

From sensing to emergent adaptations: Modelling the proximate architecture for decision-making



Sigrunn Eliassen^a, Bjørn Snorre Andersen^a, Christian Jørgensen^b, Jarl Giske^{a,*}

^a Department of Biology and Hjordt Centre for Marine Ecosystem Dynamics, University of Bergen, Bergen, Norway

^b Uni Research and Hjordt Centre for Marine Ecosystem Dynamics, Bergen, Norway

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ABSTRACT

During the past 50 years, evolutionary theory for animal behaviour has branched into different methodological frameworks focussing on age-, state-, density-, and frequency-dependent processes. These approaches have led to valuable insights in optimal responses, state dependent choices, and behavioural strategies in social contexts. We argue that time is ripe for an integration of these methodologies based on a rigorous implementation of proximate mechanisms. We describe such a modelling framework that is based on the architectural structures of sensing and information processing, physiological and neurological states, and behavioural control in animals. An individual-based model of this decision architecture is embedded in a genetic algorithm that finds evolutionary adaptations. This proximate architecture framework can be utilized for modelling behavioural challenges in complex environments, for example how animals make behavioural decisions based on multiple sources of information, or adapt to changing environments. The framework represents the evolution of the proximate mechanisms that underlie animal decision making, and it aligns with individual-based ecology by emphasizing the role of local information, perception, and individual behaviour.

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1. Introduction

Most theories for animal behaviour have traditionally assumed that individuals have accurate perception of the current environment, that they have full information on which to base their decisions, and that they make optimal choices independent of time constraints or the amount of computation required. This is in contrast to observations of animal behaviour where one would most likely conclude that animals are not smart but quite often do clever things. This apparent cleverness may stem from two sources at different time scales:

- (1) Animals are flexible as they e.g. can respond fast and adequately in situations they have never experienced before. This suggests that behaviour is controlled by heuristics (Gigerenzer, 2004), where the proximate mechanism (the decision-making process) has an architecture that allows efficient information use and decision-making. This architecture enables minor changes

in sensory input (e.g. stronger signals of predator presence) to lead to very different behaviours (e.g. termination of feeding behaviour) or experience from one situation to be made useful in a novel context.

- (2) Small evolutionary changes in this architecture may alter the behavioural phenotype quite substantially (e.g. van der Post and Semmann, 2011a), very similar to how small mutations in the regulation of developmental pathways can open up morphological diversity and innovations (e.g. Moczek et al., 2011). In the language of Tinbergen (1963), the proximate mechanism has an architecture that is particularly good at evolving as the ultimate drivers change.

As a result animal behaviour is controlled by proximate heuristic mechanisms that rest upon an innovative architecture. Still, the proximate mechanisms have largely been ignored in evolutionary and ecological models despite that they are (i) what evolve, (ii) what cause the emergence of behaviours one can observe in the wild and in the lab, and (iii) what can be studied in terms of neurology, physiology, biochemistry, and genetics. In this paper we describe the proximate architecture for decision-making, which represents biological processes from sensing via information processing and decision making through to the physiological and behavioural response. We argue that this framework is useful for understanding

Abbreviations: GA, genetic algorithm; GOS, global organismic state; IBM, individual-based model; NR, neuronal response.

* Corresponding author. Tel.: +47 99205975; fax: +47 55584450.

E-mail address: jarl.giske@uib.no (J. Giske).

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animal behaviour and that the proximate architecture can be incorporated mechanistically within an individual-based approach. With proper rooting in evolutionary adaptation, this may become an important tool for evolutionary and ecological modelling.

2. Behaviour in the individual-based paradigm

Evolutionary theory for animal behaviour has branched into different modelling frameworks focussing on age-, state-, density-, and frequency-dependent processes, with little integration between methodologies. The American statistician Alfred Lotka was the first to model evolutionary adaptation and behaviour, by turning the population growth equation of Euler (1760) into an equation for fitness (Lotka, 1907, 1925). In his interpretation of what we now call the Euler–Lotka equation, competing resource investments and activities of the organism are evaluated with a common currency: their contributions to the organism's expected rate of offspring production. The modelling paradigm is therefore based on the premise that organisms make optimal decisions. This tradition has developed further into life history theory (Fisher, 1930; Murdoch, 1966; Roff, 1992; Stearns, 1992; Williams, 1966), optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966; Charnov, 1976), game theory (Fretwell and Lucas, 1970; Maynard Smith and Price, 1973), and adaptive dynamics (Dieckmann and Law, 1996; Geritz et al., 1998; Metz et al., 1992).

While the Euler–Lotka equation, game theory and adaptive dynamics are population-based tools to understand individuals, optimal foraging theory and state-dependent life history theory (Mangel and Clark, 1986; McNamara and Houston, 1986) can be used and understood from a purely individual perspective. Although these methods are excellent tools in evolutionary ecology, none of them are all-purpose. Optimization techniques excel at finding the best possible solution to a problem without considering potential fitness valleys which may prevent the optimum itself from being reached. State-dependent life history theory is excellent for finding optimal policies when they depend on some (physiological) state of the organism, but at the expense of policies towards other individuals. The opposite is the case for the game theory tradition.

In the 1970s a different tradition, based on Individual Based Modelling (IBM; DeAngelis and Grimm, 2014; Huston et al., 1988) arose. This paradigm merged perspectives from artificial life (Langton, 1986; von Neumann, 1966) and artificial intelligence (Newell and Simon, 1956) with another major tradition in mathematical ecology, community ecology. The early papers of IBM focused on forest ecosystems (Botkin et al., 1972; Shugart and West, 1977, 1980) and fish populations (DeAngelis et al., 1980). The new tool was used to study population and ecosystem consequences of rare phenomena, such as the death of a canopy-forming tree or the survival of a larval fish through the earliest life stages. From this beginning, the individual based approach has given more flexibility in modelling ecological interactions, by allowing detailed representations of individuals living in complex ecological landscapes (Grimm and Railsback, 2005; Stillman et al., 2015). This is important because flexible and diverse behavioural responses generally observed in nature are not found in simplified models (Evans et al., 2012, 2013; Fawcett et al., 2012, 2014; McNamara and Houston, 2009). While ecology and evolution has been integrated in the artificial life tradition (e.g. Byrski et al., 2015; de Boer and Hogeweg, 2012; Paredis, 1995; Ray, 1994), the link to evolutionary dynamics in individual-based models has often been absent (Grimm, 1999).

