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# The environment to the rescue: can physics help predict predator–prey interactions?

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## ABSTRACT

Understanding the factors that determine the occurrence and strength of ecological interactions under specific abiotic and biotic conditions is fundamental since many aspects of ecological community stability and ecosystem functioning depend on patterns of interactions among species. Current approaches to mapping food webs are mostly based on traits, expert knowledge, experiments, and/or statistical inference. However, they do not offer clear mechanisms explaining how trophic interactions are affected by the interplay between organism characteristics and aspects of the physical environment, such as temperature, light intensity or viscosity. Hence, they cannot yet predict accurately how local food webs will respond to anthropogenic pressures, notably to climate change and species invasions. Herein, we propose a framework that synthesises recent developments in food-web theory, integrating body size and metabolism with the physical properties of ecosystems. We advocate for combination of the movement paradigm with a modular definition of the predation sequence, because movement is central to predator–prey interactions, and a generic, modular model is needed to describe all the possible variation in predator–prey interactions. Pending sufficient empirical and theoretical knowledge, our framework will help predict the food-web impacts of well-studied physical factors, such as temperature and oxygen availability, as well as less commonly considered variables such as wind, turbidity or electrical conductivity. An improved predictive capability will facilitate a better understanding of ecosystem responses to a changing world.

*Key words:* predictability, physical factors, predation sequence, movement paradigm, navigation, internal state, motion, functional response, food webs.

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## I. INTRODUCTION

In nature, species are interconnected through their many interactions, forming complex ecological networks (Montoya, Pimm & Sole, 2006). The structure of these interaction networks affects not only the performance of individual species, e.g. during community assembly (Bauer *et al.*, 2022), but also the stability of communities, the functioning of the ecosystem and its resilience in response to disturbances (Schneider, Scheu & Brose, 2012; Wootton & Stouffer, 2016). Accurate knowledge of the occurrence and magnitude of species interactions in natural systems is thus crucial for ecological forecasting (Daugaard *et al.*, 2022). Species co-occurrence is a prerequisite for interactions, and interactions are often required for a species to occur in a particular site (e.g. a predator cannot survive without eating some prey; Gravel *et al.*, 2011). As a result, investigations of interactions have largely relied on empirical observations, experiments under controlled conditions, and expert knowledge, which may increase uncertainty in predictions (Stier *et al.*, 2017). A mechanistic understanding of how physical conditions and species traits shape interactions represents a key step towards increasing predictability.

Fundamental approaches have linked species traits such as body mass, metabolic type (e.g. invertebrate, ectothermic or endothermic vertebrate), locomotion mode (e.g. running, flying or swimming) and predation strategy (e.g. ambushing, group or pursuit hunting) to the likelihood of predator–prey interactions (Eklöf *et al.*, 2013; Hirt *et al.*, 2020). Predator and prey body masses, in particular, have proved useful for the prediction of trophic niche boundaries (Gravel *et al.*, 2013). However, trophic niches under natural conditions vary due to changes in physical conditions and to time-dependent adaptive responses (Ushio *et al.*, 2018). These limitations of trait-based approaches require generalised models that also account for local physical conditions that can vary or shift in space or time.

Physical conditions can prevent species co-occurrence and thus interactions, e.g. if temperature or salinity exceeds a

physiological threshold for one species (Kortsch *et al.*, 2019) – so-called environmental filtering (Kraft *et al.*, 2015). In addition to the presence or absence of an interaction, physical conditions can also modulate the strength of interactions. This modulation was documented for temperature (Uszko *et al.*, 2017; Vucic-Pestic *et al.*, 2011). The effects of other physical conditions, however, have received far less attention despite being ubiquitous (Kraft *et al.*, 2015). The modulation of interactions is critical as physical conditions can enhance or prevent the interaction of co-occurring species, e.g. if it is too dark for a visual predator to find its prey (Ranåker *et al.*, 2014). As the effects of physical conditions are often deterministic and thus predictable, they form a solid basis from which to construct mechanistic models for the assembly and quantification of interactions in networks. Such models could be immensely useful for two main reasons. Firstly, they represent an improvement over current body-mass ratio approaches by enabling more mechanistic predictions of (i) interactions that are missed by sampling, and (ii) structures of interaction networks for communities where interactions have not yet been sampled. Secondly, they could expand the utility of observational data by (i) accounting for heterogeneity in interaction networks at finer spatial scales than observational data allow, (ii) enabling extrapolation to times that were not directly sampled (e.g. seasonal fluctuations in physical conditions), and (iii) predicting the effects of future change in physical conditions on empirical and estimated interactions and networks alike. Here, we pave the way for a framework that accounts for the effects of physical factors on ecological interactions in a comprehensive and quantitative way. Specifically, we focus on predator–prey interactions, which are the building blocks of food webs. Extension of the framework to other types of ecological interactions is conceivable. We also discuss how empirical work and databases can be integrated to validate the highlighted influences of physical factors across scales, from individual interaction events to the structuring of food webs.

## II. A FRAMEWORK FOR THE INCLUSION OF PHYSICAL FACTORS IN THE STUDY OF PREDATOR–PREY INTERACTIONS

We posit that a framework for the inclusion of physical factors in the study of predator–prey interactions should include a movement-based paradigm of interactions (Nathan *et al.*, 2008) combined with a modular predation sequence (Wootton *et al.*, 2023). For a predator and prey to interact, at least one organism must move relative to the other until they reach the same spatial position and handling of the prey by the predator takes place (Jeltsch *et al.*, 2013). Movement is crucial to each of the steps in a successful predation event and hence to the outcome of all predator–prey interactions (Wootton *et al.*, 2023). The intrinsic capacity of predators and prey to move and navigate – i.e. direct their movements towards a goal (Nathan *et al.*, 2008) – will interact with physical factors to impose limits on their movements and, therefore, their ability to enact or escape a predation event. Movement also incurs significant energetic costs for both predators and prey. These costs will vary with physical factors (e.g. ambient temperature affects metabolic rate and thus the costs of active movement), affect the physiological state of the organisms, and in turn, determine their trajectories and performance (Shepard *et al.*, 2013). Thus, physical factors ultimately determine the outcome of interactions *via* movement. While the definition of a ‘physical factor’ potentially includes ‘all aspects of matter, energy, and the forces acting upon them’ (American Heritage<sup>®</sup> Dictionary of the English Language, Fifth Edition, 2011), we restrict our scope here to quantifiable abiotic features of the environment whose variations are known or expected to affect the movement of organisms.

A non-exhaustive scanning of the relevant literature reveals a very diverse set of physical factors that affect locomotion (Fig. 1). Effects of some factors, such as electromagnetism, are still under-characterised given the highly interdisciplinary nature of such investigations (Johnsen & Lohmann, 2008; England & Robert, 2022). Devising a comprehensive classification scheme for all physical factors affecting movement is therefore difficult and necessarily incomplete. Nevertheless, assessing the effects of physical factors within the movement paradigm provides a first step towards such an objective (Table 1). It is important to note that the same physical phenomenon can be named, measured and characterised differently in different fields of ecology, often because it manifests itself in different ways in different habitats. For example, gravity is mainly studied for aquatic organisms because of its role in buoyancy, while in terrestrial systems, the main focus is on how it affects stature and balance (Bender & Frye, 2009). Pressure, a fundamental macrophysical variable, is defined as hydrostatic pressure in aquatic systems where it affects body density, and hence buoyancy, and serves also as a measure of depth (Davis, Holbrook & de Perera, 2021). However, in terrestrial systems, atmospheric (also called barometric) pressure has been studied mostly in insects, where it is interpreted as a signal they use to forecast weather and adjust their behaviour

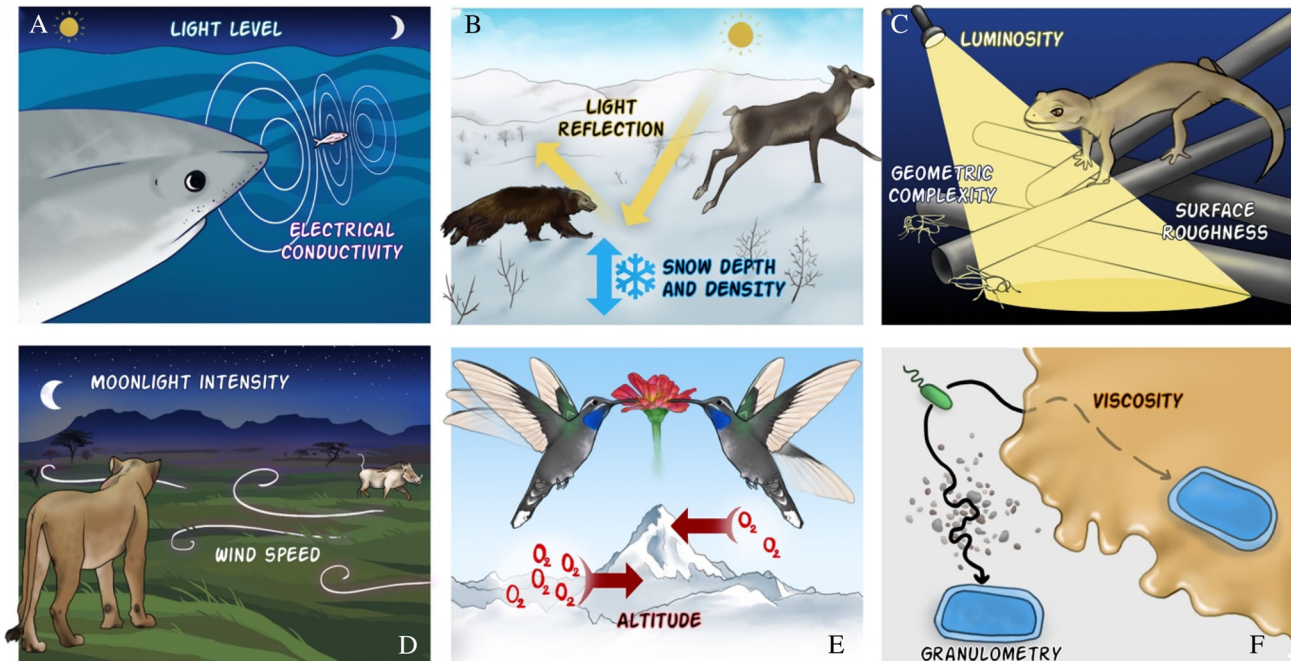
accordingly (Azevedo *et al.*, 2023). As a final example, turbidity is a term that evokes heavily particle-laden waters, but is in fact not confined to aquatic habitats (Abrahams & Kattenfeld, 1997; Ångström, 1964). Fog, a form of atmospheric turbidity, affects both visibility (Higham & Schmitz, 2019) and animal movement (Chiaradia *et al.*, 2007). These examples highlight not only the role of physical factors in species interactions, but also their varying importance in different ecosystem types.

To quantify the impacts of physical factors at the interaction level, we must estimate how they affect measurable features of movement and how this translates into changed probabilities of successful capture and conversion of prey biomass into predator biomass. Traditionally, this has been done by calculating functional and numerical responses (Holling, 1965). Translation of concrete individual-level physical effects into population-level effects requires a step-by-step approach. One must first quantify how physical factors alter the movement of the interacting organisms and then how this changes the parameters of the functional response. The modular description of the predation sequence by Wootton *et al.* (2023) provides a suitable framework to derive functional and numerical responses from the cumulative product of the probabilities of completion of consecutive steps in the sequence. Through the lens of movement, we can therefore build a framework that incorporates the movement ecology paradigm and the effects of physical factors into a detailed, generic, description of the predation sequence, and can then derive the functional and numerical responses as a function of the physical factors (Fig. 2).

The following subsections introduce the movement paradigm and explain how physical factors can be incorporated. Then, we describe the predation sequence, and show how each step in the sequence involves the components of the movement paradigm (Section III). Finally in Section IV, we highlight how, given the definition of the predation sequence we selected for our framework, effects of physical factors can be extended to the network structure and dynamics of food webs.

### (1) Inclusion of physical factors in the movement paradigm

Movement ecology as a discipline researches the effect of environmental factors on the movement and behaviour of organisms (Joo *et al.*, 2020). Its focus on environmental factors and the centrality of movement in predator–prey interactions make it a fitting starting point for our framework. The movement paradigm, formally described by Nathan *et al.* (2008) divides movement into three components (Fig. 2): (i) internal state – the integrated goal, conscious or unconscious, that results from the internal and external sensory inputs to the organism and that triggers a movement to fulfil it; (ii) navigation capacity – the intrinsic traits that allow an organism to position itself in space and time to achieve its goal; and (iii) movement capacity – the intrinsic traits that allow an organism to reach its goal by moving



**Fig. 1.** The outcome of every predator–prey interaction is determined by a set of physical factors whose importance will depend on the properties of the predator, the prey, and the surrounding environment. (A) Sharks that possess the capacity to sense changes in small electromagnetic fields detect their prey through the electromagnetic field they produce. This behaviour is important in environments where low light levels reduce the effectiveness of vision (Whitehead & Collin, 2004). (B) The depth and density of snow determines its resistance to weight. This can provide an advantage to wolverines attacking heavier prey such as reindeer (Mattisson *et al.*, 2016) because the lighter wolverine experiences less friction from the snow (Glass *et al.*, 2021). Snow cover increases light reflection, which can also affect the outcome of predation (Griffin *et al.*, 2005). (C) The ability of geckos to capture insects at night depends on the geometric complexity of their hunting ground, driving competition between native and invasive island geckos (Petren & Case, 1998). Luminosity (e.g. artificial lighting) is another driving factor, as well as surface roughness, which governs adhesion of the lizards to the solid structures over which they hunt (Persson, 2007). (D) Lions in search of prey tend to move crosswind over longer distances as wind speed increases in order to maximise odour detection probability (Wijers *et al.*, 2022). This response to wind, however, is weakened by more intense moonlight when the lion reduces its reliance on olfaction and increases its use of vision for hunting. (E) Tropical hummingbirds can inhabit a wide altitudinal range. As altitude increases, oxygen partial pressure decreases, forcing the birds to reduce wingbeat frequency due to aerobic limitation of metabolic rate. Since air density decreases as well, the only option for the birds to keep flying is to increase their stroke amplitude (Altshuler & Dudley, 2003). The resulting additional energetic requirements affect their use of nectar resources with altitude (Hainsworth & Wolf, 1972). (F) Bacterial predators, such as *Bdellovibrio* sp., feed on other bacteria. Medium viscosity affects their swimming trajectories when searching for prey (Sathyamoorthy *et al.*, 2019) and the drag forces acting on them, decreasing predation rate (Duncan *et al.*, 2018). By affecting the same parameters, geometric complexity (e.g. granulometry; Dattner *et al.*, 2017) also decreases *Bdellovibrio* sp. predation efficiency.

