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RESEARCH ARTICLE

Beyond the kill: The allometry of predation behaviours among large carnivores

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Abstract

1. The costs of foraging can be high while also carrying significant risks, especially for consumers feeding at the top of the food chain.
2. To mitigate these risks, many predators supplement active hunting with scavenging and kleptoparasitic behaviours, in some cases specializing in these alternative modes of predation.
3. The factors that drive differential utilization of these tactics from species to species are not well understood.
4. Here, we use an energetics approach to investigate the survival advantages of hunting, scavenging and kleptoparasitism as a function of predator, prey and potential competitor body sizes for terrestrial mammalian carnivores.
5. The results of our framework reveal that predator tactics become more diverse closer to starvation, while the deployment of scavenging and kleptoparasitism is strongly constrained by the ratio of predator to prey body size.
6. Our model accurately predicts a behavioural transition away from hunting towards alternative modes of predation with increasing prey size for predators spanning an order of magnitude in body size, closely matching observational data across a range of species.
7. We then show that this behavioural boundary follows an allometric power-law scaling relationship where the predator size scales with an exponent nearing 3/4 with prey size, meaning that this behavioural switch occurs at relatively larger threshold prey body size for larger carnivores.
8. We suggest that our approach may provide a holistic framework for guiding future observational efforts exploring the diverse array of predator foraging behaviours.

KEYWORDS
carnivores, dynamic programming, foraging, hunting, kleptoparasitism, predation, scavenging

1 | INTRODUCTION

Foraging can be energetically costly, and maintaining energetic reserves is crucial for survival. Consumers must interact with other organisms to obtain energy, and the form of these interactions often depends on trophic level. For example, herbivores such as folivores and frugivores consume plant tissue, but generally do not kill individual plants. Predators, by comparison, must kill their prey prior to energetic replenishment, exposing themselves to substantial risk in the process (Carbone et al., 2011; Mukherjee

& Heithaus, 2013). These risks are multifaceted: Prey resources are individually energetically rich, but may be less abundant and patchily distributed in both space and time (Bhat et al., 2020; Carbone et al., 2011; Carbone, Rowcliffe, et al., 2007; Jennings & Mackinson, 2003). This may require predators to be on the move and can impose a constant risk of starvation (Carbone et al., 2011). For larger predators that consume larger prey, the mortality risks associated with prey handling prior to consumption may also be substantial (Mukherjee & Heithaus, 2013; Yeakel et al., 2009). This is particularly true for larger mammalian carnivores in terrestrial environments because their focal prey tend to have body sizes greater than their own (Carbone, Teacher, et al., 2007; Sinclair et al., 2003), demanding increased risks to access abundant energetic rewards.

Predators are not limited to active hunting but can incorporate a wide array of behavioural tactics that alter the various costs of foraging. These alternative modes of predation allow the predator to adjust the time and energy it spends acquiring prey, the uncertainty of capturing prey and the potential for injury when handling prey (Carbone et al., 1999; Carbone, Teacher, et al., 2007; Gorman et al., 1998; Hunter et al., 2007; Iyengar, 2008; Mukherjee & Heithaus, 2013; Ruxton & Houston, 2004; Steele & Hockey, 1995; Thompson, 1986; van der Meer et al., 2011; Wilson & Wolkovich, 2011). For example, scavenging involves finding and consuming carrion (Pereira et al., 2014), thereby substituting the time and uncertainties involved in prey handling with those of searching, while lowering the risk of injury (Carbone, Teacher, et al., 2007; Mukherjee & Heithaus, 2013). However, carrion has less consumable tissue than recently deceased prey, while the tissue that remains may be of lower quality and possibly contaminated by harmful microbiota (Burkepile et al., 2006; Janzen, 1977; Moleón et al., 2019; Shivik, 2006). Kleptoparasitism, or stealing from a co-occurring predator, eliminates the handling time and mortality risks associated with hunting or the diminishing returns of scavenging, yet introduces risks associated with stealing from potentially dangerous competitors (Iyengar, 2008). Thus, while the competing predator (referred to throughout as the *competitor*) in the kleptoparasitic process may or may not be an individual of the same species (Brockmann & Barnard, 1979; Iyengar, 2008; Nishimura, 2010), such tactics may be more likely if it poses limited overall risk to the predator (Brockmann & Barnard, 1979; Iyengar, 2008).

The extent to which these different modes of predation are employed varies across species (Pereira et al., 2014), among individuals within a given species (Funston et al., 1998), and over the course of an individual's life (Ballard et al., 1987). The acts of hunting, scavenging and kleptoparasitism are thus better described as a continuum (Pereira et al., 2014), where the implementation of each mode relative to the others defines a predator's overall strategy. In many cases, the deployment of one mode over another can be opportunistic (DeVault et al., 2003; Pereira et al., 2014; Wilson & Wolkovich, 2011). For example, great white sharks (*Lamnidae*) actively hunt fur seals (Hammerschlag et al., 2006) while also obtaining significant nutritional gain from scavenging whale carcasses (Curtis et al., 2006). Albatross (*Diomedeidae*) hunt live squid and fish while supplementing their diet with scavenged prey—often from cetacean vomitus (Croxall & Prince, 1994). The extent to which different predators rely on scavenged resources can be controversial and both under- or overestimated, depending on taxa (DeVault & Rhodes, 2002; Houston, 1979; Ruxton & Houston, 2004; Wilton, 1986). For example, a standard-bearer of scavenging, the spotted hyena (*Crocuta crocuta*), may rely less on scavenged resources in some environments (ca. 30% of diet) than is widely perceived (Kruuk, 1979), whereas lions (*Panthera leo*) may rely more on scavenged resources (ca. 35% of diet) than is often assumed (Packer et al., 1990). While scavenging is ubiquitous as an opportunistic behaviour (Kane et al., 2017; Pereira et al., 2014), obligate scavenging is rare because the energetic costs associated with acquiring enough carrion to meet energetic demands is high (Ruxton & Houston, 2004).

Kleptoparasitism is largely facultative (Brockmann & Barnard, 1979; Flower et al., 2013; Iyengar, 2008). This behaviour is more common among species where predator–prey interactions are easily observed by potential kleptoparasites and is particularly well-documented among birds (Brockmann & Barnard, 1979) and large terrestrial carnivores (Gorman et al., 1998). For example, skua (*Stercorarius* spp.) are predatory seabirds that are described as specialist kleptoparasites (Furness, 1978; Hockey & Steele, 1990), even though resources obtained through active theft remain a minority component of diet (Andersson, 1976). Kleptoparasitism has also been observed in spiders (Cangialosi, 1990), hyenas (Carbone et al., 1997; Gorman et al., 1998) and marine snails (Iyengar, 2000), though these behaviours appear to supplement diet, rather than represent the primary foraging mode. Importantly, the advantages of kleptoparasitism are expected to increase when resources are rare and the length of aggressive contests between predator and competitor is short (Broom & Ruxton, 2003).

