Ecological Informatics 40 (2017) 81–92

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

Exploring the connection between emergent animal personality and fitness using a novel individual-based model and decision tree approach

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ARTICLE INFO

Keywords:
Rule extraction
Reproduction
Animal personality
Animal behavior
Internal states
Fitness

ABSTRACT

The connection between reproductive fitness and animal personality is not fully understood. Using computer simulations and machine learning, we found high accuracy rules that predict which personalities are associated with fitness for two correlated measures of components of fitness applied a posteriori for classificatory purposes: fitness component (1) in terms of survival and short-term reproductive success, and fitness component (2) in terms of long term reproductive success which is indirectly related to survival of the parents. Animals are represented in the abstract as individuals with a genome that through time develops into certain characteristic behaviors and personalities. To the best of our knowledge, this is the first simulation study of its kind that extracts rules to investigate the link between personality and fitness. Clearly separated behaviors between fit and non-fit individuals emerged through the evolution of the population over time without top-down processing. Moreover, we did not employ a pre-defined fitness function, in order to minimize any possible biases toward a specific type of behavior. With respect to fitness component (1), we found that individuals with one of two extreme values of a personality trait (either bold or fearful) tend to be most fit, which agrees with empirical studies. With respect to fitness component (2), we found that when resources are low, fit individuals search for food whereas if food is abundant, they focus on reproduction, thereby suggesting the context dependence of fitness related behaviors. Once again, these results agree with empirical studies.

1. Introduction

Although there have been a number of empirical studies conducted regarding personality variation within particular animal species, relatively few studies have focused on the possible connection between animal personality and reproductive fitness (Dingemanse and Reale, 2005; Mittelbach et al., 2014 and Smith and Blumstein, 2008). A definition of animal personality (or 'temperament' as it is sometimes called) proposed by Briffa and Weiss (2010) as well as by Patrick and Weimerskirch (2014) is the consistent variation between individuals in terms of behavioral traits such as exploration. Connected with behavioral tendencies in individuals is the concept of affective states. Bekoff (2000) observes that there is no agreed upon definition of affect for either human or non-human animals, although he proposes that so-called primary affective states (unreflective states) such as fear can be regarded as internal states that are neurologically hard-wired into animals and which can be discerned in terms of behaviors such as posture, gait and facial expressions. For example, Stankowich and Blumstein (2005) suggest that fear can be understood operationally in terms of flight distance. De Waal (2011) argues that any study of animal behavior is not complete unless it is conjoined with a consideration of internal affective states such as fear, even if only understandable on a behavioral level.

Fear, which has been discussed in the literature in connection with fitness, is understood in terms of anti-predation behavior (Stankowich and Blumstein, 2005). Stankowich and Blumstein (2005) conducted a meta-analysis of studies on anti-predation behaviors in a variety of prey species and concluded that fear and associated anti-predation measures tend to be naturally selected. Since survival is a component of reproductive fitness, it follows that fear contributes to fitness. However, the connection between fear and fitness is not quite so straightforward, since other studies support the claim that bold animals exhibiting lower levels of fear tend to have more reproductive success than their less bold counterparts (Mittelbach et al., 2014; Wilson et al., 2010). Mittelbach et al., 2014 report that in the case of both zebrafish (*Danio rerio*) and guppies (*Poecilia reticulata*), aggressive males have higher reproductive success fertilizing eggs as opposed to less aggressive fish. Wilson et al. (2010) report that there is a significant positive correlation

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http://dx.doi.org/10.1016/j.ecoinf.2017.06.004
Received 13 July 2016; Received in revised form 18 June 2017; Accepted 19 June 2017
Available online 21 June 2017
1574-9541/

between boldness and reproductive success in the Eastern Mosquitofish (*Gambusia holbrooki*). Although these results may seem to contradict the results of other studies establishing a correlation between fear and fitness, they actually go hand in hand: While fear contributes to the survival component of fitness, boldness apparently contributes to the reproductive component of fitness. This has been borne out in a meta-analysis by Smith and Blumstein (2008) where they conclude that while boldness contributes to reproductive success it also detracts from survival since bolder individuals tend to have shorter lifespans than more cautious and fearful ones, so that fear contributes to survival which is a direct or indirect component of fitness. That personality extremes tend to be more fit than intermediate personalities has been supported by a study conducted by Both et al. (2005) where the authors report that with respect to the great tit (*Parus major*), pairs of slow-exploring birds and pairs of fast-exploring birds both experienced high reproductive success and hence high fitness for different reasons: Fast-exploring birds are efficient in terms of defending territory whereas slow-exploring birds are efficient in terms of raising their young (Both et al., 2005). In the current simulation study, using individual based simulations and machine learning, we investigate the hypothesis that in some cases, the extreme values of a personality continuum such as boldness/shyness are associated with individual fitness.

