Advances in biologging can identify nuanced energetic costs and gains in predators

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Abstract

Foraging is a key driver of animal movement patterns, with specific challenges for predators which must search for mobile prey. These patterns are increasingly impacted by global changes, principally in land use and climate. Understanding the degree of flexibility in predator foraging and social strategies is pertinent to wildlife conservation under global change, including potential top-down effects on wider ecosystems. Here we propose key future research directions to better understand foraging strategies and social flexibility in predators. In particular, rapid continued advances in biologging technology are helping to record and understand dynamic behavioural and movement responses of animals, and ensuing energetic consequences, to environmental changes. Data collection can be optimised by calibrating behavioural interpretation methods in captive settings and strategic tagging decisions within and between social groups. Importantly, many species social systems are increasingly being found to be more flexible than originally described in the literature, which may be more readily detectable through biologging approaches than behavioural observation. Integrating the effects of the physical landscape and biotic interactions will be key to explaining and predicting animal movements and energetic balance in a changing world.

Keywords: predation, energetics, foraging, movement ecology, biologging, GPS, accelerometer, social system

INTRODUCTION

Animals adapt their behaviour to optimise gains and minimise losses in an environment, with energetic, ecological and evolutionary consequences [1]. Foraging is a sequence of continuous behavioural decisions made to maximise energetic gains while minimising costs in the search for food and its handling [2, 3]. Animals are faced with multiple foraging decisions, for example whether to target one prey species over another [4] or whether to forage cooperatively with conspecifics [5]. The energetic gains associated with each prey item, as well as encounter rate and handling time, determine which prey is chosen, where profitability is defined as the energy gain divided by handling time [6], with the number of individuals in a cooperatively foraging group also affecting each individual's energy gain and the profitability of a prey species [7]. The encounter rate of the most profitable potential prey dictates the diet, irrespective of the encounter rate with less profitable prey [8], and kill rate varies in response to prey density depending on predator functional response and ecological conditions [9]. The costs associated with foraging are especially pertinent in predatory animals which must invest energy in the pursuit and handling of prey, often with risk of injury to themselves [10].

Foraging strategies are shaped by external factors, such as resource availability and environmental conditions [11, 12], leading to considerable variation in foraging strategies within and between individuals, social groups, populations, species and taxa [13–17]. Flexibility in foraging strategy can occur in each of these levels from individuals displaying multiple foraging strategies (i.e., switching between multiple food types which require different handling) in complex or variable environments [18], including dynamic switches regarding the tolerance of satellites by territory owners [19], to distinct strategies associated with particular populations or habitats across temporal scales [20]. For example, foraging trip duration and rate of chick provisioning can vary between colonies of wedge-tailed shearwaters (*Puffinus* *pacificus*) [21], and bluegill sunfish (*Lepomis macrochirus*) modify their foraging search speed between open-water and vegetated habitats [22].

Predation is costly

Predation typically incurs high energetic costs, either through pursuing and subduing prey, for example in large mammalian predators such as African wild dogs (*Lycaon pictus*) and lions (*Panthera leo*) [23, 24], or shorter ambushes which require sudden bursts of energy, seen in diverse taxa including mantis shrimp [25] and snakes [26]. Collective hunting allows the takedown of large prey which individual predators could not manage alone [27, 28]. Other species, such as the red fox (*Vulpes vulpes*), target smaller prey individually, even if they live in a social group [29]. Hunting success is a central consideration in predation energetics, as a predator must intake enough energy to account for the hunt which has just taken place, but also previous unsuccessful hunts since the last meal, competition e.g., through kleptoparasitism [30, 31], their basal metabolic rate, and other non-hunting behaviours required for survival, growth and reproduction (Figure 1). Meeting these diverse demands may promote flexibility in foraging behaviour, with species implementing more diverse suites of predation strategies and prey selection than commonly captured in the literature. This is particularly true where predation events are difficult to observe, though this can now increasingly be rectified with the expanding use of animal-attached technology to reveal out-of-sight animal behaviours, which is increasingly being used to study fine-scale behaviours across multiple species [32, 33].

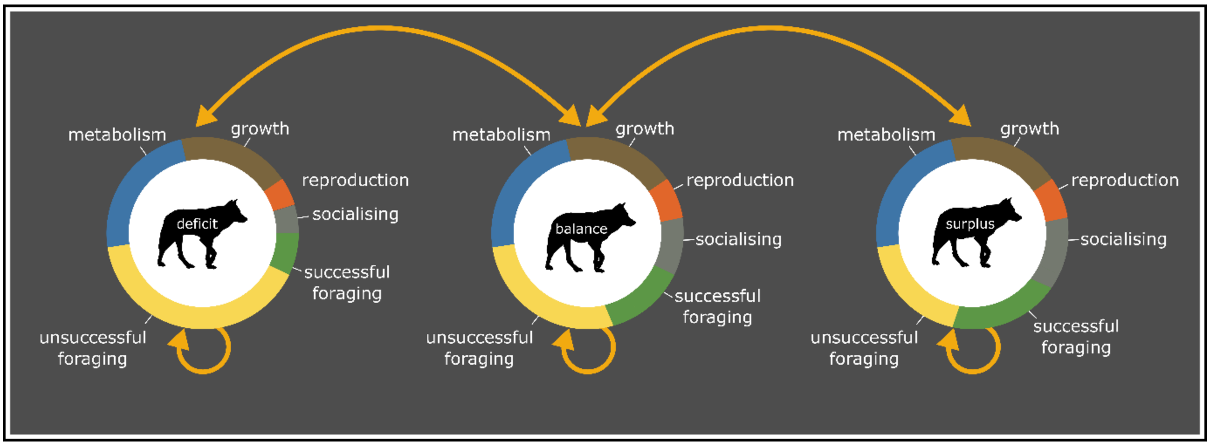


Figure 1. Animals can be in energy deficit, energy balance or energy surplus, with transition possible between these states, mediated by foraging success. Animals in energy deficit incur costs which affect body condition and eventually death will occur if animals cannot regain energy balance. Energy balance allows normal daily functioning, while surplus energy allows investment in growth, reproduction and social behaviours.