Maximizing the probability of survival requires balancing the energetic trade-offs and risks associated with different modes of predation. As such, the energetic state of a predator is expected to influence the use of alternative foraging behaviours over time (Mangel & Clark, 1988). A predator's energetic stores—in the form of body fat for most terrestrial vertebrates—determine the time over which it can survive prior to finding and acquiring additional resources. When a predator has sufficient reserves, it may be more likely to seek lower-risk resources that provide fewer energetic rewards. In contrast, predators near starvation may be more likely to engage in riskier foraging behaviours (Blecha et al., 2018; Petersen et al., 2010). Because organisms' fat stores scale with body size (Lindstedt & Boyce, 1985), starvation risks are very different for small versus larger mammals (Carbone, Teacher, et al., 2007; Rallings et al., 2022; Yeakel et al., 2018). Beyond starvation, prey and predator body sizes influence energetic expenditures and mortality risks associated with foraging (De Cuyper et al., 2019; Kane et al., 2016; Mattisson et al., 2016). In fact, the body size ratio of predators and prey is a strong predictor of whether trophic interactions are realized between pairs of species in a community (Cruz et al., 2022; Pires et al., 2015; Rohr et al., 2010; Yeakel et al., 2014).

Here, we introduce a stochastic dynamic programming (SDP) framework (Clark & Mangel, 2000) to examine the conditions resulting in active hunting, scavenging and kleptoparasitic behaviours for terrestrial carnivores foraging in a stochastic environment over time. We leverage allometric relationships governing energetic costs, physiology, and population densities to evaluate how patterns of predation are likely to change based on the body sizes of the focal predator, prey and competitor species. We then compare our model predictions to behavioural observations for a range of terrestrial mammalian predators spanning an order of magnitude in body size across several continents.

Our results point to four key findings that shed light on the nature of alternative predator foraging tactics. First, we find that whether a predator hunts, scavenges or steals is strongly correlated with starvation risk, where higher starvation risk increases the diversity of the predatory modes utilized. Second, the deployment of these modes of predation changes as a function of predator, prey and competitor body size, where both scavenging and kleptoparasitism become dominant tactics as the size of the prey relative to the predator increases. Third, our model expectations accurately predict the transition between hunting and scavenging for a range of terrestrial mammalian predators. Finally, we show that the behavioural transition predicted by our model and captured by field observations follows a power-law scaling relationship with an exponent nearing 3/4 for the threshold prey body size initiating behavioural change. Taken as a whole, we suggest that our mechanistic model offers particular insight into the role of scavenging and kleptoparasitic behaviours in the arsenal of tactics available to behaviourally flexible predators.

2 | METHODS

We construct a model to explore the conditions under which different predator foraging tactics maximize survival, where possible behaviours include the deployment of active hunting, scavenging and kleptoparasitism. We assess how these modes of predation change as a function of the risks associated with starvation, mortality induced by intra- or interspecific interactions, and time. We track two state variables: the energetic state of a focal predator $X = x$ (Joules) and time t (days in a month), where the probability of survival S is assessed at the end of the month, $t = t_{\max}$. Throughout, we maintain uppercase notation for stochastic variables and lowercase notation for specific values of these stochastic quantities.

Hunting, scavenging and kleptoparasitism are associated with different energetic costs, energetic gains and mortality risks (Figure 1). A successful hunting encounter is defined by an antagonistic encounter (moderate mortality risk, especially for large prey) involving the predator finding, pursuing and subduing prey prior to consumption (high energetic cost). Once captured, all of the high-quality prey fat and muscle mass is available to the predator, limited only by its stomach size (high energetic gain). A successful kleptoparasitic encounter is defined by the predator finding a potential

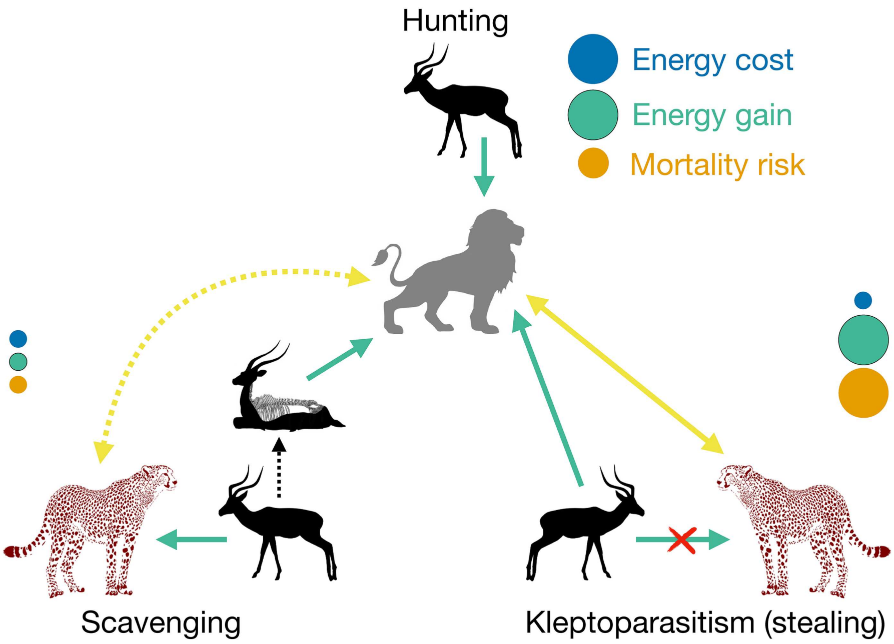

FIGURE 1 Summary of organismal interactions, energetic transactions and risks in the model: The predator (grey silhouette) obtains energy through active hunting of prey (black silhouettes), scavenging or kleptoparasitism. Green arrows represent the direction of energy gain to the predator and competitors, with the competitor's interrupted energy gain due to theft denoted by the red '×'. The dotted black arrow represents the transition of freshly killed prey to carrion (black silhouettes) available to the scavenger. The solid yellow arrow denotes a direct interaction between the predator (grey silhouette) and kleptoparasitic competitor (brown silhouette) while stealing. The dotted yellow arrow denotes the indirect interaction between the predator and competitor (brown silhouette) while scavenging. The relative energetic cost, energetic gain and the mortality risk associated with each predatory mode are represented by the relative sizes of blue, green and orange circles, respectively.

competitor and stealing prey acquired by the competitor (the same high energetic gain as for hunting). The low energetic cost due to the lack of the pursue-and-subdue phase is offset by the high mortality risk associated with the antagonistic encounter with the competitor. Finally, a successful scavenging encounter is defined by the focal predator finding and consuming the remains of prey carrion (low energetic cost, low mortality risk and low energetic gain), thereby indirectly interacting with the competitor (dashed yellow arrow in Figure 1).

