

Behavioral flexibility and novel environments: integrating current perspectives for future directions

Valeria Mazza^{a,b,*} and Vedrana Šlipogor^{c,d,e}

^aDepartment of Ecological and Biological Sciences, University of Tuscia, Largo dell'Università 1, 01100 Viterbo, Italy

^bIchthyogenic Experimental Marine Centre (CISMAR), Località Le Saline snc, 01016 Tarquinia, Italy

^cDepartment of Zoology, University of South Bohemia, Branišovská 1760, 370 05 České Budějovice, Czech Republic

^dDepartment of Ecology and Evolution, University of Lausanne, Quartier UNIL-Sorge, Bâtiment Biophore, CH-1015 Lausanne, Switzerland

^eThe Sense – Innovation and Research Center Lausanne & Sion, Avenue de Provence 82, 1007 Lausanne, Switzerland

*Address correspondence to Valeria Mazza. E-mail: valeria.mazza@unitus.it

Individuals in the process of encountering a novel environment face several new selective pressures that can lead to changes in phenotypes, which provides an exciting opportunity to study microevolutionary processes. Environmental novelty encompasses a variety of changes in the socio-ecological world of an individual, as well as situations for which animals lack eco-evolutionary experience (e.g., Saul et al. 2013; Heger et al. 2019). Individuals dispersing in non-native habitats, for example, face environmental novelty when dealing with the dangers and resources of unfamiliar habitats, in the absence of evolutionary preparedness, as well as (often) without the possibility of interacting with and learning from conspecifics (e.g., Saul et al. 2013; Heger et al. 2019). These animals thus need to memorize and navigate novel physical and social spaces, and decide which paths to take or which resources to use, while being attentive to the predatory threats and changes in the social dynamics that may be different to those of the native habitat. Similarly, animals that either disperse in or find themselves surrounded by the progressive expansion of human settlements, have to cope with the overwhelming presence of humans and their artifacts in addition to altered biotic and abiotic conditions (e.g., Sol et al. 2013; Chapple and Wong 2016; Ruland and Jeschke 2020). If the novel environmental conditions are too different from the ones animals are used to and/or evolved with, they may not survive long enough to establish a viable population (e.g., Saul et al. 2013; Sol et al. 2013; Chapple and Wong 2016). Since behavioral responses typically occur faster and are more rapidly reversible than, for example, physiological or morphological adaptations, they represent an effective “first line of defence” that animals can use to minimize immediate risks entailed by the novel conditions, and thus affect individuals’ abilities to settle and thrive in the novel environment (e.g., Duckworth 2009; Morgans and Ord 2013).

One of the key behavioral and cognitive factors that determine successful colonization or integration is behavioral flexibility, the ability to adjust behavioral outputs to better meet the environmental conditions (Izquierdo et al. 2017), which

enables individuals to find solutions to problems threatening their survival and reproduction (Sol 2009). Because there is no single cognitive ability or behavioral phenotype that is perfectly suited to all possible novel aspects of the environment, behavioral flexibility could be the key to overcoming the challenges entailed in environmental novelty, that is, allow individuals to surpass old habits, process the new information, and ultimately produce more appropriate responses. Recently there has been growing evidence that behavioral flexibility is related to many aspects of dealing with environmental novelty; from adapting to the increasing presence of human artifacts in anthropogenic environments (e.g., Estrada et al. 2020), through spreading to and colonizing new territories with different micro- and macro-environmental characteristics (e.g., Sol et al. 2013; Chapple and Wong 2016; Ruland and Jeschke 2020), to coping with conspecifics in complex social interactions (e.g., Kappeler et al. 2019).

Recent growth in the study of inter-individual variation in behavior and cognition also revealed that behavior is not completely flexible, that individuals differ consistently within a population, and that this consistent variation has fitness consequences. The most pronounced examples of the limits to behavioral flexibility are reflected in animal personality, temporally consistent inter-individual behavioral differences in animals (e.g., Gosling 2001; Réale et al. 2007). Understanding the complex interplay between animal personality and behavioral flexibility is therefore a necessary step in illuminating their potential joint role in driving individual success in a novel environment, and requires using integrative approaches.