In the following we will discuss some features of organisms that may be taken advantage of when modelling evolutionarily adaptive behaviours. These enable the integration of the ultimate perspective of optimization models with the proximate

mechanisms important in ecological interactions. There are many methods available for this, collectively termed multi-scale models by Hogeweg (2007). We will focus on the proximate architecture framework, which gives a representation of biological processes from sensing via information processing and decision making through to action for a wide range of animals. The framework can be utilized in ecological modelling, in particular for organisms that make decisions based on multiple sources of information, in complex, variable and even novel environments, where long-term fitness consequences of behavioural choices are unpredictable.

3. Behavioural control through the proximate architecture framework

In this section we describe some key elements in decision making and behavioural control in animals. As we move from the idealized environments typical for the Euler–Lotka models to moderately variable or complex environments, finding optimal responses to all possible situations would require highly advanced (Goldstein and Gigerenzer, 2011; McNamara and Houston, 2009) and energetically expensive brains (Nilsson, 2000). Natural organisms instead rely on simpler heuristics to handle large amounts and different types of information (Gigerenzer, 2004; LeDoux, 1998). These ‘rules of thumb’ have been selected to perform well in a variety of situations, including those never encountered before (Hutchinson and Gigerenzer, 2005).

Behavioural control in animals is organized as heuristics embedded within an architecture of other modules or functions of the organism. The architecture can be described as a series of weakly connected survival circuits (LeDoux, 2012) which link perceptions to behaviour. Also referred to as “the emotion system”, it plays a central role in animal decision making (Cabanac, 1979; Leknes and Tracey, 2008; Mendl et al., 2009) through evaluation of perceptions and selection of the instrumental behavioural and physiological responses (de Waal, 2011; LeDoux, 2000, 2012; Panksepp, 2005). However, this proximate architecture is not limited to those concepts psychologists call emotions (Izard, 2010), as survival circuits exist for all drives that impact attention and behaviour of the organism (LeDoux, 2012). We emphasize that in using concepts often associated with human feelings, particularly the word “emotion” with reference to LeDoux's work, we do not imply any mental awareness of these internal processes in animals.

The architectural structure described above can be implemented in individual-based modelling (Fig. 1; Giske et al., 2013), and in the following we will sketch the process of decision making in this framework, leaving the more technical modelling aspects for Appendix. We use an example from fish behaviour to illustrate the concepts, but this specific formulation is only one possible way of outlining the proximate architecture (see e.g. Evers et al., 2014, 2015).

3.1. Biological mechanisms

Specific to the architectural approach is the level of detail of the representation of the chain of events from immediate perceptions to instrumental behaviour (Giske et al., 2013; LeDoux, 2012). First, all perceptions (including signals from within the body) are evaluated in the brain, where different competing needs are weighed against each other to determine the most important task. Next, the organism focuses on solving this task. LeDoux (2012) calls this chain from perception to behaviour a survival circuit, and animals can have several such survival circuits running in parallel. These may for instance be related to hunger, thirst, sleepiness, curiosity, and fear; thus we may say the survival circuits are bundled, as illustrated in Fig. 1. Each circuit has different modules; hunger

