

Decision-making and the interdependence of behaviour and wellbeing in vertebrates

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Abstract

Many wild animal populations now live in environments to which their genes are not adapted. Further, living in captivity has become more common than living in the wild for birds and mammals. Wellbeing of both wild and captive vertebrates hinges on two important novelties in their early cognitive evolution: (1) subjective experience and (2) episodic-like memory with the ability to imagine the near future. Because their behavioural decisions use projected wellbeing as the common currency, wellbeing in vertebrates is intimately linked to behaviour and decision-making. We use an explicitly mechanistic model, illustrated by Atlantic salmon *Salmo salar* in aquaculture, to show how wellbeing is cognitively produced in vertebrates. We consider what is needed to model stress, boredom, and grades of wellbeing from the animal's perspective. To do this, we review recent developments in physiology, neuroscience and cognitive science and use this to "build" the proximate machinery for decision-making in a general vertebrate. We arrive at an operational definition of wellbeing: an animal with episodic-like memory has positive wellbeing if it expects that it can reach and maintain rewarding (as opposed to punishing) emotional states. This definition is the basis for decision-making and is observable in behaviours, making it a tool for proximately modelling behaviour in vertebrates. We illustrate the definition with a simulation that describes behaviour under stress in several types of vertebrates. Thus, we show how behaviour in vertebrates can be modelled from biological mechanisms, founded on agency and Darwinian fitness, with wellbeing in centre stage.

Keywords: Animal behaviour, animal wellbeing, Atlantic salmon, boredom, cognition, common currency, episodic-like memory, prediction, stress, subjective experience.

Introduction

This paper is prompted by three observations. First, many environments are currently changing fast (Hooke et al. 2012; Sage 2020; Sahavacharin et al. 2022), often faster than gene pools (Cowie et al. 2022; Kolbert 2014), so that many animal populations now live in environments to which their genes are not adapted (Schilthuizen 2018). Second, life completely in human captivity has become more common than life in the wild for birds and mammals (Bar-On et al. 2018; Greenspoon et al. 2023), and also for Atlantic salmon (FAO 2023). Living in captivity or altered environments impacts both wellbeing and behaviour. Thus, studies of animal behaviour that assume the evolutionarily optimal solution for behaviour and life history in a given environment are likely biased in these anthropogenically modified habitats and for animals in captivity. Third, recent advances in disciplines adjacent to animal behaviour can be utilized to develop new methods in behavioural ecology for modelling decision-making by being explicit about range of sensory and cognitive mechanisms.

Models of animal behaviour are usually written from the human perspective, we attempt here to take the animal's perspective of itself and its surroundings (Budaev et al. 2019). With this viewpoint, for example, we replace the measures of habitat profitability, such as prey encounter rates and mortality risks, with how the animal interprets its sensory data (see Box 1 for explanation of central concepts). Several philosophers in the phenomenological tradition deny that a first-person perspective is possible with animals (Chalmers 1995; McGinn 1989; Nagel 1974). However, both scientists (Churchland 1989; Ginsburg and Jablonka 2019; Irwin et al. 2022) and naturalistic philosophers (Barrett 2020; Dennett 1991; Metzinger 2009; Searle 2004) argue that approaching

first-person phenomena of individuals in non-human species is possible by employing a componential approach (Ginsburg and Jablonka 2019), which means to take apart the relevant mechanisms and processes and thereafter reassemble them. Currently, we lack the data to model the experience of a particular individual, but we may be able capture dynamics, average and variation within a group of individuals.

Box 1. Concepts in experience and wellbeing

Agency: the ability of an autonomous entity to have adaptive, goal-directed behaviour.

Allostasis: the budgeting of resources required for effective preparative regulation of the body before a need arises.

Allostatic load: the strain on the body accumulating under chronic or repeated stress.

Allostatic overload: an allostatic challenge that exceeds the individual's ability to cope.

Animal welfare: the human third-person perspective on animal wellbeing out of care for the animal.

Animal wellbeing: subjective quality of life as experienced by the animal through adaptive coping with the environment.

Arousal: the emotional excitation in a survival circuit, the currency to compare other survival circuits against

Boredom: the aversive experience to not be able to engage in satisfying activity and to not be able to keep attention engaged.

Broadcast: widespread communication in the brain's working memory.

Degeneracy: the ability of structurally different components to perform the same function so that absence of one component can be compensated elsewhere.

Emotion: cognitive mechanism that for a while may control the body and drive behavioural management.

Episodic-like memory (ELM): the ability to remember what/where/when/who from an event.

Experience: a subjective process by which an organism perceives its external and internal environment.

Global neuronal workspace: the neuroanatomy of the currently active, subjectively experienced working memory and its connections to motor control.

Global organismic state (GOS): global organismic state: the organism's centralized emotional state in terms of the specific survival circuit that is dominant.

Phenomenology: the investigation and description of phenomena as consciously experienced.

Prediction error: the difference between the *a priori* predicted state of the body or the environment and the *a posteriori* interpretation of the same by the sensory system as consequence of the action.

Robustness: an organism's ability to remain in a favourable state for future reproduction.

Stress: a non-specific physiological, behavioural, or cognitive state as well as the response to cope with anticipated challenges.

Subjective: internal processes and states of the organism that exist from its first-person point of view; their existence is inseparable from and cannot be defined independently of the experiencing organism.

Subjective internal model (SIM): an internal representation or a model of an aspect of itself or the environment currently held in the brain of the organism, available in broadcast in the global neuronal workspace.

Survival circuit: a highly integrated neural pathway that responds to a specific class of SIMs and controls a specific set of neurobiological, physiological and behavioural responses.

Unlimited associative learning: a general ability to learn from novel sensory data combinations.

We define behaviour as internally coordinated actions (or inactions) of the whole living organism, excluding internal processes and developmental changes (Levitis et al. 2009). Clearly, behaviour involves the nervous system and complex physiological (hormonal, developmental and cognitive) mechanisms; here we focus on the observable activity output that may have direct fitness consequences for the animal. Indeed, ultimately behaviour is a means for an individual's survival and reproduction (Lotka 1925; Sibly 1989). That said, our central point is that at the proximate level behaviour in vertebrates is a means to improve the individual's wellbeing. A causal link between fitness and wellbeing may sound odd, but we show below that the ability to experience wellbeing evolved in vertebrates by improving behavioural decisions. Behaviour and wellbeing are thus deeply intertwined at the proximate level, since decision-making needs a value system, also called a common currency (McCleery 1978; McFarland and Sibly 1975; McNamara and Houston 1986), to compare options (Cabanac 1992; Jablonka and Ginsburg 2022; McNamara and Houston 2009; Mendl and Paul 2020). The connection between wellbeing and behaviour – that wellbeing is the common currency for behavioural choices – has long been acknowledged (Cabanac 1979; Lotka 1925; Romanes 1883), and we show how it can be used to model behaviour in vertebrates, and thus simultaneously to predict their wellbeing (in analogy to the way that optimization models simultaneously predict behaviour and a metric of fitness). We thus embark on a new class of models of animal behaviour, and new types of theories with a smaller gap between the genotype and the phenotype (c.f. (Grafen 1984)).

The interdependence of behaviour and wellbeing stems from three major transitions in the evolution of behaviour: (i) to agency, (ii) to subjective experience and (iii) to imagination and prediction. These are also the main reasons to be concerned with the wellbeing of captive and wild vertebrates.

