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COMMENTARY

Bridging the divide in organismal physiology: a case for the integration of behaviour as a physiological process

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ABSTRACT

The role of behaviour in animal physiology is much debated, with researchers divided between the traditional view that separates physiology and behaviour, and a progressive perspective that sees behaviour as a physiological effector. We advocate for the latter, and in this Commentary, we argue that behaviour is inherently a physiological process. To do so, we outline the physiological basis for behaviour and draw parallels with recognised physiological processes. We also emphasise the importance of precise language that is shared across biological disciplines, as clear communication is foundational in integrating behaviour into physiology. Our goal with this Commentary is to set the stage for a debate and persuade readers of the merits of including behaviour within the domain of animal physiology. We argue that recognising behaviour as a physiological process is crucial for advancing a unified understanding of physiology, especially in the context of anthropogenic impacts.

KEY WORDS: Behavioural physiology, Integrative biology, Motivational state, Physiological mechanism

Introduction

All living organisms are the product of a long series of evolutionary changes that have allowed each species to persist on Earth. The resulting adaptations have evolved in response to specific conditions, becoming fine-tuned as the organism develops specialisation to its environment (Dawson et al., 1977). To meet the demands of survival, a close relationship between form and function – studied in the fields of anatomy and physiology, respectively – is required. The field of physiology, grounded in physics and chemistry, poses a universal question in science: 'how does it work?'. Occurring alongside and as a product of sets of context-dependent physiological reactions is behaviour. In the complex framework of physiological processes, behaviour serves as a pivotal element, linking an organism's internal functioning with its external environment. However, the field of animal physiology is currently divided on how to conceptualise the relationship of behaviour to physiology. Traditionally, these two aspects have been viewed as separate entities (e.g. Reese, 1996). Nevertheless, an emerging viewpoint supports the notion of behaviour as an inherent physiological effector, seamlessly integrated into the spectrum of physiological responses – a perspective we seek to clarify and advocate for in this Commentary.

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Our intention in this Commentary is not to critique differing perspectives but to stimulate discussion on integrating behaviour into the field of animal physiology. This Commentary cannot do justice to the vastly diverse subdisciplines within physiology or provide an exhaustive taxonomic overview. Instead, our goal is to engage students of physiology with the physiology–behaviour discussion. Note, also, that we are not advocating for the reduction of behaviour to its underlying physiological mechanisms (Reese, 1996); rather, we propose that behaviour should be considered alongside the myriad of other physiological processes that an animal may exhibit, thereby underscoring its inherent physiological nature. As such, the central thesis of this Commentary is that the conceptual and methodological integration of behaviour into animal physiology will allow for a more cohesive and meaningful understanding of organismal functioning, in both fundamental and applied research. A fuller realisation of this alignment would simultaneously provide and link mechanistic and functional data on the myriad internally coordinated (re)actions that organisms express in response to their environments. Indeed, the combination of traditional measures and incorporation of behavioural assays into physiological research and experimental designs already occurs quite widely, although, there is room to improve this integration and the integration itself comes with potential problems. Yet, a conceptual divide persists, hampering the productive integration of behaviour into our understanding of physiology.

In the following sections we will: (1) discuss the use of the phrase 'physiology and behaviour' (i.e. as two separate entities); (2) outline why behaviour must be fundamentally physiological in nature, from a mechanistic and motivational perspective; (3) advocate for behaviour as an integral physiological process; (4) address some of the practical and conceptual challenges with integrating behaviour into physiology; and (5) discuss why a unified approach to physiology will become increasingly more important in this era of global change.

A history of 'physiology and behaviour'

> *Biology is a continuum, but we biologists, because of our limitations, divide ourselves into categories, and then we pretend that those categories exist in the living systems that we study.*
>
> Bartholomew (1958)

George Bartholomew's reflection on the inseparability of behaviour from physiology offers insightful reasoning for the conventional use of physiology and behaviour as two separate fields of study. Historically, behavioural biologists have pursued psychological explanations for behaviour, whereas early physiologists primarily focused on the internal functioning of the body, often driven by medical curiosity. One 20th-century biologist who seemingly overcame these 'limitations' was Konrad Lorenz, considered by many to be the father of the modern study of animal behaviour. A Doctor of Medicine turned behavioural zoologist, Lorenz became

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Glossary

Cuticular lipids
The thin surface layer of lipids that protects the insect cuticle from desiccation.

Electro-osmosis
The movement of water against its chemical potential under the influence of an electric field.

Insect trachea
The tubular respiratory system of insects, which allows for gas exchange between tissues and the external environment.

Malpighian tubules
The osmoregulatory system of insects.

Nonapeptides
Nine-amino-acid neuroendocrine modulators of social behaviours (among other complex behaviours) expressed in the preoptic area and hypothalamus.

Reductionism
The idea that knowledge of one scientific discipline (typically concerning higher-level processes) can be described in terms of another more fundamental discipline (typically concerning lower-level processes).

Reflex arcs
Neural pathways consisting of a limited number of neurons that control reflexes.

Systems physiology
The physiological study concerned with the regulation and maintenance of homeostasis at the level of tissues and organ systems. (Note that systems physiology is different from systems biology, which refers to the computational and mathematical modelling of complex biological systems.)

a pioneer in advocating for a physiological view of behaviour and was among the first biologists to recognise that behavioural patterns are governed by centrally coordinated, endogenously produced impulses, much like other physiological processes (Brigandt, 2005; Lorenz, 1981).