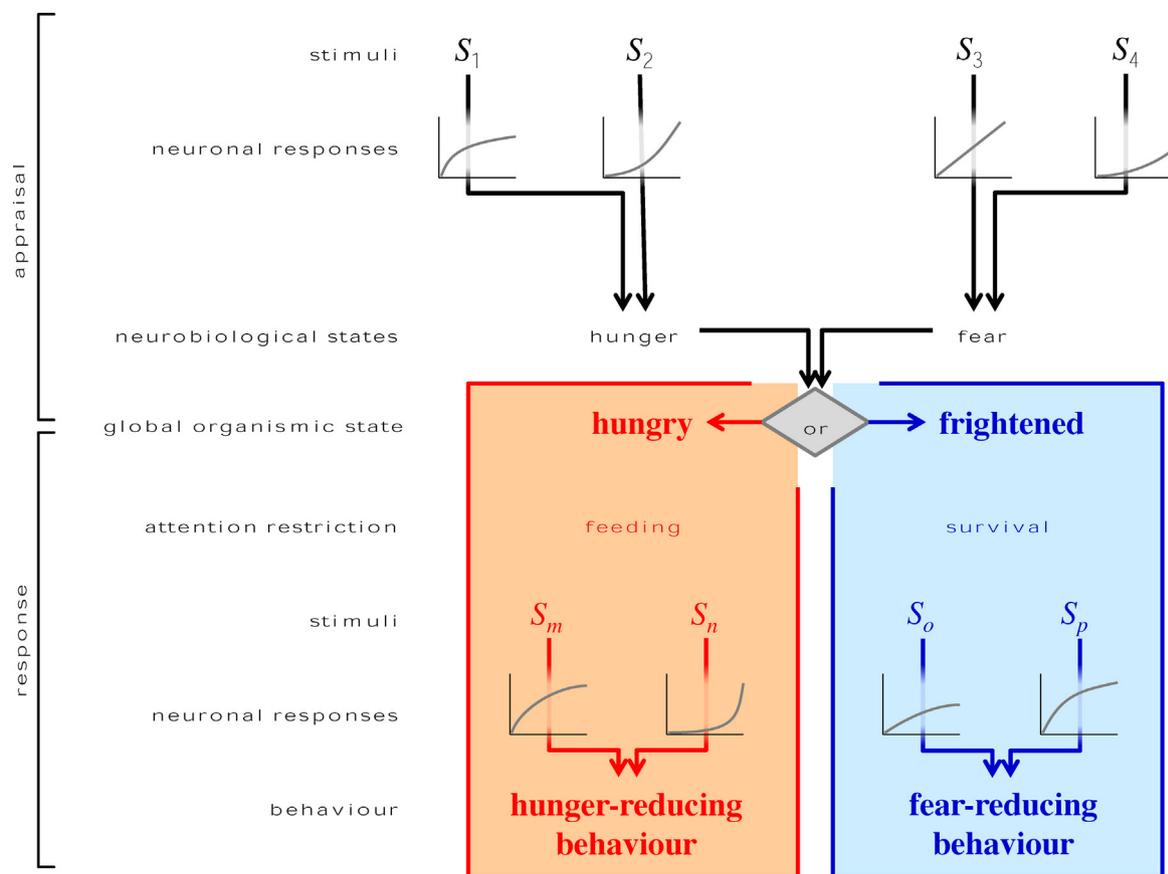


Fig. 1. A generalized framework for behavioural control through the proximate architecture of decision-making. The brain can hold several neurobiological states simultaneously (here exemplified with hunger and fear). The strength of these states depends on the combined neurological responses from one or more stimuli (internal, e.g. stomach fullness, or external, e.g. behaviour of conspecifics). Each neuronal response function is determined by genetically inherited traits, which gives the potential for different relationships between stimuli input and response strength between individuals (see Eq. (1) in Appendix and examples in Fig. 2). Inherited traits will also open for emergent adaptations due to natural selection. The relative weight given to the neuronal responses may further be modulated by processes and states (not shown), such as sex, developmental stage, physiological state, and experience. The strongest neurobiological state determines the global organismic state, in this case whether the organism is hungry or frightened. When in one of these states, the attention of the organism is focussed on making the best available physiological and behavioural response.

may for example be evoked by seeing food, seeing others eat, or by physiological needs of the organism. The survival circuit must be understood over several time scales, with the shortest one being the state-dependent response to sensory information, at intermediate scales it includes learning and memory (not included in Fig. 1), and the longest time scale involves genetic adaptation of the gene pool. As such, it belongs to the wider class of multi-scale phenomena (Hogeweg, 2007; van der Post and Semmann, 2011b; van der Post et al., 2015).

3.2. Appraisal phase

The first phase, of retrieving and comparing information, is called the appraisal phase (LeDoux, 2012). For each survival circuit, each of several sensory inputs evokes a neuronal response in the brain (see Eq. (1) in Appendix). The weight of a given response may depend on modulatory mechanisms (not shown in Fig. 1), for example short-term effects of memory, long-lasting effects of learning, and hormones more active in some life stages of the organism. There may also be life-long effects of inherited metabolic propensities, for instance linking metabolic rate, food demand, and aggression, or metabolic rate and risk willingness (Houston, 2010; Reale et al., 2010), or due to manipulation by parasites (Barber and Dingemans, 2010; Barber et al., 2000).

The sum of all the neuronal responses in a given survival circuit determines the strength of the neurobiological state in the brain, for instance hunger, thirst, sleepiness, curiosity, or fear. The

neurobiological states may compete in a winner-takes-all fashion where the strongest determines the current psychological state of the organism, which is called the global organismic state (GOS, LeDoux, 2012). The GOS is a state of the whole organism, not only the brain, and it may have neurological, physiological, and behavioural manifestations. The model outlined in Fig. 1 only considers two states; 'hunger' and 'fear' (see Evers et al. (2014, 2015) for a similar model with 'fear' and 'like' in primates). While it is mathematically straightforward to expand the model to include more neurobiological states, the benefit of a more realistic representation needs to be traded against increased model complexity.

3.3. Response phase

The determination of the GOS is the start of the second half of Fig. 1, called the response phase (LeDoux, 2012). Here, the organism will have a physiological and a behavioural response, both aimed at removing or reducing the cause of the GOS. If thirsty, the animal will seek water, if hungry it will look for food. In this process, attention restriction is an important part of the physiological response, where the animal pays more attention to information relevant to its GOS and less, or none, to other cues (Dukas and Kamil, 2000; Lima and Bednekoff, 1999; Miller et al., 2012; Purser and Radford, 2011; Tombu et al., 2011).

Although mutually exclusive behaviours, such as vigilance and feeding, has been modelled using classical optimization approaches (e.g. Houston et al., 1993; McNamara and Houston,

1992), the existence of a GOS, attention restriction, and narrowing of behavioural options, represent a major change of perspective introduced by the proximate architecture framework. The cost of attention restriction is lower sensitivity to other stimuli: frightened fish may for instance have lower efficiency in catching food (Purser and Radford, 2011). So how realistic is it? First, from an adaptationist perspective, there is no benefit in having a range of alternative global organismic states if the organism can execute its full behavioural repertoire from within any of them. The most likely purpose of being sexually aroused or of being frightened is to narrow the focus of attention to solve a task that is important for fitness. Secondly, the attention restriction mechanism exists even in sophisticated human brains (Tomblu et al., 2011), but this does not mean that organisms cannot experience aspects of several GOS simultaneously. In some situations different GOS are not in opposition, but rather complementary. An example is the combination of 'like' and 'fear' social attitudes towards other members of a primate group (Evers et al., 2014, 2015).

The model outlined in Fig. 1 does not grade the strength of the GOS, while animals do. Whether an animal is terrified or only alerted will likely impact how long it may take to consider other neurobiological states (through memory, which is not yet included in Fig. 1), and also whether it can consider more than one neurobiological state at a time. A stickleback can dynamically balance its hunger drive and its perceived predation risk (Heller and Milinski, 1979; Milinski and Heller, 1978) through a gradual regulation of its attention towards prey and predators (Milinski, 1985). Also, if all neurobiological states are weak, it may be adaptive for the animal not to focus its attention. This has been termed 'routinized behaviour' by Guilford and Dawkins (1987), and can technically be seen as yet another GOS.

3.4. Behavioural patterns

Giske et al. (2013) modelled spatial behaviour of an open-ocean midwater fish using the proximate architecture framework. The overall model output described a fish population performing diel vertical migration, residing in shallow waters at night and migrating to deeper waters during daytime (Clark and Levy, 1988; Hugie and Dill, 1994; Werner and Gilliam, 1984), as observed in pelagic planktivores (Balino and Aksnes, 1993; Goodson et al., 1995; Kaartvedt et al., 2008; Torgersen et al., 1997) and modelled (Rosland and Giske, 1997; Staby et al., 2013). All models predict a similar behavioural patterns (diel vertical migration with some vertical extension of the migrating layer), which shows that assuming some instantaneous trade-off as in optimization and game models or assuming attention restriction and sequential focussing on the most urgent task may result in the same overall space use patterns of populations.

