

Effects of the Emotion System on Adaptive Behavior

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ABSTRACT: A central simplifying assumption in evolutionary behavioral ecology has been that optimal behavior is unaffected by genetic or proximate constraints. Observations and experiments show otherwise, so that attention to decision architecture and mechanisms is needed. In psychology, the proximate constraints on decision making and the processes from perception to behavior are collectively described as the emotion system. We specify a model of the emotion system in fish that includes sensory input, neuronal computation, developmental modulation, and a global organismic state and restricts attention during decision making for behavioral outcomes. The model further includes food competition, safety in numbers, and a fluctuating environment. We find that emergent strategies in evolved populations include common emotional appraisal of sensory input related to fear and hunger and also include frequency-dependent rules for behavioral responses. Focused attention is at times more important than spatial behavior for growth and survival. Spatial segregation of the population is driven by personality differences. By coupling proximate and immediate influences on behavior with ultimate fitness consequences through the emotion system, this approach contributes to a unified perspective on the phenotype, by integrating effects of the environment, genetics, development, physiology, behavior, life history, and evolution.

Keywords: phenotype, emotion, attention, behavior, fish, animal personality.

Introduction

From physiology, via sensory biology and neurobiology, to psychology, the empirical sciences describe the mechanisms that have evolved so that animals behave and successfully reproduce in changing environments. In recent years, there have been calls for a theory that integrates proximate elements derived from empirical studies with the ultimate motivation underlying evolutionary behavioral ecology (Ricklefs and Wikelski 2002; DeAngelis and

Mooij 2003; McNamara and Houston 2009; Fawcett et al. 2013). It is even possible that the lack of a holistic theory of the phenotype prevents efficient communication between evolutionary behavioral ecology on the one side and quantitative genetics (Dingemanse et al. 2010), comparative physiology (Gilmour et al. 2005), evolutionary psychology (White et al. 2007), neurobiology (Pravosudov and Smulders 2010), or ethology (McNamara and Houston 2009) on the other.

Early models of animal behavior omitted proximate complexities with a broad-scale assumption referred to as the phenotypic gambit (Grafen 1984), in which the phenotype is considered unconstrained and only the fitness consequence of behavior was modeled (e.g., optimal foraging [Emlen 1966; MacArthur and Pianka 1966], life history [Murdoch 1966; Williams 1966], games [Fretwell and Lucas 1970; Maynard Smith and Price 1973], and state dependence [Mangel and Clark 1986; McNamara and Houston 1986; Houston et al. 1988]). The phenotypic gambit allowed the integration of individual strategies with ultimate fitness, but still today the proximate mechanisms through which organisms solve problems are largely ignored (Sih et al. 2004a; Dingemanse et al. 2010; Fawcett et al. 2013).

Many studies have included one or a few proximate constraints, such as sensory capacity, attention, learning, memory, or personality. However, the entire suite of mechanisms from sensory biology to behavior has coevolved. For example, cognitive and mental capacities are expensive (Nilsson 2000) and limited (Dukas and Kamil 2000; Sol et al. 2007), and the environment is variable and partly unpredictable. Therefore, decisions are made faster, and often better, if there are only a few alternatives or through the use of heuristics (Gigerenzer 2008), which requires filtering of sensory input, sometimes restricted according to the contextual situation (Lastein et al. 2008; Ashley et al. 2009). Genetic coding adds further proximate constraints, and from an evolutionary point of view the de-

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cision making has to be flexible and robust and must avoid fatal errors, even in situations never previously encountered (Hutchinson and Gigerenzer 2005). Unless these constraints are studied together, it is hard to infer the consequences of each one of them.

Incorporating proximate constraints is also essential to the growing interest in animal personalities (Sih et al. 2004b; Dingemanse and Reale 2005; van Oers et al. 2005; Bell 2007; Biro and Stamps 2008; Dingemanse and Wolf 2013). These arise from observations of consistencies in individual behaviors over time (McCrae et al. 2000; Gosling 2001), but the mechanisms responsible for behavioral programs are generally unknown. McNamara and Houston (2009, p. 670) argue that there is a need for models of “simple mechanisms that perform well in complex environments” rather than the traditional complex models of optimal behavior in simple environments (see also Gigerenzer 2004, 2008). Fawcett et al. (2013) argue that most behavioral ecologists unconsciously assume that behavior is independent of psychological mechanisms that constrain flexibility. They “urge behavioral ecologists to turn their attention to the evolution of decision mechanisms, as multipurpose rules which are capable of providing effective solutions to a wide range of problems” (p. 9). In this article we do so, by formulating a model based on recent insights from a range of empirical disciplines that all shed new light on processes involved with decision making.

In vertebrates, multipurpose rules are arbitrated through the “emotion system” (Rial et al. 2008; Cabanac et al. 2009; Mendl et al. 2011; LeDoux 2012), which describes the integration of information, motivation, and physiological state in determining physiological and behavioral outcomes (LeDoux 2000; Panksepp 2005; LeDoux and Phelps 2008; de Waal 2011). In turn, these outcomes affect the survival, growth, development, space use, and life history of the organism. Fish are a convenient group for studying adaptive principles of the emotion system, since they display both variation and consistency in behavior (Kalueff et al. 2012; Martins et al. 2012) but lack some of the higher cognitive functions that complicate the situation in higher vertebrates and humans (Ekman 1992; LeDoux 2000; Panksepp 2005).

According to the “survival-circuit” concept (LeDoux 2012), emotions are processes rather than states of the mind, and they contribute to the survival or fitness of the organism by focusing the attention of the organism and narrowing its behavioral interests. The first half of the survival circuit is “emotional appraisal.” It starts with sensory input, considers motivational impact related to developmental stage, and may potentially activate the organism into a “global organismic state” (LeDoux 2012), which means that not only some part of the brain but the whole organism is focusing on the situation. This is the

beginning of the second half of the survival circuit: the “emotional response,” consisting of physiological responses and instrumental behavior. Physiological activation enables the organism to focus its sensory attention, brain activity, and potentially also bodily functions, such as heartbeat and muscle tension, toward the present situation. The “instrumental behavior” will serve the needs of the global organismic state. While LeDoux (2000, 2012) concentrates on fear, we here generalize the survival-circuit concept of emotion and use it for fear and hunger. A fish in a hungry global organismic state will try to reduce its hunger, while a frightened fish will try to reduce its fear (fig. 1).

The emotion system evolved from a system of survival circuits (LeDoux 2012) as old as life itself (Macnab and Koshland 1972; Stock et al. 1989). Thus, while “emotional” has a negative connotation in everyday language, the emotion system and the ancient system of survival circuits have a vital role as integrators of information and arbitrators of conflicting behavioral options. To our knowledge, only conceptual models of the emotion system exist (Panksepp 2005; de Waal 2011; LeDoux 2012). Here we specify a mathematical model from genetic coding to reproduction, explicitly accounting for sensory input, neuronal processing, motivation, attention, and behavior, in line with the emotion system. In contrast to previous models of animal behavior, our work provides a unifying chain of proximate mechanisms, from the external environment all the way to differential reproduction and individual selection. We then show that the combination of genetics, physiology, development, and rich representation of the environment leads to stable and labile elements of personality and to spatial structure in the population. Our approach provides an integrated perspective on the phenotype and goes beyond optimality thinking and the phenotypic gambit by predicting adaptive behaviors subject to multiple constraints. This allows stronger interaction among behavioral disciplines and provides a richer template for thinking about decision making, adaptive behavior, and optimality versus constraints.