Since Lorenz's pioneering causal approach to understanding behaviour, physiologists have begun to recognise the interactions between behaviour and other physiological responses, and our comprehension of behaviour's physiological underpinnings has grown immensely. Yet, the use of the term 'physiology and behaviour' (i.e. as a phrase indicating that the two are thought of as separate disciplines) has remained commonplace in scientific literature. Recent years have seen an increasing trend towards integrative physiological publications (i.e. publications that span the levels of biological organisation and complement investigation of behavioural traits with that of their underlying mechanisms). Indeed, in the last decade (2014–2023), *Journal of Experimental Biology* has published 461 articles that discuss behaviour alongside physiology (WoS search criteria: *physiolog* AND behavio**), compared with an equal number of articles published throughout the preceding 50 years together (2004–2013, *n*=300; 1994–2003, *n*=127; 1984–1993, *n*=38; 1974–1983, *n*=10; 1964–1973, *n*=7). Nonetheless, these numbers also highlight a persistent trend in treating physiology and behaviour as separate entities, even within studies that aim to integrate them, underscoring the enduring challenge of bridging these conceptual divides.

Why behaviour is inherently physiological

To argue for behaviour as a physiological effector, we must first define physiology. At its core, physiology is the study of how an organism functions, encompassing the close relationship and interactions between numerous mechanisms and processes that operate in living organisms, including metabolism, nutrient fluxes, regulation and performance, for example. These physiological functions span from a molecular and cellular basis up to the whole-organism level, integrating complex interactions (Randall et al., 2001). The unifying concept in physiological theory is that an organism must respond to challenges in its environment in order to thrive (i.e. survive and maximise reproductive output). This response necessitates coordinated interactions between the nervous and endocrine systems to signal and generate changes in the appropriate effector systems. Although a detailed discussion of the communication between cells and the transmission of information throughout the body is beyond the scope of this Commentary, we direct readers seeking a detailed synthesis to Randall et al. (2001) or Hill et al. (2021).

Expanding on our definition of physiology, the difference between the terms 'physiological mechanism' and 'physiological process', which are often used incorrectly and interchangeably, must be clearly defined. This distinction in terminology is particularly important to understand our case for behaviour as a physiological effector. 'Physiological mechanisms' are the underlying aggregation of physicochemical events that allow a desired response to occur (i.e. based on the action of physical and chemical laws), whereas 'physiological processes' consist of the coordinated actions and interactions of cells, tissues and organs that are necessary to achieve that response (i.e. bodily functions, the regulatory effectors) (after Randall et al., 2001; Fig. 1). For example, energy metabolism – the physical and chemical reactions that occur throughout the body to generate energy – refers to a cluster of physiological mechanisms rather than a physiological process, per se. In fact, energy metabolism comprises the elementary physiological mechanisms required to sustain life, and these energy transformations are therefore necessarily involved in all physiological processes.

The incorrect use of these two terms probably fuels the debate over classifying behaviour as a physiological process. If one ignores this distinction and considers such mechanisms (e.g. energy metabolism) as physiological processes, it may appear as though behaviour is a response to these physiological 'processes', rather than a physiological process in itself. A physiological process is, after all, always driven by underlying mechanisms, and although it can and often will affect other processes, these interactions will always occur through intermediary mechanisms (Fig. 1). A good example of the failure to distinguish between these two terms can be

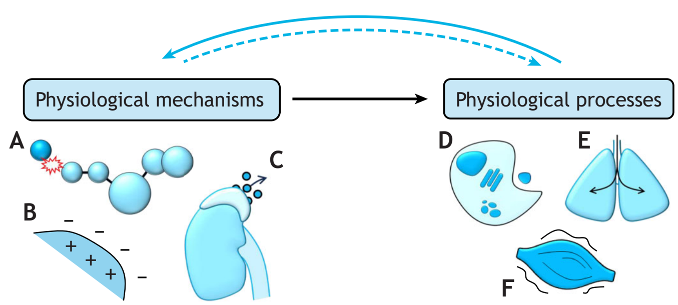

Fig. 1. Physiological mechanisms and processes. Physiological mechanisms are the underlying aggregation of physicochemical events that allow a desired response to occur (e.g. A, energy metabolism; B, membrane potentials; C, hormone signalling). Physiological processes consist of the coordinated actions and interactions of cells, tissues and organs that are necessary to achieve that response (e.g. D, immune response; E, respiration; F, behaviour). Physiological processes are driven by their underlying mechanisms (black arrow) but can and will often affect or interact with other processes through intermediary mechanisms (blue arrows).

found in efforts to address Niko Tinbergen's four problems of behaviour (i.e. causation, survival value, ontogeny and evolution; Tinbergen, 1963; discussed in more detail below). To approach one of the core problems, causation, researchers will aim to find proximate explanations – immediate mechanistic reasons – for the expression of a certain behaviour (i.e. what causes an animal to perform the behaviour?). 'Physiology' is then often cited as an important proximate mechanism underpinning the behaviour. Although physiological mechanisms can translate into behavioural responses (processes), it would be an incorrect assertion that physiology as a whole (i.e. both mechanisms and processes) causes behaviour – because behaviour is fundamentally physiological, as we will go on to argue.

Historically, physiological processes have been considered to include only effector systems that elicit internal body changes (e.g. changes in respiration, circulation, digestion). In this 'stationary animal' model of physiology, it would seem that all organs except the musculoskeletal system may change their functions in response to a challenging environment. For example, in response to a challenging temperature, an animal may regulate blood flow. In reality, however, external body changes (i.e. functional changes in the musculoskeletal system and, hence, behaviour) are fundamental effectors in maintaining homeostasis (e.g. an animal may choose to avoid certain temperature regimes). In the example of thermoregulation, this is especially true for ectotherms that rely heavily on behavioural thermoregulation as a result of their limited internal heat-production capabilities. A 'moving animal' model, therefore, offers a much more comprehensive and accurate representation of the regulation of internal conditions, recognising behaviour as a fundamental effector. Indeed, behavioural thermoregulation, in our example, is already appreciated as a core component of thermoregulation. Similarly, behaviour is recognised as an important effector in osmoregulation (discussed in more detail below) as well as in the stress response (behavioural stress coping styles). In the following two sections, we will expand on this 'moving animal' model, providing information on the mechanisms and motivations underlying behaviour to illustrate that it is an inherently physiological process.