Traditionally there have been 2 subfields of research on behavioral flexibility: one grounded in behavioral ecology, and the other in neuroscience and comparative psychology (e.g., Coppens et al. 2010; Carere and Locurto 2011). When studying behavioral flexibility in the context of adjustment to environmental novelty, behavioral ecologists focus on interactions between individuals and habitats that are novel to animals because they did not share an evolutionary history with

them, either because the species or individuals never lived in that particular region before, or simply because the habitat itself did not exist until recently (i.e., urbanized habitats). Comparative psychologists investigating behavioral flexibility in relation to environmental novelty focus on animals' abilities to withhold their innate behavioral outputs, reverse associations, and/or come up with new solutions, within a comparative evolutionary framework.

While both these separate research lines are bringing forward fundamental evidence of the complex loops between environment and individual behavioral and cognitive make-ups, an integration of these approaches is urgently needed. First, because while reaching an agreement on how to best define behavioral flexibility is tenable, we are yet to find a consensus on a standard way of measuring it. Some approaches may fit well under controlled laboratory conditions, whereas others could be more effective under natural conditions, directly in the wild. Additionally, behavioral flexibility has several facets, that can indeed be expressed in diverse contexts, encompassing decision-making, abilities to inhibit innate responses, reverse previously made links, and express innovative behaviors in all their variants, together with behavioral adjustments to anthropogenic disturbances. We advocate for considering these subtopics as integrated areas of investigation, on which a joint perspective between behavioral ecology, neuroscience, and comparative psychology is needed to advance our understanding of the role played by behavioral flexibility in coping with environmental novelty, and the selective pressures shaping this interaction.

The complementary strengths of these different subfields should be leveraged to achieve a holistic approach to the study of behavioral flexibility. For instance, evolutionary theoretical models, and the use of large sample sizes enabling powerful statistical inferences (strong assets of behavioral ecology) are needed to develop hypotheses on the evolution and development of behavioral and cognitive traits. Conceptual and empirical strengths of comparative psychology should then be applied to studies under both captive and natural conditions to go beyond the assumption that what is observed is indeed a reflection of the trait under study. In this vein, the design of rigorous empirical set-ups and the use of multiple controls should be combined with repeated testing of the same individuals to achieve robust experimental designs. We advocate for a joint effort in bringing laboratory rigor to the studies conducted in the field. Here we are aware that the control of every variable is not possible, but we believe that forethought on some of the potentially confounding factors affecting the traits under scrutiny would considerably benefit these studies. Similarly, studies that carefully describe animals' cognitive abilities should contextualize their findings, integrating the evidence of animals' capabilities with eco-evolutionary considerations, and ideally, validate the lab-based findings under appropriate field settings, and, if possible, look at long-term fitness consequences of behavior. Emphasis on conceptualizing and testing research hypotheses will contribute to developing standardized, ecologically relevant approaches and avoiding anthropocentric designs and interpretations. To get the best of both worlds and be able to work within an evolutionary framework, we need to bring together these important approaches. Since behavioral flexibility is studied in both fields, it is a more than suitable study topic for such an integrative perspective.

Integration of perspectives and approaches is urgently needed, among other things, to highlight inconsistencies between general theories and the complexities of the natural world. Since most studies on behavioral flexibility still refer to captive animals, research needs to be extended to the so-called "real world," where selective pressures, in all their complexities, act on individual traits. Further, focusing on non-traditional model species has the advantage of giving much-needed insights into taxa with less studied socio-ecological characteristics. We still know little in terms of the behavioral and cognitive adjustments to human presence and disturbance in their natural habitats, even regarding species that have been traditionally used as models for studies in captive settings. Thus, we need to extend research accordingly, to understand the generalizability of these processes and findings.

The aim of this Special Column is, therefore, to bring together different pieces of research that investigate the role of behavioral flexibility, in its broadest sense, when facing novel environments. This introduction to the topical collection of *Current Zoology* on Behavioral Flexibility and Novel Environments clarifies our operational definitions of environmental novelty and behavioral flexibility, and places the empirical contributions in context. The 10 articles that make up this Special Column collection highlight the role of behavioural flexibility in: i) dispersing into novel environments, ii) coping with human-altered, native, and non-native "natural" environments, and iii) the interplay with consistent inter-individual behavioral variation. Here, we aimed to provide a framework to integrate behavioral ecology and comparative cognition perspectives for future studies. By summarizing the contributions to the topical collection, we aimed to extract and integrate the main lessons that could be learned from the most recent work in this field.