Material and Methods

Modeling the Emotion System and Behavior

As a starting point, we model behavior related to hunger and fear. Our model (fig. 1) is consistent with the survival-circuit concept (LeDoux 2012), but as a first step we omit the processes of learning and memory.

We also omit an explicit formulation for routinized, nonmotivated behavior (Guilford and Dawkins 1987) that can be seen as the neutral ground level of the emotion system, from which sensory input can initiate motivated

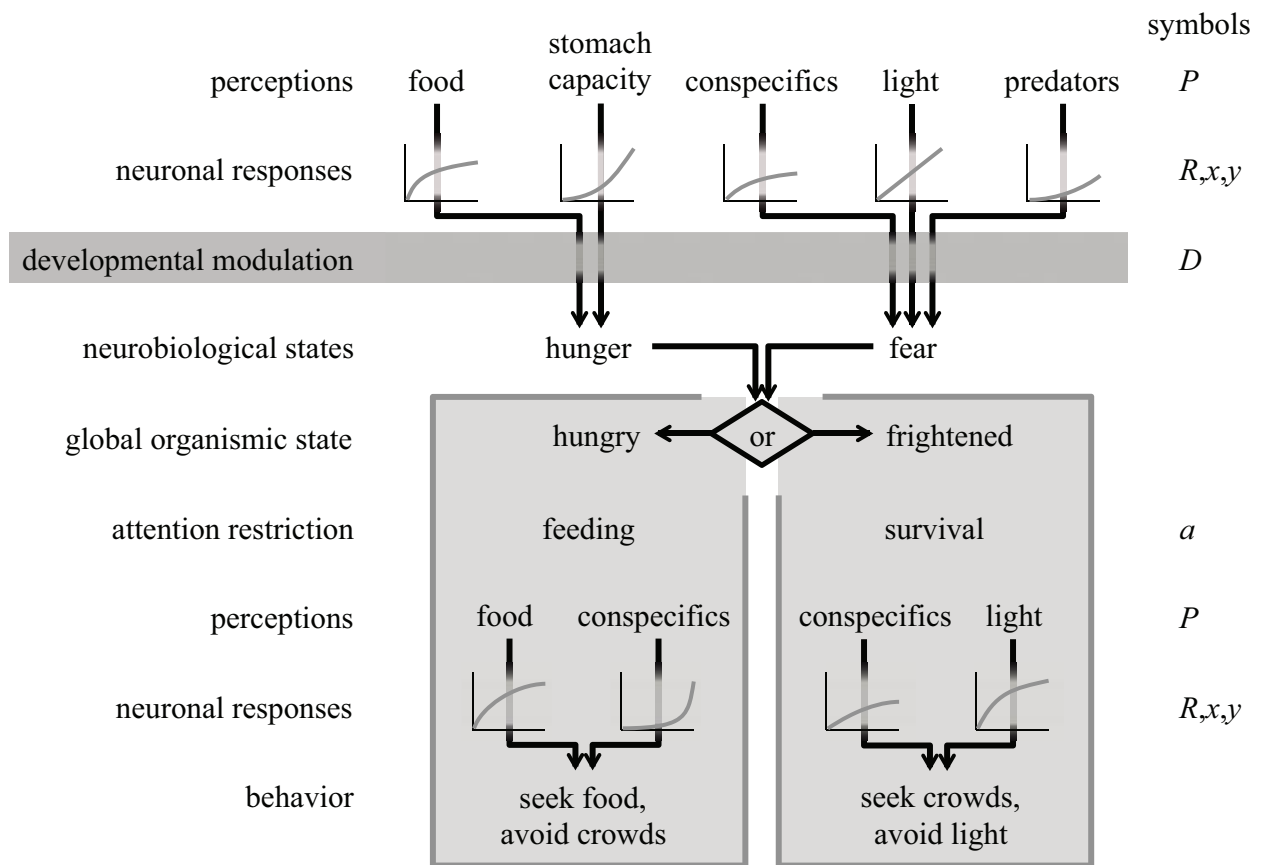


Figure 1: The emotion system’s translation of sensory stimuli into behavioral responses in our model. Each type of sensory stimulus contributes to emotional appraisal through neuronal response, developmental modulation, and competition between hunger and fear. The strength of each neuronal response is individual and depends on two genes. Internal signals related to development are also individual and may amplify the strength of inputs to hunger or fear over those to the other. The emotional response starts with the stronger neurobiological state determining the global organismic state. The physiological response to this emotional appraisal includes attention restriction. In the processing of its instrumental behaviors, the emotion system thus reevaluates a subset of its sensory information. When the relevant behavior is executed, the fish starts over at the top with new sensory stimuli. Symbols at right refer to equations (1)–(3) and equations (A4) and (A7), available online.

behavior. We assume that hungry fish retain some routinized ability to detect predators and frightened fish some ability to find food, although some studies indicate a full attention switch between competing organismic states in fish (Lastein et al. 2008; Ashley et al. 2009).

We consider six sensory inputs in our model: (1) local light intensity, (2, 3) local concentrations of food and conspecifics (visual cues), (4) overall abundance of predators (by smell or other senses), and (5, 6) internal sensing of free stomach capacity and body mass. Each sensory signal evokes a neuronal response (Kotrschal 2000; Sneddon et al. 2003) that depends on signal strength (Ashley et al. 2007) and genotype (fig. 1). We model the neuronal re-

sponse by using a sigmoidal function (Brown and Holmes 2001) to allow for response to weak signals and saturation of information (Aksnes and Utne 1997; Ashley et al. 2007). Each sensory input P (scaled between 0 and 1) is modulated by two genes, x and y (whose values range from 0.1 to 10), to give the neuronal response R :

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

Here, y is the sensory input at which the response is 0.5, while x determines how sharply the response rises with the sensory signal. We let each neuronal response have an

additive effect (Winberg et al. 1993; Höglund et al. 2005; Hills 2006; Barbano and Cador 2007) on the buildup of either fear or hunger.