There is also evidence in the literature for the context-dependence of fitness-related behaviors and personality traits. In a review article, Domenici (2010) alludes to several empirical studies showing that with respect to various fish species, reaction distance tends to decrease as predator speed (and hence risk) increases (Dill, 1974; Meager et al., 2006). Moreover, Domenici (2010) cites studies showing that reaction distances in fish species pursued by predators increase as costs associated with flight increase (Ydenberg and Dill, 1986; Krause and Godin, 1996). Thus, for various species of fish, reaction distance as a component of evasion behavior in the face of predation is a function of context. As another example of the context-dependence of fitness-related behavior, Frost et al. (2007) found that in the case of rainbow trout (*Onchorhyncus mykiss*), bold individuals became more shy based on their experiences (such as losing fights) and shy individuals became bolder also based on experiences (such as winning fights). Further, Cote et al. (2008) studied the common lizard (*Lacerta vivipara*) and found that asocial lizards were more fit than social lizards in low-density populations whereas social lizards were more fit than asocial lizards in higher density populations. Also, Coleman and Wilson (1998) conducted a study of shy and bold personalities in the pumpkinseed sunfish (*Lepomis gibbosus*) to determine if shyness and boldness are consistent traits across contexts. The results of their study demonstrated that individual differences in boldness and shyness were not consistent across contexts although these differences were consistent within contexts (Coleman and Wilson, 1998). The researchers found that individuals that were bold in contexts with high predation were generally not bold in contexts with low predation indicating that boldness is adaptive in the former context but not in the latter (Coleman and Wilson, 1998). Thus, whether boldness is adaptive in this case depends on whether predators are present, so that the fitness consequences of this behavior may be context-dependent. Similar results were obtained in a study by Brown et al. (2005) where the authors found that in situations with high predation, the poeciliid fish (*Bracbyraphis episcopi*) tended to be bold whereas in situations with low predation, shyness was adaptive. In this simulation study we also investigate the context-dependence of fitness related personality and behavior using machine learning.

In this project, we use individual-based computer simulations and inductive machine learning to investigate the possible connection between behavior and internal states of individuals and their reproductive fitness. Inductive machine learning involves learning a set of rules based on specific examples called the training set which are then tested for the predictive value (Kotsiantis, 2007). Combining individual-based models with machine learning for analyzing results is a species of hybrid modeling discussed by Parrott (2011). In particular, as mentioned above, we will be exploring the issue of whether opposite extremes of personality traits can both contribute to fitness and whether fitness-related personality traits are in some cases context dependent. It is important to point out similarities and differences between our method of modeling personality and behavior (to be outlined below) from that of Giske et al. (2013), Giske et al. (2014) and Eliassen et al. (2016). Both ourselves and the aforementioned authors employ genetic algorithms that do not depend on predefined fitness functions. Although the important studies conducted by Giske et al. (2013), Giske et al. (2014) and Eliassen et al. (2016) shed much light on the relation between internal states and adaptive behavior in animals, the approach we use in our EcoSim simulations is more general, since we are not restricted to two states but to a wider range of internal states that also includes satisfaction, nuisance, curiosity as well as the desire to search for partners. We hope that our study will contribute to the overall discussion regarding the influences on animal behavior and decision-making sparked by the seminal studies of Giske et al. (2013), Giske et al. (2014) and Eliassen et al. (2016).

Since our simulations are individual based and involve behavioral evolution, over time agents will vary from one another in terms of their behaviors and internal states thereby developing distinct personalities or temperaments. Presumably, some of these personalities will be associated with high levels of reproductive fitness whereas others will be associated with lower levels of fitness. Moreover, the fuzzy cognitive maps (see below) employed in these simulations to characterize the behavior of individuals and coded in their genomes are well suited to distinguishing between emotional concepts and behavioral concepts, which coheres with the condition proposed by de Waal (2011) that personality be un derstood in terms of both behaviors and emotions. We then use machine learning to arrive at prediction rules that spell out which behaviors and emotions will tend to lead to reproductive fitness for two senses of fitness (see below). To the best of our knowledge, this is the first study of its kind to use individual-based computer simulations and machine learning to distinguish between fitness enhancing personalities and personalities that tend to reduce fitness.

2. Methods

EcoSim (See model description according to the ODD protocol (Grimm et al., 2010) in Supplementary Material, Appendix B) is a multipurpose individual-based evolving predator-prey ecosystem computer model that simulates complex ecosystems consisting of a plethora of intelligent agents, which are called individuals, interacting and evolving in a dynamic environment (Gras et al., 2009; Mashayekhi et al., 2014a, 2014b). To model the behavior of individuals, which is an essential component in creating complex interactions with other individuals and with their environment, an extension of the Fuzzy Cognitive Map (FCM) model (Kosko, 1986) has been employed in EcoSim. The FCM is used both to model the behavior of each individual as well as functioning as a platform for implementing evolution as it is encoded (the weight of the links, where a link is defined as one concept's being excitatory or inhibitory for another concept) in the genome of each individual. The initial prey FCM is shown in Fig. 1. In this figure, the leftmost column boxes represent sensory inputs, such as *Friend close* and *Partner far*. (By way of clarification, for prey individuals, “Friend” refers to other prey individuals, male or female, whereas “Partner” refers to a reproductive partner of the opposite gender in the same prey species (or in a prey species genetically close enough for successful mating). The middle column boxes represent the internal states of the individual such as *Fear* and *Hunger*. Finally, the boxes in the rightmost column represent the individual's actions such as *Escape* and *Search for food*. The arrows known as ‘edges’ show the weighted effect of one concept on another, where each such link or ‘edge’ is representative of a gene locus. The idea here is that a gene is depicted as a so-called functional state, that is, in terms of its causal roles in ultimately explaining behavior. Blue lines illustrate excitatory effects and red arrows illustrate inhibitory effects.