Across alternative behavioural tactics, or modes of predation, we assume that an individual predator's energetic state is equivalent to its endogenous fat reserves, which change over time as

$$x_n^i(t+1) = x(t) - \lambda_n^i + \min\left(r_n^i, r_{\text{stom}}\right), \tag{1}$$

where $x_n^i(t+1)$ is the energetic state associated with predation modality i at time $t+1$, while the metabolic cost accrued by the predator λ_n^i, and the consumable prey mass r_n^i are summed across n successful encounters within a day, limited by the individual's stomach size r_{stom}. The energetic costs and gains ultimately depend on the mode of predation, where $i = h, s$, or k denote hunting, scavenging and kleptoparasitism, respectively. Energetic reserves are bounded between a maximum capacity $X = x_{\max}$ and the critical state at which starvation occurs $X = x_c$. The amount of energetic reserves $(x_{\max} - x_c)$, stomach size, energetic costs and consumable prey mass increase sublinearly with the body sizes of predators M_p, prey M_r and competitors M_c (see Appendix S1).

The search and interaction processes associated with hunting, scavenging and kleptoparasitism were independently simulated to derive numerical approximations of modality-specific probability distributions for the number of successful encounters. We denote the probability of a successful encounter as p_n^i for $n = 0,1,2, \ldots, n_{\max}^i$ encounters for predation modality i, where the maximum number of successful encounters $n_{\max}^i = r_{\text{stom}} / r_{n=1}^i$, given $r_{n=1}^i$ is the consumable prey mass available to the predator in a single encounter. Search and interaction processes are constrained by organismal movement rates (Pawar et al., 2012) and both herbivore and carnivore population densities (Carbone & Gittleman, 2002; Damuth, 1987), all of which were parameterized from allometric relationships associated with predator, prey and competitor body masses (see Appendix S1). Encounter probability distributions for each predation modality were obtained by simulating 5×10^4 independent realizations of the predator's search process for each behavioural tactic (see Appendices S1 and S2 for details), where results were averaged over 15 replicates to account for stochastic effects (see Appendix S3 for details).

We use a stochastic dynamic programming (SDP) framework to assess how predator interactions with potential prey and competitors, and associated energetic consequences alter the probability of survival, where the survival-maximizing behavioural tactic is determined for a given energetic state and time (x, t). We first assume that the predator's probability of survival at the terminal time $S(x, t = t_{\max})$ increases with energetic state, saturating at $X = x_{\max}$ such that

$$S(x, t_{\max}) = 1 - e^{-x/x_{\max}}. \tag{2}$$

The saturating dependence on x captures the diminishing returns on survival with increasing energetic reserves near capacity (Clark & Mangel, 2000; Yeakel et al., 2020), where alternative increasing functions did not qualitatively change model results (Appendix S5).

The predator's probability of survival given predation modality i at times previous to the terminal time is written as

$$S^i(x, t) = \sum_n p_n^i \left(1 - \delta_n^i\right) S\left(x_n^i, t+1\right), \tag{3}$$

where δ_n^i is the probability of mortality associated with n successful prey encounters. The overall probability of survival is then given as

$$S(x, t) = \max\left(S^h(x, t), S^s(x, t), S^k(x, t)\right), \tag{4}$$

where the survival-maximizing modality at time t determines the predator's foraging tactic as a function of its energetic state x. We assess survival-maximizing foraging tactics of terrestrial mammalian carnivores with masses ranging from 10 to 500 kg as a function of x and t, for a range of prey masses (10–3000 kg) and competitor masses (10–500 kg). Survival-maximizing tactics were then assessed for the focal predator within each predator–prey–competitor triad across all combinations of predator, prey and competitor body masses. All code used in model formulation and analysis is provided on a Zenodo Digital Repository (Ritwika et al., 2024).

3 | RESULTS

3.1 | State dependence of predator tactics

When to hunt, scavenge or steal emerges from the cumulative risks and rewards associated with finding and successfully acquiring prey while negotiating the potential for serious injury or death. While these behaviours can be viewed through an allometric lens, where the masses of predator, potential prey and potential competitors scale associated risks, our framework points to important generalities that lay the foundation for this more nuanced perspective. Specifically, the results of our model reveal that alternative predator tactics—modes of predation—are strongly predicted by predator energetic state. When the predator's energetic state is replete, there is a heavier reliance on hunting, where reliance is measured by the proportion of states resulting in hunting as the survival-maximizing tactic across predator, prey and competitor masses (Figure 2a). As the predator's energetic state declines towards starvation, both scavenging and stealing increase in frequency, whereas stealing is employed across an order of magnitude fewer states than scavenging (Figure 2b,c). As time advances to the terminal time $t_{\max}$, hunting increases in frequency for a larger proportion of energetic states, with scavenging and to a lesser extent stealing serving as fallback tactics for predators near starvation. These patterns reveal a behavioural switch: near starvation and far from the terminal time,

