What is an apex predator?

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Large 'apex' predators influence ecosystems in profound ways, by limiting the density of their prey and controlling smaller 'mesopredators'. The loss of apex predators from much of their range has lead to a global outbreak of mesopredators, a process known as 'mesopredator release' that increases predation pressure and diminishes biodiversity. While the classifications apex- and meso-predator are fundamental to current ecological thinking, their definition has remained ambiguous. Trophic cascades theory has shown the importance of predation as a limit to population size for a variety of taxa (top–down control). The largest of predators however are unlikely to be limited in this fashion, and their densities are commonly assumed to be determined by the availability of their prey (bottom–up control). However, bottom–up regulation of apex predators is contradicted by many studies, particularly of non-hunted populations. We offer an alternative view that apex predators are distinguishable by a capacity to limit their own population densities (self-regulation). We tested this idea using a set of life-history traits that could contribute to self-regulation in the Carnivora, and found that an upper limit body mass of 34 kg (corresponding with an average mass of 13–16 kg) marks a transition between extrinsically- and self-regulated carnivores. Small carnivores share fast reproductive rates and development and higher densities. Large carnivores share slow reproductive rates and development, extended parental care, sparsely populated territories, and a propensity towards infanticide, reproductive suppression, alloparental care and cooperative hunting. We discuss how the expression of traits that contribute to self-regulation (e.g. reproductive suppression) depends on social stability, and highlight the importance of studying predator–prey dynamics in the absence of predator persecution. Self-regulation in large carnivores may ensure that the largest and the fiercest do not overexploit their resources.

The ecological role of large predators is expressed by their classification as 'apex predators'; a term used to denote their elevated position on the trophic ladder. Apex predators are primarily known for their role as inhibitors of population irruptions of prey and smaller predators, an effect that cascades throughout ecological communities and promotes biodiversity. The keystone role of apex predators as ecosystem regulators is now firmly embedded in ecological theory (Estes et al. 2011, Ripple et al. 2014). Medium-sized predators, termed 'mesopredators', also drive community structure through a variety of pathways, including predation on small prey (Roemer et al. 2009). Apex predators limit the density of mesopredators so that total predation pressure is contained (Ripple et al. 2014). The loss of apex predators removes this inhibiting factor, resulting in 'mesopredator release' (Crooks and Soulé 1999, Prugh et al. 2009).

'Apex predator', 'mesopredator' and 'mesopredator release' are terms that have set the tone for our understanding of a wide range of ecological processes (Estes et al. 2011). However, the categorization of predators remains ambiguous. Within each ecosystem the largest extant predators are often classed as apex predators even if these same species are considered typical mesopredators elsewhere. For example, cats and foxes fall easily into the mesopredator group (Crooks and Soulé 1999), but as introduced species on islands they are often the largest mammal present and are therefore classed as apex predators (Rayner et al. 2007, Bergstrom et al. 2009, Roemer et al. 2009). The mesopredator release concept in itself was developed from the study of the coyote *Canis latrans* as an apex predator (Crooks and Soulé 1999), a species frequently placed in the mesopredator group when in the presence of wolves *Canis lupus* (Prugh et al. 2009, Ripple et al. 2013). Some regions contain a rich guild of large predators making it difficult to determine where to draw the line between apex- and meso-predators (Prugh et al. 2009). Indeed, some of the world's iconic apex predators coexist with larger and fiercer predators (Palomares and Caro 1999), and many of the world's largest predators are now extinct. Is the gray wolf therefore a mesopredator in the presence of larger carnivores?

Predators of all sizes harass, kill and scare predators smaller than themselves: tigers dominate wolves (Miquelle et al. 2005), wolves exclude coyotes (Ripple et al. 2013), coyotes control foxes (Crooks and Soulé 1999), foxes kill cats (Glen and Dickman 2005), cats suppress rats (Rayner et al. 2007), and rats displace mice (Wanless et al. 2007).

Predators of all sizes can also induce trophic cascades: pumas promote tree recruitment by controlling deer (Ripple et al. 2014), sea otters recover kelp forests by eating herbivorous sea urchins (Estes et al. 2011), cats maintain island productivity by suppressing rabbits (Bergstrom et al. 2009), plants benefit when fish reduce dragonfly predation on pollinating insects (Knight et al. 2005), and nutrient cycling is influenced by the stress response of herbivorous grasshoppers to hunting spiders (Hawlena and Schmitz 2010).

Despite these similarities there appears to be little functional redundancy between large and small predators. The loss of the largest of predators has had a disproportionately disruptive influence on ecosystem structure and function (Ripple et al. 2014); a process coined 'trophic downgrading' (Estes et al. 2011). Defining predator status comparatively within each system is problematic because it implies that mesopredators can step into the role of apex predators as these disappear from the landscape. Studies suggest the opposite: mesopredators are not effective replacements for apex predators (Prugh et al. 2009). Size may in fact be a reliable predictor of a predator's ecological status, reflecting differences in evolutionary pressures and adaptation. A mesopredator may therefore remain a mesopredator even in systems devoid of larger predators, and an apex predator need not be the single largest.

What then distinguishes apex predators from mesopredators? One fundamental consequence of size is that large predators are relatively safe from predation (Promislow and Harvey 1990). In the absence of an effective extrinsic source of predation, there can be two main mechanisms limiting population growth: 1) the decline in the abundance of their prey (a bottom–up force), and 2) an internal mechanism of self-regulation (a socially mediated force). Although ecologists have traditionally supported the bottom–up view (Hayward et al. 2007), trophic cascades theory highlights the role of top–down regulation in population dynamics. It would be surprising if top–down forcing influences all but the largest. Indeed, studies frequently find negative rather than positive correlations between apex predators and their prey (Estes et al. 2011), hinting that apex predator may not be bottom–up driven. While habitat productivity is not ruled out as a contributing factor to population density (Carbone and Gittleman 2002, Jedrzejewski et al. 2007), large predators may be unique in maintaining their own populations at sustainable levels.