The similarity in movement patterns is mainly due of the strong structuring force of light in aquatic environments. Light decays rapidly with water depth and impacts detection distances of predators as well as the fish's own encounter rate with prey (Aksnes and Utne, 1997). Modelling vertical distribution either as a density-dependent game through ideal free distribution (Fretwell and Lucas, 1970) by ignoring the physiological state of individuals (Giske et al., 1997) or as a state-dependent life history optimization (Mangel and Clark, 1986; McNamara and Houston, 1986) by ignoring competition in a physiology-driven optimization model (Fiksen and Giske, 1995) resulted in the same overall picture. The proximate architecture framework can on one hand be used to evaluate the importance of each factor, but it also allows for even more detailed descriptions of organisms and environments. As we will discuss in the following, one of the main differences between classical optimization and game theory models and the proximate

architecture framework is that coexisting behavioural types with dissimilar preferences and space use can emerge in the latter.

3.5. Consistent behavioural types

Incorporating proximate costs and constraints are essential for studies of animal personalities (Bell, 2007; Biro and Stamps, 2008; Budaev, 1997; Dingemanse and Reale, 2005; Dingemanse and Wolf, 2013; Sih et al., 2004; van Oers et al., 2005). The growing interest in animal personalities arose from observations of consistencies in individual physiology and behaviour over time (Gosling, 2001; Houston, 2010; McCrae et al., 2000), but the mechanisms underlying these behavioural differences are generally unknown (Fawcett et al., 2014, 2015). Individuals in a proximate architecture framework are less flexible than 'optimal' individuals. They are restricted by local information and the architecture of their heuristics (in this case their individual neuronal response functions, see Appendix) and do not behave according to unconstrained calculations of detailed optimal policies. The populations modelled by Giske et al. (2013) evolved to maintain two or more variants of some neuronal response functions, i.e. individuals showed variation in 'personality' with a strong genetic basis. In particular, consistent individual differences emerged along the social/solitary-dimension, predominantly when hungry. In the neuronal response function this was related to how the presence of competitors was evaluated during feeding, some individuals had alleles coding for weak discomfort, while others had neuronal responses that gave strong discomfort when many competitors were present (Fig. 2). Individuals with strong discomfort would more often be found in low densities in the outskirts of the vertically migrating population, while individuals who tolerated competitors were usually found at high densities near the peak food concentration (Fig. 2). Thus, in the architectural model, the emergence of persistent behavioural types led to a wider space use of the fish populations. Coexistence of behavioural types has also been observed in evolutionary models without representation of proximate architecture, e.g. Eliassen et al. (2006) and van der Post et al. (2015).

The classical textbook explanations for diversity within populations are negative frequency-dependent selection (Ayala and Campbell, 1974; Fisher, 1930) and gene-environment interactions (Lewis, 1954) in spatially or temporally variable environments. However, an explicit representation of the behavioural architecture is in itself sufficient to generate and maintain phenotypic variation (Giske et al., 2014). The ultimate reason is that random mutations in the genes underlying the architecture of the heuristics are a source of *internal* variation among individuals, with the same principal effects as external environmental variation for differences in behaviours and phenotypes.

4. Evolving solutions: the genetic algorithm (GA)

Integrating ecological and behavioural aspects of the model with evolutionary dynamics is not a trivial task. An individual-based model embedded in a genetic algorithm is one way of studying complex, near-realistic ecological problems for which pure game or optimization techniques are not well suited. The GA is a powerful algorithm that needs to be used with care and consideration, and the method represents a shift in focus from the equilibrium solutions to evolutionary change in varying fitness landscapes.

A variety of methodologies can be used to model behaviour in individuals. If we assume that organisms do not interact, then no feedbacks are involved and optimization techniques can be used to identify the fitness peak (Clark and Mangel, 2000; Houston and McNamara, 1999). In most cases, however, the behavioural decisions of individuals have consequences for others, and the

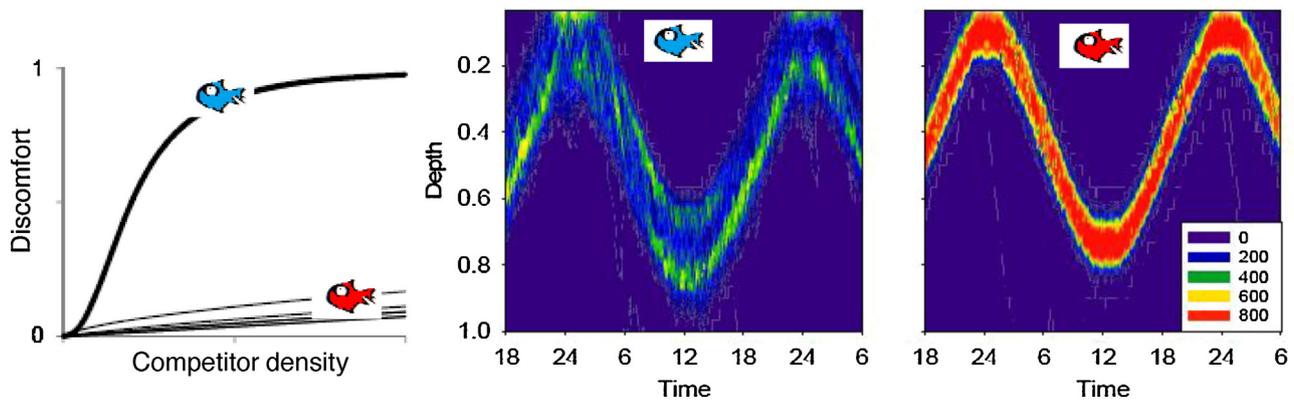


Fig. 2. Personality arising from the proximate architecture framework. A population consists of two groups of fish (left) which differ significantly in one gene determining the neuronal response towards competitors when hungry (see Fig. 1). The blue type (centre) has evolved allele values ($y=0.1-0.5$, see Eq. (1) in Appendix) that give strong discomfort even at low competitor densities, while the red fish (right, $y=9.7-10.0$) more or less ignore competitors and seek the depth with the highest initial food concentration. The blue type is hence found both shallower and deeper than the red fish, at the outskirts of the vertically migrating population. Redrawn from Giske et al. (2013).

way others behave will in turn influence the outcome of a behavioural decision. With such frequency-dependent feedback, we can use game theoretic approaches or hill-climbing algorithms such as adaptive dynamics that utilize local selection gradients to improve strategies until they reach an evolutionarily stable strategy (Dieckmann and Law, 1996; Metz et al., 1992). These methods work best when one or a few trait values characterize the strategy of each individual. A more detailed description of the organism requires several to many parameters, which allow behaviours to depend on social context and feedbacks from multidimensional environments. In such cases one is often left with individual-based simulation models as the only feasible option.