Priorities that change through life have constituted a central aspect of evolutionary biology since the work of Lotka (1926) and Fisher (1930). We represent the ontogenetic stage of a fish by its body mass and allow it to modulate the impact of sensory inputs to fear and hunger (Giske and Aksnes 1992; Brown et al. 2007; Conrad et al. 2011) through developmental-modulation genes. We let D represent the current weighting of the neuronal responses related to hunger and $1 - D$ that of responses to fear: $0 \leq D \leq 1$. We define four genes that specify this regulation of motivation at the birth size, the largest body mass observed, and two intermediate body sizes. For any other body mass, D is found by linear interpolation. The current strengths of the two neurobiological states are, then,

$$\text{Hunger} = D(R_{A_{\text{stomach}}} + R_{A_{\text{food}}}), \quad (2)$$

$$\text{Fear} = (1 - D)(R_{A_{\text{light}}} + R_{A_{\text{predators}}} - R_{A_{\text{conspicifics}}}),$$

where $R_{A_{\text{stomach}}}$, $R_{A_{\text{food}}}$, $R_{A_{\text{light}}}$, $R_{A_{\text{predators}}}$, and $R_{A_{\text{conspicifics}}}$ are the neuronal responses to sensory input of remaining stomach capacity, food encountered, ambient light intensity, predator density, and density of conspecifics, respectively. The subscript A indicates that these neuronal responses are used in emotional appraisal (upper half of fig. 1).

The global organismic state is then set by the stronger (Cabanac 1979; Braithwaite and Boulcott 2007; Leknes and Tracey 2008) of these two neurobiological states and has both physiological and behavioral consequences. Following Mendl (1999) and Tombu et al. (2011), we define “attention” as the physiological response toward stimuli relevant to the global organismic state (see also Lastein et al. 2008; Ashley et al. 2009; Lau et al. 2011). Thus, attention focuses the organism to increase its feeding success when hungry and its survival from predators when frightened. The cost of attention is lower sensitivity to other stimuli, and frightened fish may have lower efficiency in catching food (Purser and Radford 2011). This is a central difference between the emotion system and a rational or optimality approach to behavior.

On the basis of its global organismic state, the motivated fish behaves in a way that maximizes its net neuronal response (Braithwaite and Boulcott 2007; Lau et al. 2011). The options for a fish are to stay at its current depth or to move a short distance upward or downward, as determined in the depth comparisons in equations for hungry (eq. [3a]) and frightened (eq. [3b]) fish. Hungry fish will value each depth (z) positively from sensing food and negatively from sensing conspecifics (competition):

$$\max_{z-1, z, z+1} (R_{H_{\text{food}}} - R_{H_{\text{conspicifics}}}) \quad (3a)$$

Frightened fish value each depth positively from sensing conspecifics (the dilution effect on predation risk) and negatively from light intensity (increasing visual range of predators):

$$\max_{z-1, z, z+1} (R_{F_{\text{conspicifics}}} - R_{F_{\text{light}}}). \quad (3b)$$

The neuronal response functions to the same stimulus (e.g., to conspecifics) that affect the neurobiological states (eq. [2]) represent brain processes separate from those determining behavior (eq. [3]).

Since x and y genes take values between 0.1 and 10.0, this allows concave, sigmoidal, nearly linear, or convex neuronal response functions (see examples below). Details are found in the appendix, available online.

Environment

We consider a classical scenario for optimization models: planktivorous fish in a vertically stratified environment where their prey performs diel vertical migrations (Werner and Gilliam 1984; Clark and Levy 1988; Hugie and Dill 1994). Pelagic water masses have strong and predictable vertical gradients of light intensity that affect both prey encounter rate and predation risk (Aksnes and Giske 1993). Fish predators use vision to locate their prey, so that the risk of being detected by a predator increases with light intensity and body size (Aksnes and Giske 1993). The opposing density-dependent forces of competition for food and dilution of risk tend to make it profitable to reside in groups of intermediate sizes (Giske et al. 1997). The model environment, fish physiology, reproduction, and mortality functions are modified from Giske et al. (2003). See details in the appendix.

We assume that prey density, vertical distribution of prey, and risk of predation vary within and between generations. There are nine alternative, generation-long patterns of environmental variation over the 7 days that constitute a fish’s life (table A1, available online). In each generation, environmental conditions also show shorter random fluctuations around these long-term trends (see “Fluctuating” in table A1). These fluctuations prevent spurious correlations that could hinder meaningful interpretation of our results (Bandyopadhyay et al. 2004).

Reproduction and Adaptation

Females that survive to the end of a generation search locally for a male to mate with. We assume that females prefer larger males and that their fecundity is size dependent. Offspring inherit 23 traits from their parents: x and y genes in each of the nine neuronal response functions (eq. [1]), four D genes (eq. [2]), and a sex-determination

gene. The sex-determination gene and the *D* genes constitute a chromosome, as do the two genes in a neuronal response function. Generations are nonoverlapping, and random mutations occur at a rate of 0.1% per gene per individual. Offspring randomly inherit a chromosome from their father or mother.

We run an individual-based model through many generations (a genetic algorithm; Holland 1975; Goldberg 1989) to study the gradual adaptive evolution of behavioral traits, emotional responses, and life-history traits (Huse and Giske 1998; Strand et al. 2002). In this way, response functions are subject to adaptation by natural selection (ultimate), whereas behavioral responses are immediate and based on proximate mechanisms.

Simulations

We simulated 30 populations over 50,000 generations. Average fitness, as measured by egg production at the population level, very rarely increased after 2,000 generations, and 50,000 generations is well into the adaptive quasi-equilibrium stage of the simulated populations (as indicated by test runs up to 170,000 generations). Even though the life span is short (7 days), age-dependent behavior appeared in vertical migration behavior, and longer life spans did not result in major differences in general patterns. Since generations with the standard environment (table A1) are identical with respect to predation, prey, and light, we use only these generations when comparing simulations. The model is described according to the ODD (overview–design concepts–details) protocol (Grimm et al. 2006, 2010) in the appendix.

Results

Comparison of Simulations

All populations evolved a typical diel vertical migration pattern, with ascent to near-surface waters at dusk and descent at dawn (fig. 2, *top*). They also all displayed the same aggregation pattern (fig. 2, *middle*). However, the frequency of occurrences of the two competing global organismic states did not converge among simulations (fig. 2, *bottom*). Being afraid was almost twice as common in the most as in the least frequently frightened population.