Body mass may be a good predictor of apex- and meso-predator status, because it directly influences the rate of extrinsic predation pressure, thus indirectly influencing life-history traits. Across mammals both juvenile and adult mortality rates increase as body mass declines, and higher mortality is associated with r-selected life-history variables (Promislow and Harvey 1990). Among carnivores, increasing body size is associated with dietary requirements for larger prey (Carbone et al. 2007) and lower densities relative to prey biomass (Carbone and Gittleman 2002). Evolutionary pressures that influence body mass may give rise to similar adaptations in different taxonomic groups, and the emergence of a 'self-regulating ecomorph' (Flueck 2000).

Most large predator populations are subjected to lethal control (Ripple et al. 2014) and therefore studies of stable predator populations are rare. Several recent studies have pointed to the importance of considering the condition of social stability in large predators when analyzing predator–prey interactions (Wallach et al. 2009, Cariappa et al. 2011, Ordiz et al. 2013, Cubaynes et al. 2014). Evidence of social interactions that may enable self-regulation has emerged from studies of large predators including bears, large cats, large canids and large otters (Supplementary material Appendix 1 Table A1). These studies offer examples where social interactions, rather than resource availability, drive mortality and fecundity, limit population density and stability, and influence the expression of life history traits that slow population growth rates (Table 1). Where human-caused mortality is low, large predators may therefore retain relatively constant population densities despite differences in resource availability.

Here we investigate the hypothesis that predators above a certain weight threshold are self-regulating, while smaller predators require extrinsic regulation by a larger predator (Fig. 1). We conducted an analysis of life-history traits that may contribute to self-regulation in the Carnivora (hereafter carnivores). We selected the carnivores because trophic cascades effects have been consistently demonstrated for several members of this group (Ripple et al. 2014). We found that carnivores above a threshold mass have life-history traits conducive to self-regulation.

Methods

We conducted a review of life-history traits of terrestrial and semi-terrestrial species, belonging to twelve carnivore families, for which sufficient information was available (n = 121, Supplementary material Appendix 1 Table A2). We selected eleven variables representing four major life-history traits, which we considered likely to contribute to self-regulation, and analyzed them in relation to upper limit body mass (ULBM) and average body mass (ABM). Data was sourced from encyclopedias (e.g. Encyclopedia of Life), online databases (e.g. Carey and Judge 2002, de Magalhaes and Costa 2009, IUCN), life-history journals (e.g. Mammalian Species) and other peer-reviewed sources.

Human hunting can have pronounced effects on the expression of life history traits (Haber 1996, Milner et al. 2007) and few populations have escaped this impact (Ripple et al. 2014). We therefore chose upper limit values for most variables (Supplementary material Appendix 1 Table A2) to account for the potential of individuals in undisturbed

Table 1. Evidence that social interactions enable self-regulation in large carnivores. For each Family we summarize the number of studies supporting the propositions that social interactions, rather than resource availability: drive mortality and fecundity (A), limit density (B), affect population stability (C), and affect the expression of life history traits that slow population growth rates (D). The proportion of studies is shown in brackets, with some studies supporting more than one proposition. Summarized from studies compiled in the Supplementary material Appendix 1 Table A1.

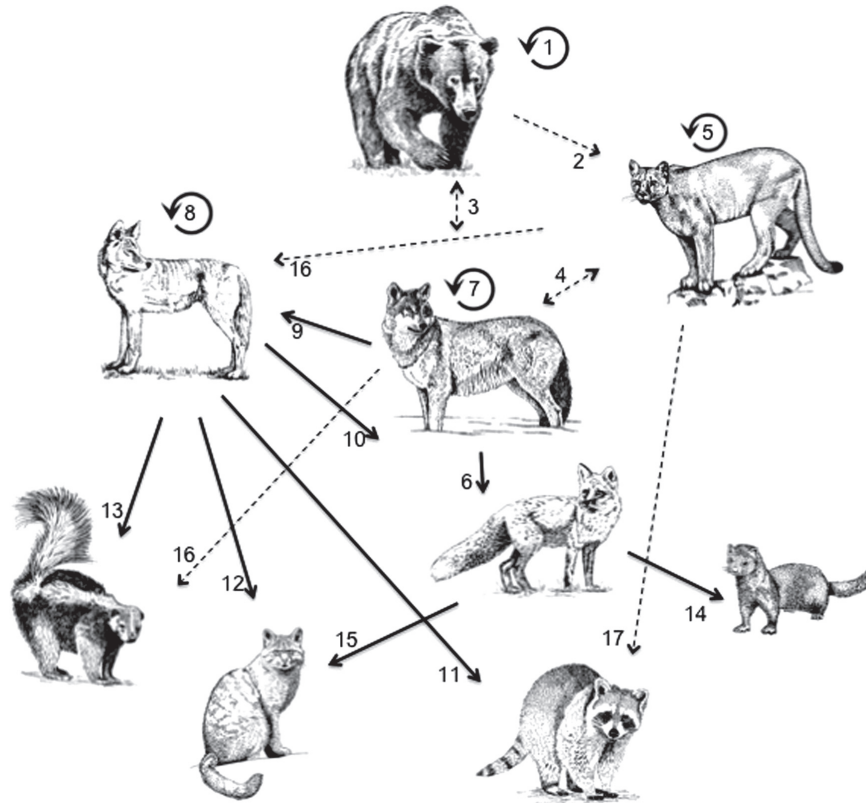| Proposition	Ursidea	Felidea	Canidea	Mustelidea	Total
A	8 (89%)	2 (18%)	4 (27%)	3 (60%)	17 (43%)
B	2 (22%)	8 (73%)	7 (47%)	1 (20%)	18 (45%)
C	4 (44%)	3 (27%)	5 (33%)	1 (20%)	13 (33%)
D	7 (78%)	2 (18%)	2 (13%)	0	11 (28%)

Figure 1. Apex- and meso-predator status are fixed ecological categories: apex predators are self-regulated and smaller predators are extrinsically regulated. Antagonistic interactions (dashed arrows) and top–down forces (thick arrows) exist within and across both groups, but the ability to self-regulate (circular arrows) is unique to large predators. Citations for interactions are: 1, 5, 7, 8 – Supplementary material Appendix 1 Table A1; 2 - Murphy et al. 1998; 3, 4, 16, 17 - Palomares and Caro 1999, Gunther and Smith 2004, Jimenez et al. 2008; 6 - Letnic et al. 2011; 9 - Ripple et al. 2013; 10–13 - Crooks and Soulé 1999; 14 - Carlsson et al. 2010; 15 - Glen and Dickman 2005. Artwork by J. Parkhurst.

populations to grow large, mature, form social bonds, hold territories and provide uninterrupted care for their young. The relation of life-history traits with ULBM and ABM showed similar trends (ULBM and ABM values are correlated r = 0.97, p < 0.0001), and we chose to present ULBM results because this variable is less likely to be influenced by human activity.