IBMs are based on one of the most significant biological structures: the organism. The most significant evolutionary characteristics of an organism are its existence and number of offspring. These bookkeeping traits were already used by Euler (1760) to explain differences in the population growth of nations. The strength of the IBM approach is to expand the description of individual traits to include changes through an organism's lifetime and variation among individuals. While the pedigree of IBM models gradually has expanded into a wide bush (Grimm and Railsback, 2005), we concentrate on IBM as a tool to study populations of high spatial and temporal resolution. An IBM allows each organism to be traced in space and time, which simplifies and improves the representation of interactions among individuals (Grimm and Railsback, 2005; Stillman et al., 2015), and it provides a link to phenomena and structures in the physical landscape. Hence, the strong restrictions in descriptions of organisms in game theory and of competitors or environmental change in state-dependent life history theory (Houston and McNamara, 1999; Railsback and Harvey, 2013) are much relaxed in IBMs (DeAngelis and Mooij, 2003, 2005). However, a link to evolutionary adaptation is not ensured by the IBM alone. For this, a mechanism for heritability of traits must be added.

4.1. The gene pool

Although "individual" by name, IBMs are tools for the study of populations (Grimm and Railsback, 2005). Even if the individual is the focus of a study, the gene pool of the population is the continuously evolving entity from which the individual gets its properties. When John Holland understood the adaptive force of natural selection on the gene pool, he invented the genetic algorithm (GA) as an evolutionarily mathematical equation solver for complex

problems (Holland, 1975). The central idea of Holland's GA was that the solution to a problem could be found by iteration of competition experiments. For each new generation of experiments, those with the lowest quality were discarded while the remaining could be slightly modified before the next round. In the context of a biological IBM, this means that some parameter values of organisms are coded as genes, where individuals that fail to reproduce do not pass their genes on to the next generation. For those that do, mutations may alter the genes while sexual reproduction mixes genes into new combinations in future organisms.

Thus, while the GA is one among many mathematical hill climbing techniques, it is unique in its ability to mimic evolutionary processes in complex environments. It is therefore a natural extension of the IBM approach (Fiksen, 2000; Hamblin, 2013; Higginson et al., 2015; Huse and Giske, 1998; Ruxton and Beauchamp, 2008; Wood and Ackland, 2007). Where the Euler-Lotka equation is an analytical solution to an implicitly evolving population (Lotka, 1925), the GA numerically simulates a gradual approach towards the solution, similar to an explicitly evolving population. Combining IBM and GA simply means to run the IBM over many generations, passing genes of the survivors on to their offspring. In addition, the GA has the capacity to utilize all the environmental and organismic diversity that an IBM can offer. The combined IBM and GA models may include processes central in life history theory, game theory, and community ecology. While the ecological toolbox contains well-established methods for studying organismal, social or environmental complexity, the situation is different when two or more of these complexity dimensions need to be considered simultaneously. The fact that evolving IBMs are not restricted to stable environments over generations, stable population sizes, and populations of identical individuals, shows how versatile they are for studying natural populations. In addition, strategies or behavioural rules need not be specified in advance but can emerge as a result of different physiological or behavioural trade-offs or life-history constraints in various environments (Burtsev and Turchin, 2006; Fiksen, 2000).

4.2. Genetic architecture

In the GA central traits are coded as genes and inherited by offspring of the surviving and reproducing parent (Hamblin, 2013; Sumida et al., 1990). There are, however, limitations in the genetic structure made in most models, as our understanding of physiological and developmental processes is still insufficient to create

genotype-to-phenotype maps. Broadly there are three approaches: to model genes and alleles explicitly as done by population genetics (Otto and Day, 2007), to use quantitative genetics which can incorporate experimentally observed variance and co-variances between phenotypic traits (Dunlop et al., 2009; Lande, 1976; Lynch and Walsh, 1998), or to assume a more loose link between inherited entity and its phenotypic effects but then losing the ability to make predictions about actual rates of evolution. One flexible and common approach is to assume that genomes are haploid, and that reproduction is asexual or a recombination of the haploid genomes of two individuals (Hamblin, 2013). For a given ecological scenario, the solution found using a GA may therefore depend on how reproduction, recombination, and mutation are implemented in the model (Hamblin, 2013; Ruxton and Beauchamp, 2008).

When genes are inherited independently of each other and mate choice is random, any allele on any gene may be paired with very different alleles of other genes in the next generations. As a consequence, alleles that are able to persist across generations (in the GA) are those that can successfully associate with most other alleles in the gene pool and still form viable offspring (Dawkins, 1976). While this may be fine in ecological landscapes with one single peak, adaptation of the gene pool to multi-peaked landscapes may require coevolution of specific alleles of several genes. This is most easily facilitated by co-location on the same chromosome so that the alleles are inherited together, or even in the same region of a chromosome to prevent separation in the offspring through recombination. Natural organisms commonly have a non-random arrangement of genes on their chromosomes, suppression of recombination outside hot-spots (Myers et al., 2005), and a non-random mating pattern. If the genome consists of more than a few genes, the modeller would need to consider which genes should be linked through inheritance, and which traits are preferred in mate choice. We illustrate this by the Giske et al. (2013) model of fish behaviour, where the behavioural decisions are explained in Fig. 1. It is not intuitive how 18 genes of 9 neuronal response functions, 4 modulatory genes and one gene for sex determination should be arranged on one or several chromosomes (Fig. 3). The chromosomal arrangement of Giske et al. (2013) was that the two parameters describing a neuronal response made up one chromosome which was never altered by recombination. Hence, only mutation could change the shape of a neuronal response function. Approximately half the neuronal response chromosomes of an offspring was inherited from each parent, which means that complex traits involving the coevolution of several neuronal response functions could not evolve as stable entities. Similarly, the modulator genes and the sex determination gene constituted one chromosome inherited without internal recombination. This means that modulation may become sex-specific, and that any sex-specific behaviour had to be rooted in these modulatory genes. Alternative configurations would be to arrange genes related to hunger or fear on the same chromosome, or all genes in the appraisal phase (Fig. 1) into one and those in the response phase into another. Such alternative genetic architectures would through avoidance of recombination within a chromosome allow coevolution of alleles and may thereby impact the number of behavioural types or animal personalities (Bell and Sih, 2007; Dingemans et al., 2010) which could coexist in a population.