Climate and land use change may cause shifts in predator-prey dynamics

Environmental conditions can add further energetic costs to foraging [34], for example, rising temperatures may subject predators to heat stress during pursuit [35]. Prey species are subject to this pressure as well, but for many predator-prey pairs, it is unclear whether the species are equally (un)affected or whether temperature changes could shift the balance in favour of one species or the other. From the predator perspective, this could shift prey preference, with cascading ecosystem effects [36]. For marine predators, endotherms seem to have a competitive advantage over ectotherms at lower water temperatures, with consequences for species distributions [37]. In terrestrial systems, cursorial predators are more likely to be adversely affected than stalk and ambush predators, due to the additional energetic costs associated with pursuing prey over large distances [38]. Though disparities in prey *versus* predator responses to rising temperatures may also work in favour of the predator, if prey become more easily exhausted under heat stress. These concepts are understudied at present, especially given the precedence of indirect climate change impacts on ecosystems. Where studies have been carried out, there is disagreement on predator-prey dynamics under rising temperatures, for example in the case of the African wild dog, where there have been contrasting findings on whether the wild dogs themselves or their prey are more impacted by heat stress associated with rising temperatures [39, 40]. These discrepancies may be partially explained by differences in prey preference across populations [35]. Assessing the energetics associated with different hunting and evasion strategies across populations is therefore a key consideration for understanding shifting predator-prey dynamics under climate change.

Land use represents another key form of global change with consequences for predator-prey dynamics, often working in tandem with climate change impacts [41]. In some cases, land use change can benefit predators by improving search efficiency as vegetation is thinned or removed [41, 42]. These dynamics can be complex, however, and vary significantly between land use types. For example, pumas (*Puma concolor*) were found to have higher body condition scores in areas of marginal anthropogenic development than in both wilderness and highly developed areas [43]. Socio-ecological phenomena must be considered as habitats are modified; land use change increases human-wildlife conflict, particularly when predators of degraded habitats target livestock [44]. Within increasingly human-dominated landscapes, some prey take advantage of carnivore avoidance of areas of high human activity, a phenomenon known as the human shield [45, 46], while others show stronger avoidance to human activity than their natural predators [47].

Energetic landscapes reveal foraging costs

Climate and land use change may cause animal populations to shift in distribution [48] with consequences for how hunting animals locate, select and subdue their prey. Shifting population distributions lead to potential re-arrangement of prey preference and cascading ecosystem effects [46]. These dynamics may be better understood by mapping predation both in the physical landscape and the so-called landscapes of fear, food and energetics [49, 50]. The landscape of fear is the spatial and temporal variation seen in prey movements in response to their perceived risk of predation, typically visualised as peaks and valleys, similarly to terrain maps [51]. For example, in Yellowstone, landscape of fear maps computed for elk were strongly affected by the crepuscular activity patterns of wolves (*Canis lupus*) [52], with more complex changes to diel activity patterns for roe deer across European landscapes responding to the threat of both the lynx predator and humans [53]. These dynamics become more complicated in multi-predator systems where prey must contend with predators using different hunting strategies, resulting in complex landscapes of fear with varying levels of risk [54]. Foodscapes, though developed for herbivores navigating immobile forage [49, 55], can also be extended further up the food chain, as prey resource selection will shape the movements and selected hunting strategies of their predators [56].

Energetic landscapes, as revealed through accelerometry (i.e., using on-board accelerometer sensors measuring the rate of change of velocity), represent efforts to put animal behaviour and physiology in the context of wider ecosystems and environments [57]. This concept was introduced by Wilson et al. (2011) assessing varying movement costs associated with foraging in a heterogeneous environment [58]. Specifically, Wilson et al (2011) compared the foraging dives of imperial cormorants (*Phalacrocorax atriceps*) and the travel costs between the foraging area and the breeding site to a model where individuals were evenly spaced. Complexity was added to the energy landscape definition through *1)* cost functions and maps visualising areas of different energetic costs, *2)* adding speed and tortuosity of animal movement paths and *3)* environmental factors such as wind conditions for aerial travel [59]. More recent considerations have assumed broader energy requirements, to account for thermoregulation and maintenance of body condition, with quantification of individual foraging strategies highlighted as a future direction in using energetic landscapes for population ecology and global change inferences, considering predator performance [60]. Integrating the landscapes of fear and energetics has been discussed elsewhere [57], but there is still little consideration of how species' social systems factor into this picture.