Variables

Reproductive strategy (r/K)

We hypothesized that self-regulating carnivores would employ a K-strategy (i.e. slow life-history) and invest more energy in fewer offspring compared to extrinsically-regulated carnivores. Five variables were assessed for this trait: 1) age at weaning, 2) age at independence (and dispersal), 3) age at sexual maturity, 4) lifespan and 5) population reproductive rate (accounting for reproductive suppression of some females).

The age at weaning and independence provide measures of parental care. To account for relative parental investment, both variables were also analyzed in relation to lifespan and reproductive rate (e.g. age at independence / lifespan / number of offspring / year). We modified the reproductive rate variable to account for social carnivores that limit the reproduction of some females (offspring / year / average number

of breeding females in a group / average number of sexually mature females in a group).

Family planning

The limitation of offspring production below the species' maximum reproductive potential is referred to here as 'family planning', and we expected this trait to contribute to self-regulation. We used two binary variables: 1) female reproductive suppression and 2) infanticide. Female reproductive suppression occurs in social species in which dominant females exclude other sexually mature females from breeding, or litters of subordinates are killed or abandoned.

Female territoriality

Territoriality is considered an important mechanism for spacing individuals or groups and limiting population density (Cariappa et al. 2011). We focused on females because territorial males may occupy the home range of several females and reproduce with all of them (e.g. felids and bears). We included a binary variable 'female territoriality' and a continuous subset variable 'female density'.

For the subset of female-territorial carnivores, we recorded the median female territory size and the average number of females in a social group to calculate an estimate of 'female density' (group size / territory size). We used the median value

because territory size may vary widely in relation to habitat conditions. To account for the differences in body mass we calculated an estimate of carnivore biomass by adjusting the density to standardized metabolic needs (group size / territory size $\times$ ABM$^{0.75}$, Gittleman and Harvey 1982). Data were obtained for 55 (of 69) female-territorial carnivores.

Cooperative behavior

Cooperative behaviors may be features of self-regulating species and associated with the ability to secure large territories and large prey (Creel and Macdonald 1995). We used cooperative hunting, and two forms of cooperative care: 1) paternal care and 2) alloparental care, as measures of cooperative behaviors, all as binary variables. Carnivores were included in both categories if their social structure was flexible and inclusive of both forms (e.g. red fox *Vulpes vulpes*, Cavallini 1996).

Data analysis

We used a principal components (PC) analysis (SPSS 20), of the eleven variables for which full datasets were available (n = 73 species), to identify groups of strongly interacting variables (Jolliffe 2002) across the Carnivora and discretely for each Family and mass group. We compared the main PCs, and each of the individual variables, with log-transformed body mass. We then fit a piecewise regression to identify a threshold in the relationships (Toms and Lesperance 2003), using the segmented package in R (Muggeo 2008). Variables were log-transformed to meet the assumption of constant variance in residuals. Binary variables were tested using a piecewise logistic regression (Toms and Lesperance 2003). We tested the threshold significance using a Davies test (Davies 1987, Piepho and Ogutu 2003). The subset variables female density and female biomass were correlated separately with the strongest PCs and with body mass. We compared the relationship between parental care and parental investment with body mass separately.

Results

The first three PCs cumulatively accounted for 70% of the variation in the dataset (Table 2). Reproductive strategy

Table 2. Scores of the eleven life-history variables in the top three models of the principal component analysis (PCA).

Variables	PC1 (33.6%)	PC2 (25%)	PC3 (11.7%)
Lifespan	0.854	0.184	−0.091
Age at sexual maturity	0.852	0.190	0.048
Age at weaning	0.814	0.174	−0.204
Age at independence	0.770	0.359	0.039
Female reproduction suppression	−0.388	0.800	−0.051
Reproductive potential	−0.601	−0.424	−0.152
Paternal care	−0.487	0.580	−0.238
Alloparental care	−0.328	0.824	−0.216
Cooperative hunting	−0.222	0.513	−0.326
Infanticide	0.044	0.631	0.558
Territoriality (female)	−0.266	0.163	0.832

variables were most strongly associated with the first PC axis (PC1), which is representative of the fast-slow (r-K) life history continuum. The piecewise regression identified a threshold in the relationship between PC1 and ULBM at 33.85 kg (ABM 13–16 kg), with a 95% confidence interval (CI) between 18.16–63.12 kg (Davies test: p < 0.001, Fig. 2A). The second PC axis (PC2) was formed by the socially complex behaviors (e.g. 'family planning' and alloparental care) on one side, and high reproductive rates on the other, with no significant threshold identified. Female territoriality only appeared as a significant variable in PC3 (Table 2). In no case was a significant threshold detected for the individual variables included in the PCA.

Across the full carnivore mass range, both PC1 and PC2 were positively correlated with body mass (Pearson's correlation LogULBM: PC1, r = 0.73, p < 0.001; PC2, r = 0.38, p < 0.01). There was no correlation between PC3 and body mass (NS). Large carnivores (ULBM ≥ 34 kg) had mostly positive PC1 values (70%) and about half (55%) had positive PC2 values, reflecting a K-strategy and a tendency towards socially complex reproductive behaviors. Small carnivores (ULBM < 34 kg) had predominantly negative PC1 (73%) and PC2 (69%) values, corresponding with an r-strategy and more solitary or biparental social groups (Fig. 2B). Both within and between taxonomic families, large carnivores had consistently higher PC1 and PC2 values (Fig. 2C). However, while small carnivore families were clustered together, each family of large carnivores was distinctly placed along the two axes (e.g. bears had the highest PC1 values and large canids had the highest PC2 values).