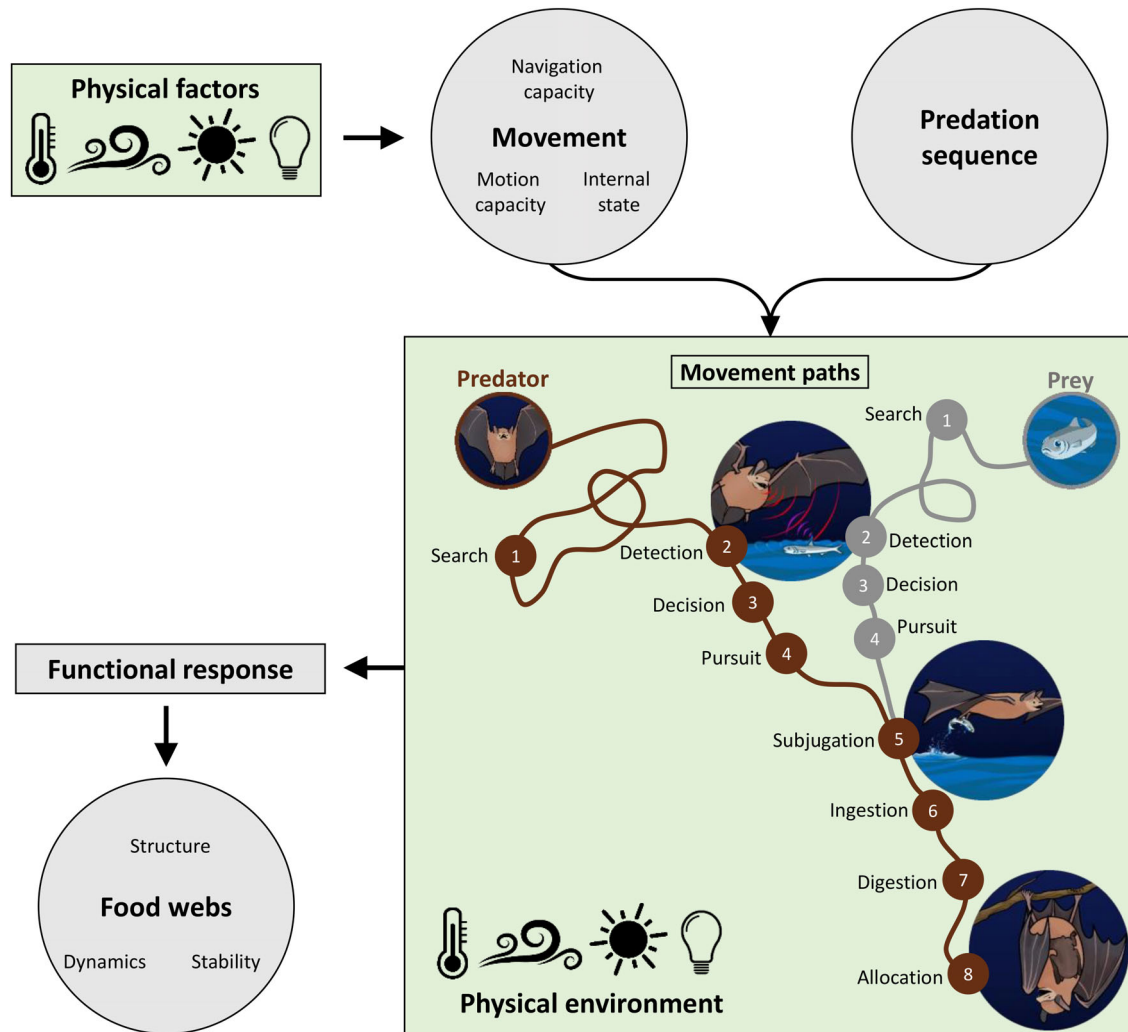
relative to its medium. Therefore, the key components of the movement paradigm include intrinsic properties of an organism and depend on its traits. For example, the ability to move in different locomotion modes (e.g. flying, swimming or running) depends upon a suite of morphological, physiological and behavioural traits (Cloyed *et al.*, 2021). Sensory and cognitive traits determine the navigation capacity of the organism (Kashetsky, Avgar & Dukas, 2021): the ability to view, hear, smell and touch the surrounding environment, to recognise and memorise elements of that environment, and to measure distance and the passage of time (Varga *et al.*, 2017).

Physical factors affect the internal state of organisms directly (detailed below). But they cannot affect navigation

and motion capacities, since these are properties intrinsic to the organisms. However, physical factors affect how these capacities are put to use by the organisms to generate a movement path. In other words, the processes of navigation and motion as they are realised are the result of an interplay between the capacities of the organism and the physical properties of the medium or terrain in which it moves (see Fig. 3 for an example). Physical factors may affect several components of movement simultaneously, albeit by different mechanisms, such as light affecting the navigation process of visual predators, as well as acting as a signal that regulates the internal clock of predators and sets the beginning and end of a foraging period (Ali, Ryder & Ancil, 1977). Conversely, a

Table 1. Mechanisms by which physical factors of the environment interact with components of movement to affect the locomotion of organisms.

	Physical factors interacting with components	Light	Gravity	Viscosity	Medium density	Temperature	Fluid motion	Turbidity	Electromagnetic fields	Pressure	Texture	Dimensionality	Topography
<b>Movement component and features</b>													
	Chemical factors (O <sub>2</sub> , pH, e, salinity, etc.)												
<b>Internal state</b>													
Body condition	Change physiological rates		Changes physiological rates			Changes physiological rates							
Hormonal levels	Change physiological rates	Signalling	Changes physiological rates			Changes physiological rates	Signalling		Signalling	Signalling			
<b>Navigation process</b>													
Circadian rhythm	Change physiological rates	Signalling	Changes physiological rates			Changes physiological rates			Signalling				
Perception	Change physiological rates	Affects vision	Affects balance and spatial orientation			Affects diffusion rates of scents, sensitivity to touch	Affects diffusion of scents	Affects vision	Affects spatial orientation	Affects balance and spatial orientation	Affects mechanoreception	Sets complexity of perception field	Affects perception field
Processing	Change physiological rates					Changes physiological rates						Sets complexity of processed information	Affects complexity of processed information
Memory	Changes physiological rates					Changes physiological rates						Sets complexity of memorised information	Affects complexity of memorised information
<b>Motion process</b>													
Propulsion													
Stability			Affects buoyancy and lift		Affects drag, lift		Affects drag, lift					Determines body support	
Manoeuvrability			Affects lift		Affects drag, lift		Perturbation				Affects friction		Affects tortuosity



**Fig. 2.** A framework for the inclusion of physical factors into the study of predator–prey interactions. The interaction between a predator and its prey follows a sequence of steps (after Wootton *et al.*, 2023): (1) Search, (2) Detection, (3) Decision, (4) Pursuit, (5) Subjugation, (6) Ingestion, (7) Digestion, and (8) Allocation. Physically, these steps are effected *via* movement of either the prey, the predator or both. Understanding the effects of any physical factors on the predator–prey interaction requires decomposition of the movement paths of each step into the three components of movement as defined in the movement paradigm: navigation capacity, motion capacity and internal state (Nathan *et al.*, 2008). Interactions between the physical factors and the components of movement will determine the movement paths and thus the success or failure of each of the steps of the predation sequence. The quantitative outcome of the sequence, the functional response, represents the building block for the derivation of the structure, dynamics and stability of food webs.

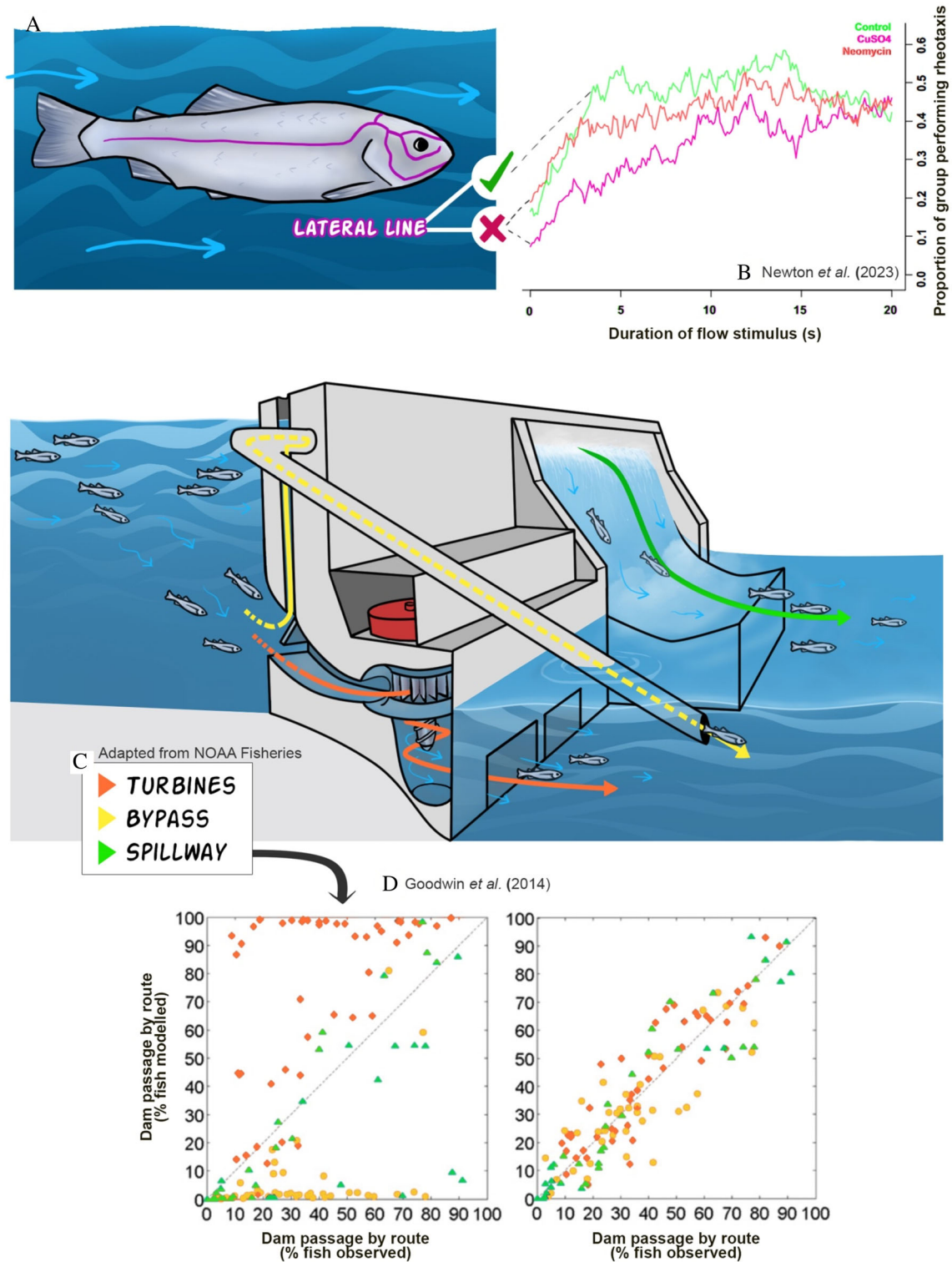
movement component may be affected by several factors in concert, such as motion that is affected by gravity and by the density and viscosity of the medium.

Consideration of the physical dimension of animal movement is far from novel. From Galen's *De Motu Muscularum* (~170 BCE), to modern textbooks on animal locomotion (Alexander, 2003; Gordon *et al.*, 2017; Biewener & Patek, 2018), *via* classical works (Pettigrew, 1873), the scientific literature shows that the topic of animal motion is inextricable from physics. Extensive work by authors such as Vogel (1988, 2000, 2013, 2020) have promoted the importance of physical constraints on life. However, it is important to note in the present context that these works focused on the role of physics on

individuals and that few attempts have been made to extend this to the study of ecological interactions and communities. Additionally, most studies have had a biomechanical focus (i.e. on motion capacity), with little consideration of the navigation and internal state components of movement. Herein we are guided by the integrative viewpoint of the movement paradigm, with the ultimate goal of explicit inclusion of the effects of physical factors into community ecology.

#### (a) *Effects of physical factors on internal state*

Although hard to define, internal state can be measured by its physiological determinants. Body condition and levels of



**Fig. 3.** Rheotaxis is the ability of an organism to orient itself in response to a current. (A) In fish, the lateral line is the main (but not the sole) organ involved in this navigation capacity. (B) Newton *et al.* (2023) showed that ablation of the lateral line in the zebrafish, *Danio rerio*, with various chemical compounds reduced the proportion of fish performing rheotaxis as a function of stimulus duration. Note the interaction with the physical factor (flow stimulus duration) that modulates the expression of rheotaxis, but does not determine the existence of this navigation capacity in the fish: a plateau is reached after a 17-s stimulus duration, above which other organs presumably are involved in rheotaxis. Rheotaxis as a navigation capacity in this species can thus be defined by this 17-s threshold, (Figure 3 legend continues on next page.)



specific hormones, such as octopamine in insects and glucocorticoids in vertebrates, are thought to be primary determinants of movement in most species (Goossens *et al.*, 2020).

Body condition, and hence internal state, is affected by physical factors that alter metabolism. Chief among these are chemical factors, such as oxygen availability, pH and salinity (Kültz, 2015; Cummins, Strowitzki & Taylor, 2020). Foremost among the non-chemical physical factors that affect body condition is temperature (Malishev, Bull & Kearney, 2018). Another factor considered less often, but also with important effects, is water content and humidity, which control water loss from the body (Chaplin, 2006). These factors act on internal state by regulating metabolic rate (e.g. reduced at low temperatures), requiring additional energetic expenditure (e.g. active secretion of salt in osmoregulatory fish under increased salinity), or by causing damage (e.g. production of reactive oxygen species under stress).

Hormone production, circulation and degradation in the body is another essential component of metabolism, and is also influenced by the same physical factors that affect body condition (Goossens *et al.*, 2020). Additionally, physical factors may function as signals that trigger hormonal cascades leading to movement-related behavioural and morphological changes (e.g. McCormick *et al.*, 1998).