Predator social interactions may be more flexible than originally described

Research into how sociality affects animal spatial behaviour and general ecology has grown significantly in recent years, as the social landscape, as well as the distribution and density of conspecifics, can strongly affect the movements and behavioural decisions of individuals [61], (see also: the social resistance hypothesis [62]). Social network analysis in particular is becoming a dominant theme within behavioural ecology [63–66]. As well as looking at interactions within groups, social networks can be used to detect interactions such as territorial intrusions related to resource abundance [67] and social dynamics of semi-social conspecifics [68]. Investigating the role of species' social systems, and intraspecific variation in these systems, as a factor influencing energetics requires attention. It is known that conspecifics can affect an individual's foraging behaviour [69]. For example, information transfer pertaining to foraging sites can occur in colonially-breeding species, such as gannets (*Morus bassanus*) [70]. Social eavesdropping has been reported in vultures, as individuals obtain information about thermals from conspecifics, helping them choose energetically efficient foraging search paths [71]. Whether an animal is social has profound implications for foraging ecology, particularly if social group members start to cooperate to obtain food. Social information transmission can influence every stage of predation, encompassing encounter, detection, identification, approach, subjugation and consumption of prey [72]. Some species that typically forage alone or in pairs can opportunistically adapt to cooperative hunting, such as the black backed-jackal *Canis mesomelas* [73]. Increasingly, there are reports of cooperative hunting in species thought to only forage alone, including harbour porpoises *Phocoena phocoena* [74], goshawks *Accipiter gentilis* [75] and yellow-throated martens *Martes flavigula* [76]. This opens research avenues focusing on dynamic behavioural decision-making, investigating spontaneous decisions on whether to cooperate to find food, mediated by internal state and animal personality [77, 78].

Aims

Here we review the development of methods for estimating animal energetics and discuss how more recent technological and conceptual advances facilitate finer-scale, multifaceted insights, primarily through approximation of energy expenditure using accelerometry. We discuss the energetics underlying predation in social and solitary contexts, as hunting alone versus with a team has significant implications for both the intake and output of energy, particularly under changing climate and land use scenarios. We suggest methods for experimental design, data collection and analysis - including the need to calibrate sensors within captive settings prior to setting up experiments in the wild - which will improve our understanding of shifting animal movement patterns and energetics in the Anthropocene. We posit that growing consideration of energetic landscapes and social networks respectively can be combined into a social-energetic landscape framework. Energetic landscapes effectively capture the influence of abiotic factors on individual movement, behaviour and survival, while social networks often lack due consideration of temporal and spatial scales. By integrating these concepts, we highlight avenues for integrating abiotic and biotic factors for a more comprehensive understanding of predator energetics.

QUANTIFYING PREDATION ENERGETICS

Due to the difficulties associated with studying energetics in wild systems, initial investigations into animal energetics were lab-based. Treadmills were, and continue to be, valuable tools in estimating the energetic costs associated with moving at different gaits across multiple species. This use of treadmills to quantify energetics associated with animal locomotion dates back to the 19th Century [79] and has expanded to include multiple species across diverse taxa including mammals [80], reptiles [81] and birds [82]. In controlled settings (including laboratories and zoos), treadmills combined with oxygen chambers allow measurement of animal speed and oxygen consumption, allowing energy expenditure to be calculated for many species performing multiple gaits. However, this experimental set-up is not possible with free-ranging wild animals; new developments were required.

The doubly-labelled water method, developed in the 1950s, allows estimation of an animal's energy expenditure during the window between two blood samples by using isotopically-labelled water to assess carbon dioxide production [83, 84]. With this, research on animal energetics in the wild could commence. It was first used outside the laboratory to assess energy expenditure during rest and flight for homing pigeons *Columba livia domestica* [85] and has since been used extensively across diverse wild species [86–89]. While facilitating inferences across diverse systems, the major limitation of this method is the requirement to recapture animals within a rigid timeframe, as the second blood sample must be taken before the isotopes have been eliminated from the body [90]. Additionally, this method provides energetic estimates from the study period as a whole and extensive behavioural observations are required to estimate the costs associated with specific behaviours [90, 91].

Technological advances leading to the development of animal-attached sensors allow the energetic intake and output associated with predation to be studied in wild systems on the level of individual behaviours and postures. Initial technological insights into wild animal energetics came from the development of VHF (Very High Frequency) telemetry, which allows triangulation of animal location using an antenna to detect pulsed radio signals emitted from an animal-attached transmitter [92–94]. This allowed studies on movements, home ranges and mortality of wild animals to proliferate, and detection of both predator foraging and prey mortality through VHF telemetry continues to provide important insights into predation [95–97]. Satellite collars were first developed in the early seventies [98, 99], allowing location data to be collected and stored at regular intervals *via* satellite communication. Continued developments expanded options for collecting location information, and the wide adoption of GPS and Argos satellite telemetry has resulted in large, fine-scale datasets of animal movements across space [100, 101]. Beyond movement trajectories, these data provide detailed insights into behavioural states, including foraging [102, 103]. More recent developments have expanded the range of animal-attached sensors and associated insights, known as biologging [104–107].

Biologging devices incorporating Inertial Measurement Units (IMUs) such as accelerometers (measuring the rate of change of velocity), magnetometers (measuring Earth’s magnetic field, which can be used to give compass-like orientation) and gyroscopes (measuring orientation through angular velocity), allow quantification of fine-scale movement patterns and the relationship between animal behaviour and energetics [108–110]. This is possible as biologging devices allow animal movement to be considered on physiological and biomechanical scales, measuring the individual movements and conditions of the body [111].

As such, these additional sensors provide data distinct from those obtained using even high-resolution locational units (such as those collecting data at the scale of seconds or minutes as opposed to hours). Using IMUs in tandem with locational units such as GPS allows fine-scale animal behaviour to be mapped in space, leading to greater insights than achievable through use of locational sensors alone. Such multi-sensor techniques can be used to advance our understanding of animal energetics through deriving field-based sub-second scale measures of movement costs using dynamic body acceleration metrics derived from tri-axial accelerometer data [112] or dead-reckoning fine-scale, tortuous animal movement paths [113]. Dead-reckoning is a path reconstruction method where the inherent tortuosity of animal movement paths is captured by combining location data with heading and speed data derived from IMUs [110, 113, 114]. Deriving energetic landscapes through mapping these measures of energy expenditure in space further represents a powerful method of testing optimal foraging theory [58] and provides opportunities to test optimal foraging theory in the field at multiple scales, e.g., penguins foraging for krill within *versus* among foraging patches [115].