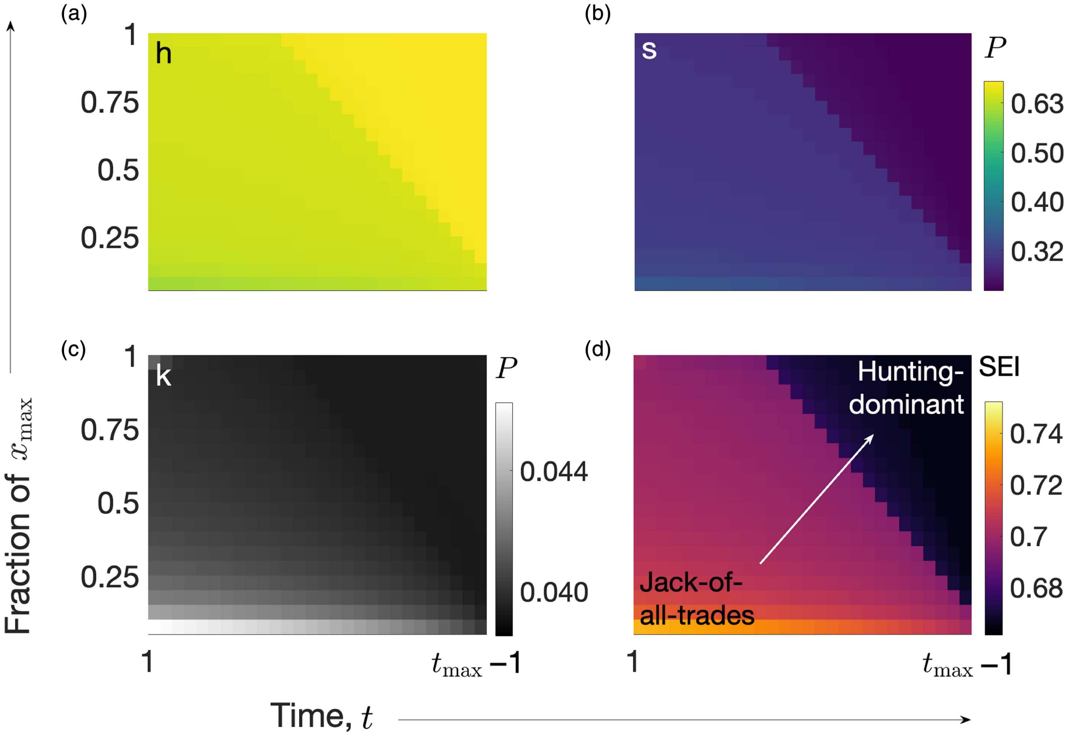

FIGURE 2 Behavioural tactics as a function of predator state. The proportion *P* of each employed behavioural tactic as a function of predator energetic reserves (fraction of the maximum energetic storage, $x_{\max}$) and time *t* for (a) hunting (h), (b) scavenging (*s*), (c) kleptoparasitism (*k*). These results are based on survival-maximizing tactics averaged across all combinations of predator, prey and competitor masses, for 15 trials (see Appendix S4 for details). (a) and (b) share a colour scheme, while (c) has a different colour scheme to emphasize smaller-scale trends. (d) shows the Shannon Evenness Index (SEI; Shannon, 1948) of employed tactics.

predation modalities are more evenly employed, which we denote as the jack-of-all-trades condition (Figure 2d). As the predator attains energetic storage and nears the terminal time, the predator switches to a hunting-dominant condition, which serves to maximize the accessibility of prey while on-boarding modest bodily risk.

3.2 | The allometry of predator tactics

Whether a predator hunts, scavenges or steals is highly constrained by predator, prey and competitor body sizes. Our model predicts that, on average, larger predators hunt across a larger proportion of states and maintain this behaviour across a larger range of prey body sizes (Figure 3a,d). As expected, as prey increase in size, both scavenging and kleptoparasitic tactics dominate (Figure 3b), whereas we observe a decline in kleptoparasitism as an effective tactic with increasing body size of the competitor (Figure 3c). Smaller to intermediate-sized predators are thus expected to deploy an increased diversity of tactics, while the largest predators tend to hunt.

Beyond the hunting-dominant region, and where prey are much larger than an associated predator, both scavenging and to a lesser extent kleptoparasitism play increasingly important roles, though observational data for both are limited and constrained to a small number of well-studied species. Kleptoparasitism is employed more frequently for larger prey (Figure 3b), attesting to the increased profitability of stealing larger prey in antagonistic encounters. In contrast, increasing competitor size—and with it mortality risk—results in decreased reliance on kleptoparasitism (Figure 3c). Together, we observe that the most diverse behavioural tool kit emerges when prey are roughly 10× larger than the predator, and when competitors are of similar size or smaller than the predator (Appendix S6).

We note that model results are robust against changes to the allometric relationships determining predator–prey–competitor encounter rates, predator mortality associated with hunting and kleptoparasitism, and the division of day-long time steps into rest and active phases (see Appendix S5). While survival-maximizing tactics are in part driven by the allometric relationships that parameterize the model, these sensitivity analyses suggest our results are ultimately the product of the complex interplay between allometric parameterizations and the energetic dynamics specified in the SDP.

The deployment of alternative predatory modes predicted by our framework aligns with observations in natural systems for well-studied species such as hyenas and lions (Pereira et al., 2014). We observe a strong correlation in our model expectations with observed hunting and scavenging behaviours for lions and hyena populations across sub-Saharan Africa ($R^2 = 0.82$; $p < 0.001$ across both behaviours; Figure 4). Across these populations, lions are predicted to have a lower reliance on scavenging (accounting for ca. 10% of states) and a larger reliance on hunting (ca. 90% of states) compared