Mechanisms behind behaviour (and other physiological processes)

Behaviour is ultimately generated by spatial and temporal patterns of musculoskeletal activity, and it is tightly regulated by neural pathways, like other physiological processes. Skeletal muscles are innervated by motor neurons, and effective movement is achieved by the controlled timing and strength of muscle contractions. The neural circuits that produce behavioural actions can be simple, yet important, reflex arcs (see Glossary; e.g. C-start/S-start behaviours in fish) or complex circuits involving the interactions of multiple neurons. To produce a desired behavioural act, these neural circuits typically engage in a sequence that includes (1) sensory input reception, (2) central processing and (3) motor output generation.

This pathway is well described in thermal physiology. For example, Antarctic penguins employ strategies such as vasoconstriction, shivering and social huddling to avoid hypothermia (Fig. 2). Under conditions of extreme cold, cutaneous thermoreceptors activate thermo-transient receptor potentials – a family of ion channels – that stimulate the thermoregulatory centre in the preoptic area and anterior hypothalamus (PO/AH) to initiate thermoregulatory mechanisms. Through a descending pathway, the PO/AH transmits information to the intermediolateral nucleus in the lateral grey column and to the anterior grey column that then activate sympathetic neurons or

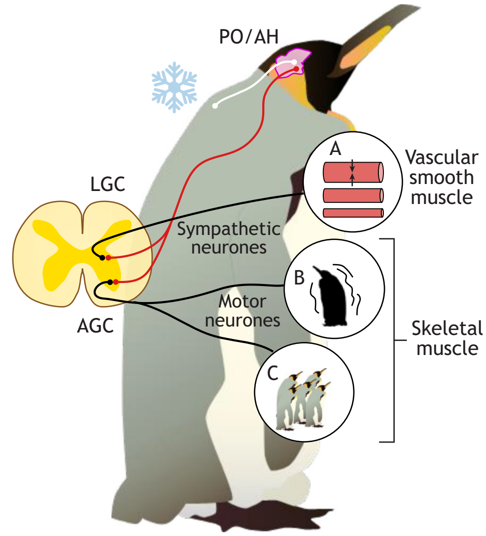

Fig. 2. Mechanisms underpinning thermoregulation in Antarctic penguins. The figure shows three physiological actions/strategies to conserve or produce heat in response to cold temperatures: (A) vasoconstriction (an insulative physiological response), (B) shivering (a metabolic physiological response) and (C) social huddling (a behavioural physiological response). AGC, anterior grey column; LGC, lateral grey column; PO/AH, preoptic area and anterior hypothalamus.

motor neurons, respectively, to mediate an appropriate response (Bohler et al., 2021; Ruuskanen et al., 2021). In Antarctic penguins, the most prominent effector systems to combat cold conditions include vascular smooth muscle and skeletal muscle. Vascular smooth muscle, innervated by sympathetic nerve fibres, can decrease peripheral blood flow through cutaneous vasoconstriction, mediated by noradrenaline release, to conserve heat (an insulative physiological process). In addition, skeletal muscles, stimulated by motor neurons, initiate shivering through rapid, repetitive contractions that are triggered by acetylcholine release at synapses to generate heat (a metabolic physiological process). In addition to these responses, skeletal muscle contractions will also modulate social huddling, influenced by central nonapeptide circuits (see Glossary) in the PO/AH, as an essential way to conserve heat (a behavioural physiological process) (Ancel et al., 1997; Gilbert et al., 2006; Goodson and Thompson, 2010; Kelly and Vitousek, 2017). This example illustrates the analogous neuroendocrine patterns involved in vasoconstriction and shivering – two well-established physiological processes in thermoregulation – and the social huddling behaviour in response to cold exposure. In all of these responses, a stimulus (cold ambient temperatures) triggers receptors (thermoreceptors) that signal a modulator (the thermoregulatory centre in the hypothalamus) that then transmits information to the effector (vascular smooth or skeletal muscle) to elicit a coordinated response.

So far, we have considered how an organism makes decisions influenced by a purely abiotic environment. In reality, however, interactions between individuals (i.e. the social environment) will often play an important role in this decision-making process: decisions that are motivated but not necessarily entirely driven by physiological changes. Indeed, behaviour is influenced by a wide array of factors, including cognitive processes, social interactions and environmental variables, and although our aim in this Commentary is to highlight the physiological nature of behaviour, we acknowledge that the complexity and multidimensionality of behaviour cannot be entirely explained by its physiological underpinnings alone. For example, although social behaviours have a physiological basis that may either enhance or constrain social interactions (Seebacher and Krause, 2017), an animal's decision to interact with others will also be determined by sentient thoughts (Brown, 2015) – such as avoidance of certain individuals because of agonistic interactions – and influenced by its motivational state. The latter is discussed in more detail in the following section.

Motivation behind behaviour (and other physiological processes)

Behavioural responses are elicited by an animal's physiological status in response to challenges in its internal or external environment. Sensory inputs to the nervous systems will evoke changes in the animal's motivational state, influencing its behaviour (Broom, 1981; McFarland and Sibly, 1975; Toates, 2002). To put 'motivational state' into context, consider an individual positioned in multi-dimensional space, where each dimension represents a behaviour (Fig. 3). By mapping the intensity of these behaviours based on their necessity for maintaining homeostasis (assuming that they are all of equal importance for maintenance), we can identify the animal's current motivational state and predict which behaviour it will prioritise. Over time, the intensities of these dimensions will change, as will the motivational state of the animal, guiding it toward the behaviour most critical at any given moment. This trade-off framework can be similarly applied to other physiological processes.