High resolution GPS and IMU sensors offer different yet complementary information, with the behaviour of the species under study and the environment in which it lives dictating the most appropriate sampling regime [116]. For example, dead-reckoning can be particularly valuable in environments where high frequency GPS sampling is prone to errors or high rates of missed fixes due to habitat composition and/or animal behaviour and posture [116]. High frequency data have been found to provide additional insights into animal behaviour where coarser datasets may result in inaccurate or incomplete interpretations, such as contrasting exploratory movements between bold and shy individuals and detecting multi-animal interactions with consequences for disease transmission [117]. Figure 2 provides a summary of the introduction of key advancements in animal-borne sensor technology.

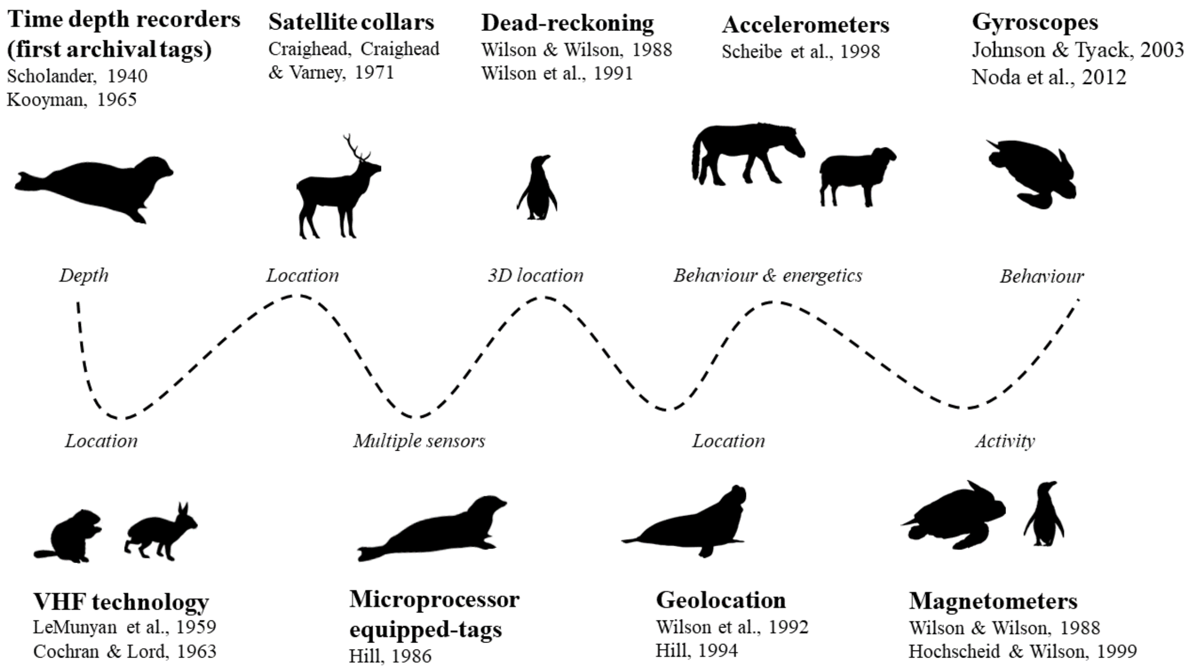


Figure 2. A summary of key developments facilitating insights into animal energetics. Note all references refer to studies of animal ecology, rather than use of these tools in other fields (e.g., engineering, physics, robotics). Figure references can be found in the reference list as entries [92, 93, 98, 114, 118–126].

Information about the type and amount of food ingested by animals can answer fundamental ecological questions relating to how animals manage their energy budgets in the wild [127]. Inter-mandibular angle sensors (IMASEN), placed on animal jaws, have been used to reliably determine prey ingestion [128]. More commonly, fine-scale movement data are used to reconstruct predation events, for example through identifying clusters of GPS locations as potential kill sites, often with field visits for verification [103, 129]; though it should be noted that this method is biased towards large predators hunting large prey, with kill sites of small prey typically classified at lower accuracies [129]. Hidden Markov models allow movement data to be categorised into discrete states [130]; although these states are typically not verified behaviours, kill sites can also be used to confirm HMM-defined predation occurrences [131].

Foraging strategies vary depending on the food items targeted, habitat type and whether foraging is cooperative or solitary [76, 132–134]. As different hunting strategies involve different body postures and energetic signatures, it should be possible to extract these separate hunting strategies from biologging data (Table 1). For example, combined tri-axial accelerometer and GPS data have shown promise in elucidating the energetics underlying prey capture by large predators like African leopards *Panthera pardus* [135] and high frequency acceleration data have been used to classify behaviours related to foraging in smaller predators such as the Arctic fox *Vulpes lagopus* [136]. As speed estimates can be derived from both GPS and acceleration data, and magnetometers can capture the tortuosity of animal movement paths [137], these technologies present opportunities to look at speed, pursuit and evasion in hunting predators and fleeing prey (Figure 3; [138]). Detailed consideration of path tortuosity fundamentally changes the classical transport cost paradigm for terrestrial animals [139].