Physical signals can serve to synchronise the circadian system with the environment. The circadian system is a fundamental regulation mechanism of internal state, an integrated system of hormonal, molecular and neuronal elements that controls the timing of physiological functions in organisms (Prokkola & Nikinmaa, 2018). This system is highly sensitive to external cues such as light and temperature (Van Someren, 2003). It is also affected by other factors that affect internal state (e.g. oxygen levels; Prokkola & Nikinmaa, 2018), as well as by other less-intuitive factors such as magnetic fields and gravity (Xue *et al.*, 2021).

Although multiple physical factors (see Table 1) affect the movement of organisms, most organisms have capacities that allow them to adapt to physical changes and maintain an optimal trajectory. Such compensation may require substantial energy expenditure and/or cause increased stress (Wilson *et al.*, 2021), thus resulting in an altered internal state (Burnett *et al.*, 2014). Hence, contrary to inanimate objects whose trajectory is determined passively by the physical forces acting on them, trajectories of even the simplest living organism are at least partly dictated by the interaction between the physical forces of the environment and the internal state of the organism. The actual trajectory is affected by conscious or unconscious decisions by the organism to resist or use

the physical forces acting on it, in a bid to bring its internal state to a desired condition. Thus, prediction of the effects of physical factors on movement must involve a detailed consideration of the internal state of the organism, e.g. its energy levels, and of the decision rules linking this state to motion, e.g. optimisation rules based on the minimisation of energy expenditure or maximisation of capture success (Portalier *et al.*, 2019).

#### (b) *Effects of physical factors on the navigation process*

Navigation depends on the physical mode used by organisms to sense their environment. Predators or prey that use vision to perceive their surroundings will find their navigation affected by physical factors that affect vision, such as light intensity and turbidity (i.e. background light scattering). Visibility may be reduced because of low light intensity or high turbidity, and these different causes of reduction in visibility can result in different effects on visual predators (Benfield & Minello, 1996).

Not all organisms rely on vision for navigation. Several aquatic organisms use electroreception as a means to detect their surroundings and other organisms (Crampton, 2019). Active electroreception (the production and detection of electric discharges) is limited to a relatively small number of species. By contrast, many more species possess passive receptors that can detect weak electric fields produced by organisms or even distortions in the Earth's electromagnetic field (Kalmijn, Gonzalez & McClune, 2002). As the magnitude of an electric field decreases with the inverse of the cube of the distance, this sense is limited to short-range distance detection of a few metres at most (Hopkins, 1999). Electroreception is likely to be highly sensitive to the electrical conductivity of the medium (von der Emde, 1993).

Magnetoreception is a much more widely distributed sense (Wiltschko & Wiltschko, 2005), with different physiological mechanisms possibly involved in sensing the magnitude, direction and inclination of the geomagnetic field (Johnsen & Lohman, 2008). However, a specific receptor has not yet been found (Nordmann, Hochstoeger & Keays, 2017), making it difficult to list the physical factors likely to affect this sense, beyond perturbations in the geomagnetic field (Tonelli, Youngflesh & Tingley, 2023) and anthropogenic electromagnetic noise (Engels *et al.*, 2014). Unexpectedly, blue/green light was found to be required for magnetic orientation in European robins, *Erithacus rubecula* (Wiltschko & Wiltschko, 2005), leading to the hypothesis that retinal pigments may be involved in magnetoreception in at least some species. Although mostly important for directing long-distance

(Figure legend continued from previous page.)

and by the slope of the curve in the intact lateral line case. (C) Rheotaxis is particularly important in fishes that need to cross dams. Fish integrity is greatly affected by the route taken, with passage through turbines most harmful, while bypasses are safest. It is thus very important to be able to predict the proportions of fish using the different routes for design-optimisation purposes. (D) Inclusion of rheotaxis in a dam-navigation model by Goodwin *et al.* (2014) significantly improved predictability (right panel), in comparison to a model in which fish follow currents passively (left panel).

movements, there are a few examples where this sense is used during foraging (Červený *et al.*, 2011).

Hearing is a pervasive sense across most animal phyla, but is achieved using a wide variety of organs (McKenna, 2020). However, in essence, as sound waves propagate in a medium, organisms can detect either the variations in pressure induced by sound waves, or the motion of particles in a medium (Nedelec *et al.*, 2016). The many physical factors that affect sound propagation include medium density, pressure, temperature, topography, winds, and currents (Larom *et al.*, 1997; Brkic, Jambrosic & Ivancevic, 2004).

Sound receptors are a special type of a larger category of mechanoreceptors. Other types of mechanoreceptors are specialised for tactile sensing of physical forces, notably those resulting from touching solid surfaces (Handler & Ginty, 2021). Among the physical factors that may affect the sense of touch, temperature may be unexpected but has been shown to increase the sensitivity of some types of mechanoreceptors (Zheng *et al.*, 2019). Texture, a multidimensional feature of solids (including roughness, friction, hardness and warmness; see Okamoto, Nagano & Yamada, 2013) also affects tactile sensing. Roughness is related to the perception of vibrations that result from contact with a surface; friction is perceived through skin stretch; hardness is related to the perception of variation in the contact surface area; and warmness is the perception of heat transfer rate [see Okamoto *et al.* (2013) and references therein]. The vibratory properties of solid substrates are also important: a surprising variety of organisms sense vibrations and use them for detection and communication (Hill, 2009). Most mechanoreceptors can sense motion in the flow of the surrounding medium (Katta, Krieg & Goodman, 2015; Casas & Dangles, 2010). Hence, the flow dynamics of the medium will affect the navigation process of organisms that are mechanosensitive: they may use information on flow direction to set the direction of their movement (Chapman *et al.*, 2011; Franks, 2001) or choose to move within beneficial features of the flow (e.g. Kármán vortex streets; see Liao, 2007). In ground animals, the ability to detect and follow airflows is called anemotaxis (Yu *et al.*, 2016).

Fluid dynamics play a major role in another sense, olfaction, that is used by a wide range of predators and prey (Finelli *et al.*, 2000; Kats & Dill, 1998). High flow rates and turbulence levels distort odour plumes, and dilute chemical signals. Other physical factors that affect olfaction as a navigation and detection mechanism are temperature and humidity levels, degradation by ultraviolet (UV) radiation and the type of substrate on which odours are deposited (Parsons *et al.*, 2018).

Organisms seldom rely on only one signal modality in order to monitor their environment. According to Munoz & Blumstein (2012), the use of multiple senses can lead to enhancement (better navigation ability overall), equivalence (all senses are equally efficient), dominance (only one sense is effectively useful) or antagonism (a decrease in navigation ability). Across species there is likely to be a trade-off in investment into different senses because of limitations in resource

allocation. This was found to be the case across the genus *Drosophila* for vision and olfaction (Keesey *et al.*, 2019). Limitations to navigation caused by different physical factors are therefore interdependent.

Limitations to sensing of their environment by organisms could also arise from their capacity to process the information collected (Fagan *et al.*, 2013; Martin *et al.*, 2022). Information processing depends on the neurophysiological abilities of organisms (e.g. Borst & Euler, 2011), but is also very sensitive to changes in the environment (Samia, Møller & Blumstein, 2015; Hemmi & Tomsic, 2012). Few physical parameters affect cognitive abilities directly, with temperature being one of these (Soravia *et al.*, 2023). However, there are limits to the amount of information that an individual can process accurately at the same time, so it is probable that complexity in the geometry of the environment (Varga *et al.*, 2017) and in the motion pattern of animals (Kramer & McLaughlin, 2001) will affect information processing and attentional state (Dukas & Ellner, 1993). More subtle effects are likely to be found for physical factors that affect proprioception (perception of body position), which is used to adapt posture to the desired spatial orientation (Massion, 1992). For example, changes in gravity, or acceleration, may lead to disorientation (Clark *et al.*, 2015).

### (c) Effects of physical factors on the motion process

Organisms rarely operate at maximum capacity (e.g. maximum speed), even when performing fitness-critical actions like escaping a predator (Wilson *et al.*, 2015). An organism's realised movement is a compromise between propulsion, manoeuvrability, and stability (Dickinson, 2000), all of which are affected by the physical features of their environment. Moving organisms differ both in their modes (e.g. swimming, flying, walking, crawling, etc.) and organs of locomotion (e.g. cilia, flagella, legs, fins, etc.). Despite this variety, some common principles can be found (Jung, 2021; Bejan & Marden, 2006). In many cases, the same physical constraints act similarly upon organisms moving in different media, and using different locomotion modes (Floryan, Van Buren & Smits, 2018; Dyer *et al.*, 2023), albeit with different intensities and net effects (Portalier *et al.*, 2019; Cloyed *et al.*, 2021), hence justifying our general discussion of movement without division according to locomotion mode.

(i) *Propulsion.* In order to move within a given environment, an organism has to perform external work by applying a backward force on its surroundings, by reaction enabling it to be propelled forward. At the same time, it needs to overcome the drag incurred by the medium that is pushed away by its forward movement (Jung, 2021). Where the organism is suspended in a fluid medium, it is also subjected to the force of buoyancy (the upward force that opposes weight), which must be counteracted by an opposing lift force (negative or positive, depending on whether buoyancy is smaller or larger than weight) if the organism is to control its position in the fluid column. Drag and buoyancy are intimately related to the intrinsic mechanical properties of the fluid in which the

organism moves: its viscosity and density. The relative speed of an organism is closely related to the flow speed of the medium in which it is embedded. Hence, wind and other advective currents, as well as turbulent flows may affect the velocity of a predator and its prey differently because of differences in body size and shape, and thereby modify their encounter probability (Kjørboe & Saiz, 1995).

Organisms moving over solid ground or objects can apply a force to the surface and use the ground reaction force for propulsion (Clark, Ryan & Weyand, 2016). But if they are partly, or entirely immersed in solid substrates (e.g. snow, sand or granular media), their drag will be determined by friction in addition to viscosity and hence, their performance will depend on the texture of the material (Hosoi & Goldman, 2015; Maladen *et al.*, 2011; Li, Zhang & Goldman, 2013). The result will depend on the mode of locomotion: legged organisms may use friction as leverage to pull themselves forward (Persson, 2007), while undulatory or crawling organisms will be impeded by rougher substrates (Zhang *et al.*, 2021). Roughness is thus an important physical property that affects locomotion of ground-dwelling organisms (Clifton *et al.*, 2023). Another solid property, hardness, is significant for burrowing species (Luna & Antinuchi, 2006), as well as for organisms that move over snow (Crête & Larivière, 2003).

(ii) *Stability*. Stability describes the ability of an organism to maintain a particular posture or trajectory in the presence of perturbations from the environment (Weihs, 2002). There are two main types: static stability, where an organism passively returns to a stable position after external disturbances, and dynamic stability where it needs to exert forces to return to its original state after a disturbance (Webb & Weihs, 2015).

Static stability is the result of balancing two forces, weight and buoyancy (for suspended organisms) or ground reaction force (for organisms on hard surfaces). For organisms suspended in a column of water or air, not only must these forces be in equilibrium, but they must also naturally realign with each other when changes in posture disrupt their alignment (Weihs, 2002). These two forces depend on the density of the organism relative to the medium, and hence a variety of mechanisms (e.g. swimbladders, lipid-rich livers, etc.) have evolved to allow regulation of body density to maintain neutral buoyancy (Webb & Weihs, 1994; Gleiss, Potvin & Goldbogen, 2017). Surprisingly, many aquatic organisms are either negatively or positively buoyant, or their centres of mass and buoyancy are not aligned, resulting in a pitching moment (Ehrlich & Schoppik, 2017). In the case of flying organisms, buoyancy in air is unable to counteract gravity even for the smallest species (Thomas, Ludlow & Kennedy, 1977). Dimensionality is an important physical factor affecting stability – as a general rule, organisms that live on two-dimensional surfaces are negatively buoyant, ensuring that they maintain contact with the substratum (Molloy & Cowling, 1999). Given the low density of air, terrestrial organisms need to counteract their own weight to maintain their posture and avoid falling (Dakin & Bolton, 2018), and in these organisms at rest, static stability reduces to posture

maintenance, since the ground reaction force counterbalances the effect of weight (Massion, Alexandrov & Frolov, 2004). Additional physical factors affect stability during steady movement. For example, low surface roughness results in slipperiness (Clark & Higham, 2011), and high surface roughness in unpredictability and potentially a fall (Grimmer *et al.*, 2008).

Decreased static stability will require additional energy expenditure to regain control *via* dynamic stability, i.e. through the production of lift and rotational forces by the relative movements of body parts (Weihs, 2002). Here, density and viscosity will play important roles, as environmental physical factors that determine lift. Another important physical factor is fluid motion, specifically turbulence (Combes & Dudley, 2009; Ravi *et al.*, 2015; Fish & Domenici, 2015), which can prevent animals from reaching a stable position.

(iii) *Manoeuvrability*. Motion through even the simplest environment requires the ability to alter speed, trajectory and body orientation, i.e. requires manoeuvrability (Dudley, 2002). Manoeuvrability is interlinked with the notion of stability: the more intrinsically stable an organism is, the harder it will be for it to alter its movement (Fish, 2002). There will thus be a trade-off between stability and manoeuvrability, with some species built for slow, steady motion and stability, while others have evolved high manoeuvrability but at a cost of lower stability (Gleiss *et al.*, 2017). While dynamic stability can be facilitated by high manoeuvrability (Shield *et al.*, 2021), this will require increased energy expenditure, especially at low speeds (Webb, 2002). The tight coupling between manoeuvrability and stability means that the same physical factors affect the two processes.

## (2) Integrating the movement paradigm in the predation sequence

A successful predation event between a predator and its prey can be visualised as the result of a sequence of steps (Fig. 2; Wootton *et al.*, 2023). Note that this sequence is modular and highly generic; some types of predation interaction will include some steps and exclude others, e.g. sit-and-wait predators do not search for their prey, and herbivores do not need to pursue their resources.

In the sequence shown in Fig. 2 the predator first (1) *searches* for prey, which involves the predator and/or prey moving through the habitat. Once in sufficient proximity, the predator must (2) *detect* the prey and then (3) *decide* that this prey item is worth attacking. It must then (4) *pursue* and (5) *subdue* the prey. Following the successful conclusion of these five steps, a predator will then (6) *ingest* and (7) *digest* the prey, and finally (8) *allocate* the ingested energy and nutrients to growth and/or reproduction. Each of these eight steps can be considered as a conditional probability which, when multiplied together describes the probability of a successful interaction occurring (see also Equation 1). Each step takes some amount of time to complete. The total time limits the amount of prey a predator can handle in a given period of time,

thereby driving the shape of the functional response. The time and probability associated with each step are functions of the movement path followed by both the predator and its prey, thus opening the possibility of using the movement paradigm to parameterise the predation sequence, or at least to quantify the effects of the physical factors that affect movement components. For example, small fishing bats require high metabolic rates to maintain homeothermy. In bad weather conditions, they conserve energy by entering torpor (Salinas *et al.*, 2014). Hence, the onset of foraging in these species is determined to some extent by weather factors that affect their internal state, such as wind intensity (see Fig. 4 for potential effects of wind on fishing bats). Each of the three components of movement thus are involved to varying degrees in each of the stages of the predation sequence (Table 2). Comparing Tables 1 and 2 highlights that most stages of the predation sequence are likely to be affected by multiple physical factors, including the last three stages in which the prey is processed, although the importance of these factors will vary across stages and with the habitat and mode of locomotion of the predator and prey.