Consider the maintenance of water balance in the honeybee as an illustrative example (Fig. 4). When a honeybee's water balance approaches critical levels, it employs a suite of physiological actions/strategies to conserve and acquire water, driven by a motivational state to avoid osmotic stress. Terrestrial insects mainly lose water through (1) respiration via the trachea (see Glossary) and spiracles (Woods and Smith, 2010), (2) transpiration via the cuticle, which is particularly important at elevated ambient temperatures when cuticular lipids (see Glossary) begin to melt and lose their waterproofing function (Gibbs, 1998, 2002), and (3) excretion in the form of urine and faeces (O'Donnell, 2022). The honeybee can use a number of conservation strategies to prevent this water loss. Firstly, a honeybee can minimise respiratory water loss through its tracheal system by periodically closing the trachea through centrally coordinated muscle contractions at the spiracles in the exoskeleton (Lawley et al., 2020). Secondly, in the face of high ambient temperatures, honeybees will rely heavily on behavioural thermoregulation to conserve water. Finally, to minimise water loss through excretion, the honeybee can create a local osmotic gradient in the hindgut across specialised transporting epithelia, called rectal pads (Wall and Oschman, 1970). Water and ions are thereby recycled by diffusion across the hindgut into the cells of the Malpighian tubule (see Glossary). This process is regulated by diuretic peptides through the differential movements of Na^+ and K^+, which are reabsorbed into the haemolymph (Coast, 1995). Additionally, the honeybee will become motivated to search for and feed on nectar or directly drink water, or it will acquire water through metabolic water production. Several insects can also absorb water vapour from their environment through diverse processes, such as increasing haemolymph osmolarity, producing highly concentrated solutions stored in specific bladders or sacs, or through electro-osmosis (see Glossary; O'Donnell, 2022).

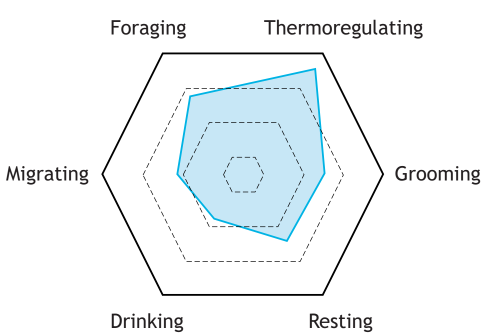

Fig. 3. The motivational state of an animal depends on the individual actions that need to be performed to maintain homeostasis. We here consider an individual in six-dimensional space, where each dimension corresponds to a behavioural action. We can plot the levels of all six behavioural actions (in blue, where intensity increases with distance from the centre of the hexagon) against one another (based on their need for maintaining homeostasis) and, in doing so, we can pinpoint the motivational state of the animal that will decide which of these six actions to perform (here, thermoregulation).

These strategies, whether aimed at conservation or acquisition, are responses to the need for water balance. Every action is linked to a control system with a feedback loop that is initiated by cues that indicate a deviation from optimal water balance. This, in turn, shifts the animal's motivational state, driving efforts to restore water balance. As actions unfold, the control system receives sensory feedback, either positive (e.g. maintain tracheal system periodically closed, increase water absorption in hindgut, continue feeding) or negative (e.g. open tracheal system, return to normal fluid excretion, stop feeding). Negative feedback eventually terminates the water conservation and acquisition cycles, shifting priority to other physiological processes. This means that the motivational drive for water balance diminishes, redirecting the animal's motivation away from water conservation and acquisition. Additionally, competing needs may shift the honeybee's motivational state. For example, when a queen bee flies out ready to mate, a male honeybee's imperative to mate, which may increase water loss, may surpass its need to conserve water. Similarly, should the honeybee detect a predator while trying to restore water balance, survival instincts necessitate an immediate shift to anti-predatory behaviours. Indeed, such trade-offs are common across many levels of biological organisation. Thus, an animal's motivational state can trigger a variety of physiological responses – behavioural or otherwise – that, while operating concurrently, all aim to satisfy an underlying 'need'.

Physiology is physiology is physiology

It is tautological to discuss physiology and behaviour as though they are two complementary branches in biology, when in fact behaviour is a fundamental part of physiology. Although some may find it convenient to maintain a verbal distinction between 'physiology' (internal body changes) and behaviour (external body changes), we challenge the necessity of this separation, although we do recognise the practical challenges of integrating these concepts (discussed in more detail in the following section; see also Cooke et al., 2014). Above, we have discussed the underpinnings of behaviour and demonstrated why behaviour is fundamentally physiological. Here, we advocate that behaviour should be considered as an integral physiological process.

The use of the term 'physiology and behaviour' implies that the user does not consider behaviour to be a physiological process, akin to the ornithologist using the phrase 'birds and fowl' (all fowl are birds, but not all birds are fowl). To avoid such tautology and to acknowledge behaviour's place within physiology, we suggest using established terms such as molecular physiology, cellular physiology, systems physiology (see Glossary) or whole-organism