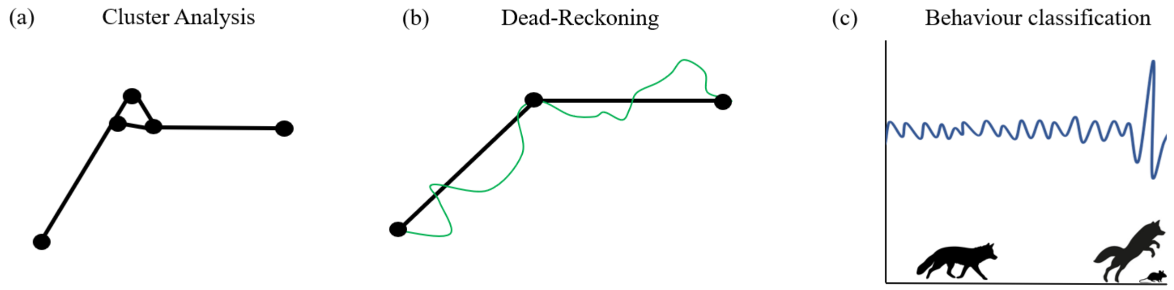


Figure 3. Examples of analysis methods for GPS and Inertial Measurement Unit data with relevance to predation energetics. (a) Cluster analysis of GPS data allows detection of kill sites, e.g. [129, 140]. (b) Dead-reckoning animal movement paths using GPS, accelerometer and magnetometer data allow the tortuosity of movement paths to be captured and can be used to reconstruct paths of hunting predators [113]. (c) Behaviour classification of data from IMU

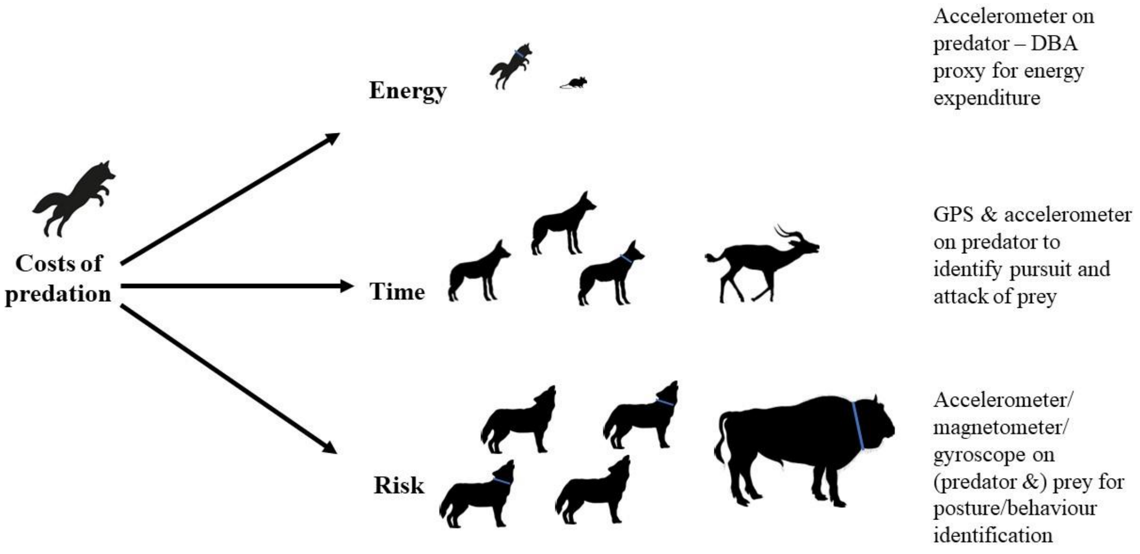
sensors such as accelerometers can be used to distinguish predation from other behaviours e.g., [141].

Table 1. A list of key sensors linked to behavioural interpretations relevant to predation energetics.

Sensor	**Behavioural inferences**	**Examples**
GPS units	Identify kill site clusters	[140]
Accelerometers	Identify postures and movements related to pursuing prey, e.g. stalk, ambush, chase	[142][143]
	Quantify predation success rate - identify predator attempts as well as successful kills	[142]
	Turn capacity	[138]
Magnetometers	Identify postures related to foraging	[144]
	Turns	[145]
	Dead-reckoning	[113]
Proximity sensors	Social interactions	[146]
	Social foraging	[147]
Intermandibular Angle Sensor (IMASEN)	Opening/closing mandible	[148]
Camera	Direct footage of all predation-related behaviours	[149]
Microphone	Recordings of prey cries	[150]

Manoeuvrability is largely determined by the prey, and turning dynamics of coursing predators during a chase has been shown to vary with prey species and the mass of both predator and prey [138]. Combining movement data with high resolution habitat data, i.e., those collected using remote sensing and LiDAR methodologies, e.g., [151], represents the highest accuracy framework for assessing manoeuvrability in predator-prey chases. Both pursuit and evasion have important energetic consequences, which ultimately determine hunt outcomes [152]. Hunt duration and success is not simply defined by the costs of the current pursuit; costs incurred by previous unsuccessful hunts and the sum of other behaviours performed by the animal should also be taken into consideration. In generalist predators, this may result in a need for balance between bouts of highly-costly exhaustive predation for more valuable prey with opportunistic scavenging, targeting of smaller prey, and foraging for other food items such as eggs or plant material [153]. For example, in some areas grey wolves seasonally exploit berries as an important food resource [154] and plant material has been detected in leopard cat *Prionailurus bengalensis* scats; its prevalence also varying with season [155]. According to optimal foraging theory, this balance between multiple strategies should be determined by energy gain, handling time and encounter rate [6]. Failed hunts, scavenging and foraging for smaller food items may also be accounted for through data from accelerometers and other IMU sensors as behaviour classification methods continue to advance [136, 141]. Developing classification methods for these complex behaviours may be assisted considerably by the increasing use of animal-attached cameras and microphones, allowing further verification of IMU sensor outputs [150, 156]. Proximity sensors can be used to detect cooperative foraging in predators [147], as well as encounters between predators and prey [157].