Female territoriality was ubiquitous and common across the Carnivora (71% of species), but within the subset of carnivores that are female-territorial, female density was negatively correlated with body mass (Spearman's r = −0.77, p < 0.001; Fig. 3A) and with PC1 (r = −0.41, p < 0.01). Female biomass (female density controlled for standardized metabolic needs) was also negatively related with body mass (r = −0.48, p < 0.001, Fig. 3B), but not with PC1 (NS). Thresholds were detected for both density (71.95 kg, 95% CI 6.67–775.88) and biomass (73.70 kg, 95% CI 4.52–1199.91), but neither threshold was significant (Davies test: p = 0.691 and p = 0.913, respectively).

Large carnivores invest more time and a larger portion of their lifetime in each offspring, relative to small carnivores. Parental care (age at weaning and independence) and parental investment (parental care controlled for lifespan and reproductive rate) were positively correlated with body mass (parental care: by weaning, r = 0.38, p < 0.001, by independence r = 0.52, p < 0.001; parental investment: by weaning r = 0.33, p < 0.001, by independence r = 0.24, p < 0.001). Thresholds were detected for parental investment (by independence: 11.87 kg, 95% CI 3.43–41.02, Davies test: p = 0.1; by weaning 14.0 kg, 95% CI 5.64–34.78, Davies test: p = 0.004), but only the threshold for weaning was significant (Fig. 4).

Discussion

Life history traits that may influence population regulation differ between large and small carnivores, lending support
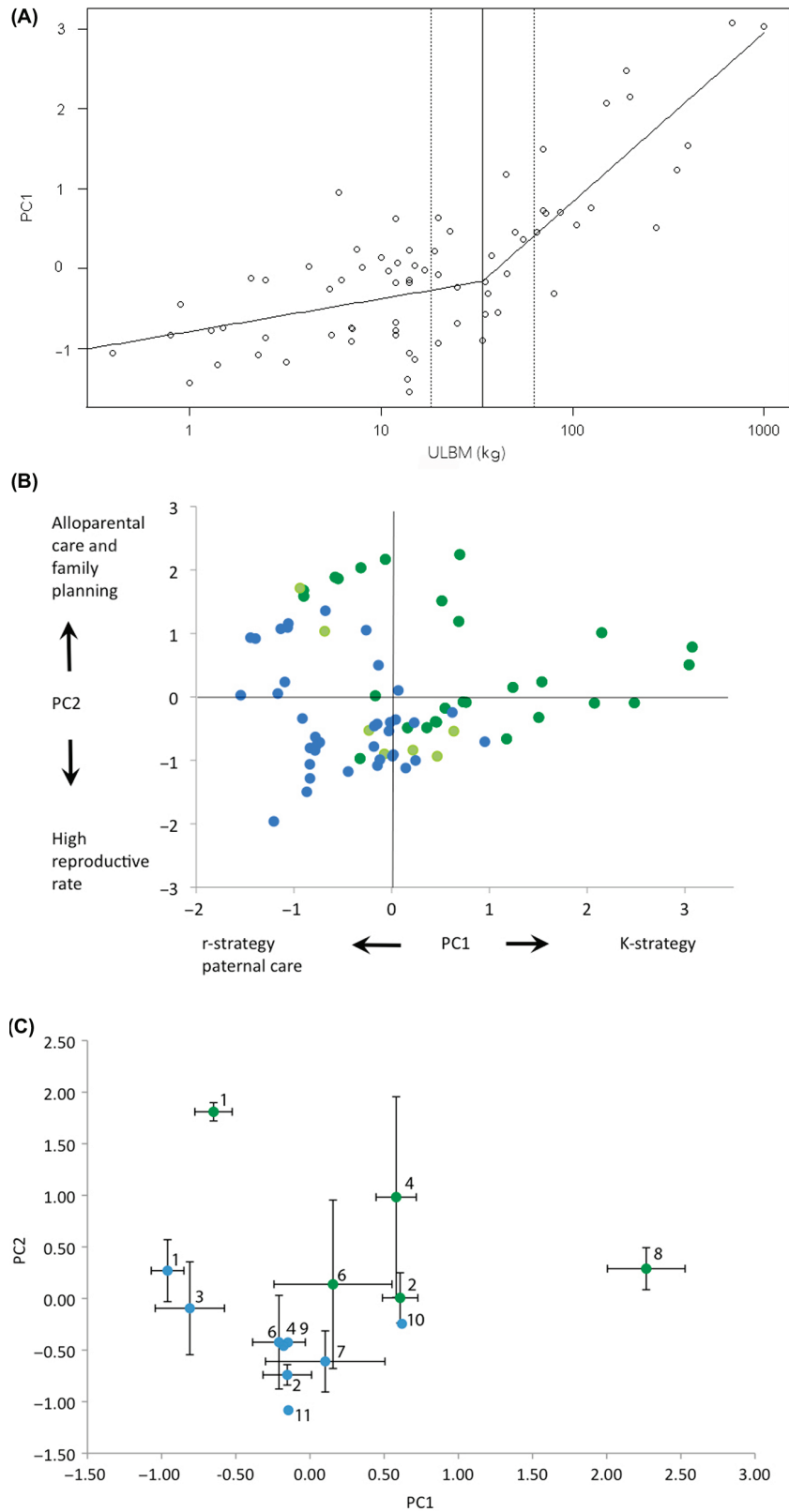
Figure 2. Relationship between the two strongest principal components (PC) and upper limit body mass (ULBM). (A) Relation of PC1 to log transformed ULBM with the estimated threshold identified at 34 kg (full line), with a 95% confidence interval of 18–63 kg (dashed lines). (B) Position of carnivores on the first two PC axes. (C) Position of family and mass groups on the two major axes (average ± SE), separated at 34 kg. Blue circles are identified as typical mesocarnivores (ULBM < 18 kg), light green circles (in B) denote carnivores that fall within the lower threshold confidence zone (ULBM 18–34 kg) and dark green circles are identified as apex carnivores (ULBM ≥ 34 kg). 1 = Canidae, 2 = Felidae, 3 = Herpestidae, 4 = Hyaenidae, 6 = Mustelidae, 7 = Procyonidae, 8 = Ursidae, 9 = Ailuridae (red panda, *Ailurus fulgens*), 10 = Eupleridae (fossa *Cryptoprocta ferox*), 11 = Viverridae (common genet, *Genetta genetta*).
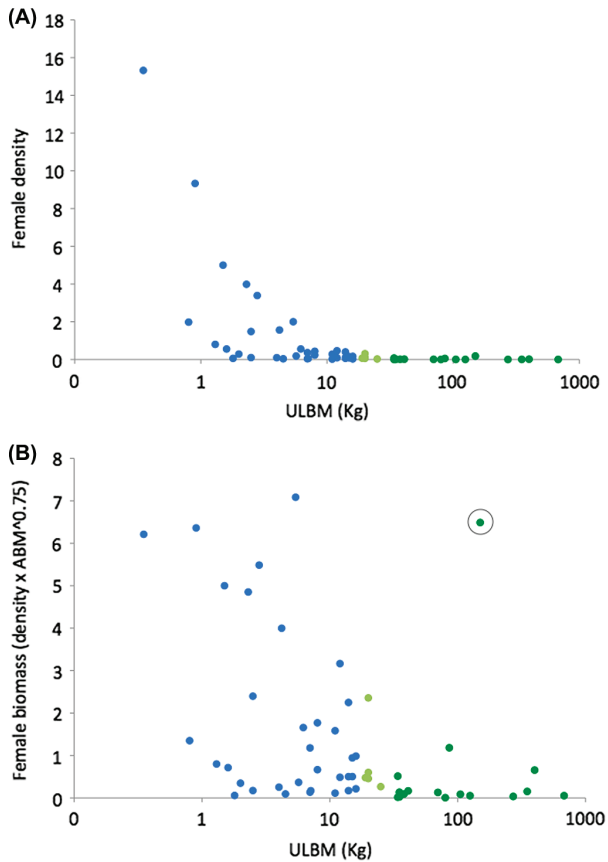
Figure 3. Density (A) and biomass (B) of territorial female carnivores relative to ULBM. The giant panda, an outlier, is circled in (B). Blue circles are identified as typical mesocarnivores (ULBM < 18 kg), light green circles denote carnivores that fall within the lower threshold confidence zone (ULBM 18–34 kg) and dark green circles are identified as apex carnivores (ULBM ≥ 34 kg).