In the search stage, as an active predator moves to locate its prey, all components of movement are involved (Table 2). The animal's internal state determines its motivation to invest in foraging at the expense of other activities such as hiding or reproduction. Its motion capacity, and associated physical factors, determine the characteristics of its motion process, such as speed, path tortuosity or higher-level random-walk parameters (Grünbaum, 1998). The navigation process may be the most important in the search stage since the ability of the predator to reach prey-rich habitats will depend on navigation tools such as gradient detection or spatial memory (Ranc *et al.*, 2021).

The navigation process is also key at the detection stage. Fishing bats, for example, use echolocation (Aizpurua *et al.*, 2015) to detect ripples produced by surfacing fish (Aizpurua & Alberdi, 2018). Wind can increase the number of waves at the surface, masking these ripples. A decline in detection ability was suggested to be the main reason for a decline in foraging activity of bats in windy conditions (Siemers & Stitz, 2001; Fig. 4).

Decision, by contrast, will mostly be determined by the predator's internal state, but it is likely that navigation and motion processes will also be involved.

After the decision is taken to pursue the prey, the predator's internal state still plays a role (balancing expected energy gain against energy losses and injury risks), but the main processes will be navigation (to target the prey) and motion (to reach the prey).

During the subjugation step, the navigation process will be of less importance, with motion remaining a key factor (as the prey attempts to escape or defend itself), and internal state should increase in importance, particularly when facing dangerous and well-defended prey (Gonzaga *et al.*, 2022).

After the prey is subjugated and ready for ingestion, movement components, and hence the physical factors of the

environment that affect them, are expected to decrease in importance as the predator and its prey are at the same location. Nonetheless the motion process may continue to play a role. For example, predators that need to maintain their position in the water column or in air while consuming their prey need to generate lift and thrust to counteract drag and buoyancy. Moreover, they need to compensate for the additional weight of their prey. Some modes of ingestion require swallowing the prey item together with the fluid surrounding it (e.g. prey suction in many fishes and lunge-feeding in baleen cetaceans), and this will have an energetic cost, depending on the viscosity and density of the fluid (Holzman *et al.*, 2012). The effects of the physical environment on the swallowing process can be illustrated by a comparison of species like amphibians and turtles that feed both underwater and on land, for which they use the same skeletomuscular apparatus but with different bite characteristics, depending on the medium (Heiss, Aerts & Van Wassenbergh, 2018; Stayton, 2011). During ingestion, the physical properties of the prey (such as its size, toughness and stiffness) become important (Diluzio *et al.*, 2017). If the prey is too large to be swallowed whole, the predator must bite, twitch, shake, or chew the prey in order to cut it into smaller pieces. All these mechanical actions will be dependent on the mechanical stiffness of the prey, on the bite force of the predator, and hence its movement capacity (e.g. muscular power), and on its internal state (e.g. energy levels). Physical factors such as medium density, viscosity and temperature are all known to affect characteristics such as bite force and duration (Stayton, 2011; Anderson, McBrayer & Herrel, 2008).

During digestion, physical factors are likely less important, but the additional weight of the prey must still be considered, and its surface area will determine the rate of digestion (Salvanes, Aksnes & Giske, 1995). Electro-resistivity was recently suggested as a physical factor controlling digestion (Sutton, 2019).

Only after allocation, when the largest part of the prey is egested, excreted or respired, does its extra weight cease to impact the predator. After digestion, it could be suggested that biochemical constraints will play a greater role than physical factors, although temperature affects all components of metabolism including assimilation efficiency (see Lang *et al.*, 2017). However, the physical environment may still place constraints on allocation, for example necessitating greater allocation towards movement capacity (e.g. in snowy conditions), navigation capacity (e.g. in a rugged landscape) or maintaining internal state (e.g. under cold conditions). External signals may also affect the internal state of the predator, for example triggering mate searching or increasing energy stores before migration.

We have based our reasoning in Table 2 on the predator's perspective, but a similar table could be constructed for the prey: prey need to search for a safe place, detect predators, navigate to safety when attacked, and defend themselves to avoid subjugation (Dugatkin & Godin, 1992). Experiments can be used to manipulate physical factors to study their



**Fig. 4.** Graphical illustration of the potential effects of wind on the parameters of the functional response for the predation sequence of fishing bats. Windy conditions may decrease (A) the proportion of daily time spent foraging ( $\varphi_{\text{forage}}$ ) (Salinas *et al.*, 2014; Santos-Moreno *et al.*, 2010) and (B) the area searched per unit foraging time ( $A_{\text{search}}$ ), as bats will forage only in sheltered areas (Russo & Jones, 2003). The impact of wind on (C) prey density ( $N$ ) and encounter probability ( $f_1$ ), and on (D) search time ( $t_1$ ) is poorly known, but there is evidence to suggest that wind will affect (E) detection probability ( $f_2$ ) and detection time ( $t_2$ ), because (Figure 4 legend continues on next page.)

Table 2. Suggested degree of involvement of the three components of the movement paradigm (Nathan *et al.*, 2008) in the steps of the predation sequence as defined in Wootton *et al.* (2023) (see Fig. 2).

	Search	Detection	Decision	Pursuit	Subjugation	Ingestion	Digestion	Allocation
Internal state	++	+	++	+	++	+	+	++
Navigation process	++	++	+	++	+	+	+	+
Motion process	+	+	+	++	++	+	+	+

effects on the functional response (e.g. Costello *et al.*, 1990; Barrios-O’Neill *et al.*, 2016). We recommend the design of experiments that distinguish between the various stages of the predation sequence and that record the different components of movement of the predator and prey.

### III. BUILDING THE FUNCTIONAL AND NUMERICAL RESPONSES

The framework outlined in Fig. 2 allows us to model the effects of different physical factors on the various stages of the predation sequence. These different stages form a series of nested conditional probabilities, which are multiplied to obtain a single probability that an individual predator successfully captures and consumes an individual prey. Wootton *et al.* (2023) derived an equation for calculation of the functional response (FR) of a predator, i.e. the number of prey items killed per unit time as a function of prey density, from these conditional probabilities and from the time taken to completion for each step of the predation sequence.

$$FR = A_{\text{search}} \frac{f_1 \times f_2 \times f_3 \times f_4 \times f_5 \times \varphi_{\text{forage}}}{1 + A_{\text{search}} \times f_1 \times f_2 \times f_3 \times f_4 \times f_5 \times t_{\text{handle}}} \times \mathcal{N}, \tag{1}$$

where  $\mathcal{N}$  is the prey density,  $A_{\text{search}}$  is the area or volume searched by the predator per unit foraging time,  $\varphi_{\text{forage}}$  is the proportion of time spent foraging,  $f_i$  is the probability of step  $i$  reaching completion, conditional on step  $i-1$  being successful, and  $t_{\text{handle}}$  is handling time, i.e. the time needed to process the prey, after a successful encounter:

$$t_{\text{handle}} = \frac{t_2}{f_2 \times f_3 \times f_4 \times f_5} + \frac{t_3}{f_3 \times f_4 \times f_5} + \frac{t_4}{f_4 \times f_5} + \frac{t_5}{f_5} + t_6 + t_7, \tag{2}$$

where  $t_i$  is the time needed for step  $i$  to reach completion. We refer the reader to the original publication for formal derivations of Equations (1) and (2).

The resulting functional response is not very different from the classical type 2 response, but differs in the explicit consideration of each step of the predation sequence, and the resulting decomposition of the classical parameters of the type-2 functional response (attack rate and handling time) into smaller building blocks (Wootton *et al.*, 2023).

Assessing the effect of a given physical factor on the functional response in our framework thus requires accounting for its effect on each of the parameters of the functional response. If possible, each effect should be derived mechanistically from a model of movement that includes the dependence of the movement paths of both the predator and the prey on the physical factor, and for each step of the sequence. Alternatively, empirical correlations or experimental results may be available. Failing that, looking for qualitative evidence for potential effects of the factor considered on each of the steps will highlight knowledge gaps still to be filled, as we illustrate in Fig. 4 for the effects of wind on fishing bats.

Another advantage of using Equation 1 is that we can derive the predator’s expected gross energy gain from a predation event by multiplying the energetic content of the prey captured by the product of the conditional probabilities extracted from the predation sequence. The energetic content of the prey can be easily extracted from its body weight, body composition, taxonomy, and/or age (e.g. Weil *et al.*, 2019; Wuenschel, Jugovich & Hare, 2006; Breck, 2008; Schindler & Eby, 1997).

(Figure legend continued from previous page.)

wind-induced waves on the water surface affect the ability of echolocating bats to identify ripples produced by surfacing fish (Aizpurua *et al.*, 2015; Siemers & Stütz, 2001; Lukas *et al.*, 2021). There is no evidence for an effect of wind on (F) decision probability ( $f_3$ ) and decision time ( $t_3$ ). Wind is likely to affect (G) pursuit probability ( $f_4$ ) and pursuit time ( $t_4$ ) due to its impact on flight speed and flight costs while trawling for the detected fish (Schnitzler *et al.*, 1994). (H) Subjugation is a rapid process in fishing bats, making it unlikely that its probability ( $f_5$ ) and duration ( $t_5$ ) are affected by wind (Altenbach, 1989). Fishing bats need to find a perch to ingest larger fish, while smaller ones are ingested in the air following subjugation (I). Strong wind may thus prolong or prevent ingestion of larger fish, thus affecting ingestion efficiency ( $f_6$ ) and ingestion time ( $t_6$ ) (Aizpurua & Alberdi, 2018; Fenton, 1990). Ingestion of smaller fishes may result in (J) more thorough and rapid digestion ( $f_7$  and  $t_7$ ; Welch *et al.*, 2015). Finally, research shows that bats may power active flight directly from their ingested food (Voigt *et al.*, 2010). Thus, it is likely that due to the increased flight costs under windy conditions, a larger proportion of the assimilated energy will be allocated to locomotion rather than to other metabolic functions, thus affecting (K) allocation efficiency ( $f_8$ ) and time ( $t_8$ ).

For a foraging strategy to permit the predator's survival, the predator's gross energy gain should be larger than the total energy cost accumulated throughout all the steps of the predation sequence. Thus, for long-term survival, the predator should have a positive net energy gain from each predation event on average. Expressed in units of newly formed predator individuals, the net energy gain becomes equivalent to the numerical response (i.e. describing changes in predator and prey densities; Holling, 1965).

For any fixed pair of predator–prey individuals, if change in a physical factor alters one or more of the probabilities or times in the predation sequence, the energy gain from that predator–prey interaction will change accordingly. The direction (increase or decrease) of this change will depend on the magnitudes of the altered probabilities or times. It is therefore possible that a change in a physical factor could make a previously productive interaction costly, or *vice versa*. For example, an increased metabolic rate at higher temperatures could mean that a predator no longer survives on small prey which do provide a net energy gain at lower temperatures (modelled in Sentis, Haegeman & Montoya, 2021). Thus, inclusion of physical factors *via* their effects on the components of movement offers an opportunity to calculate the effects of those factors on energetic costs. Using a model that included four stages in a predation sequence, Portalier *et al.* (2019) used mechanics and thermodynamics to calculate the change in energy expenditure that results from a change in a physical factor (differences in medium density and viscosity between air and water; see Fig. 5).

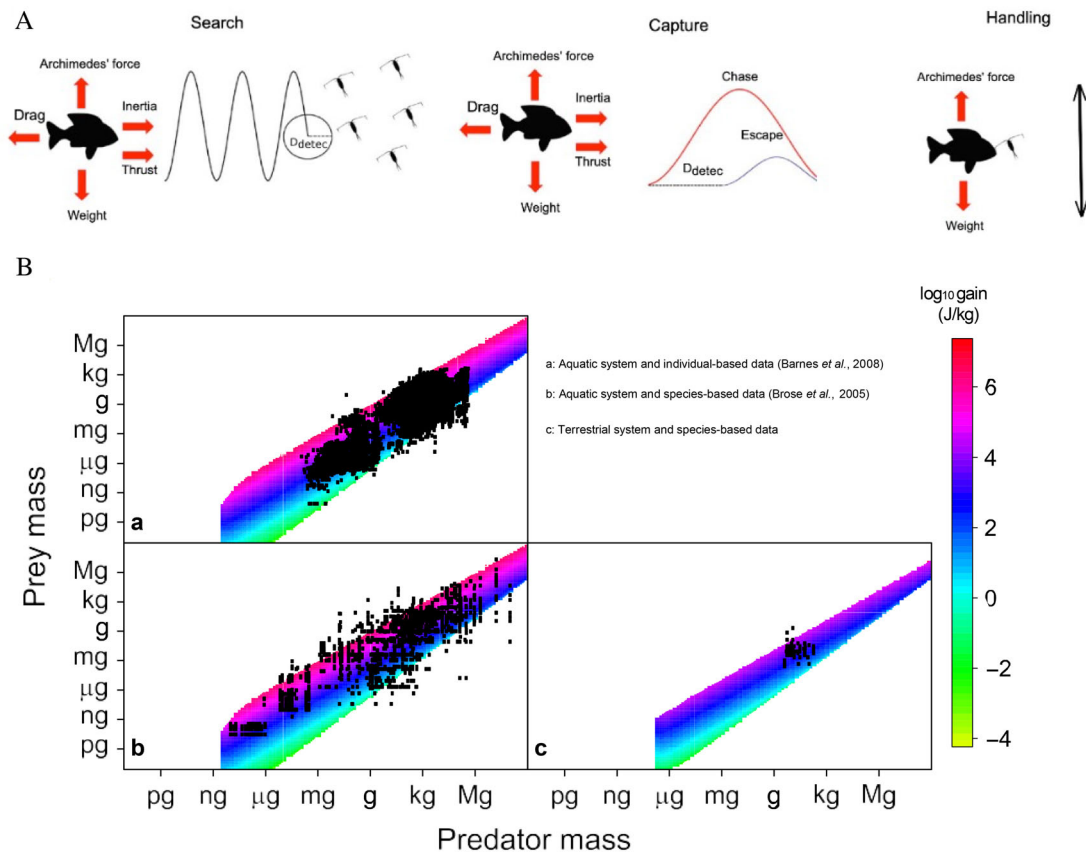
A few studies have explicitly considered the effects of physical factors on the functional response, including temperature (Englund *et al.*, 2011), ecosystem dimensionality (Pawar, Dell & Van Savage, 2012) and medium properties (Portalier *et al.*, 2022). In future, the increasing availability of functional response data (e.g. the FoRAGE database; DeLong & Uiterwaal, 2018), together with environmental information may allow detailed investigation of the effects of physical factors on functional responses.