The energetic costs of predation can be split into costs of *1)* locating prey, *2)* pursuit or ambush and *3)* restraining and killing the prey, respectively (Figure 4). The sum of these energetic costs and how they are divided across these categories varies with prey species, e.g., harbour seals *Phoca vitulina* predating cryptic *versus* conspicuous fishes [158]. The time spent on each activity is also an important consideration, as increasing duration spent on any of these aspects results in higher energy expenditure, but the costs of each step are unequal and vary between predator-prey dyads. For example, locating prey is less costly than the pursuit per unit time, where terrestrial predators switch from walking or trotting search gaits to running pursuit gaits [159]. Longer search times could involve finding easier prey with shorter pursuit and restraint times [160]. Therefore, time and energy are separate costs, but time spent on a given activity is critical to the total energetic cost of the behaviour. Further, the risk of injury and whether the prey is captured collectively and shared play important roles [28]. These costs must all be compensated by high enough energy gains to maintain metabolism and execute all necessary behaviours. Stresses such as habitat modification and environmental change may result in additional energetic costs for animals which should be considered in species conservation, as it may be the cumulative impacts of multiple costs that cause behaviour changes with knock-on demographic effects. The energy required for the separate composite behaviours comprising predation can be estimated through the collection of biologging data (Figure 4). Further, the fine-scale frequencies at which these sensors operate allows detailed activity and behavioural budgets to be estimated [161–164].



Accelerometer on predator – DBA proxy for energy expenditure

GPS & accelerometer on predator to identify pursuit and attack of prey

Accelerometer/ magnetometer/ gyroscope on (predator &) prey for posture/behaviour identification

Figure 4. A schematic representing costs of predation to the predator, in terms of energy, time and risk. Accelerometers allow the calculation of Dynamic Body Acceleration proxies which provide estimates of energy expenditure which can be matched to distinct behavioural states. GPS and accelerometer data allow the start and end points of predation to be identified so that time spent hunting can be quantified. Inertial Measurement Units can be used to assess animal posture, to detect defensive or aggressive behaviours exhibited by prey and alert postures to be detected in predators. Predator retreat may also be identifiable from dead-reckoned movement paths.

As well as facilitating fine-scale, behavioural insights, animal-attached technology can also provide important information on broader ecological scales. Understanding the energetics of predation can provide information on trophic cascades and predator-prey dynamics with consequences for whole ecosystems [165]. Integrating biologging data into Dynamic Energy Budget-Individual Population Models (DEB-IPMs) has been identified as a powerful emerging method to link individual level behavioural energetic trade-offs and metabolic processes to population dynamics including survival and reproduction, with due consideration to environmental change [166]. As such, despite the fine-scale nature of biologging data and often short deployment periods, these data can provide important, broader-scale inferences for population ecology [167, 168].

SOCIAL PREDATORS

Social foraging can decrease the time and energy an individual invests in locating and consuming prey [169, 170] and enable access to prey which cannot be obtained by a single predator [28, 171]. Whether a predator hunts alone or with a team has implications for how animal-attached sensor data should be interpreted and which wider conclusions on predation energetics can be drawn. In this section, we provide a brief overview of challenges and considerations for studies on social predators.

Often when studying social species, tags are deployed on one or a few members of multiple social groups, to gain insights into the larger population, though with consequences for our understanding of social group interactions [172]. One of the primary difficulties in interpreting tag data from social foragers is that both the energy expended in acquiring a meal and the energy intake from a successful predation attempt may be unequal between group members, particularly where group members perform different roles during a hunt [173, 174]. This makes it difficult to extrapolate energy intake and output from tagged individuals to other group members, and indeed conspecifics more generally. This is particularly complex where social group sizes are unknown or fission-fusion dynamics are at play, leading to variable numbers of predators present at each predation event. Detection of interactions between members of the social group is influenced by sampling frequency, which must also be taken into consideration when studying group dynamics [172]. The strengths of within-group and between-group social interactions may also vary depending on ecological conditions, e.g., in lions [175]. Thus an additional complication is estimating the distribution of conspecifics across the landscape; additional data, such as sightings, combined with tag data, may be used to build a social landscape providing the likely density of conspecifics from different groups [61]. This will likely require intensive sampling and surveying across potentially large areas, however. Further analysis considerations are required for behaviour classification of IMU sensor data. For example, when some but not all members of a social group have made a kill and an untagged individual does not participate in the hunt but feeds on said kill, it may not be possible to decipher whether this feeding instance represents active predation by the group or opportunistic carcass scavenging.

Studies of predation energetics should consider the range of prey species taken by a social predator, as the degree of cooperation may vary with prey size and relative risk to the predator. This is particularly relevant to generalist predators with wide distributions, the range of which may encompass different habitat types and prey species compositions. This is not static, for example larger wolf packs are more cooperative during a hunt when hunting more dangerous prey [28]. It is important to note that other factors affect the size of animal social groups, including defending vulnerable young and territories, which may explain why social groups are often larger than identified optimum group sizes for cooperative hunting [176, 177] and why some species, like the Ethiopian wolf (*Canis simensis*), occupy shared territories and breed cooperatively but forage alone [178]. Even when the hunt itself is cooperative, feeding behaviour following securing the prey may still be competitive when groups often contain more individuals than are necessary for optimised cooperative hunting [179, 180]. Dominant individuals may limit food access to more subordinate group members [181], though other factors beyond social hierarchies can also affect the roles social group members perform in hunts and the related energy intake and output from a kill.