4.3. Sensitivity analysis

The proximate architecture framework yields an element of degeneracy (many-to-one-mapping, Wainwright et al., 2005) for the evolving gene pool and for personality traits (Giske et al., 2014): One can think of Fig. 1 as a roadmap, where individuals as well as populations differ in which routes are highways. For example, an organism may be hungry because its stomach is not full or because

its appetite increases when seeing food. Hunger may also become the GOS if the organism does not sense any predators nearby, or can hide among conspecifics. This opens for several routes to states and behaviours, for many different personality types within a population, and for many differently evolved populations towards similar environments (Giske et al., 2014). Such degeneracy is also seen in artificial neural network models (Duarte et al., 2011; Enquist and Arak, 1994; Huse and Giske, 1998), in cellular innovations (Wagner, 2011) in developmental processes of animals (Doyle and Csete, 2011; Draghi and Whitlock, 2012; Kirschner and Gerhart, 2005), and even in the translation of the genetic code to amino acids and proteins. As degeneracy is natural in biological systems (Wainwright et al., 2005), a part of the sensitivity analysis should be to characterize it and study how it affects the evolution of the population and the behavioural responses through standardized virtual experiments. Here similar response patterns could result from different pathways, and lead to comparable life history traits, space use, or personality. Even with desktop computers and user-friendly programming software (e.g. NetLogo, Railsback et al., 2006; Sklar, 2007) we can use these techniques to train our intuition about effects of changing environments and produce interesting predictions that could be tested on natural populations (Evers et al., 2014, 2015).

As an illustration of the type of sensitivity analysis performed on models with explicit architecture, we have tested the effect of altering the arrangements of the 23 genes in the Giske et al. (2013) model (Fig. 3). While one can construct plausible biological arguments for all six chromosomal architectures, there is as far as we know no good a priori way to determine a preference for one over the others. The best result, measured by the population egg production which is the product of female survivorship and fecundity, was obtained by the fully adaptive chromosome structure (number 5). Three of these six chromosomal arrangements are approximately equal with respect to offspring production. Hence, there are likely many almost equally good ways of arranging genes on chromosomes. In two arrangements, egg production was considerably lower (Fig. 3), which calls for some initial caution and a need to experiment with chromosome structure. Other challenges that are not considered here may select for different chromosomal arrangements or there might be general chromosome structures that are profitable under a range of environmental conditions. Rather than predefining different architectural configurations, one could also let the chromosomal structure evolve (e.g. Crombach and Hogeweg, 2007, 2008), which would alleviate the problem of predefining and choosing a genetic structure.

4.4. Environmental variation and over-fitting

Whatever method used to investigate the effect of chromosomal structure, there is a risk of over-fitting the solution (Tetko et al., 1995), so that the evolved genetic structure excels in the current scenario but is too specific to tackle other realistic scenarios. Related to this issue is the problem of deciding the number of generations to run in the GA. There is always a chance that an improved solution will be found after more generations, but this will also increase the risk of over-fitting. Environmental stochasticity, for instance in the form of intergenerational 'climate variation', may prevent or reduce the risk of over-fitting (Giske et al., 2013). To facilitate comparisons between populations, the evolved gene pools could be simulated in a standard environment every n generations, or the behavioural responses of the final population determined in standardized tests.

Running the model for only a few generations may, on the other hand, leave insufficient time for the GA to locate peaks in the fitness landscape. We commonly observe a steep increase in fitness over the first few generations in the GA, particularly if the