Multiple Contributions to Emotional Appraisal

All genes contributed to emotional appraisal, but to different degrees (table 1). The impact of ontogeny, through the genes for developmental modulation, was strongest, but the two genes in the neuronal response from stomach capacity were also important. Hungry and frightened fish

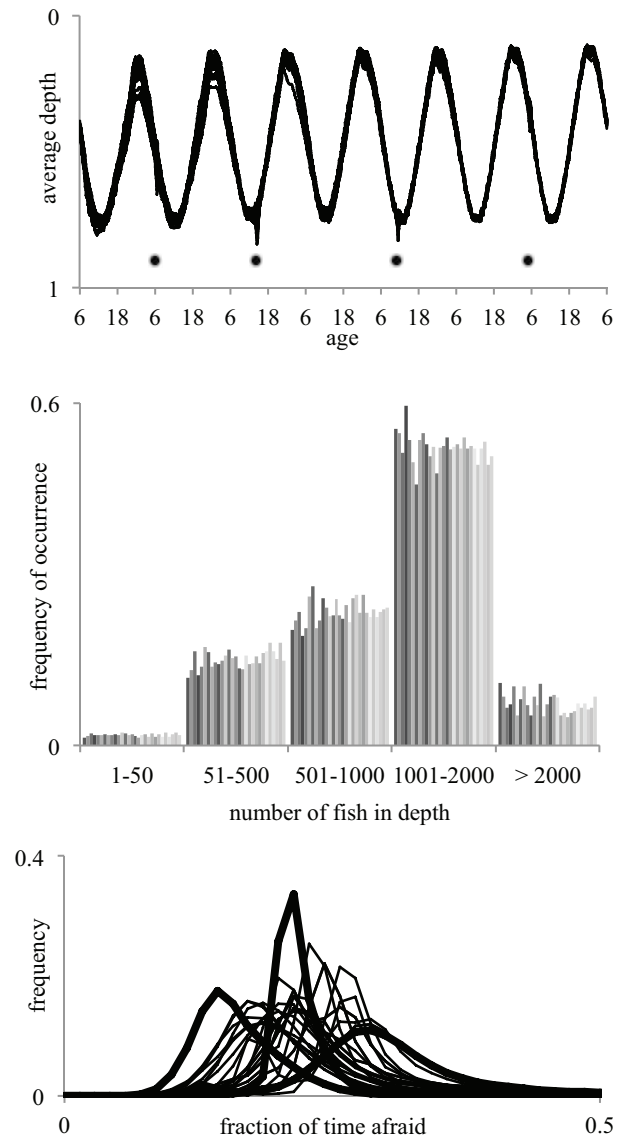


Figure 2: Comparison of 30 simulations. Data are from all individuals in the 200 last standard-environment generations (table A1, available online). *Top*, average depth through life. The timing of attacking schools of predators is identical in all generations with the standard environment and is shown by the four dots. *Middle*, aggregation: fraction of the population at each time step that is located in a depth with *N* fish. Each column represents one simulation. *Bottom*, fraction of life spent in the global organismic state “afraid” for females. Only individuals surviving until reproduction are counted. The populations denoted by thick lines are used in later figures and there are called, from left to right, the least, the intermediately, and the most frequently frightened populations.

differed more often in sensory inputs than in genes. However, because of the shapes of the neuronal response curves (see examples in fig. 6), large differences in sensory input may disappear in the neuronal response.

Table 1: Emotional appraisal

	Food	Stomach capacity	Conspecifics	Light	Predators	Body mass
Environment, P	72		86	66	86	
Physiology, P		89				84
Gene x	15	31	10	16	15	
Gene y	10	38	6	17	13	
Gene D_1						91
Gene D_2						97
Gene D_3						95
Gene D_4						89
Function, R	69	89	54	53	31	
Function, D						89

Note: Contribution to the determination of the global organismic state from environmental and physiological perceptions (P), alleles (x, y, D_1-D_4), neuronal responses (R), and developmental modulation (D). Data are percentages of the 95% confidence interval (CI) of the average value of those individuals who became hungry that did not overlap the CI of those who became frightened; $CI = \bar{X} \pm 1.96(\text{Var}(x)/N)^{1/2}$. Symbols are explained in equations (1) and (2) and in table A2, available online. Data are from all ages in the final generation in all simulations.

Developmental modulation was simultaneously forced by genes and physiological state (table 1), because the usage of the four D genes depends on the current body mass (fig. 3). However, fear was mainly environmental in origin. At any time, a fish could become afraid when hunger signals from its stomach disappeared, while the episodically approaching predator schools (fig. 2, *top*) caused most (sometimes all) individuals to switch into a frightened state (fig. 4). The interpopulation variation in being afraid (fig. 2, *bottom*) was caused by different adaptations in these two neuronal response functions.

Avoiding Danger through Attention

One of our new findings is that attention appears as both an alternative and an additional response to escape. When attacked by predators, almost all females became afraid (fig. 4a) and moved downward, as seen in the dips during predator attacks in the top panel of fig. 2. Later in life, the morning descent was only slightly faster when predators were present (fig. 4a). A quick shift of attention prevented a large increase in mortality during predator attack. More risk-prone behavior has evolved among males to achieve faster growth, since females prefer larger mates (fig. 3). This also reflects their behavior during predator attacks: males remained focused on feeding and therefore suffered high mortality (fig. 4b).

Frightened fish were not randomly distributed in time and space. When attacked by predator schools, populations exhibited a major burst of fear (figs. 4, 5). In addition, there were more frightened individuals during the morning descent to deeper waters than in the return migration in the afternoon, and frightened fish were more likely to lead the downward migration than to lag behind (fig. 5).

Personality Differences Emerge via the Emotional Response

While all populations tended to arrive at low variation in the neuronal responses to light and conspecifics when afraid, they exhibited variation in neuronal responses of hungry individuals to food and competitors (fig. 6). Frightened individuals moved away from light and slightly toward conspecifics. Hungry individuals displayed more variation in their neuronal responses and spread more widely among different depths (fig. 7, *right*). The consequences of these responses were lower mortality loss when many were afraid at the same time and lower food competition when many were hungry.

Even for the same global organismic state, individual genetic differences led to behavioral differences. The population of most rarely frightened individuals in figure 2 harbored very low genetic variation for the y gene and only two clusters of x alleles in the neuronal response to

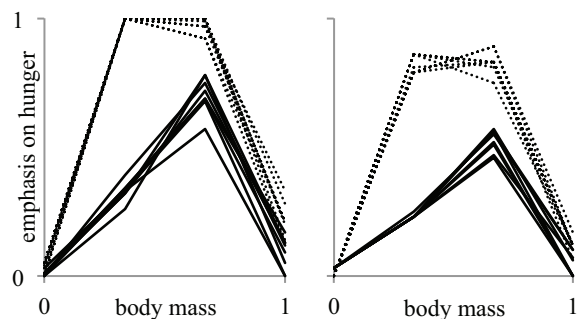


Figure 3: Developmental modulation. The eight most abundant patterns (D genes and linear interpolation between them) in females (solid lines) and males (dotted lines) in the least (left) and most (right) frequently frightened populations in the bottom panel of figure 2.