to the proposition that apex- and meso-predator status are fixed. In this analysis of terrestrial and semi-terrestrial carnivores, an ULBM of 18–34 kg (ABM 13–16 kg) marked a transition between extrinsically regulated meso-carnivores and self-regulating apex carnivores. This threshold is similar to the commonly used ABM of 15 kg to distinguish meso-carnivores from apex-carnivores (Prugh et al. 2009, Ripple
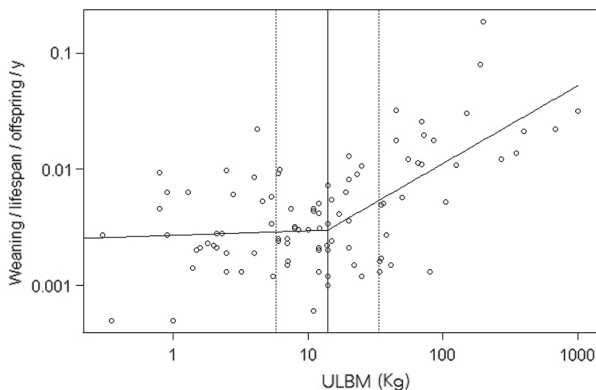
Figure 4. Relationship between parental investment (age at weaning controlled for lifespan and reproductive rate) and body mass with the estimated threshold identified at an ULBM of 14 kg (full line), with a 95% confidence interval of 6–35 kg (dashed lines).

et al. 2014), but is slightly lower than previous studies that found a dietary threshold at an ABM of 20 kg (Carbone et al. 2007). Our analysis also helps clarify the ecological position of carnivore species whose status is ambivalent (e.g. coyotes are recognized here as apex predators).

Large carnivores probably self-regulate because they typically invest more in fewer offspring, suppress the reproduction of mature females and commit infanticide ('family planning'), are socially cooperative and hold sparsely populated territories (Fig. 2–4). Mesocarnivores on the other hand are unlikely to self-regulate and are instead adapted to extrinsic-regulation pressure, as suggested by a higher reproductive rate, lower investment in each offspring, scarcity of 'family planning' and the potential to attain higher densities. Differences between large and small carnivores persist when controlling for standardized metabolic needs and group size (Fig. 3), and for lifespan and reproductive rate (Fig. 4). These life-history traits are often shared more closely within mass groups than within taxonomic groups (Fig. 2C).

Reproductive strategy, the main contributor to the first PC axis, was the most important trait defining carnivore status. Extended parental care and heavier investment in each offspring were particularly characteristic of apex carnivores. Within apex carnivores K-traits and parental investment increase relative to body mass at a faster rate than in mesocarnivores (Fig. 2A, 4). Thus apex carnivores increase their K-traits as body mass increases but this does not consistently occur in the mesocarnivore group. Predation pressure on mesocarnivores of all sizes may be consistently selecting for r-traits.

'Family planning', an important contributor to the second PC axis, was also characteristic of apex carnivores, particularly in canids. Infanticide is often associated with reproductive suppression of sexually mature females, and 65% of carnivores that exclude some females from breeding perform infanticide. In these species the dominant females kill the young of the subordinate females in their social group. Where infanticide is used to restrict the reproduction of females, it most likely acts to limit the size of social groups and ultimately population density. Overall, 52% of carnivores that practice infanticide do not suppress the reproduction of females. In these cases infanticide occurs when a rival male displaces the resident breeding male, and the sire's offspring are killed to gain reproductive advantage (sexually-selected infanticide). Male-driven infanticide has a substantial influence on population density and demography of bears and large felids (Supplementary material Appendix 1 Table A1). Male-driven infanticide may in some cases select for larger groups. In banded mongoose, reproductive suppression is selected against because pup survival increases when more females in each group reproduce due to male infanticide (Cant 2000).

