Defining the boundaries of individual plasticity in behavior: understudied mechanisms of evolution in varied contexts

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Introduction

Individual variation in morphology, physiology and behavior has been met with uneven treatment in biological studies. While scientists are beginning to realize the importance of diversity in individuals (morphology, genetics, behaviors etc.), historically the 'minority' results (i.e. outlier observations or statistically non-significant findings) of any given experiment have been dismissed from analysis. This may stem from the culture of Western science, where simple stories that garner support from many different techniques tend to be favored in high-impact journals. Our relationship with outliers may also reflect a limited ability to deal with these types of data experimentally or statistically. This is unfortunate, given that how commonly a behavior is exhibited by individuals in a population may not reflect its importance in influencing the evolutionary trajectory of the population. Indeed, rare individuals with exceptional or merely different traits can have a disproportionate impact on the population as a whole. Here, an analogy to our own process of scientific research in academia is irresistible: we all know those few scientists in our fields that have a large impact on the direction of the research as a whole. Ignoring real data because we do not know how to deal with it, or marginalizing it as experimental error, threatens to obscure our view of important biological processes. Therefore, understanding the nature and extent of individual variation would be a great leap forward in our understanding of all life forms. To do this, we need to integrate what is known about how individual variation impacts the dynamics of interacting systems in general – be it from microbial genetics to human sociological studies.

In aiming to capture variation in all its forms, technical challenges arise in the form of monitoring behavior at fine spatial and temporal resolution across long time scales in natural habitats. For example, if we are interested in how certain individuals learn to utilize a new food resource that others in the population have not learned yet, then how do we identify and quantify/measure this? Given that fields like neuroscience are still struggling to define learning and the mechanistic basis for neural variation, certain low-dimensional attributes will need to be identified for us to attack questions involving even more complexity (e.g. in the field, across evolutionary time). Another way to do this is to look to simple mathematical rules (algorithms) that describe behavior without needing to know all the details of neuroanatomy, membrane physiology, and organismal biomechanics. An example of this is in the behavior of falcons tracking their elusive prey using proportional navigation strategies. One need not know anything about the sensory capabilities of the eye or the biomechanics of flight, for example, to predict the capture success of the falcons. Other advancements that will be crucial to the success of this mission include emerging technologies to build smaller, non-invasive biologgers to infer behavior correctly from heartrate, vibration data, temperature, position, etc. We will also need advancements in machine learning to identify and classify behaviors unambiguously and without bias in complex field environments. Though there are important advances that need to be made on this front, our paper doesn't aim to tackle the issue of *how* to demonstrate and quantify individual plasticity in behavior.

What we believe to be missing, besides the requisite integration of disciplines and development of appropriate technology to identify what is an outlier, and ideally the mechanisms underlying them, is **that we lack the scientific culture to be able to appreciate what outliers are telling us**. This would include developing a funding system that would bring together scientists with diverse expertise in both the field and the lab and that would be open to long term studies, spanning generations of the model organism in question so as to track effects during evolution. Below, we offer some solutions for tackling these challenges and suggest potential benefits of changing our approach to science to identify and understand the effects of biological variation.

Challenges

Scales, collectives, and contexts

When trying to understand how behavior may be shaped, it is critical to explore the different scales on which the behavior may be changing. Often, most identification starts at the individual level. This occurs by characterizing the behavior and how it may vary by comparing other animals within a group, population, or closely-related species. To further understand how variation in behavior arises, hypotheses about proximate mechanisms may be helpful. For example, amounts of dopamine in the brain of a mammal may provide insight into whether reward systems are activated, which may indicate the animal is forming a positive association with the performance or result of that behavior (O'Connell & Hofmann 2011, Barron et al. 2010). Further, other neurological studies, such as identifying which brain areas are active during particular behaviors, could indicate what type of processing is needed for these neural systems to integrate information and respond to the behavior.

When working to understand behavior across scales, it is important to question at which level selection may be acting. For example, in a honey bee colony, there is variation on what type of food individuals forage on. Some foragers collect nectar; some foragers collect pollen (Robinson & Page 1989). However, selection acts on the colony via the amount of and nutrition content of forage – so some emergent phenotype of colony-level food collection is the trait that is being selected on (Page & Fondrk 1995). Of course, even though a collective phenotype may be selected, it is an emergent property of what phenotypes are making up the collective, therefore shifts in individual phenotypes are necessary to change the phenotype of the collective.