The cognitive machinery for decision-making and wellbeing in vertebrates

The evolution of agency and robustness

The most fundamental evolutionary transition was to agency (Ruiz-Mirazo et al. 2004; Seth and Tsakiris 2018; Thompson 2007; Tomasello 2022) with the evolution of self-regulated robustness and resilience. Agency is the ability to act towards a purpose (Kauffman 2007). For living organisms, agency ultimately translates to descendants. Robustness allows the living system to function under perturbations even if the system changes as a result (Rosslénbroich 2014). Resilience is the ability to resist and recover quickly from perturbations (Wingfield 2013b). Robustness and resilience have evolved in different ways in all life forms because they enable the agent to keep the phenotype within a window of favourable states for future reproduction (Fernandez-Leon 2011a; Fernandez-Leon 2011b; Wingfield 2013a). Behaviour is an important mechanism for both robustness and resilience in animals.

The evolution of subjective experience

The transition to subjective experience is cognitive. Subjective experience evolved in arthropods and vertebrates during or shortly after the Cambrian explosion, and in cephalopods much later (Feinberg and Mallatt 2013; Ginsburg and Jablonka 2010; Ginsburg and Jablonka 2019; Godfrey-Smith 2017). Having a sense of a self gives a “person within”: a focus that enables the animal to perceive the objects and events it encounters from a singular perspective (Damasio 1999; Damasio 2003). The evolutionary route to animals with subjective experience is still an active research question. (Godfrey-Smith 2017) emphasizes the transition from animals with separate reflex-like behavioural programs (such as in the box jellyfish and in nematodes, (Barron and Klein 2016)) to animals that balance conflicting emotions. (Ginsburg and Jablonka 2019) emphasize this transition required other transitions, and that practically unlimited associative learning is the best marker that all of them have taken place in an evolutionary lineage. It is not possible for a long-lived animal in a complex landscape to find agentic answers in a genetically determined “look-up table” (Budaev et al. 2019) but with unlimited associative learning and related cognitive abilities (Ginsburg and Jablonka 2019), the subjectively experiencing agent is more robust. Both (Godfrey-Smith 2017) and (Ginsburg and Jablonka 2019) acknowledge that learning and emotion were important in this gradual evolutionary transition into experiencing animals.

In summary, unlimited associative learning and a cognitively integrated emotion system emerged in early vertebrates. Phylogenetic comparisons suggest that it arose when the hindbrain, midbrain, and diencephalic nuclei first evolved (Damasio 2010; Feinberg and Mallatt 2013; Feinberg and Mallatt 2016; Merker 2007; Panksepp 2005; Woodruff 2017).

The cognitive production of experience and selective attention in subjectively experiencing animals

Communication between emotions in the active memory is called broadcast (Baars 1988). The ability to unify information from previously separate brain units generated a whole that is much more than its constituent parts, since it created the possibility for a unified experience across sensory and emotional systems (Anderson and Adolphs 2014; Ginsburg and Jablonka 2019; Zacks and Jablonka 2023). It also provides a basis for the judgement bias task (Mendl and Paul 2020; Neville et al. 2020), which manipulates emotions in one realm (e.g. social) and tests it in another (e.g. feeding).

While animals lacking subjective experience can, after sensing, establish simple internal models of several aspects of the body and the environment, each of their internal models is only connected to a particular emotion and from there directly to motor control (Barron and Klein 2016; Godfrey-Smith 2017). With broadcast, new kinds of complex subjective internal models (SIMs) can be formed using inputs from several senses and be useful in several emotions.

In such brains with broadcast, there may be competition between emotions for control of the body (Godfrey-Smith 2017), or, following (LeDoux 2000), between survival circuits. These survival circuits feed SIMs into neurobiological states (Andersen et al. 2016; Eliassen et al. 2016; Giske et al. 2013), such as fear, hunger, pain or tiredness. The consequence of this competition is that the subjectively experiencing animal has the ability of attaining a centralized emotional state (Anderson and Adolphs 2014; Barron and Klein 2016) that for a time controls the whole body. (LeDoux 2012) therefore calls this centralized state the Global Organismic State (GOS).

In a GOS the individual can narrow its attention to the relevant information in this state. This enables it to focus when needed on its most urgent challenge (Mendl 1999) and to increase its sensory resolution of phenomena relevant to its GOS (Feldman and Friston 2010; Trimmer et al. 2008). For example, in teleosts female Crucian carp reduce predator avoidance behaviour prior to mating (Lastein et al. 2008), acoustic noise can lead to attention shifts in three-spine sticklebacks (Purser and Radford 2011) and pain may override predator avoidance behaviour in rainbow trout (Ashley et al. 2009).

If the strength of the neurobiological state is high in more than one survival circuit simultaneously, the animal may suppress all but the strongest, as in the examples above, or it can give some attention to two or more at the same time (Budaev et al. 2018). For instance, when food-deprived three-spine sticklebacks were given the opportunity to feed on swarming *Daphnia*, the hungry sticklebacks fed in the centre of the swarm, where ingestion rates were at the highest. Some time after initiation of feeding, sticklebacks in the centre moved to the outskirts of the swarm, where prey encounter rates were lower (Heller and Milinski 1979). (Milinski and Heller 1978) also found the same retreat to the outskirts when a model of a predator was presented and (Milinski 1985) interpreted the retreat as consequence of a reduction in the strength of the need to feed, which results in some attention also given to predator avoidance.

The opposite of intensive competition between conflicting survival circuits, is that no survival circuit is activated. This happens far too often in monotonous hatcheries and in the lives of other captive animals. It also happens quite often in wild animals, but they are usually free to move to more interesting places. If no emotions are activated, the animal will not attain a GOS with restricted attention. It will then, with weak attention, be able to consider a wider range of its SIMs in its decision-making, which can then be impacted by several weak arousals (Budaev et al. 2018) and take the form of curious exploration.

The evolution of imagination and prediction

The most recent of these major cognitive transitions to imagination and prediction was the evolution of capacity for episodic-like memory (ELM, (Clayton and Dickinson 1998)) allowing animals to remember the details (where, what, when and with whom) of events. With this capacity, memory of past events (including the animal's emotion during the event) can be used in imagining possible futures (Zacks et al. 2022). The ability to experience good or poor wellbeing is evolutionarily recent among robustness/resilience mechanisms, since it builds on the abilities to experience and predict, which are not shared among all animals (Barron and Klein 2016; Ginsburg and Jablonka 2019; Godfrey-Smith 2017; Godfrey-Smith 2020). This third transition happened in vertebrates during or shortly after the Cambrian explosion (Zacks et al. 2022). Subsequent evolution may have led to gradually better episodic-like memory: amniotes may have richer imagination than fishes and amphibians (Zacks et al. 2022), but fishes can make decisions where the expected reward is sometime in the future (Aellen et al. 2021). The cucumber-grape experiment where capuchin monkeys would reject a good food if they saw others getting better (Brosnan and de Waal 2003), is also an example of a wellbeing-based prediction.

The anatomy required for prediction

In different kinds of vertebrates, internal models about the animal's resource budgeting needs, its external environment, and its own movement are processed in different parts of the midbrain, and these are combined to create a global neuronal workspace (Dehaene et al. 1998; Mashour et al. 2020; Merker 2007). In teleost brains, the global neuronal workspace seems to be located in the hippocampal homolog in the telencephalon (Zacks and Jablonka 2023), which is also the centre for long-term memory. This area for long-term memory receives information from brain areas for vision, olfaction and value, combines them into more complex models, and gives output for motor control (Zacks and Jablonka 2023). This combined neuronal model complex thus enables a teleost to integrate a range of internal models to organize its behaviour (McHaffie et al. 2005; Merker 2007).