Female reproductive suppression is clearly an important regulation mechanism in social carnivores, occurring in most large canids (88–100%) and large hyenas (67%) (Supplementary material Appendix 1 Table A2). It may however also function indirectly in solitary predators. For example, Ordiz et al. (2008) found that an adult female brown bear was less likely to produce cubs if her nearest neighbor already had cubs. They argued that this could be considered a form of reproductive suppression, probably caused by resource competition among female bears living close to each other.

In apex carnivores, female territoriality contributes to self-regulation by maintaining low densities (Fig. 3, Supplementary material Appendix 1 Table A1), but on its own territoriality is not a significant predictor of predator status (Table 2). Territoriality is unlikely to contribute to self-regulation if territories shrink in response to increased densities, as has been observed in several small carnivore populations (Cavallini 1996, Benson et al. 2006). Flexibility in territorial behavior is probably advantageous for smaller carnivores that have to adjust their space use in relation to the threat of larger carnivores (Cavallini 1996), while territorial stability is important for large predatory carnivores to buffer patchy or variable resources and for protection from dangerous conspecifics (Supplementary material Appendix 1 Table A1).

Cooperative behaviors were more pronounced in large carnivores (Table 2). The predisposition for cooperative hunting is in line with a tendency towards hypercarnivory in large carnivores (Carbone et al. 2007). While cooperative hunting of large prey is not unique to large carnivores (some ant species hunt prey thousands of times their size, Dejean et al. 2010), nor is it obligate (not all large carnivores are carnivorous), the most complex forms of cooperative hunting have been observed primarily in large carnivores (MacNulty et al. 2009, Bailey et al. 2013).

Alloparental care was more common in the large carnivore group, and was associated with 'family planning' in the second PC (Fig. 2B). In large social carnivores therefore, the association of alloparental care with female reproductive suppression and infanticide provides a high carer:offspring ratio. Paternal rearing, on the other hand, was affiliated with an r-strategy and with small carnivores in the first PC (Fig. 2B). In both solitary and biparental carnivores, female breeding is unrestricted. An r-strategy without 'family planning' is a condition conducive to high reproductive output and is more common in mesocarnivores: 48% of small carnivores versus 7% of large carnivores have negative PC1 values and are solitary or biparental.

The results of our study were robust despite the high level of 'noise' in the dataset. The quality of life history knowledge varies between species and traits: research effort is biased towards a small number of carnivores (Ripple et al. 2014); much data are derived from captive animals; and data sourced from wild populations may be equally biased due to anthropogenic effects (Milner et al. 2007). Additionally, life-history traits vary with habitat conditions (Carbone and Gittleman 2002, Jedrzejewski et al. 2007). While these biases are unlikely to be confounding in this study, we do expect that advances in life history studies of wild populations with minimal anthropogenic effects (particularly predator control) will help clarify the mechanisms regulating population size.

Our analysis identified a threshold at approximately 34 kg (ULBM), but there are several reasons not to consider this weight overly prescriptive. Firstly, the threshold mass that differentiates apex- from meso-predators is likely to vary between taxonomic groups. In this study the threshold mass was strongly influenced by three families that contributed the highest number of species: the canids, felids and mustelids. Defining a threshold mass at the Order level was necessary in order to obtain a sufficient sample size, but it may obscure differences between families. For example, the ≤ 12 kg fossa

Cryptoprocta ferox, the largest member of the Eupleridae and Madagascar's largest carnivore, shares traits with apex carnivores (Fig. 2C). The threshold mass is also likely to be much higher in the pinnipeds whose large body mass is an adaptation to their marine habitat where they are subjected to predation from even larger predators. Secondly, the threshold mass identified can also be influenced by the traits investigated and by sample size. Here, parental investment showed a threshold at a lower position (14 kg) than the eleven variables combined in PC1 (ULBM 34 kg), possibly due to the larger sample size of the former, and the absence of many medium-sized carnivores in the latter. Lastly, it remains unclear whether habitat size influences predator status and self-regulation. Several islands are too small to support large carnivores but do contain medium-sized carnivores, which our analysis suggests are mesopredators. Whether plasticity in the expression and evolution of life-history traits can enable mesopredators to self-regulate and function as apex predators on small islands remains unknown.

The ecological roles of large carnivores vary greatly, and only some function ecologically as 'apex predators'. Large carnivores that are primarily vegetarian will have ecological effects that differ from those that are carnivorous. Despite this, self-regulation within large predators may provide a distinct ecological function. For example, apex carnivores are less likely to become 'invasive'. A notable case is the contrasting ecologies of the red fox and the dingo *Canis dingo*, two canids that migrated to Australia. The fox, a mesopredator, correlates positively with resource availability, and in the absence of regulation by dingoes reaches high densities and can drive the extinction of their prey. By contrast the dingo, an apex predator, forms stable population densities across a wide productivity gradient when socially stable, and contributes significantly to the preservation of Australia's biodiversity (Wallach et al. 2009, Letnic et al. 2011).

Identifying whether predators are primarily self- or extrinsically- regulated requires long-term studies of socially stable populations. Human persecution of predators is a major influence not only on their numbers, but also on their social structure (Haber 1996, Wallach et al. 2009, Ordiz et al. 2013). In turn, social stability determines predator–prey dynamics, and the relative importance of bottom–up and top–down forces driving population size.

Influence of social stability on life-history

The expression of self-regulation in apex carnivores stems from social interactions, and is therefore subject to the condition of social stability. Reproductive strategy (r/k) variables are responsive to conditions of population density, demographics and stability. In apex carnivore populations subjected to human hunting, age at sexual maturity (and primipatry) declines, reproductive rate increases, parental care shortens and demography skews towards juveniles. In non-exploited populations of large canids, offspring often remain within their natal group for several years, delaying primipatry and reducing litter production (Haber 1996). Social stability generally acts to promote the expression of K-traits by slowing down population turnover rates (Supplementary material Appendix 1 Table A1).