Recently, more attention has been paid to variation in groups performing collective behaviors, such as flocking birds and schooling fish (Sumpter 2010). In these groups, individuals utilize local information, such as movement of a neighbor, to behave. However, the individuals that comprise those groups may differ in their ability to perceive or respond to that local information. This variation can therefore influence how each collective behaves toward similar stimuli. In collectives, certain individuals may more strongly affect the behavior of those around it. Therefore, certain "keystone" individuals have non-linear effects on the behavior of the collective (Sih et al. 2009).

Variation between individuals in populations that work together to accomplish tasks for the group may be explained by a collective phenotype that is generated by this variation. The additive or non-additive variation that emerges as a collective phenotype could be analogous to 'hybrid vigor' (i.e. heterozygote advantage). This allows the population to remain robust and adaptable, especially in changing environments.

Contexts also play a major role in shaping behavior. Therefore, it is critical to identify the contexts in which behavior is occurring. There are obvious contexts for behavior, such as a predator inducing a rodent to run. However, other more subtle contexts may shape behavior, such as ecological conditions or social environment. For example, an animal may behave one way when alone, but act differently when around other conspecifics.

Recommendations for Change

Collaborative teams, proposal development, and funding

Understanding variation is difficult because it will require multiple scales of analysis, including behavioral, neural, genetic, and ecological data from the same species to fully capture the range of variation and define what makes an outlier an outlier. These collaborations should span disciplines, including but not limited to mathematics, neuroscience, cellular/molecular, genetics, ecology, evolution, psychology, and sociology. There is also a tremendous opportunity to work with Indigenous people or other local specialists in understanding the rules of behavior and their variations in nature, given that the proper tests must be applied to correctly evaluate behavior, which in itself requires sound knowledge of a species and their ecology.

To tackle this issue, research teams will need to be large, multidisciplinary groups - a structure that has been increasing in frequency in the biological sciences for the last half-century, but with which our science culture and our funding structure hasn't kept pace. As an example, in the established way of doing things, National Science Foundation (NSF) grant proposals require collaborative teams to identify themselves and for them to have a track record of working together before they can be successful at obtaining funding. Yet, how likely is it that scientists in different disciplines are even aware of what related problems each other is addressing? What if currently existing collaborative teams are missing a critical collaborator who studies a "novel" behavioral phenotype because they publish in different venues or attend different scientific meetings? Shifting our scientific culture and practices to facilitate better team-oriented science is critical in meeting biology's "grand challenges."

Two ways to move forward are to (1) modernize current practices surrounding the formation of research teams, and (2) to revise how such large-scale, long-term research projects are structured and funded. First, collaborative work is a human endeavor, being highly influenced by disciplinary identity, academic "lineages", and stiff competition for publications and grant funding. Relying too much on published preliminary studies and established social networks to initiate and fund collaborative and interdisciplinary research likely fosters the development of research that ignores variation and diversity -- both in terms of *what* is studied and in terms of *who* studies it. For instance, senior scholars tend to have more collaborators, even though in some fields more than 80% of scholars are of young age, creating imbalances in who participates in integrative projects and perhaps limiting the influence of new ideas or approaches (Wang et al., 2017). In addition, in collaborative science, “outliers” have influence; in other words, there is an oversized impact on the field of just a few, long-term collaborations. In a recent study, 1 in 10 biologists surveyed shared 50% or more of their papers with their most frequent collaborator (the authors called this a “super tie”), and publications coauthored by these super ties received 17% more citations than other types of collaborations (Petersen et al., 2015).

To combat these trends that limit our science, NSF could encourage, reward, and adopt formal policies to promote diversity in collaborative teams. One idea is that NSF could create a process by which individuals can express interest in an interdisciplinary idea or project and self-identify where their expertise could best contribute. We need better mechanisms by which researchers can efficiently find out about and contact each other. Online social network platforms, such as VIVO (www. vivoweb.org/) and Profiles RNS (profiles.catalyst.harvard.edu/), which serve as match-making systems, could facilitate that process. NSF program officers or other staff could also play a direct role in network-building by spreading the news about who’s doing what in newsletters or on social media, and by serving as “weavers” who notice commonalities and connect scientists with each other in ways that benefit them and advance interdisciplinary science (For more on the important role of weavers in a network, see Plastrik et al. 2014). Such changes would help to widen scientists’ professional network and lead to the building of research teams composed of individuals with diverse yet complementary skill sets and intellectual interests. It would undoubtedly level the playing field for beginning researchers and those from underrepresented groups in finding new and career-impacting research collaborations, and could help place more value on variation in biological systems by exposing researchers to new organisms or experimental paradigms.