INTER-INDIVIDUAL VARIABILITY

There has been relatively little consideration of how consistent inter-individual differences (i.e., animal temperament or animal personality) might affect hunting prowess. This individual variation may lead to specialisation in solitary hunters like octopuses [182] or distinct roles in cooperative hunters such as cichlid pike *Crenicichla frenata* [77, 183]. If individuals adopt flexible foraging strategies such as exhibiting prey preference based on prey size and availability, as well as the broader ecological context, then it is reasonable to assume that differences in strategy will arise between individuals. Some differences may be linked to factors such as age and sex [11], though further variation may be attributed to consistent intra-individual variability. This can be measured by considering the repeatability and predictability of behaviours. Protocols for extracting measures of personality from biologging data have recently been developed and are growing in popularity [184]. To date, these methods have largely focused on using parameters extracted from GPS data, including distance moved and activity patterns [185] though there is considerable scope for IMU sensors to yield additional insights into individual variation in activity level and space use as influenced by foraging [186, 187]. Individual variation in activity rhythms and how prey are approached and hunted may affect predation strategies and the roles performed by cooperative hunters, with potential energetic implications.

FUTURE DIRECTIONS

In this review, we have summarised key theory in the predation energetics literature, outline the development of biologging tools for measuring animal energetics and highlight key considerations which must be accounted for when working with social predators. We conclude by proposing future directions in predation energetics research, which will be key in identifying different energetic costs and gains experienced by predators in a changing world.

1. *Integrating energetic landscapes and social networks*. Energetic landscapes, which consider the costs of navigating the physical landscape, and social networks, which define the relative strength of social interactions, can be unified as a potential method for considering the abiotic and biotic factors shaping animal movement patterns in tandem. Large-scale tracking initiatives such as ICARUS [188] and data-sharing platforms such as Movebank (which also contributes a data standardisation philosophy; [189]) make it easier to consider multi-individual interactions across both conspecifics

and heterospecifics. Though social networks are not typically spatially explicit, they can be overlaid onto maps to show the spatial distribution of individuals and assess the role of spatial proximity in determining association strength, e.g., [68]. This process can be taken a step further by overlaying social networks onto mapped energy landscapes, where individuals have been tagged with locational units and accelerometers (Figure 5), and to the social landscape of conspecifics [61]. This can be used to identify scenarios where attraction or avoidance to conspecifics and/or heterospecifics results in suboptimal use of the physical landscape (e.g., expending more energy to traverse through rough terrain to search for prey or avoid competition). Conversely, an animal may choose the least costly path to navigate the local terrain, which then affects its biotic interactions.

Social network analysis (in both intra- and inter-specific systems) offers an analytical means of assessing the role of social interactions in species ecology [65]. Social networks have typically been constructed in such a way as to disregard temporal and spatial scales in animal ecology (but see [190, 191]; see also [172] for GPS sampling designs for social species). However, animals are navigating a spatial landscape and other animals, including predators and prey, affect movement and energetics in a similar fashion to abiotic landscape factors. These biotic factors have unequal avoidance and attraction effects with consequences for how animals navigate their environment [192]. Technological approaches for deriving social networks, e.g., passive radio-frequency identification (RFID) [68, 193], are growing in popularity. This provides opportunities to better link the biotic and abiotic factors governing animal movement [117]. Recently, a new R package *aniSNA* has been developed to solve the autocorrelation issues encountered in the computation of social network metrics using radio-tracking data [194], unleashing the opportunity to test specific hypotheses on the variation of social networks as a function of, for instance, prey availability or environmental conditions such as temperatures, or how individuals modify the strength of their bonds with other group members over time. Emphasising the potential role of additional technological approaches such as proximity sensors or assessing animal interactions through GPS data may expand proposed spatial-social data insights [195] to provide new insights on how other animals affect how an individual navigates its environment.

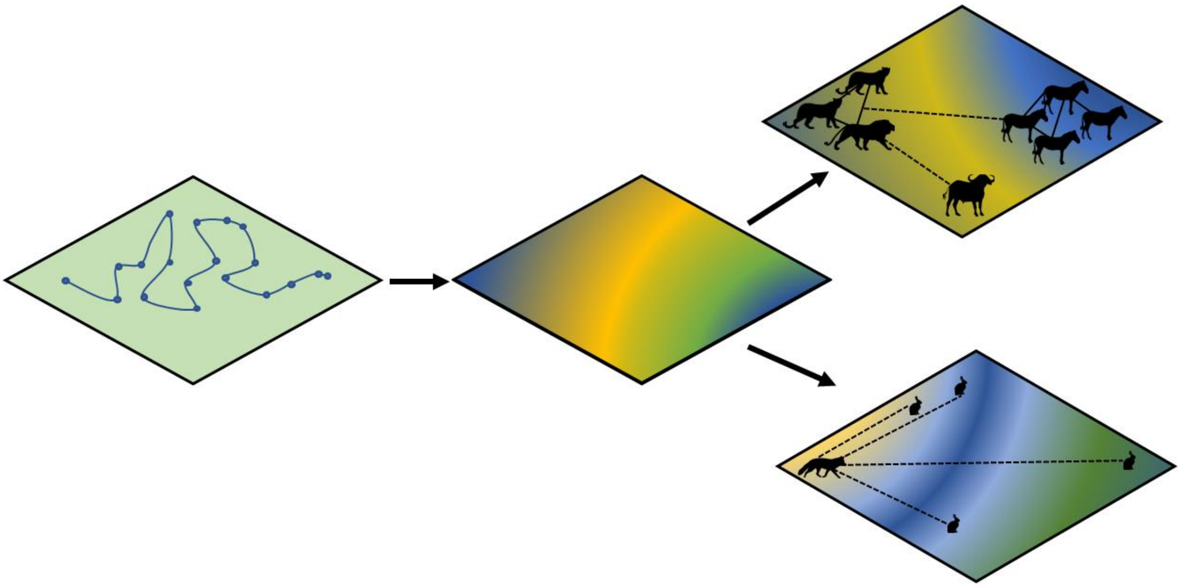


Figure 5. Infographic contrasting the energetic costs and gains between a social group of cooperative hunters and a solitary predator, incorporating energetic landscape and social network concepts. Sensor data on animal location and energetics can be computed into energy landscapes, which can in turn influence prey selection and encounter rates.