#### IV. FROM THE FUNCTIONAL RESPONSE TO FOOD-WEB STRUCTURE AND DYNAMICS

The functional response describes the *per-capita* influence of a predator on its prey population with units in individuals, biomass, or energy per unit time. This functional response, as well as its inverse, i.e. *per-capita* influence of the prey on the predator population, are often referred to as 'interaction strengths', which represent the quantitative flow of energy or biomass between the predator and prey, and drive the population dynamics of both taxa [see Berlow *et al.* (2004) for a review]. Hence, any influence of a physical factor on the probabilities or timings in the predation sequence that leads to a change in interaction strength could also affect the population dynamics of both organisms. Our framework can thus potentially be used in combination with a

population dynamics model (e.g. Yodzis & Innes, 1992) or with interaction matrices (e.g. Allesina, Alonso & Pascual, 2008) to predict influences of physical factors on predator–prey population dynamics. However, moving beyond one predator and one prey species towards trophic interactions among multiple species in a community will necessitate consideration of predator preferences when several types of prey are available. For example, if energy intake is the primary concern, optimal foraging theory (Charnov & Orians, 2006) suggests that the predator should ignore some prey types even though such links are feasible. Instead, the predator should concentrate on more profitable types of prey as they yield better long-term energetic payoffs. The predator's preference should be implemented in our framework at the decision step of the predation sequence. As for all steps of the predation sequence, it should depend on the three movement components and thus potentially be influenced by physical factors. More specifically, prey choice will involve cognitive capacities, such as sensory perception, attention, learning and memorisation of the types of prey usually encountered (Dukas & Ellner, 1993; Mitchell, 1989; Hughes *et al.*, 1992), all features which can be affected by physical factors (Table 1). Until the theory is sufficiently developed to include interactions between more than two organisms, we can combine our mechanistic framework with one of the several food-web models available that include decision mechanisms, such as the optimal foraging-based allometric diet breadth model (ADBM; Petchey *et al.*, 2008). In the absence of inclusion of prey selection, application of our framework to all possible pairs of species in a food web could help to identify which of the potential trophic links are mechanically and energetically feasible (Fig. 5; see Portalier *et al.*, 2019). Modelling can also yield for each pair an estimate of the optimal handling time and attack rate (Portalier *et al.*, 2022). To these parameters, addition of information on species densities will allow generation of predictions about food-web structure using the ADBM (Thierry *et al.*, 2011) or alternative models (Allesina, 2011).

Temperature has relatively well-understood effects on metabolism and life-history traits (e.g. Savage *et al.*, 2004; Lindmark, Ohlberger & Gårdmark, 2022). This detailed knowledge allows temperature to be incorporated into difference or differential equations related to population dynamics, facilitating highly detailed models (Beveridge, Petchey & Humphries, 2010; Binzer *et al.*, 2016). However, the biological effects of most other physical factors remain poorly understood. For example, medium properties like density and viscosity clearly affect the motion process, but are not likely to impact the navigation process or internal state (Table 1). Other factors may function as signals that set the internal state, such as sun angle above the horizon determining the activity level of migrating birds (Pokrovsky *et al.*, 2021). Through the explicit consideration of the link between the three movement components and the parameters of the functional and numerical responses, our framework provides a route for the inclusion of such factors in food-web models. Moreover, where multiple factors affect



**Fig. 5.** Inclusion of physical factors in a foraging model by Portalier *et al.* (2019). (A) The physical factors included were gravity (weight of the moving organism), viscosity (which affects drag), and medium density (which affects both drag and Archimedes' force). The predation sequence considered only four of the eight steps: search, capture (pursuit in our framework), and handling (i.e. ingestion and digestion). Internal states can be equated with the different optimisation goals set at each step: the predator is assumed to optimise (i) energy spent per unit distance travelled at the search stage; (ii) distance travelled at the capture stage; and (iii) energy spent per unit of time at the handling stage. The navigation capacities of predators and prey in the model were the ability to (i) perform a ballistic walk at the search stage, (ii) detect the other partner at a size-based minimal distance ( $D_{\text{detec}}$ ) and orient movement towards the prey for the predator and away from the predator for the prey after detection; and (iii) for the predator, maintain a constant horizontal position during handling. Motion capacity was modelled as a size-based maximum thrust force that could be allocated between a horizontal and a vertical component in different proportions, yielding a sinusoidal movement path, a capacity to sustain a constant foraging speed during search; prey capture or prey evasion was limited to only one sinusoidal oscillation, and the predator could maintain its position (hover) during handling. (B) Despite a more restricted set of stages in the predation sequence in comparison to our framework, their model was able to predict the occurrence of predator–prey interactions in pelagic and aerial media for a wide range of predator and prey masses with great accuracy, using data from (a) Barnes *et al.* (2008), (b) Brose *et al.* (2005), and (c) their own data collection. This model highlights the promise of models including physical factors to assess impacts on predator–prey interactions.

predation, models may become highly complex, with this complexity computationally prohibitive for large food webs. By incorporating the effects of all relevant physical factors into a single probability (given a set of physical conditions), our framework retains feasibility even for large systems. In addition to energetic considerations, foraging is also constrained by other filters, such as stoichiometric nutrient requirements (Hall, 2009), predator–prey trait matching (Abrams, 2000), the fear landscape (Brown, Laundre & Gurung, 1999), or phenological overlap (Renner & Zohner, 2018), and some of these have been applied to model interaction strengths in food webs (Rossberg

*et al.*, 2006). Given the large scope of processes included in our framework (physical, morphological, physiological and behavioural), such filters could possibly be incorporated by clarifying their links with the components of movement. Other filters may need to be included as additional dimensions (Eklöf *et al.*, 2013). The focus of our framework on the effects of physical factors on traits rather than only on the traits *per se*, also makes generalisation across systems easier. There remains a substantial knowledge gap, both empirically and theoretically, regarding the effects on food webs of physical factors other than temperature, and we hope that our framework stimulates future research by providing



mechanistically based, testable predictions. Ultimately, scaling up physical constraints on species interactions to food webs may provide mechanistic explanations for systematic differences in network structure between aquatic and terrestrial ecosystems (Potapov *et al.*, 2019). Given the increasing availability of large-scale food-web data (e.g. the GATEWAY database; Brose *et al.*, 2019), we are optimistic that we can move towards a more mechanistic pathway of predicting food-web structure under global change.

## V. FUTURE DIRECTIONS

Movement is central to trophic interactions. Devising accurate mechanistic models of the functional response will enable better predictions of the responses of food webs under environmental change. Most importantly, this requires the inclusion in models of physical factors of the environment that affect interactions, food webs, and thereby ecosystems and their functions *via* their impact on movement. However, much work remains to be done and many obstacles to be overcome. First, our understanding of the effects of many physical factors on the components of movement remains limited (e.g. for electromagnetism; MacIver, Sharabash & Nelson, 2001), has rarely been applied in the context of predation (e.g. wind; Cherry & Barton, 2017), or requires advanced modelling tools (e.g. turbulence; Zhou, 2021). As all models are simplifications of the systems they represent, there is also the risk of neglecting some locally important physical factor. More generally, different trophic interactions may be affected by different physical factors. Hence, it may be the case that a mechanistic food-web model needs to include as many physical factors as possible, making it appear a daunting task.

However, developments in the field of ecology may put this target within reach. Many theoretical models are already available that focus on one or several physical factors, such as dimensionality (Pawar *et al.*, 2019), medium viscosity and density (Portulier *et al.*, 2019, 2022), temperature (Binzer *et al.*, 2016), and hydrodynamics and light availability (Baird & Emsley, 1999). Empirically, the development of biologging, i.e. the measurement of biological (acceleration, heart rate, electroencephalograms, etc.) and physical (depth, temperature, salinity, etc.) data using animal-attached tags (Watanabe & Papastamatiou, 2023) offers an opportunity to test model predictions, detect patterns and formulate hypotheses.

We believe that the full potential of linking physical factors, movement, and species interactions has not been exploited due to the absence of a unifying framework such as ours. Typically, biologging studies use the collected data to answer the specific questions for which it was deployed, without making use of all the data produced (Payne *et al.*, 2014). There are already examples of the use of biologging to estimate parameters of the predation sequence from movement data [e.g. decision-making in beaked whales as a

function of the internal state (Siegal *et al.*, 2022), and ingestion rates of Eurasian spoonbills *Platalea leucorodia* (Lok *et al.*, 2023)]. Substantial progress in understanding the effects of the physical environment on trophic interactions could certainly be made by exploiting biologging data already collected, and by promoting the systematic collection of physical parameters in future biologging studies. Given the central role of acceleration according to classical mechanics in linking physical forces, energy and movement, we advocate for the use of accelerometers as a means to measure the movement of organisms, with their ease of use and methodological maturity making their widespread application realistic (Gleiss, Wilson & Shepard, 2011; Bidder *et al.*, 2015; Chakravarty *et al.*, 2019; Eikelboom *et al.*, 2020).

A research agenda combining the development of models of increasing complexity, with a fuller use of biologging data, and well-targeted experiments will be vital to understanding how changes in the environment affect the structure and dynamics of ecological communities. Predicting the species losses or successful invasions that are likely to result from climate change is a prerequisite for predicting how ecosystem services such as food production, pollination, and coastline retention will change in the near future (Domenici & Seebacher, 2020). Mechanistic models could allow us to predict the food webs of the future that will result from the strong and pervasive anthropogenic perturbations of the biosphere.

## VI. CONCLUSIONS

- (1) Accurate predictions of food-web responses to anthropogenic perturbations would benefit from an understanding of the effects of the physical factors of the local environment on food webs.
- (2) The physical factors of the environment that affect movement should also affect food webs as movement is fundamental to the realisation of trophic interactions between predators and prey.
- (3) Based on the movement paradigm of ecology, movement in living organisms is determined by three components: internal state, locomotion capacity and navigation capacity. Most physical factors affect at least one of the three components, and thus trophic interactions.
- (4) All types of predation events can be subdivided into modular steps that differ in the type of movement used, but altogether make the predation sequence: search, detection, decision, pursuit, subjugation, ingestion, digestion and allocation. Probabilities and efficiencies associated with the completion of each of the predation steps allow formulation of the functional response of any given type of predation interaction.
- (5) From the functional response, several measures of interactions between pairs of species can be derived, depending on the model used. From there, the structure and dynamics of food webs can be predicted.
- (6) The three components of movement are involved, with to a greater or lesser extent, in all the steps of the predation

sequence. Hence, a framework can be set by combining (i) the effects of given physical factors on the three components of movement, (ii) an estimation of the involvement of movement components in each of the steps of the predation sequence, (iii) a formulation of the functional response, (iv) inference of the interaction strengths between all species pairs from the functional responses, and (v) a model of food-web structure and dynamics based on pairwise interaction strengths.

(7) Altogether, these steps will permit mechanistically linking the effect of anthropogenic stressors on physical factors to their effects on food webs.

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## VIII. AUTHOR CONTRIBUTIONS

M. C. and S. M. J. P. conceived the original idea. M. C. and U. B. secured funding for the three workshops during which the initial concepts were developed into a framework. M.C. wrote the first draft. M. C., M. R. H., R. R. and V. S. constructed the figures. All other co-authors contributed substantially to revisions.

## IX. REFERENCES

ABRAHAMS, M. V. & KATTENFELD, M. G. (1997). The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology* **40**, 169–174.

ABRAMS, P. A. (2000). The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* **31**, 79–105.

AIZPURUA, O. & ALBERDI, A. (2018). Ecology and evolutionary biology of fishing bats. *Mammal Review* **48**, 284–297.

AIZPURUA, O., ALBERDI, A., AIHARTZA, J. & GARIN, I. (2015). Insight on how fishing bats discern prey and adjust their mechanic and sensorial features during the attack sequence. *Scientific Reports* **5**, 12392.

ALEXANDER, R. M. (2003). *Principles of Animal Locomotion*. Princeton University Press, Princeton, NJ.

ALI, M. A., RYDER, R. A. & ANCTIL, M. (1977). Photoreceptors and visual pigments as related to behavioral responses and preferred habitats of perch (*Perca* spp.) and pikeperch (*Stizostedion* spp.). *Journal of the Fisheries Research Board of Canada* **34**, 1475–1480.

ALLESINA, S. (2011). Predicting trophic relations in ecological networks: a test of the Allometric Diet Breadth Model. *Journal of Theoretical Biology* **279**, 161–168.

ALLESINA, S., ALONSO, D. & PASCUAL, M. (2008). A general model for food web structure. *Science* **320**, 658–661.

ALTENBACH, J. S. (1989). Prey capture by the fishing bats noctilio leporinus and myotis vivesi. *Journal of Mammalogy* **70**, 421–424.

ALTSCHULER, D. L. & DUDLEY, R. (2003). Kinematics of hovering hummingbird flight along simulated and natural elevational gradients. *Journal of Experimental Biology* **206**, 3139–3147.

AMERICAN HERITAGE DICTIONARY OF THE ENGLISH LANGUAGE. (2011). Fifth Edition, Electronic file available at <https://www.ahdictionary.com> Retrieved 10.11.2023

ANDERSON, R. A., McBRAYER, L. D. & HERREL, A. (2008). Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biological Journal of the Linnean Society* **93**, 709–720.

ÅNGSTRÖM, A. (1964). The parameters of atmospheric turbidity. *Tellus* **16**, 64–75.

AZEVEDO, K. E. X., MAGALHAES, D. M., DE ANDRADE MORAL, R. & BENTO, J. M. S. (2023). Weathering the hunt: the role of barometric pressure in predator insects' foraging behaviour. *Ecology and Evolution* **13**, e10416.

BAIRD, M. & EMSLEY, S. M. (1999). Towards a mechanistic model of plankton population dynamics. *Journal of Plankton Research* **21**, 85–126.