Second, funding agencies should also take a stronger role in setting ground rules for how large-scale collaborations are structured and how they are funded by multiple agency subdivisions. NSF had made a lot of progress toward fostering new networks of collaborating scientists through their Research Coordination Networks (RCN) program, which aims to increase communication, synthesis, and innovation of new tools to advance science. Such program structures should be expanded to reintegrate biology. Why couldn't a similar program structure be used to support primary research projects (or groups of related projects surrounding a theme) that span multiple sub-disciplines? Could these kinds of collaborative networks be funded for longer periods of time to facilitate ongoing and complex work? For example, to support longitudinal data sets and accommodate for long generation times of the organisms being studied? One improvement to the RCN program that could help to make such networks or teams more productive is that NSF could provide guidance or even require that research teams are intentional in setting up structures to evenly divide the labor, educational outreach, and scholarly impact of grant-supported activities. Hosting virtual "jumpstarts" for the NSF community to generate proposal ideas for new multidisciplinary funding tracks would undoubtedly generate better proposals, more integrative science, and enable collaboration beyond the usual two- or three-PI research project. NSF could also find proven ways of effective collaboration from diverse sources (business, non-profits, social scientists), then tell scientists how we should structure our collaborations, instead of relying on us to tell NSF how we will do this. Currently, one lab or organization often acts as the hub, with partnering labs acting as spokes to support a larger research goal of the hub. However, social scientists would tell us that science would be more impactful and efficient if multiple labs or institutions could work (and be funded) as interconnecting nodes of a network focused on big topics, such as the mechanisms and evolutionary impact of individual variation (Wei-Skillern and Marciano, 2008).

Integrating field and lab studies

Through defining the individual variation that exists, and understanding the range of individual plasticity, there could be wide-ranging effects on the integration and practice of biological research. Currently, laboratory and field experiments are typically conducted in isolation, and dominated by experts of different subdisciplines. For example, field studies are largely conducted by behavioral ecologists, whereas lab-based studies are spearheaded by cell and molecular biologists, and neuroscientists. We view the integration of field and lab studies as both necessary for and a benefit of defining the range of individual variation in populations.

In addition to merging lab and field work, in order to assess how individual variation might drive evolution in populations, we need to reconsider how we devise experiments as well as interpret our resultant data as scientists. It is common in behavioral experiments, as an example, to train animals to 'reach criterion' before collecting the data necessary to determine the function of a compound, treatment, or other variable on learning (Weitz, 1961). This design assumes that animals that do not behave in an expected way are unsuitable for study. However, this natural variation in ability, or in 'personality' (i.e. behavioral syndromes *sensu* Sih et al. 2004) in ecological contexts is a trait on which selection can occur. As it stands, this variation is a largely ignored source of potential evolution in populations. As an example, individuals often vary on their mating preferences, which can be driven by experience, physiology, genetics, neural anatomy, epigenetics (e.g. Vogel et al. 2018; Boonstra 2005; Simcox 2005; Lim et al. 2004; Johnson et al. 2016). Rarely (if ever) do we have sufficient information on how individuals have developed this behavioral plasticity of all these systems in concert. Field studies which integrate over all these subdisciplines are currently impossible due to methodological complications (one cannot observe all traits of an individual at all times and in all contexts).

An established example of individual behavioral variation driving evolution is the study of finch speciation by the Grants and colleagues in their long-term field site in the Galapagos. Over the course of many years, these data demonstrated that the mating of a native female with a heterospecific male allowed for speciation to occur (Lamichhaney et al. 2018). Why that particular female exhibited the behavioral plasticity necessary to ignore males singing conspecific song and opt to mate with a heterospecific male is unknown. As noted above, we do not have the tools necessary to attribute this event to an underlying mechanism which drove female choice.

Too often, as scientists we view these events or occurrences of behavioral plasticity as spurious outliers, when they may be catalysts for large evolutionary events. Other examples might include certain populations developing site-specific tool use through cultural learning, or the exploitation of novel food sources. However, to address the range of possible individual variation in learning, we must revise our strategies for research to integrate across biological subdivisions, to combine field and lab data, and to rethink how we deal with 'outliers' to capture the possibilities for evolution to occur. We must reassess how we measure behavior in animals to determine if our measures are relevant for individuals acting in a natural environment. To address current shortcomings, we should encourage translational scientists using animal models and behavioral ecologists and ethologists to work together to determine if experiments have relevance for naturally occurring behavior in ecologically-relevant contexts.

Potential Impact

Improved understanding of human health and behavioral disorders

Understanding variation and plasticity in animal populations can shed light on the variation and plasticity we are seeing in human populations. Common animal models such as lab rodents, fruit flies, and nematodes provide excellent genetic models to understand the mechanisms by which variation and outliers may arise.