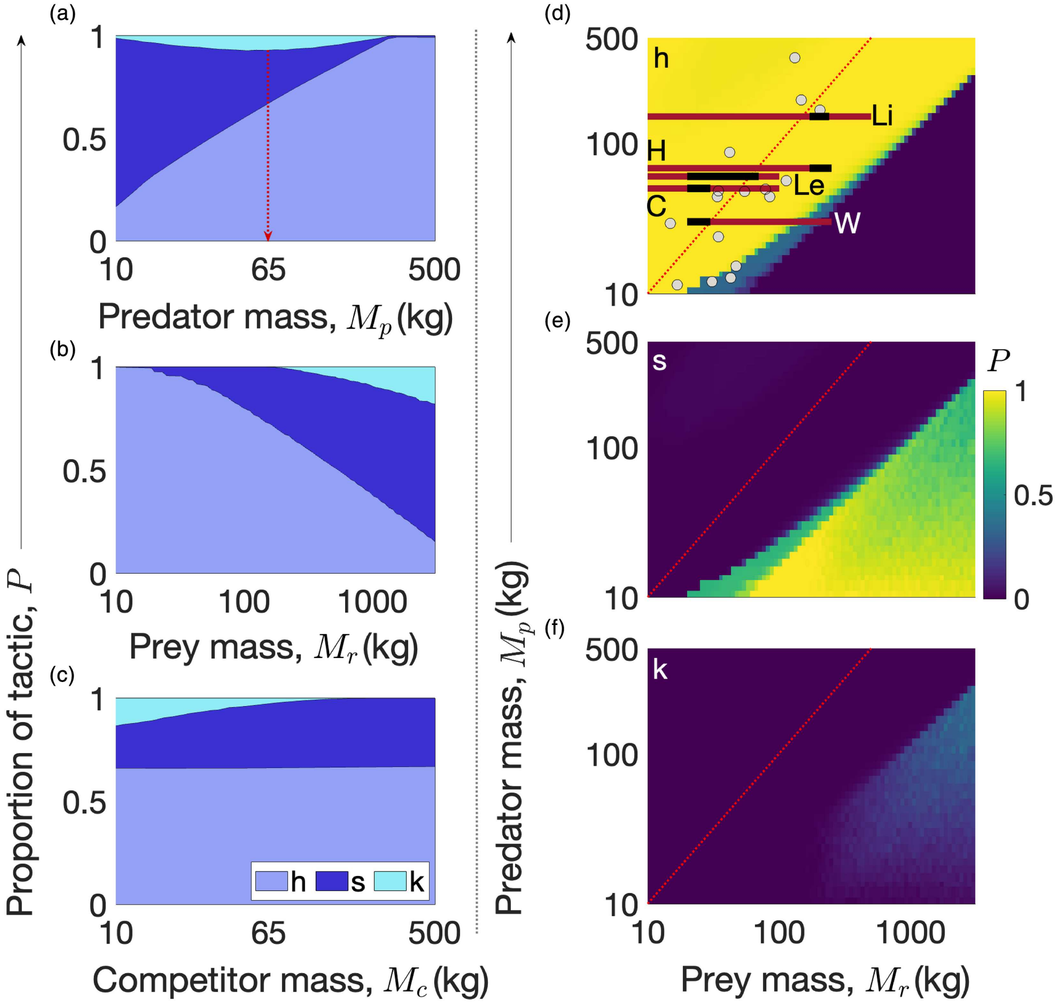

FIGURE 3 Behavioural tactics as a function of body size. (a–c) The proportion of each tactic (h = hunting, s = scavenging, k = kleptoparasitism) P as a function of predator mass M_p, prey mass M_r, and competitor mass M_c, respectively, averaged across 15 replicates (see Appendix S3). The dashed red arrow in (a) denotes the predator mass associated with the peak frequency of kleptoparasitism; note different scale in (b). (d–f) The same proportion of each tactic (P, colorbar), respectively, as a function of pairwise predator–prey body size combinations, with the dotted red line denoting the 1:1 line. The horizontal bars in (d) denote observed absolute (red) and preferred (black) prey mass ranges for predators of different body sizes (Sinclair et al., 2003), where W = African wild dog, C = cheetah, Le = leopard, H = spotted hyena and Li = lion (Le and H have been staggered for visualization). Grey circles denote the most frequently observed prey for a range of predator body sizes (Carbone et al., 1999).

with hyenas, aligning with the proportion of observed tactics in natural systems.

3.3 | Predicting transitions in predator tactics

Finally, we assess whether and to what extent the behavioural transition from hunting to scavenging, as a function of prey body mass for a given predator, predicts observations from natural systems. We examine this transition from the perspective of two predicted behavioural trends: (i) that observations of active hunting should decline at this transitional prey body mass and (ii) that exclusive scavenging should increase around the same transitional prey body mass. We rely on the abundant observations of kill percentages and prey preference among larger-bodied carnivores—including wild dogs, cheetahs, leopards, spotted hyenas, lions and tigers—to assess whether predicted declines in active hunting correlate to observed declines in the field (Hayward, 2006; Hayward et al., 2012; Hayward, Henschel, et al., 2006; Hayward, Hofmeyr, et al., 2006; Hayward & Kerley, 2005; Hayward, O'Brien, et al., 2006). In contrast, to compare our predicted transition to observed increases in exclusive scavenging, we must rely on qualitative data documenting increases in scavenging. To do so, we first calculate the probability that a trophic link exists between a predator of body size M_p and a prey of body size M_r ($\mathcal{P}_h$) from the binary presence/absence of observed trophic (hunting) interactions using the logit framework detailed by Rohr et al. (2010). We then calculate the probability that a link representing both hunting and scavenging exists between a predator and its prey as a function of the body sizes of both ($\mathcal{P}_{h\text{-}s}$) by assuming (i) that all trophic interactions may also be scavenged and (ii) including

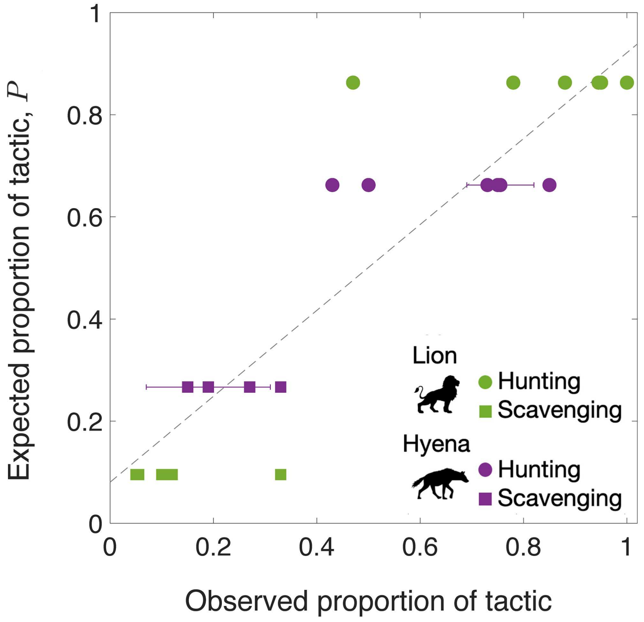

FIGURE 4 Testing model predictions against empirical data from African lion and hyena populations. Model predictions for hunting (circles) and scavenging (squares) against observations of the same behaviours for African lion (green) and spotted hyena (purple) populations, compiled by Pereira et al. (2014). Horizontal error bars indicate maximum and minimum values of observations where available, while vertical error bars are too small to be depicted. The linear best fit (dashed grey line) is given by $y = 0.84x + 0.08$ ($R^2 = 0.82$, $p < 0.001$).

documented scavenging interactions (see Appendix S4). The probability that a particular predator–prey interaction is exclusively the result of scavenging is then calculated as $\mathcal{P}_s = \mathcal{P}_{h \cdot s} \cdot (1 - \mathcal{P}_h)$. We thus expect empirical evidence of a behavioural transition from hunting to scavenging to correlate with an increase in $\mathcal{P}_s$, alongside decreases in observations of kill percentages and prey preference.