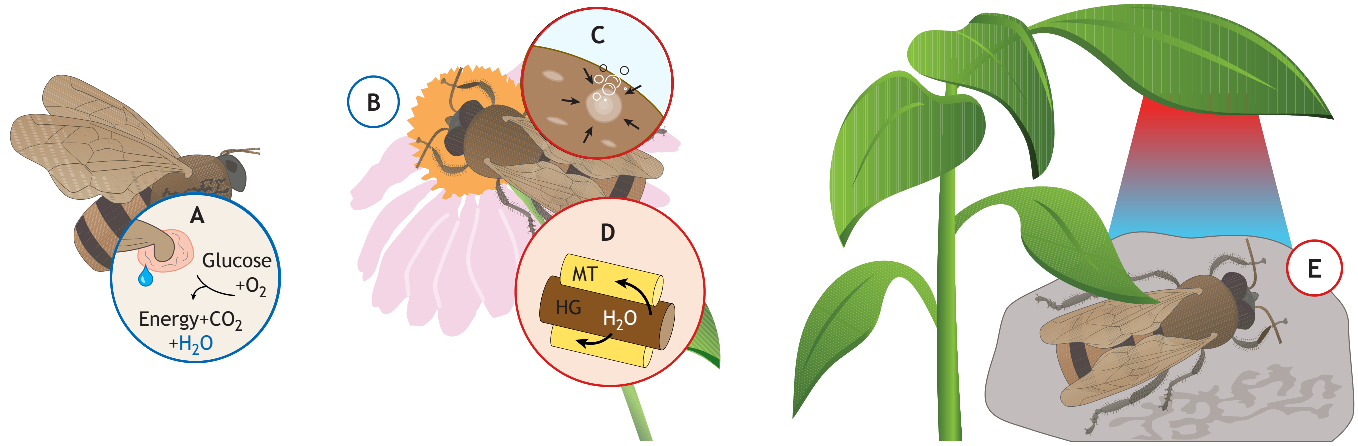

Fig. 4. Motivation behind the need for water balance in the honeybee. When its water balance declines below optimal levels, a honeybee can (A) gain supplementary water through metabolic water production and (B) become motivated to search for and feed on nectar or drink as a source of water (blue circles). To limit water loss (red circles), the honeybee can (C) periodically close its spiracles to minimise respiratory water loss, (D) create a local osmotic gradient in the hindgut (HG) and, in doing so, reabsorb water into Malpighian tubule (MT) cells to minimise water loss through excretion, and (E) avoid warm areas to minimise transpiration across the cuticle.

physiology (hierarchically ordered by level of increasing biological complexity) alongside behaviour for clarity and specificity in scientific discourse (Fig. 5). Note that these integrative levels in physiology are not restrictive or aimed to compartmentalise physiology based on biological complexity, but rather serve a semantic purpose in helping to delineate the scope of study without artificially segregating behaviour from other physiological processes.

Indeed, scientific research is essentially a product of the interactions between investigators through space and time (Bartholomew, 1982), and language therefore plays a pivotal role in research and education. It also forms the basis for integrating behaviour into physiology. It is only once we use correct and universal terminology across subdisciplines within animal physiology that we can establish an integrated field of physiology that considers all levels of biological complexity, from the molecule to the population. As long as physiology and behaviour are considered as two distinct scientific disciplines, and treated as such, a gap in communication and knowledge transfer will remain between behavioural biologists and conventional physiologists, hindering a cohesive approach to addressing contemporary scientific and conservation challenges (e.g. species conservation, population restoration, sustainable resource use).

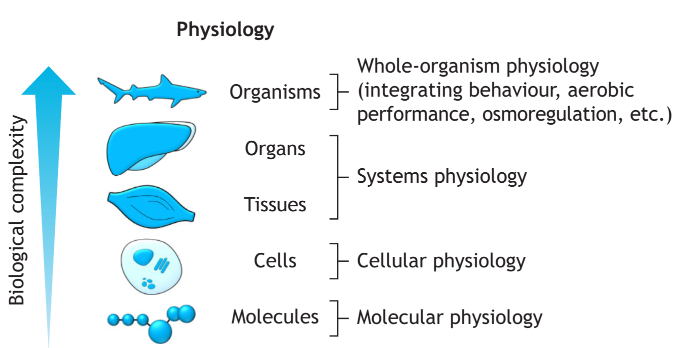

Fig. 5. Integrative levels in physiology. These integrative levels are hierarchically ordered from bottom to top with increasing level of biological complexity.

For the most part, this Commentary has focused on how molecular and cellular physiology mediate behavioural responses. However, inter-individual differences at the molecular and cellular level are, at least in part, driven by behavioural differences, which in turn can contribute to a myriad of lower-level physiological changes (i.e. changes in bodily functions at lower levels of biological organisation; see Fig. 5). For example, agonistic interactions and aggressive behaviours associated with social status can modify regional brain activity and monoaminergic activity in fishes and other vertebrates (Fernald, 2003; Gilmour et al., 2005; Summers et al., 2005). Similarly, animal personality, and the associated consistent individual behavioural variation, influences metabolic rate (Careau et al., 2008). In humans, voluntary smiling (i.e. contraction of the zygomaticus major and the orbicularis oculi muscles) stimulates the release of several neurotransmitters in the brain (i.e. dopamine, serotonin and endorphins) (Ekman and Davidson, 1993). Indeed, the interaction between lower-level organismal functions and behaviour is not a one-way process; behaviour can influence other physiological responses. Bridging these hierarchical levels of biological organisation will therefore be pivotal in providing holistic insights into physiological functioning and interactions among myriad processes and responses.

Challenges with integrating behaviour into physiology

The productive integration between any set of academic disciplines is rarely simple nor direct. Indeed, the integration of behaviour as a physiological process comes with several practical and conceptual challenges. A first significant challenge is the divergence in training and methodologies between behavioural biologists and conventional physiologists (Cooke et al., 2014). Behavioural biologists will, for example, often explore Tinbergen's four problems of behaviour (i.e. causation, survival value, ontogeny and evolution; Tinbergen, 1963) to understand behavioural phenomena. These four problems are, however, not exclusive to behaviour, and can be adapted to suit any physiological question. 'Causation' refers to the physiological mechanisms (proximate causes) underlying any physiological process; 'survival value' is the functional capacity of a process to maintain internal balance; 'ontogeny' comprises the developmental steps and environmental factors that influence the process; and 'evolution' refers to how the physiological trait has evolved to allow the animal's persistence within a certain environment. Additionally, whereas behavioural biologists have often investigated inter-individual (intra-specific) differences (e.g. personality traits, behavioural syndromes), conventional physiologists have historically overlooked such variation or considered these as statistical noise in their quest for 'the golden mean' (Bennett, 1987). However, these inter-individual differences in cellular and whole-organism physiology, in particular, are becoming increasingly better appreciated (e.g. Burton et al., 2011; Koolhaas et al., 2010; Williams, 2008).