The interdependence of wellbeing and behaviour in animals with future planning

In predictive brains (Bubic et al. 2010; Seth and Tsakiris 2018; Soylu 2016) complex SIMs about the animal and its world are constructed from combinations of sensory data and simpler models. These animals can combine their SIMs with ELM in the global neuronal workspace (Zacks and Jablonka 2023) and re-use the body's nervous system to model (Soylu 2016) what the outcomes of its behavioural options would feel like, before they are chosen (Crump et al. 2020; Damasio 1999; Giske et al. 2013). Vertebrates have used their "prediction machine" (Bubic et al. 2010) for time-travelling into the future and back again since the Cambrian explosion (Ginsburg and Jablonka 2010). The prediction of feeling is the value in the common currency (Cabanac 1992), and the chosen behaviour is therefore the option that gives the best feeling for the current GOS. The central point of our paper is that the ability of future prediction enabled the vertebrate to assess the wellbeing it may expect from each of its available behavioural options. This emotional evaluation is the crucial link between behaviour and wellbeing: we have now shown how a vertebrate will assess and compare its wellbeing benefits before a decision (Bubic et al. 2010; Soylu 2016). Therefore: a behavioural decision in a vertebrate is the option that maximizes the predicted wellbeing.

After the subsequent action, a vertebrate will compare its prediction to its interpretation of new sensory data in which the difference between the expected and the observed [i.e. prediction error (Adams et al. 2013; Bubic et al. 2010)] is the basis for learning and for updating its SIMs. With universal associative learning, an animal with ELM, and its global neuronal workspace linked to emotional value and SIMs from sensing, can learn to associate novel sensory data with their value and with the appropriate behaviour towards them. This allows the individual to establish a new SIM and link it to a neurobiological state and further to wellbeing and behaviour (Budaev et al. 2018). Even older types of learning, sensitization and habituation (Cheng 2021), allow an animal to increase or decrease the impact of a given sensory data on the relevant neurobiological state, e.g. to be less scared of an unfamiliar sound, such as urban noise (Schilthuizen 2018).

Wellbeing challenges in salmon aquaculture: boredom and stress

While our overall focus is the intertwined relationship between wellbeing and behaviour in all vertebrates, we illustrate our ideas using the welfare of salmon aquaculture. Here boredom (Braithwaite and Salvanes 2005; Mes et al. 2019; Näslund et al. 2019; Salvanes et al. 2013) and stress (Overton et al. 2019; Vindas et al. 2016) are major challenges.

To improve salmon welfare, we want to understand how wellbeing is produced in the salmon. This work can thus be placed in ‘Pasteur’s Quadrant’ (Mangel 2023; Stokes 1997) in which one addresses a fundamental research question (animal decision-making) through an important application (animal welfare).

Stress is often defined as both a state and as the response to cope with anticipated challenges (Del Giudice et al. 2018; Koolhaas et al. 2011; Peters et al. 2017; Schreck et al. 2016). Allostasis is the most advanced framework for analysing stress (Sterling 2012): the organism predicts its near-future needs and prepares by adjusting its hormones, physiology, attention, and behaviour. Costs of allostatic regulation can become disproportionately high if there is excessive prediction error in the estimation of the upcoming challenge, the challenge exceeds the capacity of the organism, or the challenge is chronic and will continue for a long time (Korte et al. 2007). Because allostatic responses have costs, when prolonged these mechanisms do likely contribute substantially to salmon mortality in aquaculture.

Boredom can be defined as the aversive experience of wanting, but being unable, to engage in satisfying activity, with inability to keep attention engaged (Eastwood et al. 2012). Boredom occurs in monotonous environments, such as hatcheries (Dunlap 2016; Ebbesson and Braithwaite 2012) and in the daily life of many captive animals.

Stress and boredom are directly related to the cognitive transitions described above. Atlantic salmon use ELM to form predictions about their future and act accordingly: The fish learn to associate sounds from feed pipes with an upcoming feeding event and react anticipatorily (Fernö et al. 2011). This anticipatory behaviour can change for several days if a fish has been chased and it is not certain that the danger is over (Folkedal et al. 2012). Furthermore, salmon that have used ELM to expect feeding, can become agitated and aggressive if food does not come (Vindas et al. 2012). Some salmon in a fish farm have been characterized by a depression-like state: they are small and thin, behaviourally inhibited and easily catchable at the surface. Fish farmers call them ‘drop outs’ and ‘loser fish’ (Vindas et al. 2016). They show chronically elevated levels of the stress hormone cortisol, and contrary to healthy individuals they cannot respond to new stress with elevated cortisol levels (Vindas et al. 2014). Further, treatment with the anti-depressant ketamine can reverse the behavioural inhibition (Vindas et al. 2019).

Operationalizing the concept of wellbeing

A valid and useful concept of welfare should be built on bodily control by allostasis (Korte et al. 2007). According to (Korte et al. 2007), p. 426), ‘good animal welfare is characterized by a broad predictive physiological and behavioural capacity to anticipate environmental challenges ... only conditions that produce high allostatic load or inadequately low allostatic load may threaten good health and good animal welfare.’

Stress and boredom occur in situations of mismatch between the expected states of the internal and external environments and the actual experience; they can be viewed as “too much” or “too little” of a challenge. While stress is an evolved robustness mechanism that most animals experience from time to time (Del Giudice et al. 2018; Korte et al. 2005; Taborsky et al. 2021), boredom is predominantly observed in animals kept in captivity (Špinko 2019). We will show below, in line with the above statement by (Korte et al. 2007), that a computational model can combine ELM with

allostasis and robustness. Then, a vertebrate will have positive wellbeing if it predicts that it can reach and maintain a rewarding (as opposed to punishing) emotional states via its decision-making.

Modelling behaviour based on wellbeing

We now show how proximate modelling of wellbeing and the resultant behaviour of a vertebrate can be done by explicit representation (Figure 1) of the most important survival circuits and their subjective internal models, competing neurobiological states, the GOS, prediction, emotional evaluation, decision, sensing, prediction error and learning. This is the basic framework, which can be expanded to include other mechanisms such as hormonal factors that modify (Budaev et al. 2024; Jensen et al. 2021) e.g. appetite (Rønnestad et al. 2017) or fear (Giske and Aksnes 1992) during life (Figure 1).