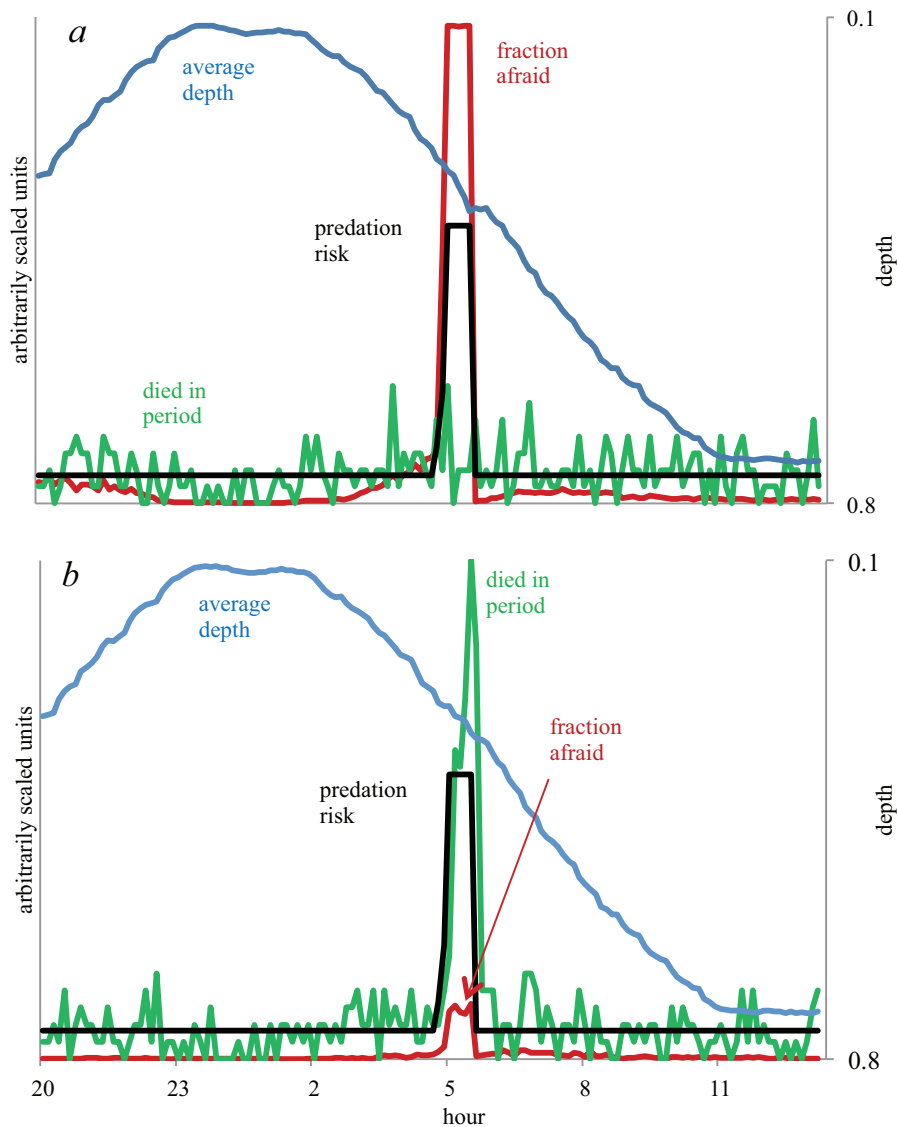


Figure 4: Effect of attention. Females (a) and males (b) react differently to the last attack by schooling predators (fig. 2, top). When the last attack occurred (see burst of fear in fig. 5), almost all females became afraid, while males remained hungry. As a consequence, few females but many males were killed by the predators. Data from final generation of the intermediately frightened population in the bottom panel of fig. 2.

food when hungry (fig. 6a). In addition, it also contained only two clusters of genotypes for responses to competitors when hungry, where one genotype yielded only weak neuronal responses to the presence of competitors, while the other responded strongly (fig. 6b). Thus, the population harbored four behavioral phenotypes when hungry, of which two avoided competitors while the other types sought dense food concentrations despite more intense competition (fig. 7). Hence, the competition-avoiding phenotypes ended up in the deep and shallow outskirts of the vertically migrating population (figs. 7 [right], 8a).

Frequency Dependence in a Fluctuating Environment Maintains Personality Diversity

Both the competition-avoiding and the competition-ignoring phenotypes competed for food most strongly with individuals of the same behavioral type (fig. 8), and all were under negative frequency-dependent selection. As the environment varied between generations (table A1), the competition-avoiding types did best in “low-food” generations, and the competition-ignoring phenotypes did best in “high-food and high-risk” generations (fig. 8c, 8d).