Another major challenge is that developing interdisciplinary training programmes and new methodologies to effectively integrate behaviour into physiology will require substantial time and resources. Additionally, bridging different hierarchical levels of biological complexity may generate diverse datasets that will necessitate new analytical tools and techniques. Yet, several academic programmes are already incorporating courses such as behavioural physiology, behavioural neurobiology or behavioural endocrinology into their curricula. This integrative approach in training the next generation of animal physiologists/behavioural biologists will foster a more cohesive field, bridging theoretical divides and promoting a comprehensive understanding of organismal biology. Technologically, biotelemetry and biologging tools, which fundamentally enable the measurement of behaviour (e.g. activity patterns, kinematics of locomotion, foraging behaviours, social interactions, vertical and horizontal migrations) as well as other physiological functions (e.g. heart rate, breathing frequency, body temperature, brain activity, tissue oxygenation patterns, gastric activity), are becoming increasingly widespread and well-integrated in both laboratory and field studies (Watanabe and Papastamatiou, 2023). The development of these increasingly sophisticated tools is likely to open the door to new integrative research avenues in organismal physiology (Gilmour et al., 2023).

Additionally, collaborative efforts between behavioural biologists and conventional physiologists – because of our limitations as biologists – are key to avoid an oversimplification of either field to make it fit one's models, paradigms or theories. As already touched upon in the Introduction in this Commentary, we are not advocating for the reduction of behaviour to its underlying physiological mechanisms. Nevertheless, with the integration of academic disciplines, there is always the risk of reductionism (see Glossary) or simplification while searching for a holistic understanding of complex phenomena (Brigandt and Love, 2023). Although molecular and cellular measures of physiological function may provide insight into the underlying complexity and drivers of behaviours, they may also fail to capture the variability and external drivers of these behaviours.

Another challenge is the differing approaches that behavioural biologists and conventional physiologists may take when treating their animals in experimental studies. For example, conventional physiologists often fast their study animals to obtain basal physiological measurements, aiming to minimise variation caused by digestion. However, from a behavioural perspective, fasting can lead to the misinterpretation of behavioural measurements, as fasted animals typically exhibit different behaviours – such as increased risk taking – when compared with their satiated counterparts. Although these controlled conditions are valuable for isolating specific physiological processes, they may not accurately reflect real-life situations. Note, however, that fasting is an equally common practice in behavioural experiments (e.g. in predation experiments, predators will often be fasted to increase motivation). Therefore, when designing new integrative experimental studies, researchers must carefully consider how their treatments might alter both the behaviour and other physiological processes of the animals being studied. Balancing these considerations is crucial to ensuring that the results are both physiologically relevant and ecologically meaningful.

Conclusion

Establishing a unified field of physiology – including behaviour – is becoming increasingly important against the backdrop of human disturbances and their effects on animal populations. Anthropogenic activities and their associated stressors, both direct and indirect, pose significant threats to global biodiversity, necessitating comprehensive investigations into all aspects of an organism's physiological responses. The emerging discipline of conservation physiology, for example, seeks to provide a functional and mechanistic understanding of the effects of global change on organisms and populations by leveraging an array of physiological concepts, tools and techniques, i.e. the conservation physiology toolbox (Cooke et al., 2013; Madliger et al., 2018; Sutherland et al., 2004). As this toolbox continues to expand, new conservation tools are being integrated, stemming, for example, from stress physiology, ecotoxicology, immunology, reproductive physiology and bioenergetics. Yet, so far, behavioural tools, although plentiful (e.g. the diverse array of biotelemetry and biologging tools; see Kotler et al., 2007), remain relatively underused in conservation physiology – relative to, for example, measurements of haematological parameters, energy budgets and metabolic rates – despite their potential for conservation purposes, particularly considering their application in population management (Cooke et al., 2014; Sutherland, 1998).

Quantifying behavioural responses can provide valuable insights into the whole-organism status of an animal. Furthermore, behavioural responses are often easier to observe/quantify *in situ* or in a non-invasive way than the actual mechanisms underpinning a behavioural action. There is, therefore, merit in making integrative assessments of an animal's molecular physiology, cellular physiology, systems physiology and/or whole-organism physiology (i.e. including behaviour; Fig. 5) for conservation purposes. A good number of examples of such integrative approaches to conservation physiology already exist. For example, such work has revealed that behavioural alterations in coral reef fishes in response to ocean acidification occur through GABAergic disruption (Heuer et al., 2016; Nilsson et al., 2012); impaired swimming performance of mahi-mahi (*Coryphaena hippurus*) is driven by oil-induced reductions in aerobic scope (Mager et al., 2014; Stieglitz et al., 2016); and reduced agonistic behaviour and alterations in predatory behaviour are due to impaired glycolytic muscle action following prolonged ammonia exposure in brown trout (*Salmo trutta*) (Tudorache et al., 2008). Integrative studies like these may prove critical to strengthening the evidence base for meaningful and impactful conservation actions. Indeed, adding behavioural information to conservation physiology studies probably provides more tangible and relatable findings that can be communicated to diverse stakeholders and the general public and that are more relevant to the natural environment with which the animal interacts (Cooke et al., 2013, 2014).

By the conclusion of this Commentary, we hope to have encouraged readers to naturally integrate behaviour into their understanding of physiology. Our goal was to initiate a discussion on the inclusion of behaviour in the field of animal physiology, emphasising the significance of precise language across biological disciplines. In this Commentary, we have clarified terminology related to physiology, and we have discussed how behaviour is regulated by mechanisms and motivations that are similar to those governing any other physiological process. Although we acknowledge the challenges associated with integrating behaviour as a physiological process, we believe that this effort will contribute to developing a more cohesive field of physiology, one which can effectively address the complex challenges of conservation in the face of global change.