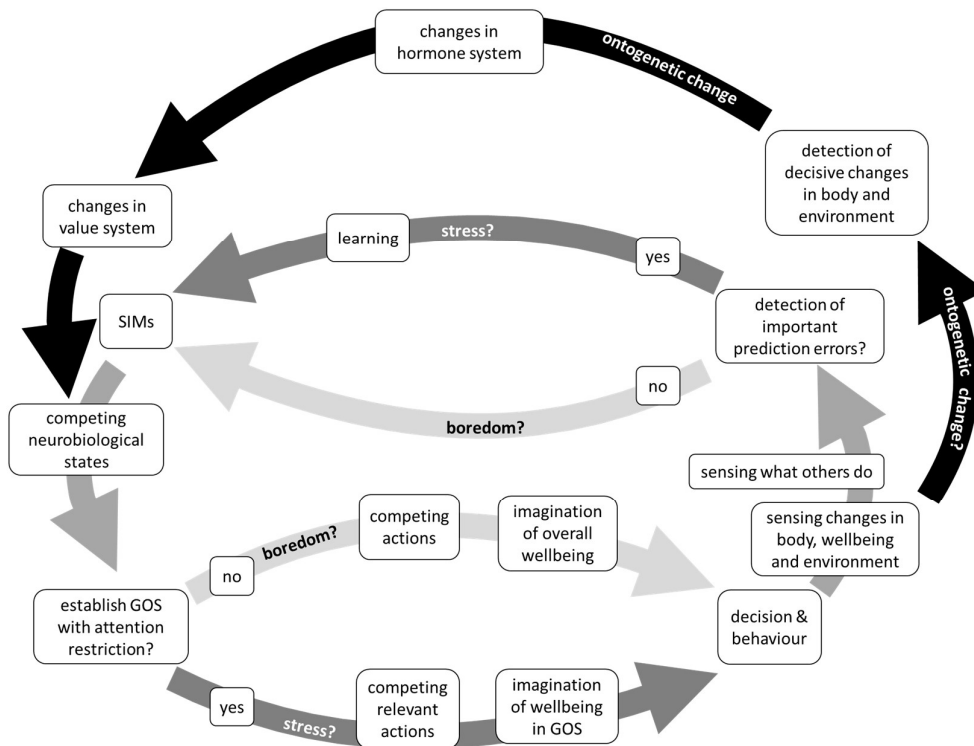


Figure 1. The cognitive production of wellbeing and behaviour in a vertebrate. Decision-making and behaviour in animals with episodic-like memory and prediction emerge from a cycle where the wellbeing-assessment of the available options is the final procedure in decision-making. The cognitive loop (in light and dark grey) has two branching points where processing may take different routes. One is that sensing may or may not reveal important prediction error. The other is that competition between neurobiological states may or may not set the animal in a global organismic state (GOS) with attention restriction. Outside the cognitive loop is a much slower ontogenetic loop (in black) that can change the value system via the hormonal profile. Poor wellbeing can only occur along the dark grey routes. However, in the long run, wellbeing can also be threatened if the animal generally follows the light grey paths: Boredom may follow when subjective internal models (SIMs) are only rarely changed, survival circuits are generally too weak to activate a GOS and sensing rarely reveals severe prediction

errors. Stress may occur along the dark grey route, due to high activation of one or more neurobiological states, resulting in a GOS and the following realization that the negative affect cannot quickly be reduced cognitively or behaviourally. Modified from (Budaev et al. 2024).

The AHA model (Adapted Heuristics and Architecture, (Budaev et al. 2018)) provides a starting point for modelling wellbeing-based proximate behaviour (see Appendix for explanation of the model). The AHA model uses a genetic algorithm (Huse and Giske 1998; Sumida et al. 1990) to evolve a population of adapted individuals with senses, emotions, cognition and behaviour (Andersen et al. 2016; Budaev et al. 2018; Eliassen et al. 2016; Giske et al. 2013; Giske et al. 2014). These individuals may have competing neurobiological states (Figure 1) with associated levels of arousal.

However, wellbeing is not explicitly part of the AHA model. Still, the AHA model reproduces a pattern that is often found in a variety of vertebrate species, namely the reduction of behavioural complexity with increasing stress. For example, chicks stressed by food limitation (María et al. 2004) and parasitised sheep (Burgunder et al. 2018) display reduced complexity of locomotion. Two species of goats display reduction of exploratory behavioural complexity under stress (Alados et al. 1996). Anthropogenic disturbances lead to reduced complexity of diving behaviour patterns in bottlenose dolphins and killer whales (Seuront and Cribb 2017). Finally, a range of environmental pollutants affect the complexity of fish behaviour, which often decreases the diversity of behaviour (measured by entropy) with stress (Eguiraun et al. 2014).

This reduction of behavioural complexity has been difficult to account for, perhaps because it is a high-level system-wide response to stress that cannot be explained at the level of a single behaviour or context. However, using the AHA model (Figure 2) we are able to reproduce this pattern simply by assuming that a heightened emotional arousal in the AHA model captures stress caused by a chronically unsatisfied need. The illustrative trajectories show the same overall pattern: The behavioural diversity (within a block of time steps) is high (measured by entropy) when the average arousal in the period is low, and low when average arousal is high. All these individuals had low arousal most of the time, which means that the environment was overall not very challenging. The time periods with high arousal and low entropy are ones in which the individual did not find a behaviour that could take it out of its current GOS, which kept the arousal high over time and fixed its attention and behaviour towards this GOS. The behavioural differences between individuals may originate in genetics, physiological state, or environmental randomness.

Thus, even a simple model that represents unobservable subjective cognitive mechanisms that account for (and output) observable behaviours can help us understand subtle aspects of subjective wellbeing. This makes it a potentially useful tool for both understanding the internal processes that account for wellbeing and for developing early warning metrics.

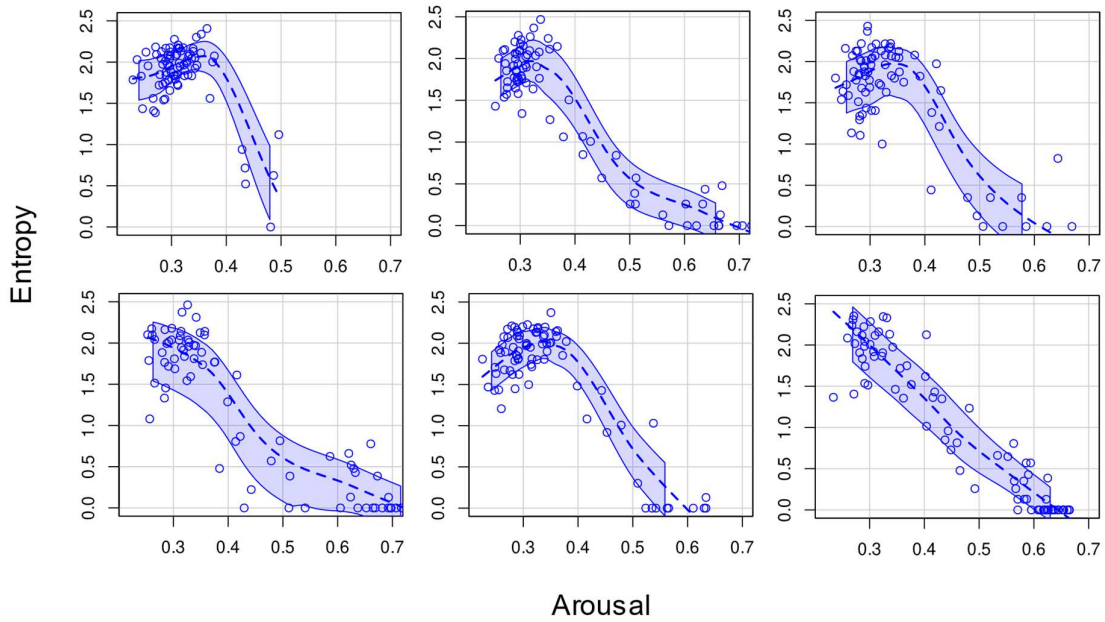


Figure 2. Negative relationship between arousal (stress) and behavioural complexity: examples of typical simulated individuals from the AHA model. Higher arousal is associated with lower entropy (complexity) of the sequential pattern of categorical behavioural units (vertical motion, random movement, quick escape darts, freezing, approaching conspecifics and feeding). The plots show the loess smoothing line and its confidence area. The data are based on a single-generation multiagent simulation of 4489 timesteps after 200 generations of adaptive evolution. Each point refers to a block of 56 sequential timesteps: average arousal and first-order entropy were calculated for each block. Arousal is rescaled so the maximum observed in an individual in the simulation is 1.0. See Appendix for model details.

Discussion

Evolutionary optimisation has been and is very valuable for studies of animal behaviour and behavioural ecology. It can be expanded if we also utilize progress made in surrounding disciplines to obtain deeper understanding of animal behaviour. Multiple advances in many disciplines now make it realistic to model near-natural animals by their robustness mechanisms. We have shown how the strong interdependence in the assessment of wellbeing and the production of behaviour in animals with ELM can be modelled through competing survival circuits with imagination and prediction. The capacity for experiencing variation in wellbeing (Broom 2001) evolved because it improved robustness and helped organisms maintain a state compatible with future reproduction (Spruijt et al. 2001; Wingfield 2013a; Wingfield 2013b) through better behavioural decisions. (Romanes 1883) and (Lotka 1925) wrote about this vision, our lay-out of a simulation model of wellbeing, decision-making and behaviour (Figure 1) is novel, because many of the mechanisms we have discussed in this paper have been understood and brought together only in the last decade.

