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The Philosophy of Outliers: Reintegrating Rare Events Into Biological Science

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Synopsis Individual variation in morphology, physiology, and behavior has been a topic of great interest in the biological sciences. While scientists realize the importance of understanding diversity in individual phenotypes, historically the "minority" results (i.e., outlier observations or rare events) of any given experiment have been dismissed from further analysis. We need to reframe how we view "outliers" to improve our understanding of biology. These rare events are often treated as problematic or spurious, when they can be real rare events or individuals driving evolution in a population. It is our perspective that to understand what outliers can tell us in our data, we need to: (1) Change how we think about our data philosophically, (2) Fund novel collaborations using science "weavers" in our national funding agencies, and (3) Bridge long-term field and lab studies to reveal these outliers in action. By doing so, we will improve our understanding of variation and evolution. We propose that this shift in culture towards more integrative science will incorporate diverse teams, citizen scientists and local naturalists, and change how we teach future students.

Introduction

Individual variation in morphology, physiology, and behavior has been a topic of great interest in the biological sciences. While scientists realize the importance of understanding diversity in individual phenotypes, historically the "minority" results (i.e., outlier observations or rare events) of any given experiment have been dismissed from further analysis. Statistical outliers are defined as "an observation that deviates so much from other observations as to arouse suspicions that it was generated by a different mechanism" (Hawkins 1980, p. 1). Our relationship with outliers may reflect our limited ability to deal with these types of data philosophically, experimentally, and statistically. This is unfortunate, given that how common a behavior is might not reflect its importance in influencing the survival of the individual or the evolutionary trajectory of the population. For example, predation events are rare, but it is hard to argue that they are not important. At the population level, rare individuals with exceptional or merely different traits can have a disproportionate impact on the population as a whole.

The importance of understanding rare events is not exclusive to biology. Physicists have long searched for dark matter to explain the rare events that do not fit within the standard model (Bertone and Tait 2018). In biology, however, there is a tendency for these rare individuals or events to be excluded from broader discussion because we often have insufficient data to fully understand how these individuals might shape a

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population, or we might prefer to highlight the data that are easier to interpret. Yet, ignoring real data because we do not know how to deal with it, or marginalizing it as experimental error, threatens to limit our interpretation of important biological processes. Developing ways to re-integrate outliers into our science and scientific practice in order to understand the nature and extent of individual variation would be a more inclusive approach to science and a great leap forward in our understanding of all life forms.

Here, we highlight a well-known case study (Grant and Grant 1993, 2002, 2006) as an example of how outlier observations can become important scientific discoveries under the right conditions. While this case is a "success story", it helps make apparent the barriers that exist in identifying and incorporating meaningful outlier data. Though there are important advances that need to be made to help scientists determine whether outliers are spurious or whether they contain meaning, our paper does not aim to tackle the issue of how to demonstrate what is a rare observation or what is the mechanism underlying outlier observations. What we believe to be missing is that **we lack the scientific culture to be able to appreciate what outliers are telling us**. This culture includes what we choose to study, what we consider "data", how we approach understanding variation (e.g., a "continuous-video" vs "snapshot" approach, see below) and, importantly, our funding system's ability to bring together scientists with diverse expertise and to sustain long-term studies to track outlier effects and their evolution. Below, we identify three major challenges to re-integrating outliers, offer some solutions for tackling these challenges, and suggest potential benefits of changing our approach to science.

Case study

In the early 1980s, *Geospiza fortis* (the medium ground finch) and *G. scandens* (the cactus finch) were known inhabitants of the Daphne Major island in the Galápagos. *G. fuliginosa* (the small ground finch), as well as *G. fortis* would occasionally travel to Daphne Major from the nearby Santa Cruz island (Grant and Grant 1993). Immigration tended to be rare, with fewer than one breeding immigrant per generation (Grant and Grant 2010). Hybridization between these species (and other ground finches on these islands) occurred, but also tended to be rare events. Indeed, rates of hybridization were between 0 and 4%, and survival of these offspring was extremely low (Grant and Grant 1992).