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Competing interests
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References
Ancel, A., Visser, H., Handrich, Y., Masman, D. and Le Maho, Y. (1997). Energy saving in huddling penguins. *Nature* **385**, 304-305. doi:10.1038/385304a0
Bartholomew, G. A. (1958). The role of physiology in the distribution of terrestrial vertebrates. In *Zoogeography* (ed. C. L. Hubbs). Washington DC: Publ. 51. American Association for the Advancement of Science.
Bartholomew, G. A. (1982). Scientific innovation and creativity: a zoologist's point of view. *Am. Zool.* **22**, 227-235. doi:10.1093/icb/22.2.227
Bennett, A. F. (1987). Interindividual variability: an underutilized resource. In *New Directions in Ecological Physiology* (ed. M. E. Feder, A. F. Bennett, W. W. Burggren and R. B. Huey). Cambridge, UK: Cambridge University Press.
Bohler, M. W., Chowdhury, V. S., Cline, M. A. and Gilbert, E. R. (2021). Heat stress responses in birds: a review of the neural components. *Biology* **10**, 1095. doi:10.3390/biology10111095
Brigandt, I. (2005). The instinct concept of the early Konrad Lorenz. *J. Hist. Biol.* **38**, 571-608. doi:10.1007/s10739-005-6544-3
Brigandt, I. and Love, A. (2023). Reductionism in biology. In *The Stanford Encyclopedia of Philosophy* (ed. E. N. Zalta and U. Nodelman). https://plato.stanford.edu/entries/reduction-biology/
Broom, D. M. (1981). The biology of behaviour. *Sch. Sci. Rev.* **62**, 442-451.
Brown, C. (2015). Fish intelligence, sentience and ethics. *Anim. Cogn.* **18**, 1-17. doi:10.1007/s10071-014-0761-0
Burton, T., Killen, S. S., Armstrong, J. D. and Metcalfe, N. B. (2011). What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proc. R. Soc. B* **278**, 3465-3473. doi:10.1098/rspb.2011.1778
Careau, V., Thomas, D., Humphries, M. M. and Réale, D. (2008). Energy metabolism and animal personality. *Oikos* **117**, 641-653. doi:10.1111/j.0030-1299.2008.16513.x
Coast, G. M. (1995). Synergism between diuretic peptides controlling ion and fluid transport in insect malpighian tubules. *Regul. Pept.* **57**, 283-296. doi:10.1016/0167-0115(95)00042-A
Cooke, S. J., Sack, L., Franklin, C. E., Farrell, A. P., Beardall, J., Wikelski, M. and Chown, S. L. (2013). What is conservation physiology? Perspectives on an increasingly integrated and essential science. *Conserv. Physiol.* **1**, cot001. doi:10.1093/conphys/cot001
Cooke, S. J., Blumstein, D. T., Buchholz, R., Caro, T., Fernandez-Juricic, E., Franklin, C. E., Metcalfe, J., O'Connor, C. M., St. Clair, C. C., Sutherland, W. J. et al. (2014). Physiology, behavior, and conservation. *Physiol. Biochem. Zool.* **87**, 1-14. doi:10.1086/671165
Dawson, W. R., Bartholomew, G. A. and Bennett, A. F. (1977). A reappraisal of the aquatic specializations of the Galapagos marine iguana (*Amblyrhynchus cristatus*). *Evolution* **31**, 891-897. doi:10.2307/2407452
Ekman, P. and Davidson, R. J. (1993). Voluntary smiling changes regional brain activity. *Psychol. Sci.* **4**, 342-345. doi:10.1111/j.1467-9280.1993.tb00576.x
Fernald, R. D. (2003). How does behavior change the brain? Multiple methods to answer old questions. *Integr. Comp. Biol.* **43**, 771-779. doi:10.1093/icb/43.6.771
Gibbs, A. G. (1998). Water-proofing properties of cuticular lipids. *Am. Zool.* **38**, 471-482. doi:10.1093/icb/38.3.471
Gibbs, A. G. (2002). Lipid melting and cuticular permeability: new insights into an old problem. *J. Insect Physiol.* **48**, 391-400. doi:10.1016/S0022-1910(02)00059-8
Gilbert, C., Robertson, G., Le Maho, Y., Naito, Y. and Ancel, A. (2006). Huddling behavior in emperor penguins: dynamics of huddling. *Physiol. Behav.* **88**, 479-488. doi:10.1016/j.physbeh.2006.04.024
Gilmour, K. M., Wilson, R. W. and Sloman, K. A. (2005). The integration of behaviour into comparative physiology. *Physiol. Biochem. Zool.* **78**, 669-678. doi:10.1086/432144
Gilmour, K. M., Daley, M. A., Egginton, S., Kelber, A., McHenry, M. J., Patek, S. N., Sane, S. P., Schulte, P. M., Terblanche, J. S., Wright, P. A. et al. (2023). Through the looking glass: attempting to predict future opportunities and challenges in experimental biology. *J. Exp. Biol.* **226**, jeb246921. doi:10.1242/jeb.246921
Goodson, J. L. and Thompson, R. R. (2010). Nonapeptide mechanisms of social cognition, behavior and species-specific social systems. *Curr. Opin. Neurobiol.* **20**, 784-794. doi:10.1016/j.conb.2010.08.020
Heuer, R. M., Welch, M. J., Rummer, J. L., Munday, P. L. and Grosell, M. (2016). Altered brain ion gradients following compensation for elevated CO_2 are linked to behavioural alterations in a coral reef fish. *Sci. Rep.* **6**, 33216. doi:10.1038/srep33216
Hill, R. W., Anderson, M. and Cavanaugh, D. (2021). *Animal Physiology*. Oxford University Press.
Kelly, A. M. and Vitousek, M. N. (2017). Dynamic modulation of sociality and aggression: an examination of plasticity within endocrine and neuroendocrine systems. *Philos. Trans. R. Soc. B Biol. Sci.* **372**, 20160243. doi:10.1098/rstb.2016.0243
Koolhaas, J. M., De Boer, S. F., Coppens, C. M. and Buwalda, B. (2010). Neuroendocrinology of coping styles: towards understanding the biology of individual variation. *Front. Neuroendocrinol.* **31**, 307-321. doi:10.1016/j.yfrne.2010.04.001
Kotler, B. P., Morris, D. W. and Brown, J. S. (2007). Behavioral indicators and conservation: wielding "the biologist's tricorder". *Israel J. Ecol. Evol.* **53**, 237-244. doi:10.1560/IJEE.53.3.237
Lawley, S. D., Reed, M. C. and Nijhout, H. F. (2020). Spiracular fluttering increases oxygen uptake. *PLoS ONE* **15**, e0232450. doi:10.1371/journal.pone.0232450
Lorenz, K. Z. (1981). *The Foundations of Ethology*. New York: Springer Science+Business Media.
Madliger, C. L., Love, O. P., Hultine, K. R. and Cooke, S. J. (2018). The conservation physiology toolbox: status and opportunities. *Conserv. Physiol.* **6**, coy029. doi:10.1093/conphys/coy029
Mager, E. M., Esbaugh, A. J., Stieglitz, J. D., Hoenig, R., Bodinier, C., Incardona, J. P., Scholz, N. L., Benetti, D. D. and Grosell, M. (2014). Acute embryonic or juvenile exposure to Deepwater Horizon crude oil impairs the swimming performance of mahi-mahi (*Coryphaena hippurus*). *Environ. Sci. Technol.* **48**, 7053-7061. doi:10.1021/es501628k
McFarland, D. J. and Sibly, R. M. (1975). The behavioural final common path. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **270**, 265-293. doi:10.1098/rstb.1975.0009
Nilsson, G. E., Dixson, D. L., Domenici, P., McCormick, M. I., Sørensen, C., Watson, S. A. and Munday, P. L. (2012). Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nat. Clim. Change* **2**, 201-204. doi:10.1038/nclimate1352
O'Donnell, M. J. (2022). A perspective on insect water balance. *J. Exp. Biol.* **225**, jeb242358. doi:10.1242/jeb.242358
Randall, D., Burggren, W. and French, K. (2001). *Eckert's Animal Physiology: Mechanisms and Adaptations*. New York: W.H. Freeman & Co. Ltd.
Reese, H. W. (1996). How is physiology relevant to behavior analysis? *Behav. Anal.* **19**, 61-70. doi:10.1007/BF03392739
Ruuskanen, S., Hsu, B. Y. and Nord, A. (2021). Endocrinology of thermoregulation in birds in a changing climate. *Mol. Cell. Endocrinol.* **519**, 111088. doi:10.1016/j.mce.2020.111088
Seebacher, F. and Krause, J. (2017). Physiological mechanisms underlying animal social behaviour. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **372**, 20160231. doi:10.1098/rstb.2016.0231
Stieglitz, J. D., Mager, E. M., Hoenig, R. H., Benetti, D. D. and Grosell, M. (2016). Impacts of Deepwater Horizon crude oil exposure on adult mahi-mahi (*Coryphaena hippurus*) swim performance. *Environ. Toxicol. Chem.* **35**, 2613-2622. doi:10.1002/etc.3436
Summers, C. H., Korzan, W. J., Lukkes, J. L., Watt, M. J., Forster, G. L., Øverli, Ø., Höglund, E., Larson, E. T., Ronan, P. J., Matter, J. M. et al. (2005). Does serotonin influence aggression? Comparing regional activity before and during social interaction. *Physiol. Biochem. Zool.* **78**, 679-694. doi:10.1086/432139
Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Anim. Behav.* **56**, 801-809. doi:10.1006/anbe.1998.0896
Sutherland, W. J., Pullin, A. S., Dolman, P. M. and Knight, T. M. (2004). The need for evidence-based conservation. *Trends Ecol. Evol.* **19**, 305-308. doi:10.1016/j.tree.2004.03.018
Tinbergen, N. (1963). On aims and methods of ethology. *Z. Tierpsychol.* **20**, 410-433.