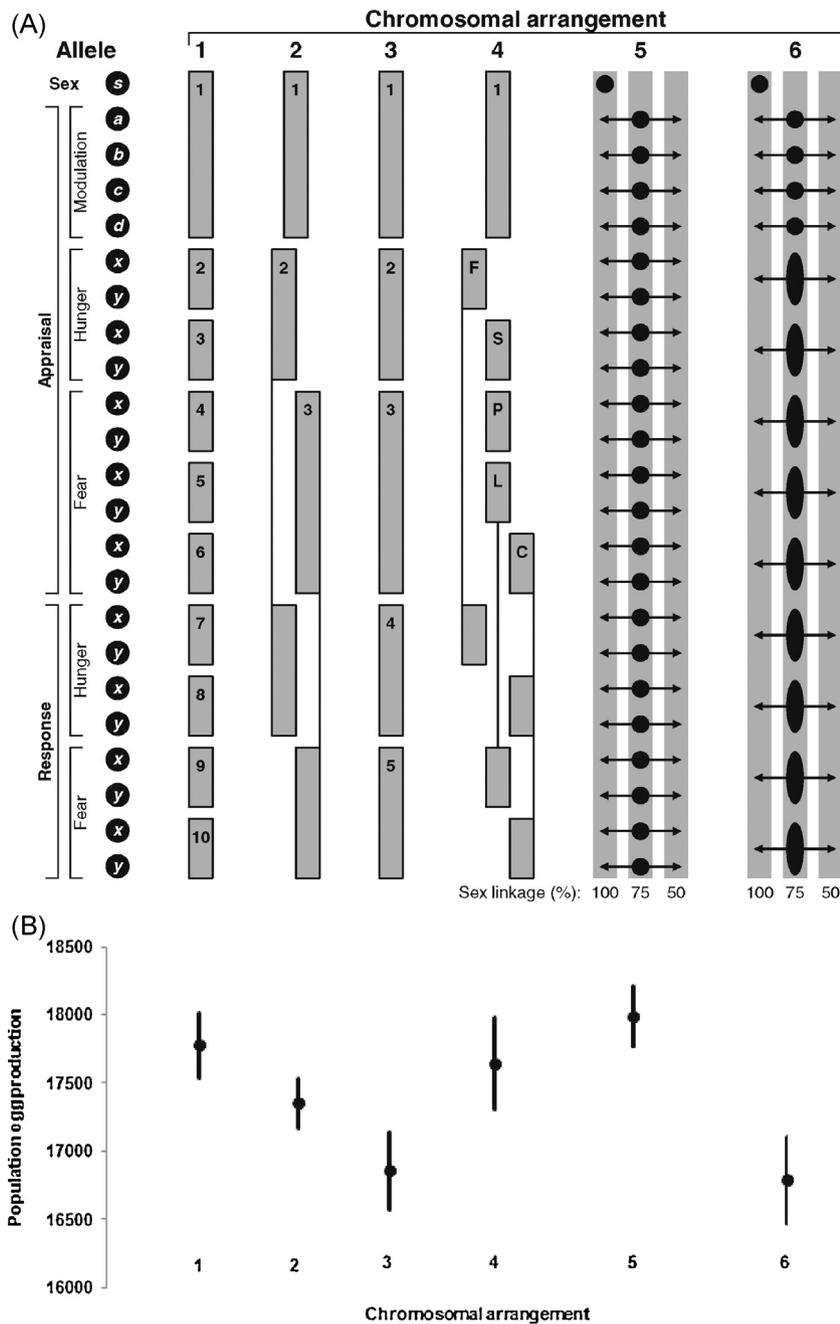


Fig. 3. Sensitivity to chromosomal arrangement. (A) Arrangements of genes coding for neuronal responses, modulation and sex on 6 different chromosome structures. The F, S, P, L and C labels on chromosomes are for genes related to neuronal responses to food, stomach fullness, predation, light and conspecifics, respectively. (1) The Giske et al. (2013) chromosomal architecture: one chromosome for each of 9 neuronal response (NR) functions and one for gender and modulation, in total 10 chromosomes. (2) One chromosome for gender and modulation, one for all NRs related to fear, and one for all NRs related to hunger, in total 3 chromosomes. (3) As (2), but separate chromosomes for fear and hunger in appraisal and response phases of Fig. 1, in total 5 chromosomes. (4) One chromosome for gender and modulation, one for all NRs related to food, conspecifics and light, respectively, and separate chromosomes for the two NRs related to predators and stomach fullness, in total 6 chromosomes. (5) Three equally large adaptive chromosomes, where each gene can mutate position. Offspring will inherit the chromosome structure of its same-sex parent, and the probability of inheritance of all (or none) genes on the chromosome from same-sex parent is 100%, 75%, and 50% on chromosomes 1–3, respectively. (6) As (5), but where both genes in one NR must be on the same chromosome. (B) The egg production in fish populations (from the Giske et al. (2013) model) with these chromosomal arrangements. Each simulation is initiated with 10,000 fish larvae and run for 30,000 generations, with substantial stochastic environmental variation at short-term and generational time scales. The bars show the mean egg production and 95% confidence interval among 10 replicate simulations between generation 20,000 and 30,000.

population is seeded with random allele values. In the fish model of Giske et al. (2013, 2014), population egg production levelled off after around 1000 generations, and Andersen (2014) did not find quality improvements in the model output after 1000 generations. As there is always an inherent uncertainty in evolutionary modelling whether the algorithm has arrived at or near a fitness peak, we recommend running multiple populations with some very long

simulations to determine a reasonable number of generations. The adaptation period depends on the goal of the modelling, as the time to adapt a trait depends on the fitness costs of suboptimal solutions (Fisher, 1930). Life history, growth, or space use patterns in the Giske et al. (2013) model generally converge early in simulations whereas genetics or personality-related traits, takes longer to stabilize.

4.5. Effects of implicit assumptions

The reproduction scheme will influence the evolutionary process as well as the output of the model. Mate choice is important in sexually reproducing organisms, and different rules for mate selection may be implemented in ecological modelling. For instance, Giske et al. (2013) allowed females to choose a mate among males located at the same depth. Females mated with the largest of the first three males encountered and this resulted in sexual selection favouring faster growth and more risk-prone behaviour in males. In other modelling scenarios, females had no mate preference which resulted in smaller males that were rewarded for higher survival rather than faster growth (Giske et al., 2014). As illustrated by this example, it is quite likely that patterns predicted by a model may depend on factors not considered by the modeller or presented to the reader. This problem is not specific to GA, but because the algorithm is designed to solve complex problems, a side effect is that it also finds and exploits weaknesses in such assumptions. At the other end of the model complexity spectrum, organisms are represented by simple processes and few variables. When comparing the predictions of these models to natural systems, the processes that are not considered in the model need to be represented by fixed parameters or the few processes that are explicitly modelled. In practice, this implies that many of the degrees of freedom in a complex model are hardwired in a simpler one.

4.6. “Handle with care”

While our methodology is one step nearer the behavioural architecture of natural organisms, it may also be computationally more intensive and require attention to technical details. Thinking in terms of architecture of behavioural control will be useful for a wide range of theoretical, experimental and field studies, but important insights can also be obtained through individual-based evolutionary simulations without being explicit about the proximate architecture (e.g. Higginson et al., 2015; Hogeweg, 2007; van der Post and Semmann, 2011b; van der Post et al., 2015; Wood and Ackland, 2007). Using GA to simulate behavioural responses may invoke costs and benefits which yield a surplus only when analytical methods are insufficient (Ruxton and Beauchamp, 2008). Such situations are when environmental variation is important, or when behaviour is simultaneously impacted by a range of factors which makes pure optimization or pure game approaches too simplistic. However, it is hard to anticipate what is lost when using simpler models. As discussed above, a model of vertical migration with explicit architecture was not only able to combine density-dependent and state-dependent trade-offs, it also revealed a potential for vertical structuring based on consistent behavioural types.