Wellbeing is not an agentic goal. The ultimate agentic goal, perhaps even the *meaning of life*, is revealed by fitness-maximizing models: to live so as to maximize the expected number of future descendants (Lotka 1925; Sibly 1989; Williams 1966), which is to maximize the individual's genetic contribution to its gene pool. For animals with episodic-like memory, and thus with predictive brains,

the *meaning in life* becomes maximizing wellbeing, through their behavioural decisions. In the AHA model, the link between the ultimate and proximate goals is achieved by mutation and natural selection via a genetic algorithm. While no non-human animals are aware of the agentic goal, many are aware of their wellbeing status. With more than half of the world's birds and mammals living in captivity (Bar-On et al. 2018; Greenspoon et al. 2023) humans have taken on a huge responsibility for this wellbeing.

Since the cognitive building blocks in Figure 1 apply to all vertebrates (Ginsburg and Jablonka 2019; Zacks et al. 2022), the model for wellbeing and behaviour there also describes how fishes, birds, mammals and other taxa assess their wellbeing and make their decisions. We have been explicit in limiting the model to vertebrates, since capacities for emotion, broadcast, imagination and prediction are far from universal among animals (Barron and Klein 2016; Ginsburg and Jablonka 2019; Godfrey-Smith 2020; Levin 2021). However, many of the components we have described will also apply to decision-making in some lineages of arthropods (Barron and Klein 2016; Chittka 2022; Ginsburg and Jablonka 2019) and cephalopods (Ginsburg and Jablonka 2019; Godfrey-Smith 2017). Less is known about episodic-like memory, prediction and wellbeing than about subjective experience in these other lineages (Elwood 2021; Farnsworth and Elwood 2023; Godfrey-Smith 2020). The history of biology tells us that more is found when looked for. Subjective experience and episodic-like memory should be looked for.

A population of proximate animals is behaviourally diverse (Figure 2), even in environments of low complexity (Giske et al. 2013). An algorithmic architecture for production of behaviour (Figure 1) will by itself lead to variation between animals in a population (Giske et al. 2014). Since the chosen behaviour often depends on attaining a particular GOS, natural selection will favour degeneracy (Chen and Crilly 2014); for instance that an animal can become hungry from signals from its digestive system, or from sensing food or from seeing others eat. Thus, degeneracy leads to several routes to attain the same GOS or to same number of descendants (Giske et al. 2013; Giske et al. 2014). Degeneracy makes the cognitive architecture robust (Whitacre 2010) and simplifies its evolvability (Clune et al. 2013; Wagner and Altenberg 1996).

(Nagel 1974) was probably right when claiming that to understand how it is to be a bat, one must become one. With today's computational powers, it is easier to let our computer become the bat, and understand the computer, which readily answers questions about processes, states, and causation. The behavioural complexity analysis in Figure 2 suggests that models of unobservable subjective cognitive mechanisms that produce observable behaviour as output of the model, can be instrumental for developing deeper behavioural theories that link subjective wellbeing to apparent behaviour. This illustrates how the componential approach (Ginsburg and Jablonka 2019) – to take the mechanisms and processes for experience apart and then piece them back together – can bring us much closer to what it is to be another kind of being. We follow Richard Feynman, who said “What I cannot create, I do not understand” (Way 2017).

Appendix: explanation to model in Figure 2

Model outline. The AHA model (Adapted Heuristics and Architecture, (Budaev et al. 2018)) is a simple discrete-time, agent-based model framework that is grounded in basic general neurobiological mechanisms. A large population of agents (modelled individuals) live and reproduce (or die) in a variable environment with density-dependent food competition and predation risk

dilution. The central component of AHA architecture is the survival circuit (LeDoux 2012) that integrates multiple sources of perceptual information into a unitary internal emotional state. The internal state depicted by the survival circuit has continuously graded arousal. Each agent has two survival circuits encapsulating basic emotional states: fear and hunger. These trade priority with each other by competing through lateral inhibition so that only one can be the global organismic state (GOS) at a time. The GOS exerts an arousal-attuned top-down attention modulation effect suppressing perceptions that are not linked to the current GOS. The life cycle of the agent involves a flow of perception to action (via subjective internal models, SIMs) at each timestep. Actions are based on arousal and are categorical and fixed. Actions include vertical motion: up and down, random movement, quick escape darts, freezing, approaching conspecifics and feeding. Feeding results in the growth of the agent. Actions are based on arousal and are categorical and fixed (Table A1). Feeding results in the growth of the agent.

Table A1. Behavioural units implemented in the model.

| Behaviour | Index |
|-----------------------|-------|
| Eat food item | E |
| Random movement | G |
| Freeze immobile | F |
| Escape dart | D |
| Approach conspecifics | C |
| Go up | U |
| Go down | W |

Genetic algorithm. Parametrization of the agents is based on the Genetic Algorithm (GA) that mimics the evolutionary adaptation process (Huse and Giske 1998; Sumida et al. 1990). All adaptable parameters are set by individual genes, initially set at random. Then a large population of agents goes through a life cycle and individuals who survive and achieved the biggest body mass reproduce most, passing their genes to the next generation. The genetic values are also subject to random mutations and genetic recombination. Thus, the GA brings about evolutionary adaptation of the agents and the gene pool over repeated generations.

Simulation experiment. The results presented here are aimed for a simple illustration and do not include detailed analysis. After 200 generations of adaptive evolution with GA, the genomes of the resulting population were used in an experimental simulation. Here the agents run through 4480 timesteps with detailed individual-level recording of external and internal data, GOS, emotion activation, arousal, and behaviour. The resulting sequence of behavioural units is the main focus of this analysis. For the purpose of a simple example, we consider six agents randomly chosen among those who survived all timesteps. We then split the behavioural sequence of these agents into blocks of 56 timesteps. For each block, we calculated the average level of arousal as well as the first order entropy of the sequence of the behavioural units, considered as a string of characters (see below). For calculations, we used the methods described in (Gauvrit et al. 2016).

Results and discussion. The typical pattern found in the agents comprise a clear reduction of entropy at higher levels of arousal, often occurring in various non-linear patterns (Figure 2). We assume that high arousal signals stress because a basic need of the agent (such as feeding) has not been satisfied.

That is, a high level of stress is associated with lower level of behavioural complexity and more stereotypic behaviour. To illustrate the differences, we show below two contrasting examples of such behavioural sequences (see Table A1) and the associated values of entropy:

UUGUGGUGUEEUGUGUGUDGDWUUGUFDUWWGWUWWWFGDUUFGUGWWGFUUGDUG: Entropy=2.24
 EEWEEEEEEEEEEEEEEEE: Entropy=0.22

Our simple interpretation for the results in Figure 2 is as follows. When one of the basic needs is not satisfied for a prolonged time, the animal gets stuck in one GOS and the respective motivation builds up, as reflected in the increasing arousal. For example, remaining hungry for a long time is a signal that the agent's SIMs are not providing correct expectations of the environment. The hungry agent will then increasingly focus on a single adaptive need, such as food. This, in turn, reduces the behavioural repertoire and complexity.

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References

Adams, R. A., S. Shipp, and K. J. Friston. 2013. Predictions not commands: active inference in the motor system. *Brain Structure & Function* 218:611-643.

Aellen, M., V. Dufour, and R. Bshary. 2021. Cleaner fish and other wrasse match primates in their ability to delay gratification. *Animal Behaviour* 176:125-143.