2. *Refining data collection and analysis procedures using captive and domestic animals*. Pilot studies on captive and domestic animals allow refinements before wild tag

deployments. Zoos provide settings where sensor data can easily be verified for improved data analysis procedures ahead of wild deployments [187]. Captive studies can also have welfare benefits by piloting device attachment and deployment methods and detecting potential species-specific considerations required ahead of long-term field deployments e.g., maned wolves *Chrysocyon brachyurus*; English et al., unpublished data. While there are limitations to using surrogates [196], with careful interpretation, data from captive and domestic animals can improve behaviour classification procedures for biologging data [197]. This can be particularly useful when investigating complex postures and motions such as those associated with feeding.

3. *Tagging multiple or all individuals in a social group*. Simultaneously tagging multiple or all individuals in a single social group is rarely done for multiple reasons. Most studies typically have limited numbers of tags and aim to spread them across multiple social units so that broader population insights can be gained [172]. Deploying tags in discrete social groups can also address statistical assumptions of independence of data points, depending on the analysis methods used. These constraints are valid, but currently limit our fine-scale knowledge of within-group interactions, including distinct roles which may be performed during coordinated hunting behaviour. Studies which target an entire social group can reveal whether a hunt is truly cooperative and quantify the influence of habitat on pursuit predation, with important considerations for how focal species may adapt in changing land-use and climate scenarios [24]. While tackling entire social groups is easier where groups are small, it is becoming increasingly feasible and common to also tag larger social groups (e.g., [198]). While tagging multiple or all members of a social group will lead to advances in our understanding of

animal societies, tag burden should be kept in mind and research questions should be well formulated to ensure maximum information gain from studies with potential higher overall tag burden. Researchers can also implement non-invasive technologies to collect empirical data on group size, such as camera traps and drones, for example in scenarios where tagging all members of a social group is not feasible due to economic or logistical constraints, or to verify social bonds where these cannot easily be ascertained by an observer, e.g. red foxes [29].

4. *Taking social groups as individual units to compare inter-group communication and interactions.* Complementary to studies of within-group interactions, there is scope for further consideration of between-group interactions, where territoriality may (at least occasionally) be weaker than described in classical literature of species ecology. This also applies to solitary species which may interact socially with conspecifics in neighbouring territories more readily than previously thought (e.g., maned wolves [199]). These interactions may be aggressive or affiliative and include communication through scent-marking and vocalisations. These interactions also shape how an animal perceives and therefore navigates its environment, with consequences for territoriality and therefore the resources available to the territory holder. These interactions are more difficult to visualise and frame in a social-energetic landscape context, but mapping instances of scent-marking behaviour classified through IMU sensor data [200] and continued advancements in acoustic recording research [201] may improve our understanding of these non-visual communication channels in shaping how animals move through their environment.

5. *Account for factors such as hunting success rate and relative prey energy value in statistical model structures*. Fine-scale biologging data and related behaviour classification can also contribute additional variables to include in models of predation energetics. For example, where hunting can be defined, the approximate energetic costs of distinct prey species and their energy value when obtained (either estimated from time spent feeding if clear from IMU sensor traces or through a proxy derived from prey body size or estimated caloric value) can be included in model structures. Models explaining the likelihood of successful predation of a given prey would benefit from including the approximate energy value of the prey, encounter rate, handling time (i.e., profitability), and individuality. Conversely, failed predation attempts can be an important consideration when considering a more general model of a predator's energetic balance.

6. *Increasing the diversity of species tagged and included in such studies*. One of the limitations of animal-attached sensors is that tag size and weight can limit the potential for the use of such technology on smaller animals. Considerable advancements have been and continue to be made, however, such as biologger sensor networks developed for tracking bats [202]. Though the development of smaller tags facilitates deployments on smaller species, these developments should also aim to facilitate the use of reduced mass tags on individuals to minimise potential deleterious effects [203]. Biologging studies are also biased towards mammals, and to a lesser extent fish and birds [204]; efforts should be made to increase the diversity of species represented in such studies.

7. *Sampling designs tackling the influence of climate and habitat modification on foraging behaviour*. Predator-prey interactions are key to trophic ecology and it is therefore important to assess energy balance in these relationships in a changing world. Further, robust understanding of energy intake and output is required to understand species responses to climate and habitat change. These questions can be tackled, for example, by comparing energetics across populations with different weather patterns to approximate species responses to climatic shifts [40]. Studies on wildlife in human-dominated landscapes such as urban areas or agricultural land can yield insights for areas undergoing current land-use change.

Advances in animal-attached tagging technology have rapidly expanded the ecologist's toolkit for understanding animal energetics. These tools, coupled with thoughtful study designs and integrated analysis concepts, can facilitate substantial advances in our understanding of predation energetics in a changing world.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

HME lead conceptualisation of the review with contribution from SC, LB and AK. HME wrote the original draft. Figures were designed by HME and AK. Supervision was provided by SC and LB. All authors revised the manuscript. All authors approved the submitted version of the manuscript and agree to be accountable for the work.

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