5. Individual-based ecology: building on the gene pool

The Alfred Lotka tradition in evolutionary ecology has led to elegant analytical and numerical findings through life history theory (Fisher, 1930; Mangel and Clark, 1986; McNamara and Houston, 1986; Murdoch, 1966; Williams, 1966), optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966), and game theory (Fretwell and Lucas, 1970; Maynard Smith and Price, 1973). While there are many reasons for continuing the development of these methods, it is not straight-forward to combine them in population models (Houston and McNamara, 1999; Railsback and Harvey, 2013). While Individual-based Neural network genetic algorithms (Huse and Giske, 1998), hedonic modelling (Giske et al., 2003), and eco-genetic IBMs (Dunlop et al., 2009) can integrate across age-, state-, and density-dependent processes, and solve the

computational challenge, the proximate architecture framework described in this paper is based on mechanisms of decision making found in a wide range of natural organisms (Cabanac, 1979; Macnab and Koshland, 1972; Mendl et al., 2009; Stock et al., 1989) and it can also be implemented in models.

Models that consider the effect of individual variation and evolving gene pools lead to two important insights that differ from predictions based on traditional optimality models. First, as organisms need to solve immediate problems and respond to the current and local environmental conditions, their responses may not be optimal in the classical sense. Strategies that are robust and perform well under a variety of situations are often more beneficial in the long run (Yoshimura and Clark, 1991; Yoshimura and Jansen, 1996) and inter-dependencies between behaviour, physiology or life-history traits may allow for several coexisting solutions to similar problems (Mangel and Stamps, 2001; Stamps, 2007). Next, at the population level there is a similar analogy, as the diversity in the evolved gene pool has evolved for being resilient to changing conditions and the coarser contours of the fitness landscape. The adaptive diversification within the gene pool or between populations is facilitated by the proximate architecture for decision-making, which allows many different but equally valuable pathways from sensing through to behaviour (Giske et al., 2014).

Human impact on the planet makes it increasingly important to understand complex problems and interactions on multiple scales. Community ecology is the sum of social interactions and local environmental effects on single individuals, which again are consequences of adapted and often coevolving gene pools. The proximate architecture framework is not only a useful tool for finding adaptive behaviour in complex situations, but also a better representation of the behavioural responses and the underlying genetic architecture typical for natural populations. As a modelling framework it may also bridge the individual focus of behavioural ecology with the population focus in many other ecological disciplines.

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Appendix. Examples and functions

Giske et al. (2013, 2014) modelled spatial behaviour in an IBM of a fish population using the proximate architecture framework (Fig. 1), and a GA to evolve adaptive values of genes. All perceptions P were scaled linearly relative to the strongest observation of each perception, and the neuronal response R to each perception P was modelled as a sigmoidal function (Brown and Holmes, 2001)

$$R = \frac{(P/y)^x}{1 + (P/y)^x} \quad (1)$$

where x and y are genes with allele values in the 0.1–10.0 range, which give responses $0 \leq R \leq 1$. The allele of the y -gene determines the perception P at which the response $R = 0.5$, and the x gene determines how rapidly the response increases with P . Depending on the values of x and y , the shape of the function may range from near linear to a threshold-type response within this parameter range ($0 \leq P \leq 1$). This allows for graded responses to weak signals as well as saturation of information (Aksnes and Utne, 1997; Ashley et al.,

2007). A clear benefit of this approach relative to that of artificial neural networks is that the function in Eq. (1) has a clear biological interpretation as it displays how the organism evaluates a single perception.

We have tested whether this function is flexible enough by allowing the individuals to use a neuronal response function with three additive elements (and six genes):

$$R = \frac{(P/y_1)^{x_1}}{1 + (P/y_1)^{x_1}} + \frac{(P/y_2)^{x_2}}{1 + (P/y_2)^{x_2}} + \frac{(P/y_3)^{x_3}}{1 + (P/y_3)^{x_3}} \quad (2)$$

We found that for the ecological scenario of Giske et al. (2013), decisions based on Eqs. (1) and (2) were the same for all organisms in all time steps of their life, except for a few individuals who utilized all three additive components in Eq. (2) when evaluating fear during predator attacks (Andersen, 2014). Thus, except in very complex model environments, Eq. (1) will do the job.

Each neuronal response R has an additive effect on one neurobiological state (Fig. 1).

$$\text{Hunger} = M \times (R_{A_{\text{stomach}}} + R_{A_{\text{food}}}) \quad (3)$$

$$\text{Fear} = (1 - M) \times (R_{A_{\text{light}}} + R_{A_{\text{predators}}} + R_{A_{\text{conspecifics}}}) \quad (4)$$

The subscript A indicates that the neuronal response is used in the appraisal phase (Fig. 1, top). The modulatory mechanism (M) is in this example (Giske et al., 2013) a life-history trade-off between growth and survival that may vary with the developmental state of the organism. In the model, four genes give the M values at four different body masses (with other values for M found by linear interpolation between these points). The global organismic state (GOS) of the individual is then determined by the stronger of the neurobiological states of hunger and fear in this case.

The response phase depends on the global organismic state, where attention narrows the behavioural response to one adequate for the situation (Fig. 1). In the case of habitat selection for a pelagic planktivore, the organism could choose to move up or down in the water column or to stay at its current location. The surrounding depths (z) are evaluated by new neuronal responses and the fish moves to the depth that maximizes net neuronal response (Fig. 1, bottom). For hungry fish (Eq. (5)) the response from seeing food gives a positive effect while the response from seeing conspecifics has a negative effect. For frightened fish (Eq. (6)) the response from conspecifics have a positive effect while light have a negative effect, since risk is strongly linked to light intensity in pelagic environments, which decays fast with depth (Giske et al., 1994):

$$\text{Hungry fish} : \max_{z=-1, z, z+1} (R_{H_{\text{food}}} - R_{H_{\text{conspecifics}}}) \quad (5)$$

$$\text{Frightened fish} : \max_{z=-1, z, z+1} (R_{F_{\text{conspecifics}}} - R_{F_{\text{light}}}) \quad (6)$$

Each individual had 23 genes (9 x - and 9 y -genes, 4 M genes and one sex-determination gene) that determined response functions and modulatory mechanism. Evolving in a genetic algorithm, it took a few thousand generations to find quasi-stable solutions. Much of the adaptive evolution was done within the first couple of generations, and most was done in the first hundred. The long tail in slower improvement is due to the weaker selection gradient near the optimum (Fisher, 1930), plus undulations in the fitness landscape caused by density-dependent growth and survival and frequency-dependent selection (Giske et al., 2013).

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