Comparing prey kill percentage and preference metrics for six carnivore species spanning nearly an order of magnitude in body size, we observe that our model accurately predicts this behavioural boundary—a transitional prey body size where active hunting by the predator tapers off (Figure 5a–f). We define the transition from hunting to scavenging or kleptoparasitic behaviours by the critical prey body size, which we denote as M_r^*. This critical prey size marking a decline in both kill percentages and prey preference is different for each examined carnivore: it is both predicted and observed to occur at a smaller prey body size for smaller carnivores (e.g., wild dogs) and at a much larger prey body size for larger carnivores (e.g., tigers). To assess whether our model quantitatively predicts the prey body size at which active hunting tapers off, we extract the empirical behavioural transition by first discarding prey kill percentages $\leq 5\%$ because they identify the absence rather than the presence of predator–prey hunting interactions. We then calculate the observed critical prey body mass M_r^* from the remaining non-negligible kill percentages, where M_r^* describes the point where all prey masses $M_r < M_r^*$ cumulatively account for 90% of prey kill percentage observations (Figure 5g). We compare this empirical measure of critical prey mass against the expected prey mass at which the proportion of hunting falls to 10% in our model. Our expectations of this boundary align with observational data for 5 out of 6 species, though the relationship falls just short of statistical significance ($R^2 = 0.73$, $p = 0.06$; Figure 5h). We note that we cannot evaluate the accuracy for wild dogs given the coarseness of kill percentage data available (Hayward, O'Brien, et al., 2006). To examine whether the predicted behavioural transition documents a simultaneous increase in the probability of exclusive scavenging, we calculated $\mathcal{P}_s$ for both hyenas and lions, which have well-documented observations of scavenging interactions (see Appendix S4). We observe that the predicted decline in hunting and increase in scavenging (solid-filled and line-filled curves in Figure 5d,e, respectively) qualitatively align with the increase in the empirical $\mathcal{P}_s$ for hyena and lion prey, respectively (dashed lines in Figure 5d,e).

While expectations of this behavioural boundary are a function of the survival maximization procedure implemented in the SDP (see Section 2) and emerge at different prey body sizes for different predators, we observe that they collapse together, such that the behavioural transition is observed to occur at roughly $M_r^* / M_p^{1.45} \approx 1$ (Figure 5i), where M_r^* is the critical prey mass. This points to a scaling relationship for this behavioural boundary where the transitional prey mass $M_r^* \approx M_p^{1.45}$, meaning that predators of larger body size transition from hunting to alternative modes of predation at proportionally larger prey masses. Because larger prey deliver both greater energetic rewards and increased risk to the hunter, we interpret the suspension of hunting behaviours at larger prey body sizes as a signal of the potential energetic gain falling below the increased risk. Rearranging, this relationship can also be written $M_p \approx M_r^{*0.69}$ which is not far from a value of 3/4, a common scaling exponent observed for many ecological and physiological phenomena (Lindstedt & Calder III, 1981).

4 | DISCUSSION

4.1 | Predator energetics predict modes of predation

The behavioural shift from hunting-dominant to jack-of-all-trades behaviours tracks declining energetic reserves of the predator. A general prediction of our model follows: an increasingly diverse behavioural tool kit is expected to be employed when the risk of starvation-induced mortality is increased. While energetic data on carnivores and their resultant foraging behaviours are very limited, there is some evidence to support such a switch. For example, coyote reliance on ungulate carrion increases during periods when primary prey populations (snowshoe hare) decline (Prugh, 2005). Similarly, Australian dingos (Allen, 2010) and arctic foxes (Roth, 2003) have been observed to rely more on scavenging during periods of resource scarcity, while hyenas have been observed to increase their reliance on scavenging as a result of an effective decrease in