To uncover the deep evolutionary roots of such variation, a broader phylogenetic approach is required. Further, being able to explore animals with different ecological and social life histories (i.e. many contexts) can provide insight into the environmental conditions which may select for or cause variation to be exhibited. For example, recent studies looking at how birds and elephants exhibit sophisticated tool use and theory of mind, show their capabilities rivals humans' (Nissani 2004, Emery & Clayton 2004). Understanding variation may also shed light on the evolutionary roots of some diseases, such as autism, which has been studied using honey bees that exhibit fewer social interactions than nestmates, as well as in solitary bees (Shpigler et al. 2017, Kocher et al. 2018). From these comparative animal social systems, we can form translational hypotheses about what might happen in human societies when behaviors shift, and may be able to understand how genes for certain behaviors or plasticity may be conserved.

However, humans are a unique species with an incredible ability to modify their environment and thus quickly alter the selection pressures that are acting on them. Thus, studying other animals may not provide complete insight into how human populations are evolving.

Conservation

By defining the individual variation in learning and behavior, we may yield deeper insight into how individuals can adapt to novel situations. The influence of behavioral plasticity on an animal's ability to adapt to human-induced rapid environmental change has been well-addressed in previous work (Sih et al. 2011; Snell-Rood 2013). However, improving our understanding of the variation that exists for individuals and populations may improve our ability to predict how animals will respond to changes in their environment. These data could then be applied to conservation efforts to identify species which would be most impacted by environmental change. We could then selectively allocate resources or land for conservation which would have the most positive impact in conservation efforts globally.

Broader impacts

Open science, citizen science, collaborations with local people will increase

Understanding variation means being able to study enough individuals, populations, and contexts over time and space to obtain the full range of behavior, including novel behavioral expressions. Though tools that remotely record behavior exist, increasing the number of avenues through which we collect data about animal behavior is necessary to accurately capture variation. Video monitoring programs, camera traps, and citizen science initiatives allow us to collect information on more individuals in more geographic regions. Increasing focus on these alternative means of data collection will put scientists in increasing contact with their communities, some of which may have specialized knowledge, and will give those communities a larger role in directing or contributing to the science that utilizes local landscapes or study species. Increasing the network of individuals that participate directly or indirectly in a research project can benefit non-scientists by making research projects more transparent, accessible, and open for people of many different backgrounds to participate and take ownership.

Use of "outlier" cases in undergraduate and graduate education

Similar to clinical case studies, in which one patient's illness used to provide a framework for problem-solving, outlier cases that emerge from studies of individual variation can serve as teaching tools in the biology classroom. Case-based instruction has been repeatedly demonstrated to build students' skills in analytical thinking, problem-solving, and cooperative learning (Bonney 2015; Herreid 1994; Duch et al; 2001; AAAS, 2010 Vision and Change; NRC 2011), and better prepares students to contribute productively to research work in and outside the classroom. Case-based instruction can also facilitate interdisciplinary learning and help students make connections between understanding the nature of individual variation and its application to real-world problems (e.g., species conservation), which are critical skills of a future science workforce that will need to tackle big, multi-faceted problems (Dori and Herscovitz 1998). Using the study of outliers and individual variation as teaching tools will help raise a future cohort of scientists who understand modern biological research as a collaborative, interdisciplinary process.

Summary

If our goal is to understand individual plasticity in behavior and its potential impacts on evolution, we must 1) consider outliers, contexts, and collectives and 2) support collaborative teams by changing the way we 'do science' and improving integration across disciplines. Through this, in addition to improving our understanding of individual variation in behavior, we foresee benefits in translational research for human health and in conservation of at-risk species. Finally, we posit that this shift in culture towards more integrative science will incorporate citizen scientists and local naturalists, and change how we teach future students.

References

American Association for the Advancement of Science (2010) Vision and change in undergraduate biology education: a call to action. (Brewer C, Smith D., eds). Washington, D.C.: AAAS

Barron, A. B., Søvik, E., & Cornish, J. L. (2010). The roles of dopamine and related compounds in reward-seeking behavior across animal phyla. *Frontiers in behavioral neuroscience* 4:163.

Bonney, K.M. (2015). Case study teaching method improves student performance and perceptions of learning gains. *Journal of Microbiology and Biology Education* 16(1):21-28.

Boonstra, R. (2005). Equipped for life: The adaptive role of the stress axis in male mammals. *Journal of Mammalogy* 86(2): 236-247.

Dori. Y.J., & Herscovitz, O. (1998). Question-posing capability as an alternative evaluation method: analysis of an environmental case study. *Journal of College Science Teaching* 36:411-430.