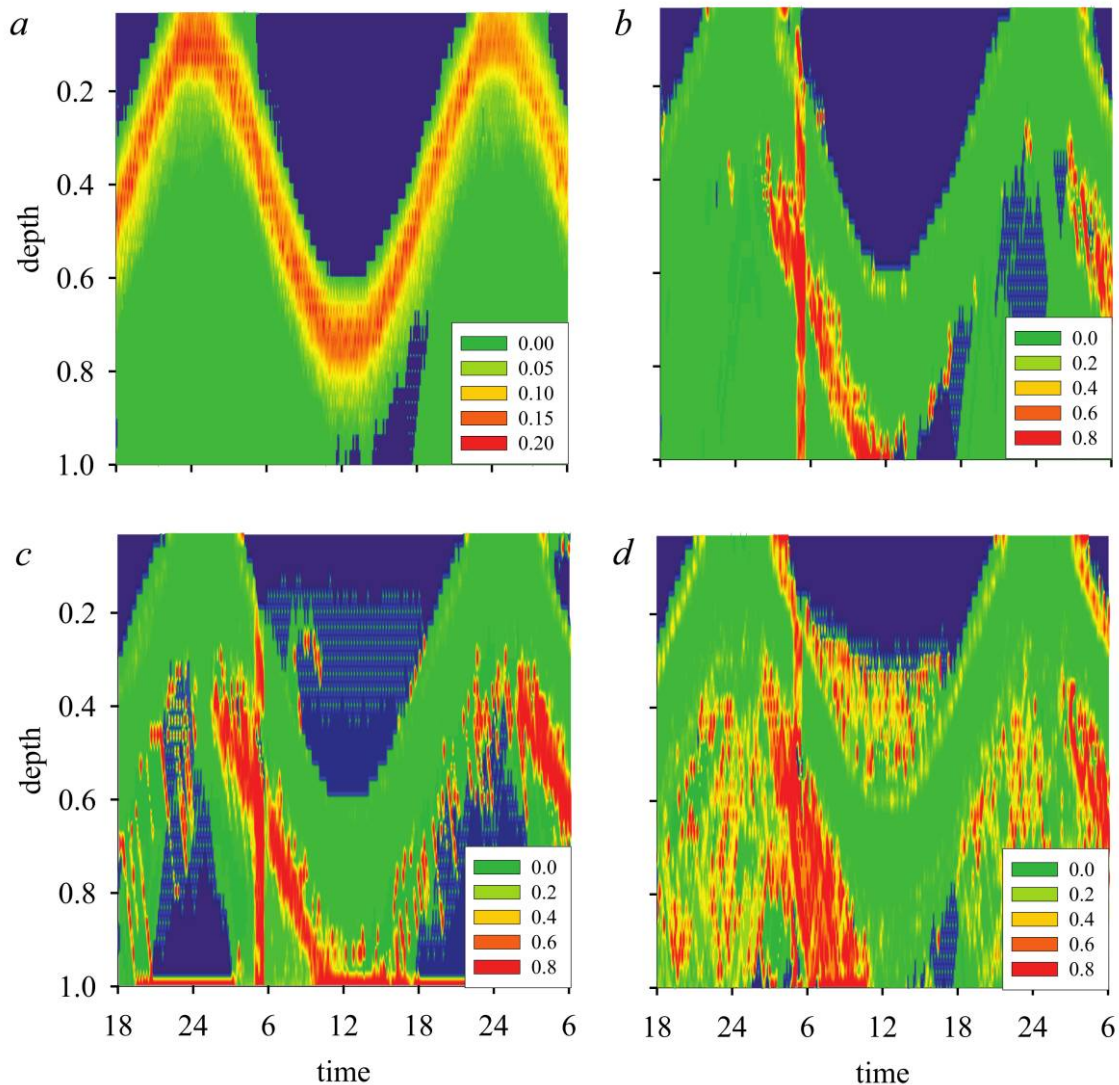


Figure 5: Vertical distribution and global organismic state. *a*, Population density. *b–d*, Fraction of individuals frightened. Time axis covers the latter 20% of lifetime of the final generation in the simulations marked with thick lines in the bottom panel of figure 2, with the least and most frequently frightened population in *b* and *d*, respectively. Population density (scaled against the newborn population size) is shown for only the least fearful population, as variation among populations is small except for the location of stray individuals. The burst of fear in *b–d* is caused by a school of predators, as in figure 4.

Discussion

Emotion as a Tool for Understanding Phenotypes

We have shown that the emotion system is central in producing a unified perspective of the phenotype, linking the external environment, through genetics, development, and physiology, to behavior, life history, and evolution. Further, we show in figure 1 that the emotion system can deliver “multipurpose rules which are capable of providing effective solutions to a wide range of problems” (Fawcett et al.

2013, p. 9). In our model, this happens through the global organismic state, which can be activated from different sensory signals or combinations of them. The behavioral rules a fish will use when being afraid can be activated by perception of predators, by light, or by the perception that there are few conspecifics nearby, and they can be aided by internal signals from developmental stage. Thus, in contrast to previous quantitative models of animal behavior, our model integrates environmental and bodily information and the arbitration of opposing options in

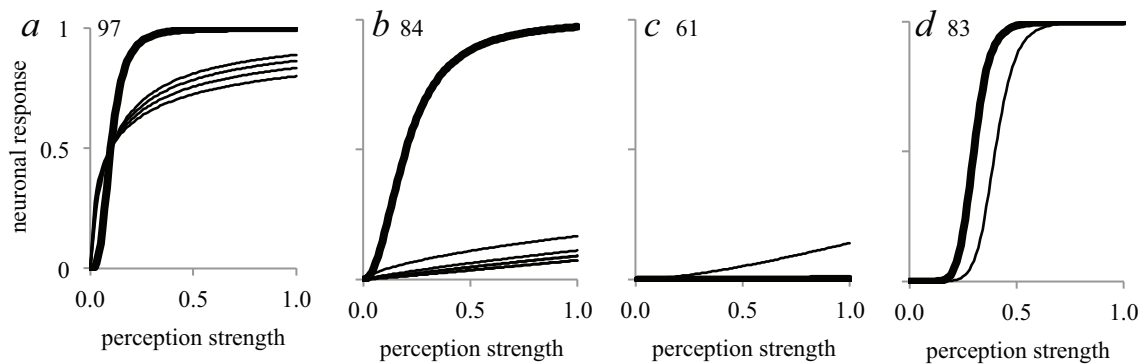


Figure 6: Emotional response. The eight most abundant neuronal responses to food (*a*) and conspecifics (*b*) when hungry, and to conspecifics (*c*) and light when frightened (*d*). Some curves are so similar that they mask each other. The curves are for the final generation of the least frightened population in the bottom panel of figure 2. Neuronal-response curves occurring in 20% or more of individuals are shown as thicker lines. Numbers in upper left corners show percentage of the population covered by these eight curves.

the same principal way as natural organisms do (Panksepp 2005; de Waal 2011; LeDoux 2012).

Although the discussion goes back to the Stoics (Dixon 2012), there is still no consensus understanding of what emotion is (Izard 2010). A mathematical formulation may sharpen the arguments, and new experiments can then confront these assumptions (Hilborn and Mangel 1997) and facilitate dialogue between empiricists and theoreticians and across behavioral disciplines (Gilmour et al. 2005; White et al. 2007; McNamara and Houston 2009; Dingemans et al. 2010; Pravosudov and Smulders 2010).

Animal personalities are an example. Our model does not contain personality in its construction, but it is able to explain why and when personalities emerge. It is difficult to empirically investigate the components of personality in nonhuman organisms, since the state of mind can be very difficult to sample. Thus, mechanistic models can be valuable tools for studying processes and can help generate testable predictions. For example, simulations predict that there are several routes in the organism to the same behavior, that occurrence of fear in a population may be hard to predict from environmental variables, that there is a clear difference in sensitivity to conspecifics between hungry and frightened fish, that personality differences in the pelagic occur over competition rather than over risk avoidance, that depth distribution may be personality dependent, and that males may be less attentive and more vulnerable than females to predator attacks.

Emergence of Animal Personalities

We found that populations evolved a narrow range of neuronal response patterns to almost all perceptions and that almost all frightened individuals showed the same evaluation of light and conspecifics (fig. 6c, 6d). Only the

behavioral response of hungry individuals tended to yield intrapopulation diversity and potential personality-type differences (fig. 6a, 6b).

As simple as this model is (since individuals can choose only between staying and moving vertically), we observe distinct behavioral types within populations. Individual physiological states affect the global organismic state, while the behavioral decisions of motivated individuals are controlled by genes. Hence, there is the potential for strong state dependency in labile behavioral responses and simultaneously a possibility for genetically differentiated behavioral types (Dingemans and Wolf 2013). Individual variation in responses toward food and conspecifics among hungry individuals (fig. 6a, 6b) emerged in all simulations, with clear divergence into two types in some populations. Personalities are often defined by correlated behavioral traits (Gosling 2001) across a range of ecological situations and motivational states (Huntingford 1976; Conrad et al. 2011). We considered only two global organismic states, a single behavioral choice at each time step, and partner choice only through body size and depth selection in last time step, and our model of reproduction does not allow related neuronal responses to cluster in chromosomes or regions to establish physical proximity and thus establish genetic correlations that persist across generations. But even so, the results that emerge (figs. 3, 6–8) indicate that richer personality traits are to be expected in models with more mechanistic detail.