Alados, C. L., J. M. Escos, and J. M. Emlen. 1996. Fractal structure of sequential behaviour patterns: An indicator of stress. *Animal Behaviour* 51:437-443.

Andersen, B. S., C. Jørgensen, S. Eliassen, and J. Giske. 2016. The proximate architecture for decision-making in fish. *Fish and Fisheries* 17:680-695.

Anderson, D. J., and R. Adolphs. 2014. A framework for studying emotions across species. *Cell* 157:187-200.

Ashley, P. J., S. Ringrose, K. L. Edwards, E. Wallington, C. R. McCrohan, and L. U. Sneddon. 2009. Effect of noxious stimulation upon antipredator responses and dominance status in rainbow trout. *Animal Behaviour* 77:403-410.

Bar-On, Y. M., R. Phillips, and R. Milo. 2018. The biomass distribution on Earth. *Proceedings of the National Academy of Sciences* 115:6506-6511.

Barrett, L. F. 2020, *Seven and a half lessons about the brain*, Houghton Mifflin.

Barron, A. B., and C. Klein. 2016. What insects can tell us about the origins of consciousness. *Proceedings of the National Academy of Sciences of the United States of America* 113:4900-4908.

Braithwaite, V. A., and A. G. V. Salvanes. 2005. Environmental variability in the early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. *Proceedings of the Royal Society B-Biological Sciences* 272:1107-1113.

Broom, D. M. 2001. Coping, stress and welfare *in* D. M. Broom, ed. *Coping with challenge: welfare in animals including humans*. Dahlem Workshop report, Dahlem University Press.

Brosnan, S. F., and F. B. M. de Waal. 2003. Monkeys reject unequal pay. *Nature* 425:297-299.

Bubic, A., D. Y. Von Cramon, and R. I. Schubotz. 2010. Prediction, cognition and the brain. *Frontiers in Human Neuroscience* 4:25.

Budaev, S., M. L. Dimitru, K. Enberg, S. O. Handeland, A. D. Higginson, T. S. Kristiansen, A. F. Opdal et al. 2024. Premises for a digital twin of the Atlantic salmon in its world: agency, robustness, subjectivity, and prediction. *Aquaculture, Fish and Fisheries* 4.

Budaev, S., J. Giske, and S. Eliassen. 2018. AHA: A general cognitive architecture for Darwinian agents. *Biologically Inspired Cognitive Architectures* 25:51-57.

- Budaev, S., C. Jørgensen, M. Mangel, S. Eliassen, and J. Giske. 2019. Decision-making from the animal perspective: Bridging ecology and subjective cognition. *Frontiers in Ecology and Evolution* 7:14.
- Burgunder, J., K. J. Petrzeková, D. Modry, A. Kato, and A. J. J. MacIntosh. 2018. Fractal measures in activity patterns: Do gastrointestinal parasites affect the complexity of sheep behaviour? *Applied Animal Behaviour Science* 205:44-53.
- Baars, B. J. 1988, *A cognitive theory of consciousness*, Cambridge University Press.
- Cabanac, M. 1979. Sensory pleasure. *Quarterly Review of Biology* 54:1-29.
- . 1992. Pleasure - the common currency. *Journal of Theoretical Biology* 155:173-200.
- Chalmers, D. J. 1995. Facing up to the problem of consciousness. *Journal of Consciousness Studies* 2:200-219.
- Chen, C.-C., and N. Crilly. 2014, Modularity, redundancy and degeneracy: cross-domain perspectives on key design principles 2014 IEEE International Systems Conference Proceedings:546-553.
- Cheng, K. 2021. Learning in Cnidaria: A systematic review. *Learning & Behavior* 49:175-189.
- Chittka, L. 2022, *The mind of a bee*, Princeton University Press.
- Churchland, P. S. 1989, *Neurophilosophy: Toward a unified science of the mind-brain*, MIT Press.
- Clayton, N. S., and A. Dickinson. 1998. Episodic-like memory during cache recovery by scrub jays. *Nature* 395:272-274.
- Clune, J., J. B. Mouret, and H. Lipson. 2013. The evolutionary origins of modularity. *Proceedings of the Royal Society B-Biological Sciences* 280.
- Cowie, R. H., P. Bouchet, and B. Fontaine. 2022. The Sixth Mass Extinction: fact, fiction or speculation? *Biological Reviews* 97:640-663.
- Crump, A., E. J. Bethell, R. Earley, V. E. Lee, M. Mendl, L. Oldham, S. P. Turner, and G. Arnott. 2020. Emotion in animal contests. *Proceedings of the Royal Society Biological Sciences Series B* 287:1-9.
- Damasio, A. 1999, *The Feeling of What Happens - Body and Emotion in the Making of Consciousness*. New York, Harcourt Brace.
- . 2003. Mental self: The person within. *Nature* 423:227.
- Damasio, A. 2010, *Self comes to mind: Constructing the conscious brain*. London, William Heinemann.
- Dehaene, S., M. Kerszberg, and J.-P. Changeux. 1998. A neuronal model of a global workspace in effortful cognitive tasks. *Proceedings of the National Academy of Sciences of the United States of America* 95:14529-14534.
- Del Giudice, M., C. L. Buck, L. E. Chaby, B. M. Gormally, C. C. Taff, C. J. Thawley, M. N. Vitousek, and H. Wada. 2018. What is stress? A systems perspective. *Integrative and Comparative Biology* 58:1019-1032.
- Dennett, D. C. 1991, *Consciousness explained*. Boston, Little, Brown and Company.
- Dunlap, K. D. 2016. Fish neurogenesis in context: assessing environmental influences on brain plasticity within a highly labile physiology and morphology. *Brain Behavior and Evolution* 87:156-166.
- Eastwood, J. D., A. Frischen, M. J. Fenske, and D. Smilek. 2012. The unengaged mind: Defining boredom in terms of attention. *Perspectives on Psychological Science* 7:482-495.
- Ebbesson, L. O. E., and V. A. Braithwaite. 2012. Environmental effects on fish neural plasticity and cognition. *Journal of Fish Biology* 81:2151-2174.
- Eguiraun, H., K. López-de-Ipiña, and I. Martinez. 2014. Application of entropy and fractal dimension analyses to the pattern recognition of contaminated fish responses in aquaculture. *Entropy* 16:6133-6151.
- Eliassen, S., B. S. Andersen, C. Jørgensen, and J. Giske. 2016. From sensing to emergent adaptations: modelling the proximate architecture of decision-making. *Ecological Modelling* 326:90-100.
- Elwood, R. W. 2021. Potential pain in fish and decapods: Similar experimental approaches and similar results. *Frontiers in Veterinary Science* 8.
- FAO. 2023. Atlantic Salmon, *Salmo salar* Linnaeus, 1758 [online], FAO.
- Farnsworth, K. D., and R. W. Elwood. 2023. Why it hurts: with freedom comes the biological need for pain. *Animal Cognition* 26:1259-1275.
- Feinberg, T. E., and J. Mallatt. 2013. The evolutionary and genetic origins of consciousness in the Cambrian Period over 500 million years ago. *Frontiers in Psychology* 4.
- Feinberg, T. E., and J. M. Mallatt. 2016, *The ancient origins of consciousness: How the brain created experience*, MIT Press.
- Feldman, H., and K. J. Friston. 2010. Attention, uncertainty, and free-energy. *Frontiers in Human Neuroscience* 4.
- Fernandez-Leon, J. A. 2011a. Evolving cognitive-behavioural dependencies in situated agents for behavioural robustness. *Biosystems* 106:94-110.
- . 2011b. Evolving experience-dependent robust behaviour in embodied agents. *Biosystems* 103:45-56.