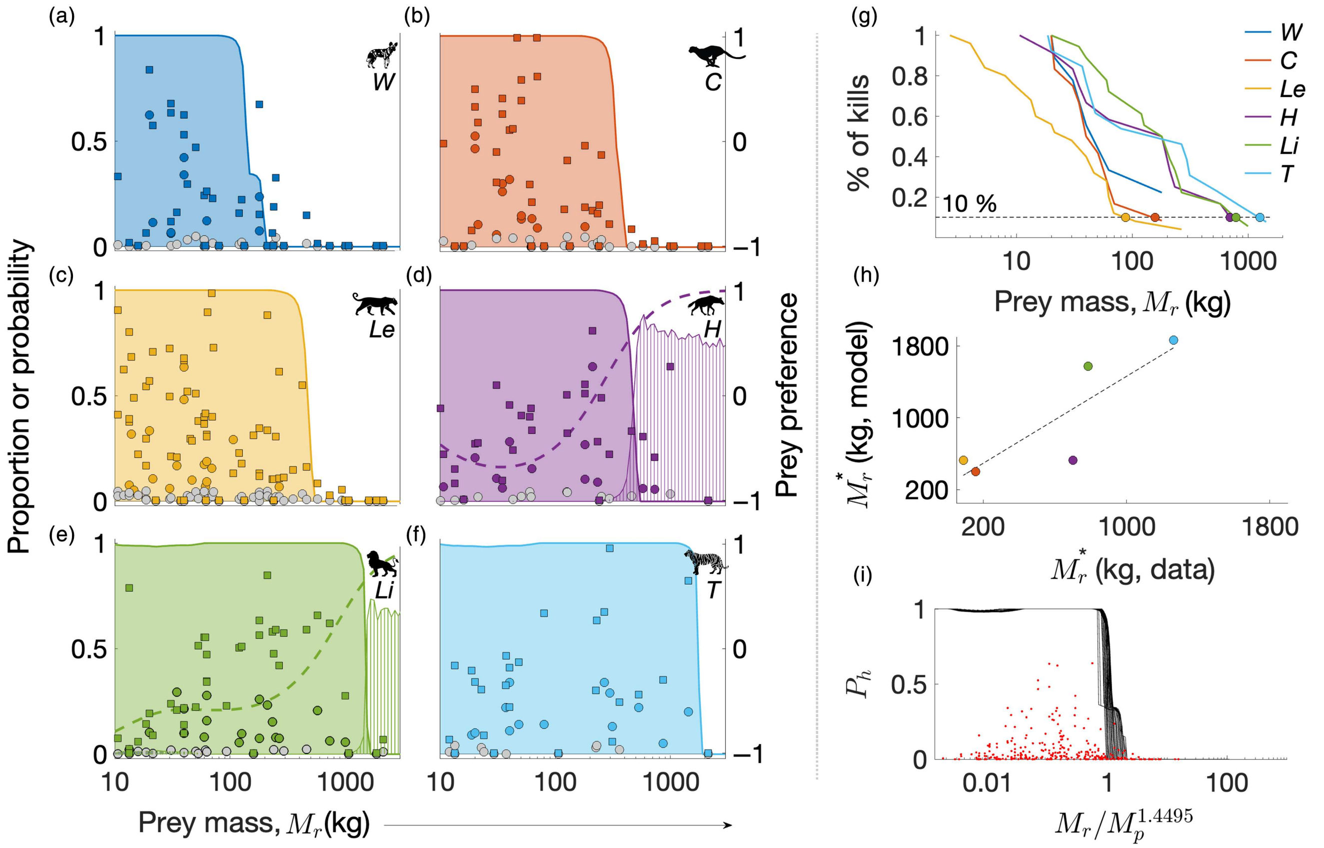

FIGURE 5 Predicting behavioural transitions in prey preference (a–f) Model predictions of the proportional utilization of hunting (solid shaded region) compared against empirical data for (a) wild dog (W), (b) cheetah (C), (c) leopard (Le), (d) spotted hyena (H), (e) lion (Li) and (f) tiger (T). Empirical data include prey kill percentage (circles; values <5% are deemed negligible and coloured grey) and prey preference (Jacob's Index; squares), ranging from −1 (avoidance) to +1 (preference; see main text for citations). Model predictions for scavenging (vertical-barred region) are shown for hyenas and lions (d, e) alongside the probability of exclusive scavenging derived from empirical data (dashed curves). (g) Cumulative distributions of empirical non-negligible prey kill percentages reveal the critical prey mass M_r^* marking the transition away from hunting, given by the prey mass boundary above which $\leq 10\,\%$ of kills contribute to predator diets. (h) Correlation between observed (g) and predicted (prey mass marking the decline in solid shaded regions in a–f) critical prey mass values M_r^*, where hunting behaviours transition to increasingly diverse tactics with the linear best fit $y = 1.21x + 252.26$ ($R^2 = 0.73$, $p = 0.06$). (i) The behavioural transition from hunting to diverse tactics reveals a common threshold given by $M_r / M_p^{1.45}$; red points denote prey kill percentages in (a–f).

prey abundance due to interspecific competition with lions (Périquet et al., 2015). However, both environmental and physiological drivers of scavenging behaviour among predators are not easily quantified (DeVault et al., 2003; Prugh & Sivy, 2020).

Because predators are more likely to experience near-starvation states in low-productivity or nutrient-stressed environments, the integration of starvation and/or kleptoparasitic behaviours would increase dependence on—and competition for—carrion subsidies in these conditions. Predator scavenging behaviours are thought to scale with environmental stress, fuelled by increasing competition (the stress gradient hypothesis; Bertness & Callaway, 1994). This may lead to higher rates of intraguild competition and significant top-down mesopredator control (Prugh & Sivy, 2020). In a broad sense, our framework offers a mechanistic reasoning for the expectation that limited carrion may promote increased intraguild competition. That is, in resource-limited environments where predators are nutrient-stressed, a greater reliance on scavenging and kleptoparasitism (Figure 2d) will promote increased competition for carrion subsidies. However, it is also reasonable to expect that the magnitude of carrion reliance depends on the body size relationships between predators, potential prey and potential competitors, which we next show may illuminate important behavioural dynamics contributing to the structure of mammalian communities.

4.2 | Pairwise allometry constrains modes of predation

The advantages of alternative tactics between interacting species reveal allometrically constrained behavioural boundaries. Across predator and prey body sizes, our framework points to a behavioural switch from a hunting-dominant region when the predator is larger than the prey, to a jack-of-all-trades region when the predator is smaller than the prey (Figure 3d–f). This behavioural transition scales sublinearly with prey body size, meaning that hunting remains the dominant mode of predation for a wider range of prey with increasing predator body size, mirroring a trend observed in terrestrial mammalian systems (Sinclair et al., 2003). While our model is relatively coarse and cannot shed light on the nuanced behaviours between species over short timescales, we observe that it successfully predicts predation limitations in diverse mammalian communities. For the most part, observed predator–prey body mass relationships (points and bars in Figure 3d from data in Carbone et al., 1999; Sinclair et al., 2003) fall within the hunting-dominant space predicted by our framework.

Of particular note is the observed nonlinearity in the role of kleptoparasitism and predator body size, with a peak frequency associated with a predator body size of ca. 65 kg (Figure 3a). This corresponds to a size similar to that of the spotted hyena (*Crocuta crocuta* at ca. 60 kg), a noted kleptoparasite of wild dogs, cheetahs and lions (Cooper, 1991; Cooper et al., 1999; Höner et al., 2002). As an oft-cited exemplar of intraguild instigation, the contributions of hunting, scavenging and kleptoparasitism to spotted hyena diet are estimated at 50%–85%, 7%–33% (Pereira et al., 2014) and ca. 20% (Höner et al., 2002), respectively. Expectations from our model are generally on par with these observations: for hyena-sized predators, our framework predicts contributions of each behavioural tactic to be ca. 66%, 27% and 7%, respectively.

Expanding our assessment of model accuracy to both lions and spotted hyenas, both well-studied large mammalian species engaged in hunting and scavenging behaviours, we find that model expectations are largely predictive of observed behavioural tendencies. Across sub-Saharan Africa, lion and hyena populations variably supplement active hunting with scavenging, with both species employing scavenging behaviours for <10% to ca. 33% of their dietary income (Pereira et al., 2014). While lions tend to acquire a greater proportion of dietary contribution from activities related to hunting compared with spotted hyenas, the range of the behaviours for both nearly overlap. These field observations of hunting versus scavenging behaviours align with expectations from our model (Figure 4), where we use the proportion of states resulting in a hunting versus scavenging survival-maximizing tactic—taken across prey and competitor body sizes—as a proxy for the per cent contribution to diet measured in the field (Pereira et al., 2014). While our proxy measurement is not one-to-one, we expect it to vary proportionately, such that increases in the percentage of states resulting in scavenging as a survival-maximizing tactic will result in behaviours that tend towards scavenging. Our ability to predict observed reliance on scavenging behaviours, particularly among larger-bodied and well-studied carnivores such as lions and hyenas (Figure 4), suggests that the included relationships governing our calculation of predator survival are important determinants of the foraging behaviours employed by large mammalian predators in terrestrial ecosystems.

4.3 | Transitioning between modes of predation

Behaviours typically emerge from an intersection of physical and biological constraints, a source from which plastic responses may adapt to rapidly changing demands. Far from these constraints, it is reasonable to expect behaviours to be idiosyncratic and subject to a diversity of (a)biotic drivers. Yet close to the constraint, behaviours may be expected to reflect the nature of the constraint itself. Because our model primarily serves to identify transitions between survival-maximizing behaviours in a foraging context, we focus assessment of model expectations against observations of these 'behavioural transitions'.