Emotion Affects Behavior Differently from Optimization

Our model arrives at the same general type of spatial distribution patterns as do optimization models (Clark and Levy 1988) and games (Hugie and Dill 1994) of pelagic planktivores: diel vertical migration with some extension

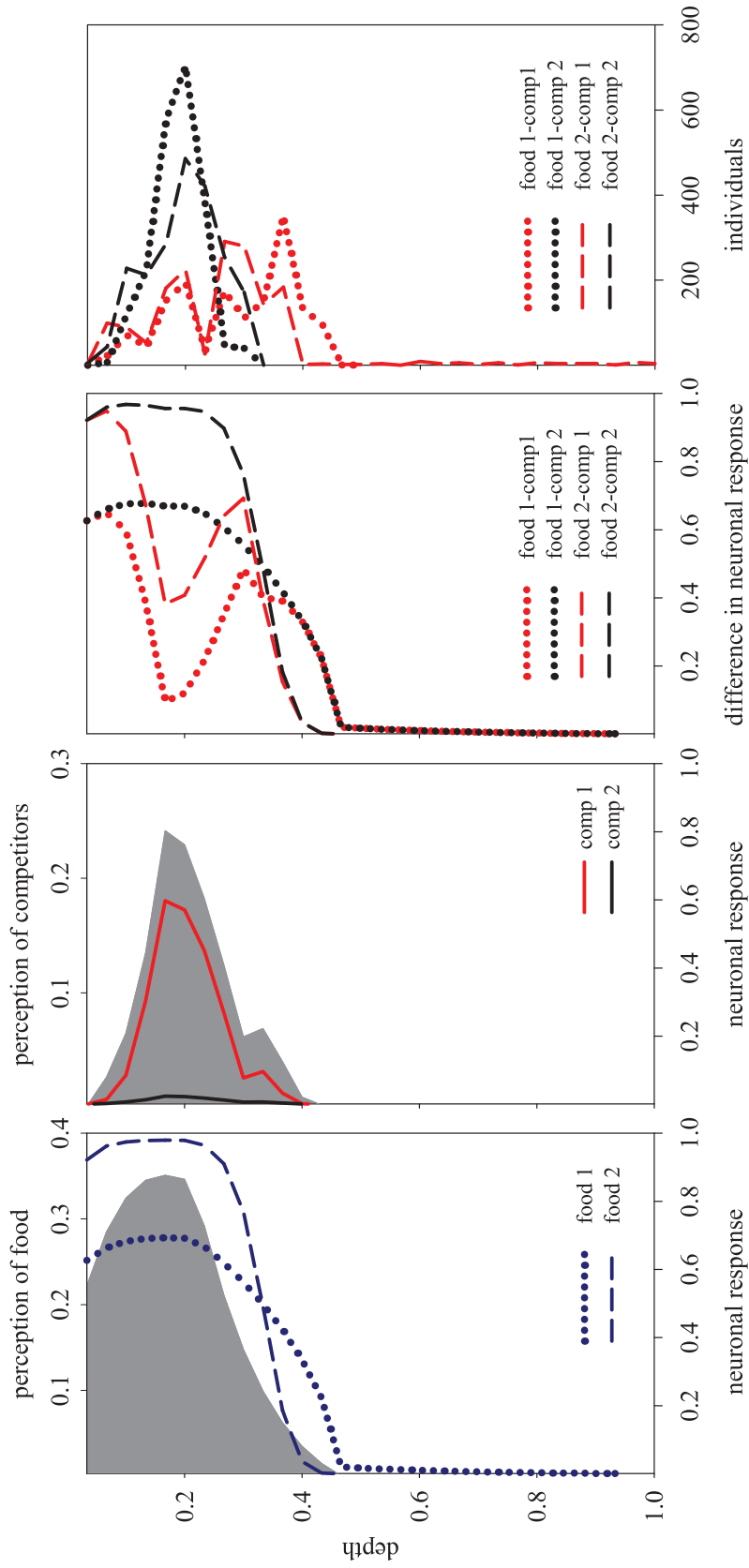


Figure 7: Vertical distribution of hungry individuals of four behavioral types in the same population as in figure 6. *Left*, The perception of food (shaded area) and the two dominant neuronal responses to food when hungry (food1 and food2) are the two groups of neuronal response functions with R_{\max} at 1.0 and ~ 0.8 , respectively, in fig. 6a); *middle left*, the same for competitors (comp1 and comp2) have R_{\max} of 1.0 and 0.1, respectively, in fig. 6b); *middle right*, the four possible combinations for net differences in neuronal responses when hungry (see eq. [3a]); *right*, the observed vertical distribution of hungry fish of these four genotypes. The two genotypes with strong aversion to competitors (red curves) are located deeper than the food maximum. Deepest of all is the genotype with low tolerance for competitors and high acceptance of low food concentrations. The four behavioral types (food1, comp1), (food1, comp2), (food2, comp1), and (food2, comp2) comprised 20.8%, 28.4%, 22.3%, and 28.5%, respectively, of the hungry fish at this time, while 2% of the population were afraid. Data from 2130 hours on the first evening in figure 8a, 8b.