Social traits that limit densities are similarly dependent upon a condition of social stability, and hunting influences carnivore densities beyond the loss of the individuals killed. Female reproductive suppression is a social phenomenon, and in hunted populations social groups are fragmented, resulting in more alpha pairs and thus more breeding females (Haber 1996, Bryan et al. 2014). Social stability also influences infanticide rates and it's role in populations. Human hunting reduces female-driven infanticide associated with social regulation (Canidea), but increases male-driven infanticide related to reproductive competition (Ursidae and Felidae, Supplementary material Appendix 1 Table A1).

Cooperative behaviors require a state of social stability to develop and are often lost in populations subjected to culling. For cooperative-hunting carnivores, group size and composition are important factors contributing to the hunting success of large and dangerous prey (Creel and Macdonald 1995, MacNulty et al. 2009, Mukherjee and Heithaus 2013). Increased sociality in large canids, for example, is associated with delayed independence and dispersal (Bekoff et al. 1981) and higher pup survival (Stahler et al. 2013). In apex carnivores subjected to hunting, the loss of cooperative behaviors increases mortality rates beyond the individuals directly culled (Haber 1996).

Territoriality can only act to limit population density if territories are large and stable. The breakdown of territory boundaries may contribute to higher densities by increasing immigration rates and reducing spacing behaviors. This has been shown to occur in several large carnivores (Supplementary material Appendix 1 Table A1), but also in the European badger (McDonald et al. 2008), a small carnivore with 'apex' characteristics.

Reduced expression of self-regulation traits in socially disrupted populations can lead to both increases and declines in population density (Supplementary material Appendix 1 Table A1). For example, attempts to control dingoes with poison-baiting and shooting, can inadvertently result in higher population densities, while protected populations tend to be stable (Wallach et al. 2009). Similarly, banning wolf hunting resulted in the establishment of kin-based packs but not in higher densities (Rutledge et al. 2010). Population dynamics may vary widely between those that are socially stable and those that are disrupted. This is relevant to studies that attempt to interpret the effect of productivity on apex predators. Cariappa et al. (2011) argued that wolf populations are limited through social interactions (self-regulated) rather than prey availability alone. They showed that although wolf density can be positively correlated with ungulate biomass, a threshold limit to density is more strongly supported for wolf populations protected from hunting. Similarly, Cubaynes et al. (2014) found that the socially stable wolf population of Yellowstone National Park is primarily limited by intraspecific aggressive interactions rather than by prey availability.

Unfortunately socially stable apex predator populations are rare (Ordiz et al. 2013). Human hunting is threatening 87% of large carnivore species worldwide (ABM of > 15 kg) and most populations are decreasing (Ripple et al. 2014). Life-history traits associated with self-regulation may increase the sensitivity of carnivores to exploitation. High population size alone is an insufficient measure of population health (Wallach et al. 2009, Ordiz et al. 2013). Carnivores subjected to hunting undergo markedly different population dynamics. There are few studies that have investigated how the loss of individual animals influences populations, and fewer still that have determined the drivers of population density in protected populations. We are only recently beginning to appreciate the profound importance of large carnivores for the health of ecosystems. Apex predators may keep the proverbial 'balance of nature' not only by limiting the populations of those they hunt, but also by limiting themselves. Whether humanity can achieve a similar feat is an important question to consider.

Are we apex primates?

Our earliest ancestors were prey species most likely top–down regulated by large carnivores (Rose and Marshall 1996), but we have evolved into the fiercest predator on the planet, free of extrinsic top–down regulation and are arguably apex predators in our own right. In the words of Louis C. K. "we got out of the food chain" (Oh My God, HBO, 2013). And yet, after surpassing a population size of 7 billion in 2012, triggering a sixth mass extinction and severely depleting non-renewable resources, one would hesitate to argue that humans are self-regulating. Current human society appears to be a classic case of mesopredator release, destined to end in a Malthusian collapse (Ehrlich and Ehrlich 2013). However, when we consider that self-regulation in apex carnivores is dependent upon a state of social stability, we can reflect upon our own condition as that of a socially disrupted apex primate. And social instability can be redressed.

References

Bailey, I. et al. 2013. Group hunting within the Carnivora: physiological, cognitive and environmental influences on strategy and cooperation. – Behav. Ecol. Sociobiol. 67: 1–17.

Bekoff, M. et al. 1981. Life-history patterns and sociality in canids: body size, reproduction and behavior. – Oecologia 50: 386–390.

Benson, J. F. et al. 2006. Regulation of space use in a solitary felid: population density or prey availability. – Anim. Behav. 71: 685–693.

Bergstrom, D. M. et al. 2009. Indirect effects of invasive species removal devastate World Heritage Island. – J. Appl. Ecol. 46: 73–81.

Bryan, H. M. et al. 2014. Heavily hunted wolves have higher stress and reproductive steroids than wolves with lower hunting pressure. – Funct. Ecol. doi: 10.1111/1365-2435.12354 in press.

Cant M. A. 2000. Social control of reproduction in banded mongooses. – Anim. Behav. 59: 147–158.

Carbone, C. and Gittleman, J. L. 2002. A common rule for the scaling of carnivore density. – Science 295: 2273–2276.

Carbone, C. et al. 2007. The costs of carnivory. – PLoS Biol 5(2): e22.

Carey, J. R. and Judge, D. S. 2002. Longevity records: life spans of mammals, birds, amphibians, reptiles and fish. – In: Monographs on population aging. No. 8. Odense Univ. Press.

Cariappa, C. A. et al. 2011. A reappraisal of the evidence for regulation of wolf populations. – J. Wildlife Manage. 75: 726–730.

Carlsson, N. O. L. et al. 2010. Long-term data on invaders: when the fox is away, the mink will play. – Biol. Invas. 12: 633–641.

Cavallini, P. 1996. Variation in the social system of the red fox. – Ethol. Ecol. Evol. 8: 323–342.