BARNES, C., BETHEA, D. M., BRODEUR, R. D., SPITZ, J., RIDOUX, V., PUSINERI, C., CHASE, B. C., HUNSICKER, M. E., JUANES, F., KELLERMANN, A., LANCASTER, J., MÉNARD, F., BARD, F.-X., MUNK, P., PINNEGAR, J. K., ET AL. (2008). Predator and prey body sizes in marine food webs. *Ecology* **89**, 881–881.

BARRIOS-O'NEILL, D., KELLY, R., DICK, J. T. A., RICCIARDI, A., MACISAAC, H. J. & EMMERSON, M. C. (2016). On the context-dependent scaling of consumer feeding rates. *Ecology Letters* **19**, 668–678.

BAUER, B., BERTI, E., RYSER, R., GAUZENS, B., HIRT, M. R., ROSENBAUM, B., DIGEL, C., OTT, D., SCHEU, S. & BROSE, U. (2022). Biotic filtering by species' interactions constrains food-web variability across spatial and abiotic gradients. *Ecology Letters* **25**(5), 1225–1236.

BEJAN, A. & MARDEN, J. H. (2006). Unifying constructal theory for scale effects in running, swimming and flying. *Journal of Experimental Biology* **209**, 238–248.

BENDER, J. A. & FRYE, M. A. (2009). Invertebrate solutions for sensing gravity. *Current Biology* **19**, R186–R190.

BENFIELD, M. C. & MINELLO, T. J. (1996). Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. *Environmental Biology of Fishes* **46**, 211–216.

BERLOW, E. L., NEUTEL, A.-M., COHEN, J. E., DE RUITER, P. C., EBENMAN, B., EMMERSON, M., FOX, J. W., JANSEN, V. A. A., IWAN JONES, J., KOKKORIS, G. D., LOGOFET, D. O., MCKANE, A. J., MONTROYA, J. M. & PETCHEY, O. (2004). Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology* **73**, 585–598.

BEVERIDGE, O. S., PETCHEY, O. L. & HUMPHRIES, S. (2010). Direct and indirect effects of temperature on the population dynamics and ecosystem functioning of aquatic microbial ecosystems. *Journal of Animal Ecology* **79**, 1324–1331.

BIDDER, O. R., WALKER, J. S., JONES, M. W., HOLTON, M. D., URGE, P., SCANTLEBURY, D. M., MARKS, N. J., MAGOWAN, E. A., MAGUIRE, I. E. & WILSON, R. P. (2015). Step by step: reconstruction of terrestrial animal movement paths by dead-reckoning. *Movement Ecology* **3**, 23.

BIEWENER, A. & PATEK, S. (2018). *Animal locomotion*. Oxford University Press, New York, NY.

BINZER, A., GULLI, C., RALL, B. C. & BROSE, U. (2016). Interactive effects of warming, eutrophication and size structure: impacts on biodiversity and food-web structure. *Global Change Biology* **22**, 220–227.

BORST, A. & EULER, T. (2011). Seeing things in motion: models, circuits, and mechanisms. *Neuron* **71**, 974–994.

BRECK, J. E. (2008). Enhancing bioenergetics models to account for dynamic changes in fish body composition and energy density. *Transactions of the American Fisheries Society* **137**, 340–356.

BRKIC, I., JAMBROSIĆ, K. & IVANCEVIĆ, B. (2004). Perception of sound by animals in the ocean. In *Proceedings. Elmar-2004. 46th International Symposium on Electronics in Marine*, pp. 258–264. Croatian Society Electronics in Marine - ELMA, Zadar.

BROSE, U., ARCHAMBAULT, P., BARNES, A. D., BERSIER, L.-F., BOY, T., CANNING-CLODE, J., CONTI, E., DIAS, M., DIGEL, C., DISSANAYAKE, A., FLORES, A. A. V., FUSSMANN, K., GAUZENS, B., GRAY, C., HÄUSSLER, J., ET AL. (2019). Predator traits determine food-web architecture across ecosystems. *Nature Ecology & Evolution* **3**, 919–927.

BROSE, U., CUSHING, L., BERLOW, E. L., JONSSON, T., BANASEK-RICHTER, C., BERSIER, L.-F., BLANCHARD, J. L., BREY, T., CARPENTER, S. R., BLANDENIER, M.-F. C., COHEN, J. E., DAWAH, H. A., DELL, T., EDWARDS, F., HARPER-SMITH, S., ET AL. (2005). Body sizes of consumers and their resources. *Ecology* **86**, 2545–2545.

BROWN, J. S., LAUNDRE, J. W. & GURUNG, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* **80**, 385–399.

BURNETT, N. J., HINCH, S. G., BRAUN, D. C., CASSELMAN, M. T., MIDDLETON, C. T., WILSON, S. M. & COOKE, S. J. (2014). Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon. *Physiological and Biochemical Zoology* **87**, 587–598.

- CASAS, J. & DANGLES, O. (2010). Physical ecology of fluid flow sensing in arthropods. *Annual Review of Entomology* **55**, 505–520.
- CERVENÝ, J., BEGALL, S., KOUBEK, P., NOVÁKOVÁ, P. & BURDA, H. (2011). Directional preference may enhance hunting accuracy in foraging foxes. *Biology Letters* **7**, 355–357.
- CHAKRAVARTY, P., COZZI, G., OZGUL, A. & AMINIAN, K. (2019). A novel biomechanical approach for animal behaviour recognition using accelerometers. *Methods in Ecology and Evolution* **10**, 802–814.
- CHAPLIN, M. (2006). Do we underestimate the importance of water in cell biology? *Nature Reviews Molecular Cell Biology* **7**, 861–866.
- CHAPMAN, J. W., KLAASSEN, R. H. G., DRAKE, V. A., FOSSETTE, S., HAYS, G. C., METCALFE, J. D., REYNOLDS, A. M., REYNOLDS, D. R. & ALERSTAM, T. (2011). Animal orientation strategies for movement in flows. *Current Biology* **21**, R861–R870.
- CHARNOV, E. & ORIAN, G. H. (2006). Optimal foraging: some theoretical explorations. Electronic file available at [https://digitalrepository.umn.edu/biol\\_fsp/45](https://digitalrepository.umn.edu/biol_fsp/45).
- CHERRY, M. J. & BARTON, B. T. (2017). Effects of wind on predator–prey interactions. *Food Webs* **13**, 92–97.
- CHIARADIA, A., MCBRIDE, J., MURRAY, T. & DANN, P. (2007). Effect of fog on the arrival time of little penguins *Eudyptula minor*: a clue for visual orientation? *Journal of Ornithology* **148**, 229–233.
- CLARK, A. J. & HIGHAM, T. E. (2011). Slipping, sliding and stability: locomotor strategies for overcoming low-friction surfaces. *Journal of Experimental Biology* **214**, 1369–1378.
- CLARK, K. P., RYAN, L. J. & WEYAND, P. G. (2016). A general relationship links gait mechanics and running ground reaction forces. *Journal of Experimental Biology* **220**(2), 247–258.
- CLARK, T. K., NEWMAN, M. C., OMAN, C. M., MERFELD, D. M. & YOUNG, L. R. (2015). Modeling human perception of orientation in altered gravity. *Frontiers in Systems Neuroscience* **9**, 68.
- CLIFTON, G., STARK, A. Y., LI, C. & GRAVISH, N. (2023). The bumpy road ahead: the role of substrate roughness on animal walking and a proposed comparative metric. *Journal of Experimental Biology* **226**, jeb245261.
- CLOYED, C. S., GRADY, J. M., SAVAGE, V. M., UYEDA, J. C. & DELL, A. I. (2021). The allometry of locomotion. *Ecology* **102**(7), e03369.
- COMBES, S. A. & DUDLEY, R. (2009). Turbulence-driven instabilities limit insect flight performance. *Proceedings of the National Academy of Sciences* **106**, 9105–9108.
- COSTELLO, J. H., STRICKLER, J. R., MARRASE, C., TRAGER, G., ZELLER, R. & FREISE, A. J. (1990). Grazing in a turbulent environment: behavioral response of a calanoid copepod, *Centropages hamatus*. *Proceedings of the National Academy of Sciences* **87**, 1648–1652.
- CRAMPTON, W. G. R. (2019). Electroreception, electrogenesis and electric signal evolution. *Journal of Fish Biology* **95**, 92–134.
- CRÈTE, M. & LARIVIÈRE, S. (2003). Estimating the costs of locomotion in snow for coyotes. *Canadian Journal of Zoology* **81**, 1808–1814.
- CUMMINS, E. P., STROWITZKI, M. J. & TAYLOR, C. T. (2020). Mechanisms and consequences of oxygen and carbon dioxide sensing in mammals. *Physiological Reviews* **100**, 463–488.
- DAKIN, C. J. & BOLTON, D. A. E. (2018). Forecast or fall: Prediction's importance to postural control. *Frontiers in Neurology* **9**, 924.
- DATTNER, I., MILLER, E., PETRENKO, M., KADOURI, D. E., JURKEVITCH, E. & HUPPERT, A. (2017). Modelling and parameter inference of predator–prey dynamics in heterogeneous environments using the direct integral approach. *Journal of the Royal Society Interface* **14**, 20160525.
- DAUGAARD, U., MUNCH, S. B., INAUEN, D., PENNEKAMP, F. & PETCHEY, O. L. (2022). Forecasting in the face of ecological complexity: number and strength of species interactions determine forecast skill in ecological communities. *Ecology Letters* **25**, 1974–1985.
- DAVIS, V. A., HOLBROOK, R. I. & DE PERERA, T. B. (2021). Fish can use hydrostatic pressure to determine their absolute depth. *Communications Biology* **4**, 1208.
- DELONG, J. & UITERWAAL, S. (2018). The FoRAGE (functional responses from around the globe in all ecosystems) database: a compilation of functional responses for consumers and parasitoids, v. 2021. KNB Data Repository. Electronic file available at <https://knb.ecoinformatics.org/view/doi:10.5063/DB807S> Accessed 26.6.2023.
- DICKINSON, M. H. (2000). How animals move: an integrative view. *Science* **288**, 100–106.
- DILUZIO, A. R., BALIGA, V. B., HIGGINS, B. A. & MEHTA, R. S. (2017). Effects of prey characteristics on the feeding behaviors of an apex marine predator, the California moray (*Gymnothorax mordax*). *Zoology* **122**, 80–89.
- DOMENICI, P. & SEEBACHER, F. (2020). The impacts of climate change on the biomechanics of animals. *Conservation Physiology* **8**, coz102.
- DUDLEY, R. (2002). Mechanisms and implications of animal flight maneuverability. *Integrative and Comparative Biology* **42**, 135–140.
- DUGATKIN, L. A. & GODIN, J.-G. J. (1992). Prey approaching predators: a cost-benefit perspective. *Annales Zoologici Fennici* **29**, 233–252.
- DUKAS, R. & ELLNER, S. (1993). Information processing and prey detection. *Ecology* **74**, 1337–1346.
- DUNCAN, M. C., FORBES, J. C., NGUYEN, Y., SHULL, L. M., GILLETTE, R. K., LAZINSKI, D. W., ALI, A., SHANKS, R. M. Q., KADOURI, D. E. & CAMILLI, A. (2018). *Vibrio cholerae* motility exerts drag force to impede attack by the bacterial predator *Bdellovibrio bacteriovorus*. *Nature Communications* **9**, 4757.
- DYER, A., BROSE, U., BERTI, E., ROSENBAUM, B. & HIRT, M. R. (2023). The travel speeds of large animals are limited by their heat-dissipation capacities. *PLoS Biology* **21**, e3001820.
- EHRLICH, D. E. & SCHOPPIK, D. (2017). Control of movement initiation underlies the development of balance. *Current Biology* **27**, 334–344.
- EIKELBOOM, J. A. J., DE KNEGT, H. J., KLAVER, M., VAN LANGEVELDE, F., VAN DER WAL, T. & PRINS, H. H. T. (2020). Inferring an animal's environment through biologging: quantifying the environmental influence on animal movement. *Movement Ecology* **8**, 40.
- EKLÖF, A., JACOB, U., KOPP, J., BOSCH, J., CASTRO-URRAL, R., CHACOFF, N. P., DALSGAARD, B., DE SASSI, C., GALETTI, M., GUIMARAES, P. R., LOMÁSCOLO, S. B., MARTÍN GONZÁLEZ, A. M., PIZO, M. A., RADER, R., RODRIGO, A., ET AL. (2013). The dimensionality of ecological networks. *Ecology Letters* **16**, 577–583.
- ENGELS, S., SCHNEIDER, N.-L., LEFELDT, N., HEIN, C. M., ZAPKA, M., MICHALIK, A., ELBERS, D., KITTEL, A., HORE, P. J. & MOURITSEN, H. (2014). Anthropogenic electromagnetic noise disrupts magnetic compass orientation in a migratory bird. *Nature* **509**, 353–356.
- ENGLAND, S. J. & ROBERT, D. (2022). The ecology of electricity and electroreception. *Biological Reviews* **97**, 383–413.
- ENGLUND, G., ÖHLUND, G., HEIN, C. L. & DIEHL, S. (2011). Temperature dependence of the functional response. *Ecology Letters* **14**, 914–921.
- FAGAN, W. F., LEWIS, M. A., AUGER-MÉTHÉ, M., AVGAR, T., BENHAMOU, S., BREED, G., LADAGE, L., SCHLÄGEL, U. E., TANG, W., PAPASTAMATIOU, Y. P., FORESTER, J. & MUELLER, T. (2013). Spatial memory and animal movement. *Ecology Letters* **16**, 1316–1329.
- FENTON, M. B. (1990). The foraging behaviour and ecology of animal-eating bats. *Canadian Journal of Zoology* **68**, 411–422.
- FINELLI, C. M., PENTCHEFF, N. D., ZIMMER, R. K. & WETHEY, D. S. (2000). Physical constraints on ecological processes: a field test of odor-mediated foraging. *Ecology* **81**, 784–797.
- FISH, F. E. (2002). Balancing requirements for stability and maneuverability in cetaceans. *Integrative and Comparative Biology* **42**, 85–93.
- FISH, F. E. & DOMENICI, P. (2015). Introduction to the symposium—unsteady aquatic locomotion with respect to eco-design and mechanics. *Integrative and Comparative Biology* **55**, 642–647.
- FLORYAN, D., VAN BUREN, T. & SMITS, A. J. (2018). Efficient cruising for swimming and flying animals is dictated by fluid drag. *Proceedings of the National Academy of Sciences* **115**, 8116–8118.
- FRANKS, P. J. S. (2001). Turbulence avoidance: an alternate explanation of turbulence-enhanced ingestion rates in the field. *Limnology and Oceanography* **46**, 959–963.
- GLASS, T. W., BREED, G. A., LISTON, G. E., REINKING, A. K., ROBARDS, M. D. & KIELLAND, K. (2021). Spatiotemporally variable snow properties drive habitat use of an Arctic mesopredator. *Oecologia* **195**, 887–899.
- GLEISS, A. C., POTVIN, J. & GOLDBOGEN, J. A. (2017). Physical trade-offs shape the evolution of buoyancy control in sharks. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20171345.
- GLEISS, A. C., WILSON, R. P. & SHEPARD, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution* **2**, 23–33.
- GONZAGA, L. E. A., SALOMAO, R. P., MOURA, G. J. B. & LIRA, A. F. A. (2022). Predation strategy of the brown widow spider *Latrodectus geometricus* Koch, 1841 against prey with different defensive mechanisms. *Journal of Ethology* **40**, 159–165.
- GOODWIN, R. A., POLITANO, M., GARVIN, J. W., NESTLER, J. M., HAY, D., ANDERSON, J. J., WEBER, L. J., DIMPERIO, E., SMITH, D. L. & TIMKO, M. (2014). Fish navigation of large dams emerges from their modulation of flow field experience. *Proceedings of the National Academy of Sciences* **111**, 5277–5282.
- GOOSSENS, S., WYBOUW, N., VAN LEEUWEN, T. & BONTE, D. (2020). The physiology of movement. *Movement Ecology* **8**, 1–13.
- GORDON, M. S., BLICKHAN, R., DABIRI, J. O. & VIDELER, J. J. (2017). *Animal Locomotion: Physical Principles and Adaptations*. CRC Press, Boca Raton.
- GRAVEL, D., MASSOL, F., CANARD, E., MOUILLOT, D. & MOUQUET, N. (2011). Trophic theory of Island biogeography. *Ecology Letters* **14**, 1010–1016.
- GRAVEL, D., POISOT, T., ALBOUY, C., VELEZ, L. & MOUILLOT, D. (2013). Inferring food web structure from predator–prey body size relationships. *Methods in Ecology and Evolution* **4**, 1083–1090.
- GRIFFIN, P. C., GRIFFIN, S. C., WAROQUIERS, C. & MILLS, L. S. (2005). Mortality by moonlight: predation risk and the snowshoe hare. *Behavioral Ecology* **16**, 938–944.