Journal of Experimental Biology (2024) 227, jeb247685. doi:10.1242/jeb.247685

Toates, F. (2002). Physiology, motivation and the organization of behaviour. In *The Ethology of Domestic Animals: an Introductory Text* (ed. P. Jensen). Wallingford, UK: CABI Publishing.

Tudorache, C., Blust, R. and De Boeck, G. (2008). Social interactions, predation behaviour and fast start performance are affected by ammonia exposure in brown trout (*Salmo trutta* L.). *Aquat. Toxicol.* **90**, 145-153. doi:10.1016/j.aquatox.2008.08.009

Wall, B. J. and Oschman, J. L. (1970). Water and solute uptake by rectal pads of *Periplaneta americana*. *Am. J. Physiol.* **218**, 1208-1215. doi:10.1152/ajplegacy.1970.218.4.1208

Watanabe, Y. Y. and Papastamatiou, Y. P. (2023). Biologging and biotelemetry: tools for understanding the lives and environments of marine animals. *Ann. Rev. Anim. Biosci.* **11**, 247-267. doi:10.1146/annurev-animal-050322-073657

Williams, T. D. (2008). Individual variation in endocrine systems: moving beyond the 'tyranny of the Golden Mean'. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **363**, 1687-1698. doi:10.1098/rstb.2007.0003

Woods, H. A. and Smith, J. N. (2010). Universal model for water costs of gas exchange by animals and plants. *Proc. Natl Acad. Sci. USA* **107**, 8469-8474. doi:10.1073/pnas.0905185107