The age of the Anthropocene has far-reaching consequences on the living organisms, and we are only beginning to realize the negative effects of sudden human-induced environmental disturbances on biodiversity (e.g., McKinney 2006; Grimm et al. 2008; Wong and Candolin 2015; Johnson and Munshi-South 2017). The organisms that are able to flexibly adapt and thrive in anthropogenic environments despite these abrupt changes have an evolutionary advantage over the less apt ones (e.g., Candolin et al. 2012). Usually we expect urban dwellers to be bolder and more neophilic than rural conspecifics (e.g., Carrete and Tella 2017; Charmantier et al. 2017; Mazza et al. 2020), but more and more studies are painting a different picture (e.g., Echeverría and Vassallo 2008; Bókonyi et al. 2012), that paves the way for a better understanding of the concept of "novelty within novelty," that is, how individuals respond to novel stimuli while in a novel environment (e.g., as pioneer colonizers or urban dwellers).

Lazzaroni et al. (2024) found that urban red foxes (*Vulpes vulpes*) showed explorative behavior towards novel stimuli that was comparable to that of their rural counterparts, thereby indicating that responses to novelty can be quite conserved even in established urban dwellers. While expressing comparable fear responses at the beginning of the study, urban foxes were also adjusting faster to the presented stimulus (a potential resource), showing that heightened flexibility may not necessarily be associated with specific behavioral types and that living in novel environments could require both heightened caution (or boldness in other species) and heightened flexibility. Therefore, if we aim to understand the

processes driving successful colonization of novel environments, flexibility in adjusting behavioral responses may thus be more worth looking into than single responses or traits, like learning or innovation capabilities, boldness, or aggression. This approach is quite challenging, because of both theoretical and practical considerations, particularly in field settings. However, it is imperative we give it our best shot, because flexible animals brought into captive settings may adjust too quickly to new conditions (e.g., Mazza et al. 2020), thus losing valuable information and/or obtaining incomplete descriptions of these adjustments.

Ellington et al. (2024) investigated vervet monkey (*Chlorocebus pygerythrus*) object curiosity in captivity, semi-urban and wild habitats, and showed that a positive experience combined with habituation often motivates object exploration, regardless of habitat differences. In line with previous studies detecting no differences in responses to novelty between wild and urbanized populations (e.g., Echeverría and Vassallo 2008; Bókony et al. 2012; Mazza et al. 2021), here the novel stimuli elicited comparable responses in the semi-urban and wild troops, whereas it was only in the captive, habituated, well-fed troop that the object curiosity was at its peak. While some non-human primates are suitable urban dwellers (e.g., Sha et al. 2009), many species face high rates of human-wildlife conflicts (e.g., Nyhus 2016). The study by Ellington and colleagues shows that for vervet monkeys, behavioral flexibility may have an important role regarding the interactions with (possibly hostile) heterospecifics, rather than the physical environment, and that the experience with humans and their artifacts will inform decisions on future approaches to human-made structures.

Cimarelli et al. (2024) also addressed the role of humans in the social landscape of urban dwellers, showing that free-ranging dogs (*Canis familiaris*) can use heterospecific social information to make decisions during a foraging task. Studying both domesticated and urbanized animals to investigate interspecific social learning is a very promising approach to understand social interactions. Since in cities different species are living more closely together than in natural habitats (e.g., Duckworth 2013; Cronk and Pillay 2020), behavioral flexibility can be of the utmost importance to navigate the novel social information scenario. This also offers a unique opportunity to study how species' interactions shape information use and transmission within and across the urban community (e.g., Damas-Moreira et al. 2018; Ratnayake et al. 2021).

Damas-Moreira et al. (2024) investigated inhibitory control, a cognitive ability that enables animals to halt innate responses and replace them with behaviors more suited to the current context, in 2 lizard species, the Italian wall lizard (*Podarcis siculus*), and the common wall lizard (*Podarcis muralis*), via a detour task. It is generally assumed that urban animals show higher levels of flexibility and inhibitory control because they outperform urban avoiders in tasks like problem-solving (e.g., Sol et al. 2013). While more than half of the subjects successfully solved the detour task, and female lizards showed higher cognitive flexibility than males, the authors did not find differences in performance between these 2 syntopic species, nor between lizards living in urban and semi-natural environments. These results are in line with the above-mentioned studies, and also other studies that did not find differences in, for instance, caching intensity and spatial

memory accuracy along an urban gradient (e.g., Thompson and Morand-Ferron 2019), or in learning ability between urban and non-urban populations (e.g., Kang et al. 2018), and suggest that our current understanding of the role of behavioral flexibility in dealing with environmental novelty is incomplete. Some species or populations living under different amounts of anthropogenic pressure may adapt to challenges in a similar way, and this may be particularly true for species that have lived alongside humans for millennia. In those organisms, differences in flexibility may have been eroded, and are thus no longer visible in living individuals of the species, at least under some conditions, tasks, or settings.