- GRIMMER, S., ERNST, M., GÜNTHER, M. & BLICKHAN, R. (2008). Running on uneven ground: leg adjustment to vertical steps and self-stability. *Journal of Experimental Biology* **211**, 2989–3000.
- GRÜNBAUM, D. (1998). Using spatially explicit models to characterize foraging performance in heterogeneous landscapes. *The American Naturalist* **151**, 97–113.
- HAINSWORTH, F. R. & WOLF, L. L. (1972). Crop volume, nectar concentration and hummingbird energetics. *Comparative Biochemistry and Physiology Part A: Physiology* **42**, 359–366.
- HALL, S. R. (2009). Stoichiometrically explicit food webs: feedbacks between resource supply, elemental constraints, and species diversity. *Annual Review of Ecology, Evolution, and Systematics* **40**, 503–528.
- HANDLER, A. & GINTY, D. D. (2021). The mechanosensory neurons of touch and their mechanisms of activation. *Nature Reviews Neuroscience* **22**, 521–537.
- HEISS, E., AERTS, P. & VAN WASSENBERGH, S. (2018). Aquatic–terrestrial transitions of feeding systems in vertebrates: a mechanical perspective. *Journal of Experimental Biology* **221**, jeb154427.
- HEMMI, J. M. & TOMSIC, D. (2012). The neuroethology of escape in crabs: from sensory ecology to neurons and back. *Current Opinion in Neurobiology* **22**, 194–200.
- HIGHAM, T. E. & SCHMITZ, L. (2019). A hierarchical view of gecko locomotion: photic environment, physiological optics, and locomotor performance. *Integrative and Comparative Biology* **59**, 443–455.
- HILL, P. S. M. (2009). How do animals use substrate-borne vibrations as an information source? *Naturwissenschaften* **96**, 1355–1371.
- HIRT, M. R., TUCKER, M., MÜLLER, T., ROSENBAUM, B. & BROSE, U. (2020). Rethinking trophic niches: speed and body mass colimit prey space of mammalian predators. *Ecology and Evolution* **10**, 7094–7105.
- HOLLING, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* **97**, 5–60.
- HOLZMAN, R., COLLAR, D. C., MEHTA, R. S. & WAINWRIGHT, P. C. (2012). An integrative modeling approach to elucidate suction-feeding performance. *Journal of Experimental Biology* **215**, 1–13.
- HOPKINS, C. D. (1999). Electric communication. *The Journal of Experimental Biology* **202**, 1217–1228.
- HOSOI, A. E. & GOLDMAN, D. I. (2015). Beneath our feet: strategies for locomotion in granular media. *Annual Review of Fluid Mechanics* **47**, 431–453.
- HUGHES, R. N., KAISER, M. J., MACKNEY, P. A. & WARBURTON, K. (1992). Optimizing foraging behaviour through learning. *Journal of Fish Biology* **41**, 77–91.
- JELTSCH, F., BONTE, D., PE'ER, G., REINEKING, B., LEIMGRUBER, P., BALKENHOL, N., SCHRÖDER, B., BUCHMANN, C. M., MUELLER, T., BLAUM, N., ZURELL, D., BÖHNING-GAESE, K., WIEGAND, T., ECCARD, J. A., HOFER, H., ET AL. (2013). Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology* **1**, 6.
- JOHNSON, S. & LOHMANN, K. J. (2008). Magnetoreception in animals. *Physics Today* **61**, 29–35.
- JOO, R., PICARDI, S., BOONE, M. E., CLAY, T. A., PATRICK, S. C., ROMERO-ROMERO, V. S. & BASILLE, M. (2020). A decade of movement ecology. *arXiv*. Electronic file available at <http://arxiv.org/abs/2006.00110> Accessed 6.5.2024.
- JUNG, S. (2021). Swimming, flying, and diving behaviors from a unified 2D potential model. *Scientific Reports* **11**, 15984.
- KALMIJN, A. J., GONZALEZ, I. F. & McCLUNE, M. C. (2002). The physical nature of life. *Journal of Physiology-Paris* **96**, 355–362.
- KASHETSKY, T., AVGAR, T. & DUKAS, R. (2021). The cognitive ecology of animal movement: evidence from birds and mammals. *Frontiers in Ecology and Evolution* **9**, 724887.
- KATS, L. B. & DILL, L. M. (1998). The scent of death: chemosensory assessment of predation risk by prey animals. *Écoscience* **5**, 361–394.
- KATTA, S., KRIEG, M. & GOODMAN, M. B. (2015). Feeling force: physical and physiological principles enabling sensory mechanotransduction. *Annual Review of Cell and Developmental Biology* **31**, 347–371.
- KEESEY, I. W., GRABE, V., GRUBER, L., KOERTE, S., OBIERO, G. F., BOLTON, G., KHALLAF, M. A., KUNERT, G., LAVISTA-LLANOS, S., VALENZANO, D. R., RYBAK, J., BARRETT, B. A., KNADEN, M. & HANSSON, B. S. (2019). Inverse resource allocation between vision and olfaction across the genus *Drosophila*. *Nature Communications* **10**, 1162.
- KIØRBOE, T. & SAIZ, E. (1995). Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. *Marine Ecology Progress Series* **122**, 135–145.
- KORTSCH, S., PRIMICERIO, R., ASCHAN, M., LIND, S., DOLGOV, A. V. & PLANQUE, B. (2019). Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography* **42**, 295–308.
- KRAFT, N. J. B., ADLER, P. B., GODOY, O., JAMES, E. C., FULLER, S. & LEVINE, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* **29**, 592–599.
- KRAMER, D. L. & MCLAUGHLIN, R. L. (2001). The behavioral ecology of intermittent locomotion. *American Zoologist* **41**(2), 137–153.
- KÜLTZ, D. (2015). Physiological mechanisms used by fish to cope with salinity stress. *Journal of Experimental Biology* **218**, 1907–1914.
- LANG, B., EHRES, R. B., BROSE, U. & RALL, B. C. (2017). Temperature and consumer type dependencies of energy flows in natural communities. *Oikos* **126**, 1717–1725.
- LAROM, D., GARSTANG, M., PAYNE, K., RASPE, R. & LINDEQUE, M. (1997). The influence of surface atmospheric conditions on the range and area reached by animal vocalizations. *The Journal of Experimental Biology* **200**, 421–431.
- LI, C., ZHANG, T. & GOLDMAN, D. I. (2013). A terradynamics of legged locomotion on granular media. *Science* **339**, 1408–1412.
- LIAO, J. C. (2007). A review of fish swimming mechanics and behaviour in altered flows. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362**, 1973–1993.
- LINDMARK, M., OHLBERGER, J. & GÄRDMARK, A. (2022). Optimum growth temperature declines with body size within fish species. *Global Change Biology* **28**, 2259–2271.
- LOK, T., VAN DER GEEST, M., BOM, R. A., DE GOEIJ, P., PIERSMA, T. & BOUTEN, W. (2023). Prey ingestion rates revealed by back-mounted accelerometers in Eurasian spoonbills. *Animal Biotelemetry* **11**, 5.
- LUKAS, J., ROMANCZUK, P., KLENZ, H., KLAMSER, P., ARIAS RODRIGUEZ, L., KRAUSE, J. & BIERBACH, D. (2021). Acoustic and visual stimuli combined promote stronger responses to aerial predation in fish. *Behavioral Ecology* **32**, 1094–1102.
- LUNA, F. & ANTINUCHI, C. D. (2006). Cost of foraging in the subterranean rodent *Ctenomys talarum*: effect of soil hardness. *Canadian Journal of Zoology* **84**, 661–667.
- MACIVER, M. A., SHARABASH, N. M. & NELSON, M. E. (2001). Prey-capture behavior in electric fish. *The Journal of Experimental Biology* **204**, 543–557.
- MALADEN, R. D., DING, Y., UMBANHOWAR, P. B., KAMOR, A. & GOLDMAN, D. I. (2011). Mechanical models of sandfish locomotion reveal principles of high performance subsurface sand-swimming. *Journal of the Royal Society Interface* **8**, 1332–1345.
- MALISHEV, M., BULL, C. M. & KEARNEY, M. R. (2018). An individual-based model of ectotherm movement integrating metabolic and microclimatic constraints. *Methods in Ecology and Evolution* **9**, 472–489.
- MARTIN, B. T., GIL, M. A., FAHIMIPOUR, A. K. & HEIN, A. M. (2022). Informational constraints on predator–prey interactions. *Oikos* **2022**, e08143.
- MASSION, J. (1992). Movement, posture and equilibrium: interaction and coordination. *Progress in Neurobiology* **38**, 35–56.
- MASSION, J., ALEXANDROV, A. & FROLOV, A. (2004). Why and how are posture and movement coordinated? In *Progress in Brain Research*, pp. 13–27. Elsevier, Amsterdam.
- MATTISSON, J., RAUSET, G. R., ODDEN, J., ANDRÉN, H., LINNELL, J. D. C. & PERSSON, J. (2016). Predation or scavenging? Prey body condition influences decision-making in a facultative predator, the wolverine. *Ecosphere* **7**, e01407.
- MCCORMICK, S. D., HANSEN, L. P., QUINN, T. P. & SAUNDERS, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 77–92.
- McKENNA, M. F. (2020). The sounds around us. *Physics Today* **73**(1), 28–34.
- MITCHELL, W. A. (1989). Informational constraints on optimally foraging hummingbirds. *Oikos* **55**, 145.
- MOLLOY, P. J. & COWLING, M. J. (1999). Buoyancy mechanisms of marine organisms: lessons from nature. *Underwater Technology* **24**, 41–49.
- MONTOYA, J. M., PIMM, S. L. & SOLE, R. V. (2006). Ecological networks and their fragility. *Nature* **442**, 259–264.
- MUNOZ, N. E. & BLUMSTEIN, D. T. (2012). Multisensory perception in uncertain environments. *Behavioral Ecology* **23**, 457–462.
- NATHAN, R., GETZ, W. M., REVILLA, E., HOLYOAK, M., KADMON, R., SALTZ, D. & SMOUSE, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052–19059.
- NEDELEC, S. L., CAMPBELL, J., RADFORD, A. N., SIMPSON, S. D. & MERCHANT, N. D. (2016). Particle motion: the missing link in underwater acoustic ecology. *Methods in Ecology and Evolution* **7**, 836–842.
- NEWTON, K. C., KACEV, D., NILSSON, S. R. O., SAETTELE, A. L., GOLDEN, S. A. & SHEETS, L. (2023). Lateral line ablation by ototoxic compounds results in distinct rheotaxis profiles in larval zebrafish. *Communications Biology* **6**, 84.
- NORDMANN, G. C., HOCHSTOEGER, T. & KEAYS, D. A. (2017). Magnetoreception—a sense without a receptor. *PLoS Biology* **15**, e2003234.
- OKAMOTO, S., NAGANO, H. & YAMADA, Y. (2013). Psychophysical dimensions of tactile perception of textures. *IEEE Transactions on Haptics* **6**, 81–93.
- PARSONS, M. H., APFELBACH, R., BANKS, P. B., CAMERON, E. Z., DICKMAN, C. R., FRANK, A. S. K., JONES, M. E., MCGREGOR, I. S., McLEAN, S., MÜLLER-SCHWARZE, D., SPARROW, E. E. & BLUMSTEIN, D. T. (2018). Biologically meaningful scents: a framework for understanding predator-prey research across disciplines: multidisciplinary framework for olfaction studies. *Biological Reviews* **93**, 98–114.
- PAWAR, S., DELL, A. I., LIN, T., WIECZYNSKI, D. J. & SAVAGE, V. M. (2019). Interaction dimensionality scales up to generate bimodal consumer-resource size-ratio distributions in ecological communities. *Frontiers in Ecology and Evolution* **7**, 202.