- Fernö, A., G. Huse, P. J. Jakobsen, T. S. Kristiansen, and J. Nilsson. 2011. Fish behaviour, learning, aquaculture and fisheries, Pages 359-404 in C. Brown, K. Laland, and J. Krause, eds. Fish cognition and behavior, 2nd ed. Fish and aquatic resources series, Blackwell Publishing.
- Folkedal, O., T. Torgersen, R. E. Olsen, A. Fernö, J. Nilsson, F. Oppedal, L. H. Stien, and T. S. Kristiansen. 2012. Duration of effects of acute environmental changes on food anticipatory behaviour, feed intake, oxygen consumption, and cortisol release in Atlantic salmon parr. *Physiology & Behavior* 105:283-291.
- Gauvrit, N., H. Singmann, F. Soler-Toscano, and H. Zenil. 2016. Algorithmic complexity for psychology: a user-friendly implementation of the coding theorem method. *Behavior Research Methods* 48:314-329.
- Ginsburg, S., and E. Jablonka. 2010. The evolution of associative learning: A factor in the Cambrian explosion. *Journal of Theoretical Biology* 266:11-20.
- . 2019. *The evolution of the sensitive soul: learning and the origins of consciousness*, MIT Press.
- Giske, J., and D. L. Aksnes. 1992. Ontogeny, season and trade-offs - vertical-distribution of the mesopelagic fish *Maurollicus muelleri*. *Sarsia* 77:253-261.
- Giske, J., S. Eliassen, Ø. Fiksen, P. J. Jakobsen, D. L. Aksnes, C. Jørgensen, and M. Mangel. 2013. Effects of the emotion system on adaptive behavior. *American Naturalist* 182:689-703.
- Giske, J., S. Eliassen, Ø. Fiksen, P. J. Jakobsen, D. L. Aksnes, M. Mangel, and C. Jørgensen. 2014. The emotion system promotes diversity and evolvability. *Proceedings. Biological sciences / The Royal Society* 281.
- Godfrey-Smith, P. 2017. Animal evolution and the origins of experience, Pages 51-71 in D. Smith, ed. *How biology shapes philosophy: New foundations for naturalism*, Cambridge University Press.
- . 2020. *Metazoa: animal life and the birth of the mind*, Farrar, Straus and Giroux.
- Grafen, A. 1984. Natural selection, kin selection and group selection, Pages 62-84 in J. R. Krebs, and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. Oxford, Blackwell.
- Greenspoon, L., E. Krieger, R. Sender, Y. Rosenberg, Y. M. Bar-On, U. Moran, T. Antman et al. 2023. The global biomass of wild mammals. *Proceedings of the National Academy of Sciences of the United States of America* 120:e2204892120.
- Heller, R., and M. Milinski. 1979. Optimal foraging of sticklebacks on swarming prey. *Animal Behaviour* 27:1127-1141.
- Hooke, R. L., J. F. Martín-Duque, and J. Pedraza. 2012. Land transformation by humans: a review. *GSA today* 12:4-10.
- Huse, G., and J. Giske. 1998. Ecology in Mare Pentium: an individual-based spatio-temporal model for fish with adapted behaviour. *Fisheries Research* 37:163-178.
- Irwin, L. N., L. Chittka, E. Jablonka, and J. Mallatt. 2022. Editorial: Comparative animal consciousness. *Frontiers in Systems Neuroscience* 16.
- Jablonka, E., and S. Ginsburg. 2022. Learning and the evolution of conscious agents. *Biosemiotics* 15:401-437.
- Jensen, C. H., J. Weidner, J. Giske, S. Budaev, C. Jørgensen, and S. Eliassen. 2021. Hormonal adjustments to future expectations impact growth and survival in juvenile fish. *Oikos* 130:41-51.
- Kauffman, S. 2007. Origin of life and the living state. *Origins of Life and Evolution of Biospheres* 37:315-322.
- Kolbert, E. 2014. *The sixth extinction: An unnatural history*, A&C Black.
- Koolhaas, J. M., A. Bartolomucci, B. Buwalda, S. F. de Boer, G. Flugge, S. M. Korte, P. Meerlo et al. 2011. Stress revisited: A critical evaluation of the stress concept. *Neuroscience and Biobehavioral Reviews* 35:1291-1301.
- Korte, S. M., J. M. Koolhaas, J. C. Wingfield, and B. S. McEwen. 2005. The Darwinian concept of stress: benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. *Neuroscience and Biobehavioral Reviews* 29:3-38.
- Korte, S. M., B. Olivier, and J. M. Koolhaas. 2007. A new animal welfare concept based on allostasis. *Physiology & Behavior* 92:422-428.
- Lastein, S., E. Höglund, I. Mayer, Ø. Øverli, and K. B. Døving. 2008. Female crucian carp, *Carassius carassius*, lose predator avoidance behavior when getting ready to mate. *Journal of Chemical Ecology* 34:1487-1491.
- LeDoux, J. 2012. Rethinking the emotional brain. *Neuron* 73:653-676.
- LeDoux, J. E. 2000. Emotion circuits in the brain. *Annual Review of Neuroscience* 23:155-184.
- Levin, M. 2021. Life, death, and self: Fundamental questions of primitive cognition viewed through the lens of body plasticity and synthetic organisms. *Biochemical and Biophysical Research Communications* 564:114-133.
- Levitis, D. A., W. Z. Lidicker, and G. Freund. 2009. Behavioural biologists do not agree on what constitutes behaviour. *Animal Behaviour* 78:103-110.
- Lotka, A. J. 1925. *Elements of Physical Biology*. Baltimore, Williams & Wilkins Company.
- Mangel, M. 2023. Pest science in Pasteur's Quadrant. *Journal of Pest Science*.