Štolhoferová et al. (2024) showed that rodents represent a valuable source of information regarding behavioral adjustments to novel environments. Despite their successful history of colonization, immediate association to humans, and long-standing commensalism, this taxon is rarely studied in this context. Through a highly original approach to assess exploratory tactics of black rats (*Rattus rattus*) in the laboratory, the authors highlighted how overlooked species-relevant behaviors like climbing may contribute to a partial differentiation of micro-habitats that could facilitate resource distribution and coexistence. The authors' detailed analysis of exploration patterns shows that individual rats have consistent exploration tactics and distribute themselves along a gradient of "even-uneven" exploration that is akin to a "fast-slow" exploration continuum (e.g., Verbeek et al. 1994; Koolhaas et al. 1999; Carere et al. 2005; Sih and DelGiudice 2012). Further, a few individuals changed strategy across tests, having first an even exploration of the arena followed by a more detailed search on a second attempt. This flexible use of information-gathering strategies highlights the importance of designing studies that can measure both the repeatability of behavioral responses across time and contexts, as well as evaluate habituation patterns to the same context, thereby gaining a thorough understanding of the dynamics between habituation, behavioral consistency, and flexibility.

Bobadilla et al. (2024) also detected different tactics in the use of space between pioneer and established non-native rabbits (*Oryctolagus cuniculus*) along their expansion range through Argentina. Contrary to the often-held assumptions that pioneers should be more broadly adaptable and more behaviourally flexible (e.g., Duckworth and Badyaev 2007), in this study the animals at the expansion edge showed higher selectivity in space use compared to conspecifics that had already established themselves in non-native areas. Expanding the taxonomic range to study colonization dynamics thus builds a more complete and complex picture of range expansion processes, where pioneers at the expansion edge are usually expected to be reliably bolder, more aggressive, and overall more risk-prone in their approaches (e.g., Duckworth and Badyaev 2007; Phillips et al. 2007; Gruber et al. 2018; Damas-Moreira et al. 2019).

Mazza and Eccard (2024) found that pioneer bank voles (*Myodes glareolus*) at the edge of their expansion through Ireland are actually more careful and thorough explorers compared to conspecifics settled in the source population. Colonizing an area that is void of conspecifics, and for which there is no previous eco-evolutionary experience, calls for more detailed information about the environment, which in turn requires a careful and thorough strategy of information acquisition that favors accuracy over speed (e.g., Hall

and Kramer 2008; Carvalho et al. 2013). Slow explorers are expected to be favored in unfamiliar or unpredictable environments because they are more sensitive to changes in their surroundings and thus run a lower risk of neglecting some key environmental features (e.g., Carere et al. 2010; Guillette et al. 2011; Šlipogor et al. 2022). The authors conclude that considering the species' ecology, and the respective priority that is attributed to resource discovery and acquisition versus the maintenance of safety and crypticity (i.e., danger avoidance) could resolve the apparent contrast between these and similar findings (e.g., Hudina et al. 2015; Ashenden et al. 2017) with current models predicting pioneers to be bold, aggressive fast-explorers.

Macali et al. (2024) compared the behavior of 3 nudi-branch species: 2 sympatric native Mediterranean species (*Cratena peregrina* and *Caloria quatrefagesi*) and an invasive South African species (*Godiva quadricolor*). Flexibility in behavior is particularly important when encountering new physical and social environments, and as such may be one of the determinants of successful biological invasions (e.g., Chapple and Wong 2016; Jeschke and Heger 2018; Chapple et al. 2022). Comparisons between native and invasive species may yield further insights into the potential traits involved in the early phases of colonization of novel habitats. Thus, in a series of experiments, the authors looked at how these 3 species differ in their activity, alertness, and habituation during a simulated introduction and acclimatization phase into a new environment, which simulated how these species would behave during an invasion process. The invasive species considerably differed from the other 2 species, showing higher levels of exploration activity, thigmotaxis, alertness and sensitization, and thereby indicating that these traits may be linked with its invasion success in new habitats. These findings corroborate previous studies that found individuals at the invasion front showing higher activity levels compared to settled populations (e.g., Llewelyn et al. 2010; Burstal et al. 2020).