Empirical evidence of a predator's behavioural transition from hunting to alternative modes of predation with increasing prey body size is expected to be characterized by a decline in the per cent of kills as well as prey preference (Hayward & Kerley, 2008), alongside an increase in the tendency to scavenge and/or kleptoparasitise increasingly large prey. Observations of active hunting among predators are plentiful (especially for larger-bodied species), and we find good alignment between the predicted switch away from hunting with observed declines in kill percentages and prey preference around the predicted critical prey mass M_r^* (Figure 5). Instead, while observations of exclusive scavenging by predators on particular prey are comparatively rare, our quantification of the probability of exclusive scavenging based on empirical observations also aligns with the predicted behavioural transition (dashed lines, Figure 5d,e). These alternative lines of evidence indicate that the predicted transition is capturing a switch in behaviours emerging alongside changes to the costs, benefits and risks of mortality associated with depredation of larger prey.

The role of scavenged resources in contributing to biomass flow within food webs is thought to be vastly underestimated (Wilson & Wolkovich, 2011), potentially biasing our understanding of the indirect effects between species (Mellard et al., 2021) and the factors that influence system stability (Beasley et al., 2012). For example, seal subsidies from polar bear kills can contribute to >50% of arctic fox diet, particularly when lemming populations—their preferred prey—are low (Roth, 2003). These scavenged subsidies may serve to buoy fox populations, decoupling their dynamics from those of their preferred prey, with potentially negative effects on lemming recovery (Roth, 2003). Such missing links can alter our assumptions of both the structure and function of food webs (Selva & Fortuna, 2007), potentially influencing forecasts of species' vulnerability in response to current or future disturbances (Wilson & Wolkovich, 2011). Mass mortality events in particular, which appear to be on the rise (Fey et al., 2015), can make available enormous amounts of carrion to generalist scavengers, though the effects of these events on ecosystems can be surprising complex (Fey et al., 2019) and their impact on facultative scavengers is not well understood (Baruzzi et al., 2023).

The importance of scavenging in mammalian ecosystems may have played an even more central role in the past when the diversity and abundance of megafauna was magnified (Van Valkenburgh et al., 2016), compared with that of contemporary communities. Prior to the expansion and dominance of grasslands in the early Pliocene (ca. 5 Myrs BP), megafaunal grazer and browser species diversity was much greater than it is today, declining alongside a downward trend in atmospheric $p\mathrm{CO}_2$ and the simultaneous increase in C_4-photosynthetic grasslands (Faith et al., 2018, 2019). Within mammalian communities, a large proportion of total biomass is carried by megafaunal populations (Hempson et al., 2015), suggesting that greater diversity among these species may have allowed increased scavenging subsidies for predators, as has been reconstructed for condors during the Pleistocene (Chamberlain et al., 2005), where a loss in megafauna resulted in a loss of inland populations without access to marine carrion (Fox-Dobbs et al., 2006). Increased rates of tooth breakage among Pleistocene carnivorans additionally point to greater reliance on scavenged resources than among comparable species today (Van Valkenburgh, 2009).

That the observed and predicted behavioural transitions collapse onto a single scaling relationship, where the transitional prey mass $M_r^* \approx M_p^{1.45}$ (Figure 5i), has a number of important implications. The relationship, in words, means that the prey mass at which predator tactics switch from hunting to alternative modes (scavenging and kleptoparasitism) increases more steeply than a 1:1 relationship with larger predator body mass. For example, following this relationship, a hyena-sized predator at ca. 80 kg has a predicted transition at the prey mass $M_r^* = 574$ kg (roughly the mass of a large wildebeest or eland). In contrast, a lion-sized predator at ca. 150 kg has a predicted transition at $M_r^* = 1430$ kg (roughly the mass of a giraffe). While the latter represents one of the largest terrestrial mammalian predators in contemporary systems, the Cenozoic is replete with examples of mammalian predators reaching sizes of up to 1000 kg (e.g., the Eocene artiodactyl *Andrewsarchus*). It is unknown to what extent these megapredators actively hunted or scavenged, however application of our scaling relationship suggests a transitional prey mass of ca. $M_r^* = 22,000$ kg for a predator the size of *Andrewsarchus*. Such a prey size is clearly beyond the range of contemporary fauna—for example, savanna elephants tend to weigh ca. 3000–6000 kg—but is not far outside the range of the largest land mammals, including the Oligocene paraceratheres and Miocene deinotheres, with body sizes estimated ca. 17,000 kg (Smith et al., 2010). If these extinct megapredators followed similar energetic trade-offs as assumed in our model, it would suggest that active depredation on these size classes is not outside the bounds of feasibility.

Unlike obligate scavengers such as condors, mammalian scavenging is largely facultative (Pereira et al., 2014), such that the biomass flow attributed to carrion changes dynamically with environmental conditions and attendant pressures on individual predators. Our framework enables a mechanistic understanding of the general processes that contribute to the intersection of predator foraging tactics and their dynamic prey environments. We suggest that the relationships that we have explored here could be integrated into larger food web models to incorporate conditional biomass flow originating from a diversity of predatory modes, potentially better informing assessment of community function and stability. As the effects of climate change and other anthropogenic drivers continue to push ecological communities into novel, and potentially hazardous, states, understanding the larger effects of such behavioural variability may be vital for predicting system-level responses to future disturbances.

5 | CONCLUSIONS

The energetic risks and rewards associated with hunting, scavenging and stealing vary with predator, prey and competitor body size. We have shown that integrating these energetic relationships into a framework premised on maximizing the probability of survival predicts key transitions in the predator behaviours spanning an order of magnitude in body size (Figures 4 and 5). This framework, while applied to terrestrial mammalian carnivores and their potential prey, is general in both its energetic principles and allometric relationships, and could be applied to investigate similar behaviours in other taxa. While we consider here a triad of interacting species, the inclusion of a greater diversity of interactions may be required for exploring behaviours far from these transitions. Our model operates from the perspective of individual predators interacting with other prey or competitor individuals, though many species that we examine engage in cooperative groups (Fanshawe & Fitzgibbon, 1993; Holekamp et al., 1997). Including the advantages that group formation introduces to both predator and prey species (Fryxell et al., 2007) may provide additional insight into the behavioural complexity characterizing carnivore foraging behaviours. Predation comprises a complex suite of behaviours, and accounting for this complexity in ecological models may be essential for predicting outcomes of trophic interactions in natural systems.

AUTHOR CONTRIBUTIONS

VPSR, AG and JDY conceived the ideas and designed the methodology; VPSR and JDY performed the research; VPSR, AG and JDY analysed data; VPSR, AG and JDY led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Code and data are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.10533788.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Allometric scaling of predatory modes.

Appendix S2: Summary schematics of search processes for hunting, scavenging, and kleptoparasitism.

Appendix S3: Computing the proportion of different foraging tactics.

Appendix S4: The probability of exclusive scavenging.

Appendix S5: Sensitivity analyses.

Appendix S6: Additional visualizations of results.

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