Duch, B.J., Groh, S.E., & Allen, D.E. (2001). The power of problem-based learning. Sterling, VA: Stylus Publishing.

Emery, N.J., & Clayton, N.S. (2004). The mentality of crows: Convergent evolution of intelligence in Corvids and Apes. *Science* 306(5703):1903-1907.

Herreid, C.F. (1994). Case studies in science: a novel method of science education. *Journal of College Science Teaching* 23:221-229.

Johnson, Z.V., Walum, H., Jamal, Y.A., Xiao, Y., Keebaugh, A.C., Inoue, K., & Young, L.J. (2016). Central oxytocin receptors mediate mating induced partner preferences and enhance correlated activation across forebrain nuclei in male prairie voles. *Hormones and Behavior* 79: 8-17.

Kocher, S. D., Mallarino, R., Rubin, B. E., Douglas, W. Y., Hoekstra, H. E., & Pierce, N. E. (2018). The genetic basis of a social polymorphism in halictid bees. *Nature communications* 9(1):4338.

Lamichhaney, S., Han, F., Webster, M.R., Andersson, L., Grant, B.R., & Grant, P.R. (2018). Rapid hybrid speciation in Darwin's finches. *Science* 359(6372): 224-228.

Lim, M.M., Wang, Z., Olazábal, D.E., Ren, X., Terwilliger, E.F., & Young, L.J. (2004). Enhanced partner preference in a promiscuous species by manipulating the expression of a single gene. *Nature* 429(6993): 754-757.

National Research Council (2011) Promising practices in undergraduate science, technology, engineering, and mathematics education. In: National Research Council (Niellson, N., ed). Washington, D.C.: National Academies Press.

Nissani M. (2004) Theory of Mind and Insight in Chimpanzees, Elephants, and Other Animals?. In: Rogers L.J., Kaplan G. (eds) Comparative Vertebrate Cognition. Developments in Primatology: Progress and Prospects. Springer, Boston, MA

O'Connell, L. A., & Hofmann, H. A. (2011). The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis. *Journal of Comparative Neurology* 519(18):3599-3639.

Page, R. E., & Fondrk, M. K. (1995). The effects of colony-level selection on the social organization of honey bee (Apis mellifera L.) colonies: colony-level components of pollen hoarding. *Behavioral ecology and sociobiology* 36(2):135-144.

Petersen, A. M. (2015). Quantifying the impact of weak, strong, and super ties in scientific careers. Proceedings of the National Academy *of Sciences* 112(34):E4671–E4680.

Robinson, G. E., & Page, R. E. (1989). Genetic determination of nectar foraging, pollen foraging, and nest-site scouting in honey bee colonies. *Behavioral Ecology and Sociobiology* 24(5):317-323.

Shpigler, H. Y., Saul, M. C., Corona, F., Block, L., Ahmed, A. C., Zhao, S. D., & Robinson, G. E. (2017). Deep evolutionary conservation of autism-related genes. *Proceedings of the National Academy of Sciences* 114(36):9653-9658.

Plastrik, P., Taylor, M., & Cleveland, J. (2014) *Connecting to Change the World: Harnessing the Power of Networks for Social Impact*. Washington, D.C.: Island Press

Sih, A., Bell, A., & Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* 19(7): 372-378.

Sih, A., Ferrari, M.C.O., & Harris, D.J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary applications* 4(2): 367-387.

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology* 63(7):975-988.

Simcox, H., Colegrave, N., Heenan, A., Howard, C., & Braithwaite, V.A. (2005). Context-dependent male mating preferences for unfamiliar females. *Animal Behaviour* 70(6): 1429-1437.

Snell-Rood, E.C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour* 85(5): 1004-1011.

Sumpter, D. J. (2010). *Collective animal behavior*. Princeton University Press.

Vogel, A.R., Patisaul, H.B., Arambula, S.E., Tiezzi, F., & McGraw, L.A. (2018). Individual variation in social behaviours of male lab-reared prairie voles (*Microtus ochrogaster*) is non-heritable and weakly associated with V1aR density. *Scientific Reports* 8(1): 1-9.

Wang, W., Yu, S., Bekele, T.M. et al. (2017). Scientific collaboration patterns vary with scholars' academic ages. *Scientometrics* 112: 329-343. https://doi.org/10.1007/s11192-017-2388-9

Wei-Skillern, J. and Marciano, S. (2008). The Networked Non-Profit. Stanford Social Innovation Review, Spring 2008. p.38-43. https://ssir.org/articles/entry/the_networked_nonprofit

Weitz, J. 1961. Criteria for criteria. *American Psychologist* 16(5): 228-231.