Besides responses to novel physical environments, behavioral flexibility influences many different social contexts, such as partner choice, reproductive success, and parental care, and is tightly linked with decision-making, that is, like many behavioral and cognitive traits, in turn, influenced by both the internal and external factors that act upon an individual (e.g., Horn et al. 2022). Peignier et al. (2024) investigated how internal factors (i.e., animals' personality) and external factors (i.e., olfactory cues) affect males in locating and using new resources, using neotropical brilliant-thighed poison frog (*Allobates femoralis*) that are well-known for parental care (e.g., Ringler et al. 2013). The authors experimentally manipulated the location and olfactory cues of these new reproductive resource sites, measured personality traits, and inferred parent-offspring relationships with molecular parentage analyses, and found that reliable external sources, but not internal ones like exploration or boldness were the main drivers in finding and using new tadpole deposition sites in the dynamic tropical rainforest environment. While there is evidence that some personality traits are linked with parental care and reproductive success (e.g., Mutzel et al. 2013), the authors suggest that neotropical poison frogs in this study rely entirely on the external olfactory cues, closeness to their natal territory, and their spatial memory (see also Pašukonis et al. 2016; Ringler et al. 2018).

Lopez-Hervas et al. (2024) tested how changes in resource quality affect wild house mice (*Mus musculus domesticus*)

personality and life-history traits, both in adulthood and in a subsequent generation. In the past it has been suggested that "fast" personality types are less flexible in adjusting to changing conditions than "slow" types (e.g., Coppens et al. 2010). Disentangling the effects of external factors, like physical and social environment (modified by both anthropogenic and natural causes), and internal factors like personality on the expression of behavioral flexibility is indeed not trivial and requires careful empirical considerations, as these factors are likely to interact in driving animals' long-term fitness consequences. Lopez-Hervas et al. (2024) found that adult mice experiencing a change in resource quality, all switched to the same, passive stress-coping behavior and immediately reduced growth and reproduction rates. In contrast, the offspring of the mice that grew up with different food quality compared to their parents showed more active stress-coping than their parents, and maintained effects of the resource quality change only in regard to the body-mass development. This indicates that personality and life-history traits adjust in different ways to changing environmental conditions, and that studies over multiple generations may be needed to capture the long-term effects of environmental alterations, and the interplay between behavioral flexibility and other traits.

In sum, the 10 empirical studies in this collection encompass the role of behavioral flexibility, and its interplay with animal personality, during colonization of or dispersal to novel human-altered, native and non-native "natural" environments, across a wide taxonomic range. The role of behavioral flexibility and novel environments has so far been studied in both behavioral ecology and comparative psychology, yet with little integration of perspectives across these fields. Thus, to instill the best practices from these fields, we advocate future studies to i) design tests and their respective controls based on theoretical evolutionary models; ii) use the rigor of the laboratory approach when designing and, if possible, when conducting such tests in the field; iii) account for the species' natural socio-ecological characteristics when designing tests under captive (and wild) conditions; iv) have clear and concrete a priori research predictions on what certain empirical outcomes may signify; v) strive to avoid anthropocentric bias in the experimental design and interpretation of findings. Additionally, future studies integrating behavioral ecology and comparative psychology perspectives will benefit from the general good practices of: vi) collecting reliable quantitative data, that are neither overly reductionist nor too complex, to thoroughly capture behavioral expressions; vii) acknowledging limitations, but also the potential of own research design, analyses, as well as findings; and viii) providing thorough information about settings, subjects, and confounds, reporting all aspects that may have an effect on the final results, thus placing the findings in a wider context. Current technological advances such as camera traps, GPS tags, AI tools, and community-based initiatives like Citizen Science may further help in these endeavors, especially with elusive species. We draw attention to the taxonomic breadth of species highlighted in this Special Column, which range from invertebrates to non-human primates, as well as to the range of habitats these species live in, from captive, through anthropogenic, to native and non-native "natural" habitats. Furthermore, this Special Column highlights scientific efforts from multidisciplinary international teams across the globe. We hope that this Special Column will stimulate further discussions on the topic of behavioral flexibility and novel

environments, and potentially lead to new big-scale collaboration projects, in line with the Big Team Science efforts (e.g., Alessandroni et al. 2024a, 2024b). We also hope that this topical collection will help readers in designing new studies, whether conceptual or empirical in nature, allowing further insights into the role of behavior and cognition, and their potential for flexibility, in facing novel environments.

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