- María, G. A., J. Escós, and C. L. Alados. 2004. Complexity of behavioural sequences and their relation to stress conditions in chickens (*Gallus gallus domesticus*): a non-invasive technique to evaluate animal welfare. *Applied Animal Behaviour Science* 86:93-104.
- Mashour, G. A., P. Roelfsema, J. P. Changeux, and S. Dehaene. 2020. Conscious processing and the Global Neuronal Workspace hypothesis. *Neuron* 105:776-798.
- McCleery, R. 1978. Optimal behaviour sequences and decision making, Pages 377-410 in J. Krebs, and N. Davies, eds. *Behavioural ecology: An evolutionary approach*, Blackwell.
- McFarland, D. J., and R. M. Sibly. 1975. The behavioural final common path. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 270:265-293.
- McGinn, C. 1989. Can we solve the mind-body problem? *Mind* 98:349-366.
- McHaffie, J. G., T. R. Stanford, B. E. Stein, W. Coizet, and P. Redgrave. 2005. Subcortical loops through the basal ganglia. *Trends in Neurosciences* 28:401-407.
- McNamara, J. M., and A. I. Houston. 1986. The common currency for behavioral decisions. *American Naturalist* 127:358-378.
- . 2009. Integrating function and mechanism. *Trends in Ecology & Evolution* 24:670-675.
- Mendl, M. 1999. Performing under pressure: stress and cognitive function. *Applied Animal Behaviour Science* 65:221-244.
- Mendl, M., and E. S. Paul. 2020. Animal affect and decision-making. *Neuroscience and Biobehavioral Reviews* 112:144-163.
- Merker, B. 2007. Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behavioral and Brain Sciences* 30:63-+.
- Mes, D., R. van Os, M. Gorissen, L. O. E. Ebbesson, B. Finstad, I. Mayer, and M. A. Vindas. 2019. Effects of environmental enrichment on forebrain neural plasticity and survival success of stocked Atlantic salmon. *Journal of Experimental Biology* 222.
- Metzinger, T. 2009. *The ego-tunnel. The science of the mind and the myth of the self* New York, Basic Books.
- Milinski, M. 1985. The patch choice model - no alternative to balancing. *American Naturalist* 125:317-320.
- Milinski, M., and R. Heller. 1978. Influence of a predator on optimal foraging behavior of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* 275:642-644.
- Nagel, T. 1974. What is it like to be a bat? *Philosophical Review* 83:435-450.
- Neville, V., J. King, I. D. Gilchrist, P. Dayan, E. S. Paul, and M. Mendl. 2020. Reward and punisher experience alter rodent decision-making in a judgement bias task. *Scientific Reports* 10.
- Näslund, J., M. Rosengren, and J. I. Johnsson. 2019. Fish density, but not environmental enrichment, affects the size of cerebellum in the brain of juvenile hatchery-reared Atlantic salmon. *Environmental Biology of Fishes* 102:705-712.
- Overton, K., T. Dempster, F. Oppedal, T. S. Kristiansen, K. Gismervik, and L. H. Stien. 2019. Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. *Reviews in Aquaculture* 11:1398-1417.
- Panksepp, J. 2005. Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition* 14:30-80.
- Peters, A., B. S. McEwen, and K. Friston. 2017. Uncertainty and stress: Why it causes diseases and how it is mastered by the brain. *Progress in Neurobiology* 156:164-188.
- Purser, J., and A. N. Radford. 2011. Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). *Plos One* 6.
- Romanes, G. J. 1883, *Mental evolution in animals: WITH a posthumous essay on instinct* by Charles Darwin, Kegan Paul, Trench.
- Rosslénbroich, B. 2014, *On the origin of autonomy: A new look at the major transitions in evolution: History, Philosophy and Theory of the Life Sciences*, v. 5, Springer.
- Ruiz-Mirazo, K., J. Pereto, and A. Moreno. 2004. A universal definition of life: Autonomy and open-ended evolution. *Origins of Life and Evolution of Biospheres* 34:323-346.
- Rønnestad, I., A. S. Gomes, K. Murashita, R. Angotzi, E. Jonsson, and H. Volkoff. 2017. Appetite-controlling endocrine systems in teleosts. *Frontiers in Endocrinology* 8.
- Sage, R. F. 2020. *Global change biology: a primer*. *Global Change Biology* 26:3-30.
- Sahavacharin, A., P. Sompongchaiyakul, and D. Thaitakoo. 2022. The effects of land-based change on coastal ecosystems. *Landscape and Ecological Engineering* 18:351-366.
- Salvanes, A. G. V., O. Moberg, L. O. E. Ebbesson, T. O. Nilsen, K. H. Jensen, and V. A. Braithwaite. 2013. Environmental enrichment promotes neural plasticity and cognitive ability in fish. *Proceedings of the Royal Society B-Biological Sciences* 280.

- Schilthuizen, M. 2018, Darwin comes to town: How the urban jungle drives evolution, Picador.
- Schreck, C. B., L. Tort, A. P. Farrell, and C. J. e. Brauner. 2016, Biology of stress in fish: Fish physiology, Academic Press.
- Searle, J. R. 2004, Mind: A brief introduction, Oxford University Press.
- Seth, A. K., and M. Tsakiris. 2018. Being a beast machine: Somatic basis of selfhood. Trends in Cognitive Sciences 22:969-981.
- Seuront, L., and N. Cribb. 2017. Fractal analysis provides new insights into the complexity of marine mammal behavior: A review, two methods, their application to diving and surfacing patterns, and their relevance to marine mammal welfare assessment. Marine Mammal Science 33:847-879.
- Sibly, R. M. 1989. What evolution maximizes. Functional Ecology 3:129-135.
- Soylu, F. 2016. An embodied approach to understanding: Making sense of the world through simulated bodily activity. Frontiers in psychology 7:1914.
- Špinko, M. 2019. Animal agency, animal awareness and animal welfare. Animal Welfare 28:11-20.
- Spruijt, B. M., R. van den Bos, and F. T. A. Pijlman. 2001. A concept of welfare based on reward evaluating mechanisms in the brain: anticipatory behaviour as an indicator for the state of reward systems. Applied Animal Behaviour Science 72:145-171.
- Sterling, P. 2012. Allostasis: A model of predictive regulation. Physiology & Behavior 106:5-15.
- Stokes, D. E. 1997, Pasteur's quadrant: Basic science and technological innovation, Brookings Institution Press.
- Sumida, B. H., A. I. Houston, J. M. McNamara, and W. D. Hamilton. 1990. Genetic algorithms and evolution. Journal of Theoretical Biology 147:59-84.
- Taborsky, B., S. English, T. W. Fawcett, B. Kuijper, O. Leimar, J. M. McNamara, S. Ruuskanen, and C. Sandi. 2021. Towards an evolutionary theory of stress responses. Trends in Ecology & Evolution 36:39-48.
- Thompson, E. 2007. Mind in Life: Biology. Phenomenology and the Sciences.
- Tomasello, M. 2022, The evolution of agency: Behavioral organization from lizards to humans, MIT Press.
- Trimmer, P. C., A. I. Houston, J. A. R. Marshall, R. Bogacz, E. S. Paul, M. T. Mendl, and J. M. McNamara. 2008. Mammalian choices: combining fast-but-inaccurate and slow-but-accurate decision-making systems. Proc. R. Soc. B-Biol. Sci. 275:2353-2361.
- Vindas, M. A., O. Folkedal, T. S. Kristiansen, L. H. Stien, B. O. Braastad, I. Mayer, and Ø. Øverli. 2012. Omission of expected reward agitates Atlantic salmon (*Salmo salar*). Animal Cognition 15:903-911.
- Vindas, M. A., S. H. Helland-Riise, G. E. Nilsson, and Ø. Øverli. 2019. Depression-like state behavioural outputs may confer beneficial outcomes in risky environments. Scientific Reports 9.
- Vindas, M. A., I. B. Johansen, O. Folkedal, E. Höglund, M. Gorissen, G. Flik, T. S. Kristiansen, and Ø. Øverli. 2016. Brain serotonergic activation in growth-stunted farmed salmon: adaption versus pathology. Royal Society Open Science 3.
- Vindas, M. A., C. Sørensen, I. B. Johansen, O. Folkedal, E. Höglund, U. W. Khan, L. H. Stien et al. 2014. Coping with unpredictability: dopaminergic and neurotrophic responses to omission of expected reward in Atlantic salmon (*Salmo salar* L.). Plos One 9.
- Wagner, G. P., and L. Altenberg. 1996. Complex adaptations and the evolution of evolvability. Evolution 50:967-976.
- Way, M. 2017. "What I cannot create, I do not understand". Journal of Cell Science 130:2941-2942.
- Whitacre, J. M. 2010. Degeneracy: a link between evolvability, robustness and complexity in biological systems. Theoretical Biology and Medical Modelling 7.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687-690.
- Wingfield, J. C. 2013a. The comparative biology of environmental stress: behavioural endocrinology and variation in ability to cope with novel, changing environments. Animal Behaviour 85:1127-1133.
- . 2013b. Ecological processes and the ecology of stress: the impacts of abiotic environmental factors. Functional Ecology 27:37-44.
- Woodruff, M. L. 2017. Consciousness in teleosts: There is something it feels like to be a fish. Animal Sentience 2:1.
- Zacks, O., S. Ginsburg, and E. Jablonka. 2022. The futures of the past. The evolution of imaginative animals. Journal of Consciousness Studies 29:29-61.
- Zacks, O., and E. Jablonka. 2023. The evolutionary origins of the Global Neuronal Workspace in vertebrates. Neuroscience of Consciousness 2023.