterns illustrated here interact with the other two main determinants of the overall demographic impact of predation: predation intensity and prey life-history traits. We suggest that a comprehensive model of predation impact should take into account the fact that greater predation on adult individuals often corresponds with a reduced kill rate, and that the different predation pressure on the senescent segment of a prey population can modulate the potential demographic impact inherent in different predation strategies. Such a model must include the fact that prey generation time interacts with predation patterns to determine the overall prey population growth rate, and that slow-living species are more sensitive than fast-living species to a high level of adult mortality (Gaillard et al. 2005). The results presented here on factors affecting age composition should be considered a suitable starting point for a more comprehensive assessment of top–down control of ungulates by carnivores.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Body mass estimates for predator and prey species, used to study carnivore–ungulate patterns of predation, and references.

Appendix S2. Complete list of the predation studies included in the review, in excel worksheet format. For each study, the table shows the predator–prey couple, the average predator group size, the gender of the individual predators included in the study, the geographical location and period of the study, the season during which it was performed, the methodology used, predator and prey body masses, and the resulting age composition of kills at the highest resolution available. References are also shown.