Creel, S. and Macdonald, D. 1995. Sociality, group size, and reproductive suppression among carnivores. – Adv. Stud. Behav. 24: 203–257.

Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. – Nature 400: 563–566.

Cubaynes, S. et al. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). – J. Anim. Ecol. doi: 10.1111/1365-2656.12238.

Davies, R.B. 1987. Hypothesis testing when a nuisance parameter is present only under the alternative. – Biometrika 74: 33–43.

Dejean, A. et al. 2010. Arboreal ants use the "Velcro® principle" to capture very large prey. – PLoS ONE 5(6): e11331.

de Magalhaes, J. P. and Costa, J. 2009. A database of vertebrate longevity records and their relation to other life-history traits. – J. Evol. Biol. 22: 1770–1774.

Ehrlich, P. R. and Ehrlich A. H. 2013. Can a collapse of global civilization be avoided? – Proc. R. Soc. B. 280: 20122845.

Estes, J. A. et al. 2011. Trophic downgrading of planet earth. – Science 333: 301–306.

Flueck, W. T. 2000. Population regulation in large northern herbivores: evolution, thermodynamics and large predators. – Eur J. Wildl. Res. 46: 139–166.

Gittleman, J. L. and Harvey, P. H. 1982. Carnivore home-range size, metabolic needs and ecology. – Behav. Ecol. Sociobiol. 10: 57–63.

Glen, A. S. and Dickman, C. R. 2005. Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. – Biol. Rev. 80: 387–401.

Gunther, K. and Smith, D. W. 2004. Interactions between wolves and female grizzly bears with cubs in Yellowstone National Park. – Ursus 15: 232–238.

Haber, G. C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. – Conserv. Biol. 10: 1068–1081.

Hawlena, D. and Schmitz, O. J. 2010. Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. – Proc. Natl Acad. Sci. 107: 15503–15507.

Hayward, M. W. et al. 2007. Carrying capacity of large African predators: prediction and tests. – Biol. Conserv. 139: 221–229.

Jedrzejewski, W. et al. 2007. Territory size of wolves *Canis lupus*: linking local (Bialowieza Primeval Forest, Poland) and Holarctic-scale patterns. – Ecography 30: 66–76.

Jimenez, M. D. et al. 2008. Gray wolves, *Canis lupus*, killed by cougars, *Puma concolor*, and a grizzly bear, *Ursus arctos*, in Montana, Alberta, and Wyoming. – Can. Field Nat. 122: 76–78.

Jolliffe, I. T. 2002. Principal component analysis, 2nd edn. – Springer.

Knight T. M. et al. 2005. Trophic cascades across ecosystems. – Nature 437: 880–883.

Letnic, M. et al. 2011. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. – Biol. Rev. 87: 390–413.

MacNulty, D. R. et al. 2009. Predatory senescence in ageing wolves. – Ecol. Lett. 12: 1–10.

McDonald, R. A. et al. 2008. Perturbing implications of wildlife ecology for disease control. – Trends Ecol. Evol. 23: 53–56.

Milner, J. M. et al. 2007. Demographic side effects of selective hunting in ungulates and carnivores. – Conserv. Biol. 21: 36–47.

Miquelle, D. G. et al. 2005. Tigers and wolves in the Russian Far East: competitive exclusion, functional redundancy, and conservation implications. – In: Ray, J. C. et al. (eds), Large carnivores and the conservation of biodiversity. Island Press, pp. 179–207.

Muggeo, V. M. R. 2008. Segmented: an R package to fit regression models with broken-line relationships. – R News 8: 20–25.

Mukherjee, S. and Heithaus, M. R. 2013. Dangerous prey and daring predators: a review. – Biol. Rev. 88: 550–563.

Murphy, K. M. et al. 1998. Encounter between bears and cougars: some ecological implications. – Ursus 10: 55–60.

Ordiz, A. et al. 2008. Distance-dependent effect of the nearest neighbor: spatiotemporal patterns in brown bear reproduction. – Ecology. 89: 3327–3335.

Ordiz, A. et al. 2013. Saving large carnivores, but losing the apex predator? – Biol. Conserv. 168: 128–133.

Palomares, F. and Caro, T. M. 1999. Interspecific killing among mammalian carnivores. – Am. Nat. 153: 492–508.

Piepho, H. P. and J. O. Ogutu. 2003. Inference for the break point in segmented regression with application to longitudinal data. – Biometrical J. 45: 591–601.

Promislow, D. E. L. and Harvey P. H. 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. – J. Zool. Lond. 220: 417–437.

Prugh, L. R. et al. 2009. The rise of the mesopredator. – BioScience 59: 779–791.

Rayner, M. J. et al. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. – Proc. Natl Acad. Sci. USA 104: 20862–20865.

Ripple, W. J. et al. 2013. Widespread mesopredator effects after wolf extirpation. – Biol. Conserv. 160: 70–79.

Ripple W. J. et al. 2014. Status and ecological effects of the world's largest carnivores. – Science 343: 1241484

Roemer, G. W. et al. 2009. The ecological role of the mesocarnivore. – BioScience 59: 165–173.

Rose, L. and Marshall, F. 1996. Hominid sociality and home bases revisited. – Curr. Anthropol. 37: 307–338.

Rutledge, L. Y. et al. 2010. Protection from harvesting restores the natural social structure of eastern wolf packs. – Biol. Conserv. 143: 332–339.

Stahler, D. R. et al. 2013. The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. – J. Anim. Ecol. 82: 222–234.

Toms, J. D. and Lesperance, M. L. 2003. Piecewise regression: a tool for identifying ecological thresholds. – Ecology 84: 2034–2041.

Wallach, A. D. et al. 2009. More than mere numbers: the impact of lethal control on the social stability of a top-order predator. – PLoS ONE 4(9): e6861.

Wanless, R. M. et al. 2007. Can predation by invasive mice drive seabird extinctions? – Biol. Lett. 3: 241–244.

Supplementary material (available online as Appendix oik.01977 at <www.oikosjournal.org/readers/appendix>). Appendix 1.