- PAWAR, S., DELL, A. I. & SAVAGE, V. M. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature* **486**, 485–489.
- PAYNE, N. L., TAYLOR, M. D., WATANABE, Y. Y. & SEMMENS, J. M. (2014). From physiology to physics: are we recognizing the flexibility of biologging tools? *Journal of Experimental Biology* **217**, 317–322.
- PERSSON, B. N. J. (2007). Biological adhesion for locomotion on rough surfaces: basic principles and a theorist's view. *MRS Bulletin* **32**, 486–490.
- PETCHEY, O. L., BECKERMAN, A. P., RIEDE, J. O. & WARREN, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences* **105**, 4191–4196.
- PETREN, K. & CASE, T. J. (1998). Habitat structure determines competition intensity and invasion success in gecko lizards. *Proceedings of the National Academy of Sciences* **95**, 11739–11744.
- PETTIGREW, J. B. (1873). *Animal Locomotion or Walking, Swimming, and Flying, with a Dissertation on Aeronautics*. HS King & Company, London.
- POKROVSKY, I., KÖLZSCH, A., SHERUB, S., FIEDLER, W., GLAZOV, P., KULIKOVA, O., WIKELSKI, M. & FLACK, A. (2021). Longer days enable higher diurnal activity for migratory birds. *Journal of Animal Ecology* **90**, 2161–2171.
- PORTALIER, S. M. J., FUSSMANN, G. F., LOREAU, M. & CHERIF, M. (2019). The mechanics of predator–prey interactions: first principles of physics predict predator–prey size ratios. *Functional Ecology* **33**, 323–334.
- PORTALIER, S. M. J., FUSSMANN, G. F., LOREAU, M. & CHERIF, M. (2022). Inferring size-based functional responses from the physical properties of the medium. *Frontiers in Ecology and Evolution* **9**, 761984.
- POTAPOV, A. M., BROSE, U., SCHEU, S. & TIUNOV, A. V. (2019). Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *The American Naturalist* **194**, 823–839.
- PROKKOLA, J. M. & NIKINMAA, M. (2018). Circadian rhythms and environmental disturbances – underexplored interactions. *Journal of Experimental Biology* **221**, jeb179267.
- RANÄKER, L., PERSSON, J., JÖNSSON, M., NILSSON, P. A. & BRÖNMARK, C. (2014). Piscivore–prey Fish interactions: mechanisms behind diurnal patterns in prey selectivity in Brown and Clear water. *PLoS One* **9**, e102002.
- RANC, N., MOORCROFT, P. R., OSSI, F. & CAGNACCI, F. (2021). Experimental evidence of memory-based foraging decisions in a large wild mammal. *Proceedings of the National Academy of Sciences* **118**, e2014856118.
- RAVI, S., CRALL, J. D., MCNEILLY, L., GAGLIARDI, S. F., BIEWENER, A. A. & COMBES, S. A. (2015). Hummingbird flight stability and control in freestream turbulent winds. *Journal of Experimental Biology* **218**, 1444–1452.
- RENNER, S. S. & ZOHNER, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics* **49**, 165–182.
- ROSSBERG, A. G., MATSUDA, H., AMEMIYA, T. & ITOH, K. (2006). Food webs: experts consuming families of experts. *Journal of Theoretical Biology* **241**, 552–563.
- RUSSO, D. & JONES, G. (2003). Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography* **26**, 197–209.
- SALINAS, R. V. B., HERRERA, M. L. G., FLORES-MARTÍNEZ, J. J. & JOHNSTON, D. S. (2014). Winter and summer torpor in a free-ranging subtropical desert bat: the fishing myotis (*Myotis vivesi*). *Acta Chiroptologica* **16**, 327–336.
- SALVANES, A. G. V., AKSNES, D. L. & GISKE, J. (1995). A surface-dependent gastric evacuation model for fish. *Journal of Fish Biology* **47**, 679–695.
- SAMIA, D. S. M., MÖLLER, A. P. & BLUMSTEIN, D. T. (2015). Brain size as a driver of avian escape strategy. *Scientific Reports* **5**, 11913.
- SANTOS-MORENO, A., RUIZ VELÁSQUEZ, E. & SÁNCHEZ MARTÍNEZ, A. (2010). Efecto de la intensidad de la luz lunar y de la velocidad del viento en la actividad de murciélagos filostómidos de Mena Nizanda, Oaxaca, México. *Revista Mexicana de Biodiversidad* **81**, 839–845.
- SATHYAMOORTHY, R., MAOZ, A., PASTERNAK, Z., IM, H., HUPPERT, A., KADOURI, D. & JURKEVITCH, E. (2019). Bacterial predation under changing viscosities. *Environmental Microbiology* **21**, 2997–3010.
- SAVAGE, V. M., GILLOOLY, J. F., BROWN, J. H., WEST, G. B. & CHARNOV, E. L. (2004). Effects of body size and temperature on population growth. *The American Naturalist* **163**, 429–441.
- SCHINDLER, D. E. & EBV, L. A. (1997). Stoichiometry of fishes and their prey: implications for nutrient recycling. *Ecology* **78**, 1816–1831.
- SCHNEIDER, F. D., SCHEU, S. & BROSE, U. (2012). Body mass constraints on feeding rates determine the consequences of predator loss: allometric predator effects. *Ecology Letters* **15**, 436–443.
- SCHNITZLER, H.-U., KALKO, E. K. V., KAIPF, I. & GRINNELL, A. D. (1994). Fishing and echolocation behavior of the greater bulldog bat, *Noctilio leporinus*, in the field. *Behavioral Ecology and Sociobiology* **35**, 327–345.
- SENTIS, A., HAEGEMAN, B. & MONTÓYA, J. M. (2021). Stoichiometric constraints modulate temperature and nutrient effects on biomass distribution and community stability. *Oikos* **2022**, e08601.
- SHEPARD, E. L. C., WILSON, R. P., REES, W. G., GRUNDY, E., LAMBERTUCCI, S. A. & VOSPER, S. B. (2013). Energy landscapes shape animal movement ecology. *The American Naturalist* **182**, 298–312.
- SHIELD, S., JERICEVICH, R., PATEL, A. & JUSUFI, A. (2021). Tails, flails, and sails: how appendages improve terrestrial maneuverability by improving stability. *Integrative and Comparative Biology* **61**, 506–520.
- SIEGAL, E., HOOKER, S. K., ISOJUNNO, S. & MILLER, P. J. O. (2022). Beaked whales and state-dependent decision-making: how does body condition affect the trade-off between foraging and predator avoidance? *Proceedings of the Royal Society B: Biological Sciences* **289**, 20212539.
- SIEMERS, B. M. & STILZ, P. (2001). The acoustic advantage of hunting above water. *The Journal of Experimental Biology* **204**, 3843–3854.
- SORAVIA, C., ASHTON, B. J., THORNTON, A. & RIDLEY, A. R. (2023). High temperatures are associated with reduced cognitive performance in wild southern pied babblers. *Proceedings of the Royal Society B: Biological Sciences* **290**, 20231077.
- STAYTON, C. T. (2011). Terrestrial feeding in aquatic turtles: environment-dependent feeding behavior modulation and the evolution of terrestrial feeding in Emydidae. *Journal of Experimental Biology* **214**, 4083–4091.
- STIER, A. C., SAMHOURI, J. F., GRAY, S., MARTONE, R. G., MACH, M. E., HALPERN, B. S., KAPPEL, C. V., SCARBOROUGH, C. & LEVIN, P. S. (2017). Integrating expert perceptions into food web conservation and management: expert opinion and ecosystem management. *Conservation Letters* **10**, 67–76.
- SUTTON, J. A. (2019). The iso-osmo-resistivity theory of digestion. *Medical Hypotheses* **130**, 109282.
- THIERRY, A., PETCHEY, O. L., BECKERMAN, A. P., WARREN, P. H. & WILLIAMS, R. J. (2011). The consequences of size dependent foraging for food web topology. *Oikos* **120**, 493–502.
- THOMAS, A. A. G., LUDLOW, A. R. & KENNEDY, J. S. (1977). Sinking speeds of falling and flying *Aphis fabae* Scopoli. *Ecological Entomology* **2**, 315–326.
- TONELLI, B. A., YOUNGFLESH, C. & TINGLEY, M. W. (2023). Geomagnetic disturbance associated with increased vagrancy in migratory landbirds. *Scientific Reports* **13**, 414.
- USHIO, M., HSIEH, C., MASUDA, R., DEYLE, E. R., YE, H., CHANG, C.-W., SUGIHARA, G. & KONDOH, M. (2018). Fluctuating interaction network and time-varying stability of a natural fish community. *Nature* **554**, 360–363.
- USZKO, W., DIEHL, S., ENGLUND, G. & AMARASEKARE, P. (2017). Effects of warming on predator–prey interactions – a resource-based approach and a theoretical synthesis. *Ecology Letters* **20**, 513–523.
- VAN SOMEREN, E. J. (2003). Thermosensitivity of the circadian timing system. *Sleep and Biological Rhythms* **1**, 55–64.
- VARGA, A. G., KATHMAN, N. D., MARTIN, J. P., GUO, P. & RITZMANN, R. E. (2017). Spatial navigation and the central complex: sensory acquisition, orientation, and motor control. *Frontiers in Behavioral Neuroscience* **11**, 4.
- VOGEL, S. (1988). *Life's Devices: The Physical World of Animals and Plants*. Princeton University Press, Princeton.
- VOGEL, S. (2000). *Cats' Paws and Catapults: Mechanical Worlds of Nature and People*. WW Norton & Company, New York, NY.
- VOGEL, S. (2013). *Comparative Biomechanics: life's Physical World*. Princeton University Press, Princeton, NJ.
- VOGEL, S. (2020). *Life in Moving Fluids: The Physical Biology of Flow-Revised and Expanded*, second Edition. Princeton University Press, Princeton, NJ.
- VOIGT, C. C., SÖRGE, K. & DECHMANN, D. K. N. (2010). Refueling while flying: foraging bats combust food rapidly and directly to power flight. *Ecology* **91**, 2908–2917.
- VON DER EMDE, G. (1993). The sensing of electrical capacitances by weakly electric mormyrid fish: effects of water conductivity. *Journal of Experimental Biology* **181**, 157–173.
- VUCIC-PESTIC, O., EHNE, R. B., RALL, B. C. & BROSE, U. (2011). Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Global Change Biology* **17**, 1301–1310.
- WATANABE, Y. Y. & PAPANASTATI, Y. P. (2023). Biologging and biotelemetry: tools for understanding the lives and environments of marine animals. *Annual Review of Animal Biosciences* **11**, 247–267.
- WEBB, P. W. (2002). Control of posture, depth, and swimming trajectories of fishes. *Integrative and Comparative Biology* **42**, 94–101.
- WEBB, P. W. & WEIHS, D. (1994). Hydrostatic stability of fish with swim bladders: not all fish are unstable. *Canadian Journal of Zoology* **72**, 1149–1154.
- WEBB, P. W. & WEIHS, D. (2015). Stability versus maneuvering: challenges for stability during swimming by fishes. *Integrative and Comparative Biology* **55**, 753–764.
- WEIHS, D. (2002). Stability versus maneuverability in aquatic locomotion. *Integrative and Comparative Biology* **42**, 127–134.
- WEIL, J., TRUDEL, M., TUCKER, S., BRODEUR, R. D. & JUANES, F. (2019). Percent ash-free dry weight as a robust method to estimate energy density across taxa. *Ecology and Evolution* **9**, 13244–13254.
- WELCH, K. C. JR., OTÁLORA-ÁRDILA, A., HERRERA, M. L. G. & FLORES-MARTÍNEZ, J. J. (2015). The cost of digestion in the fish-eating myotis (*Myotis vivesi*). *Journal of Experimental Biology* **218**, 1180–1187.
- WHITEHEAD, D. & COLLIN, S. (2004). The functional roles of passive electroreception in non-electric fishes. *Animal Biology* **54**, 1–25.

- WIJERS, M., TRETOWAN, P., DU PREEZ, B., LOVERIDGE, A. J., MARKHAM, A., MACDONALD, D. W. & MONTGOMERY, R. A. (2022). Something in the wind: the influence of wind speed and direction on African lion movement behavior. *Behavioral Ecology* **33**, 1180–1187.
- WILSON, R. P., ROSE, K. A. R., METCALFE, R. S., HOLTON, M. D., REDCLIFFE, J., GUNNER, R., BÖRGER, L., LOISON, A., JEZEK, M., PAINTER, M. S., SILOVSKÝ, V., MARKS, N., GAREL, M., TOÏGO, C., MARCHAND, P., *ET AL.* (2021). Path tortuosity changes the transport cost paradigm in terrestrial animals. *Ecography* **44**, 1524–1532.
- WILSON, R. S., HUSAK, J. F., HALSEY, L. G. & CLEMENTE, C. J. (2015). Predicting the movement speeds of animals in natural environments. *Integrative and Comparative Biology* **55**, 1125–1141.
- WILTSCHKO, W. & WILTSCHKO, R. (2005). Magnetic orientation and magnetoreception in birds and other animals. *Journal of Comparative Physiology A* **191**, 675–693.
- WOOTTON, K. L., CURTSDOTTER, A., ROSLIN, T., BOMMARCO, R. & JONSSON, T. (2023). Towards a modular theory of trophic interactions. *Functional Ecology* **37**, 26–43.
- WOOTTON, K. L. & STOFFER, D. B. (2016). Species' traits and food-web complexity interactively affect a food web's response to press disturbance. *Ecosphere* **7**, e01518.
- WUENSCHER, M. J., JUGOVICH, A. R. & HARE, J. A. (2006). Estimating the energy density of fish: the importance of ontogeny. *Transactions of the American Fisheries Society* **135**, 379–385.
- XUE, X., ALI, Y. F., LUO, W., LIU, C., ZHOU, G. & LIU, N.-A. (2021). Biological effects of space hypomagnetic environment on circadian rhythm. *Frontiers in Physiology* **12**, 643943.
- YODZIS, P. & INNES, S. (1992). Body size and consumer-resource dynamics. *The American Naturalist* **139**, 1151–1175.
- YU, Y. S. W., GRAFF, M. M., BRESEE, C. S., MAN, Y. B. & HARTMANN, M. J. Z. (2016). Whiskers aid anemotaxis in rats. *Science Advances* **2**, e1600716.
- ZHANG, X., NAUGHTON, N., PARTHASARATHY, T. & GAZZOLA, M. (2021). Friction modulation in limbless, three-dimensional gaits and heterogeneous terrains. *Nature Communications* **12**, 6076.
- ZHENG, W., NIKOLAEV, Y. A., GRACHEVA, E. O. & BAGRIANTSEV, S. N. (2019). Piezo2 integrates mechanical and thermal cues in vertebrate mechanoreceptors. *Proceedings of the National Academy of Sciences* **116**, 17547–17555.
- ZHOU, Y. (2021). Turbulence theories and statistical closure approaches. *Physics Reports* **935**, 1–117.

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