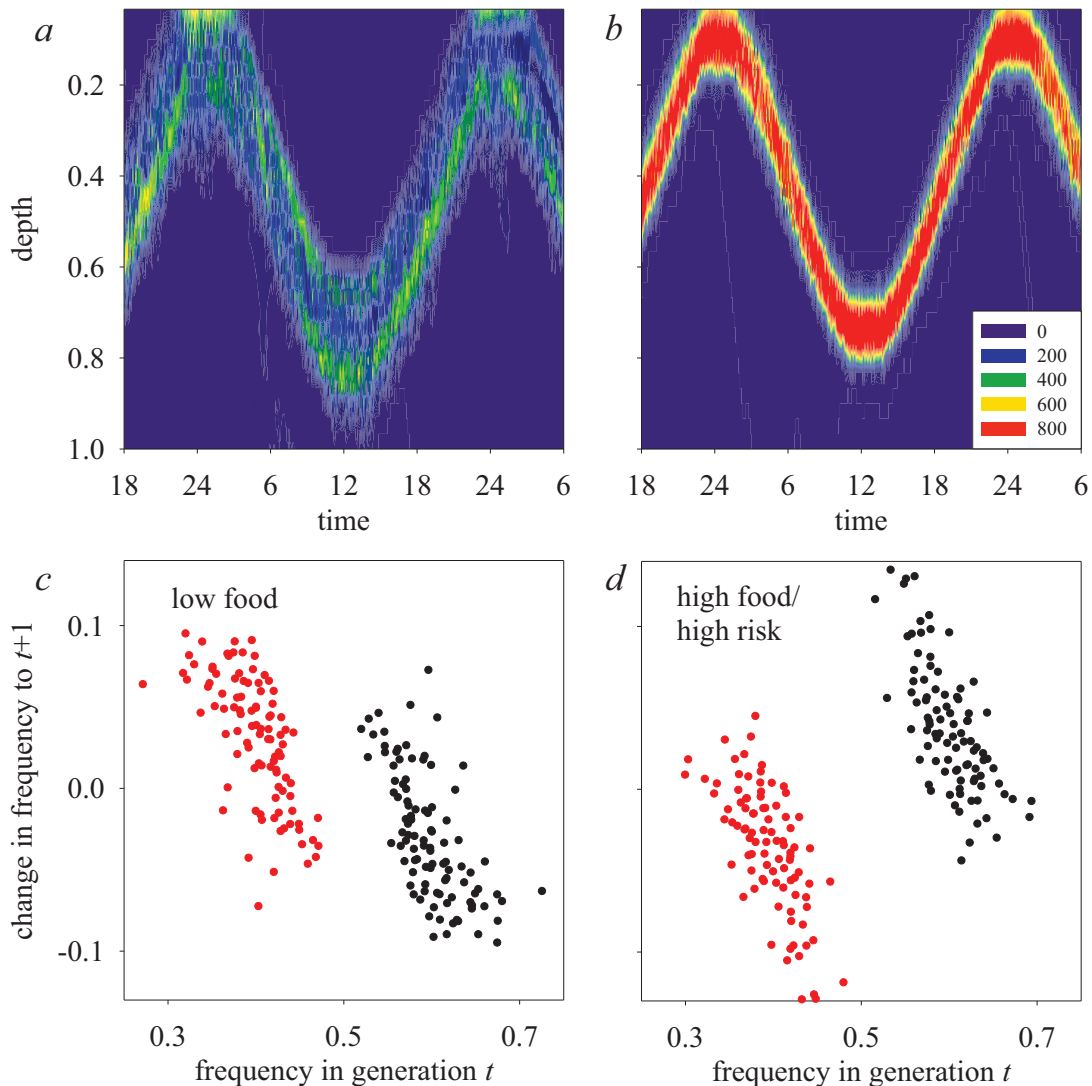


Figure 8: Behavioral types and gene-environment interactions in the same population as in figures 6 and 7. *a, b*, Vertical distribution pattern in the last 36 hours of life of individuals with low (*a*; 0.1–0.5; red curves in fig. 7 [right]) and high (*b*; 9.7–10.0; black curves in fig. 7 [right]) allele values for the y gene in the neuronal response to conspecifics when hungry (eq. [3a]). Lower values in y alleles yield increasing aversion (neuronal response) to crowds (see fig. 7, middle left). *c, d*, Frequency-dependent fitness and gene-environment interactions of the 0.1–0.5 (red circles) and 9.7–10.0 (black circles) allele groups in low-food (*c*) and combined high-food and high-risk (*d*) environments. Other environments (table A1, available online) are intermediate to these two extremes with regard to average fitness for these allele groups in this y gene and are not shown here. Data in *c* and *d* are from the last 200 generations with either a “low-food” or a “combined high-food and high-risk” environment in this population. These two allele clusters comprised 39.7% and 60.0% of this y gene this period, respectively.

around the average. This is a consequence of the strong impact of light on encounter rates with both food and predators (Aksnes and Giske 1993). However, where optimization and game models calculate the long-term consequences of opposing selective factors, such as the gain from feeding and the risk of predation (McLaren 1963; Werner and Gilliam 1984), organisms in our model respond at immediate timescales to food or perceived risk. Danger is avoided because of an evolved proximate pref-

erence to stay with others or in darker waters when afraid, while danger is largely ignored when hungry. Developmental-modulation genes lead to individual differences through life, while the temporal variation in stomach fullness will affect the neurobiological state of hunger in the brain in shorter terms. The genetic algorithm reinforces preferences during production of offspring. In this respect, our modeled fish are one step nearer natural fish (Brodin et al. 2013) than are those of optimization models. Indeed,

the quite messy vertical distributions (fig. 5) bear clear resemblances to those of natural fish populations (Staby et al. 2011; Dypvik et al. 2012).

A second difference between our model and classical optimization is that individuals with different long-term (genetic) personality traits may have evolved different spatial preferences (fig. 7). Attention is a third difference. It is the physiological consequence of the global organismic state (LeDoux 2012), which is typically not considered in state-dependent (Mangel and Clark 1986; McNamara and Houston 1986) optimization models. Attention allows more intensive feeding or more efficient escapes but also comes with a risk of neglecting the second-most-important factor (fig. 4*b*). Finally, since our fish react only to near-field perceptions, they may make mistakes in the sense of behaviors that are suboptimal from a fitness perspective.

We have combined a general, individual-based modeling approach with simple functional relationships that can easily be adapted and expanded to a variety of organisms and scenarios. Experimental studies in several disciplines (Gerlai 2010; Kalueff et al. 2012; Martins et al. 2012) may contribute to species-specific versions of figure 1 with higher fidelity to nature and then yield specific, testable predictions about individual and population behavior.

The pillars of our method are (1) the linkage of local environmental information with genetics and physiological states, (2) a general function for neuronal responses that allows for individual variation, (3) restricted attention as part of the physiological response, and (4) coupling of proximate constraints in determining behavior, while the behavior's consequences are evaluated in terms of the ultimate and adaptive value. While fish in spatially explicit models avoid danger by moving away (Werner and Gilliam 1984; Clark and Levy 1988; Hugie and Dill 1994; Rosland and Giske 1994), our approach allows reduction in danger by a shift of attention (fig. 4). The emotion system determines how the sensory information is interpreted by the organism and translates it into behavioral decisions. The genetic basis for these response functions evolves organisms that are better adapted to their changing conditions in their environment.

A model of behavior based in specific emotions may be restricted to organisms with certain brain structures. However, while the phylogenetic emergence of emotion remains unclear (Rial et al. 2008; Cabanac et al. 2009; Mendl et al. 2011; LeDoux 2012) and some important cognitive changes may have emerged in the terrestrial vertebrates (Cabanac et al. 2009), dopamine, serotonin, and opioids used in aggression, depression, reward, pleasure, and pain in humans are highly conserved in evolution (Blenau and Baumann 2001; Andretic et al. 2005; Mustard et al. 2005; Iliadi 2009; Curran and Chalasani 2012). The appropriate design question might therefore be how to accommodate

relevant survival circuits and behaviors for the particular species studied (Panksepp 2005, 2011; LeDoux 2012). This is fruitful ground for the collaboration between modelers and empiricists (Kalueff et al. 2012).

Emotion as a Tool in Understanding Populations

During the past decade, population modeling has increased in importance as a tool for understanding human impacts on the environment (Purves et al. 2013). In most population models, behavior is represented poorly, if at all, simply because there is no easy way to model organisms that shift between being constrained by physiology and being constrained by conspecifics or are constrained by both simultaneously. Indeed, it is a considerable problem that until this article, we have lacked unifying mathematical tools for studying populations of individuals with behavior. Methods such as optimal-foraging theory, life-history theory, game theory, and state-dependent life-history theory are excellent tools for finding optimal policies for individuals when they are under a single dominant constraint (physiology for state-dependent life history, actions of others in game theory, and life stage in life-history theory). Here we have shown that the emotion system can prioritize among competing constraints in modeled organisms, as in natural organisms. We found that individual differences in neuronal responses (fig. 6) are important for population ecology (fig. 7) and are maintained by frequency-dependent selection (fig. 8) caused by the processes leading from perception to behavior. Our method is also a tool for studying populations with higher fidelity to nature than is allowed by the established tools.

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Should I stay or flee? A challenge for the curious cod. Photograph by J. Giske.