In 1981, the arrival of a uniquely large *G. fortis-scandens* hybrid male immigrant from Santa Cruz started what became an endogamous lineage of large-billed *G. fortis* that sang a lineage-specific type of *G. fortis* song (Grant and Grant 2006). This rare hybrid male immigrant bred with a rare female hybrid and reproductive isolation and speciation in the lineage followed (Grant and Grant 2009). This case study highlights the importance of "outliers" in driving evolution: rare hybrid individuals and rare immigrants to the island significantly impacted the phenotypic variance on the island. Hybridization and immigration were followed by a rare weather event (Grant and Grant 1993), and these "outlier" events together set the populations of Daphne Major on a path that was previously unforeseen.

The example of finches on Daphne Major underlines the importance of rethinking or reintegrating "outliers". Without the long-term ecological research done by the Grants on these islands (Grant and Grant 2002), we would have missed the changes in body size, beak shape, hybrid survival, and rare event(s) that led to evolutionary change in these populations. Short-term projects are only snapshots in time and would have almost certainly missed the events that precipitated these longer-term changes. With long term data, we have a "continuous-video" dataset, where changes and rare events are more easily detected, compared to "snapshot" approaches. In a typical season on Daphne Major, hybrid animals were unlikely to survive, yet a change in environmental context shifted selection parameters and created a unique confluence of variables that enabled these hybrid animals to outcompete others. This example shows how well-funded, long-term studies are essential for identifying how often rare events (e.g., hybridization) occur, and for allowing the detection of critical biological patterns (e.g., speciation).

Current challenges

Identifying outliers

One challenge to re-integrating outliers into mainstream science is: how do we determine whether observations are spurious or real events? What we choose to study and how we study it is important in making this distinction. The Grants' work on *Geospiza* suggests that the impact of rare events may only be realized after some time is spent in observing a population and meticulously documenting change. However, several 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 measure this? One technological solution is to continue to adapt machine learning and algorithms to help us identify complex, rare traits and work to create "big data" analyses (Valletta et al. 2017). Given that fields like neuroscience are still struggling to define even well-studied processes, such as learning and the mechanistic basis for neural variation, certain low-dimensional attributes in biology will need to be identified for us to attack questions involving even more complexity (e.g., in the field, across evolutionary time). A potential solution is to look to simple mathematical rules (algorithms) that describe behavior without needing to know all the details (e.g., of neuroanatomy, membrane physiology, and organismal biomechanics; Hein et al. 2020). An example of this is in the behavior of falcons tracking their elusive prey using proportional navigation strategies (Brighton et al. 2017). 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 heart rate, vibration data, temperature, position, etc. (e.g., Ripperger et al. 2020). We will also need advancements in machine learning to identify and classify behaviors unambiguously and without bias in complex field environments. To begin addressing these issues, biology needs integration of disciplinary tools and knowledge, along with the appropriate technology to identify outliers. Because rare events can be meaningful for populations (see Grant and Grant 1993, 2002), we should work to develop interdisciplinary tools and technologies to reintegrate these occurrences whenever possible.

Another point that the case study highlights is that it is critical to explore different scales on which behavior may be changing in order to understand how behavior is shaped. Often, most identification starts at the individual level. This occurs by characterizing the behavior and how it may vary by comparing animals within a group, population, or closely related species. To find true rare events or individuals, we need to consider variation at multiple scales. For example, in a honeybee colony, there is variation on what type of food individuals forage on. Some foragers collect nectar; some foragers collect pollen (Robinson and Page 1989). However, selection acts on the colony via the amount of and nutrition content of forage, therefore some emergent phenotype of colony-level food collection is the trait that is being selected on (Page and 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. In addition, rare individuals with exceptional or merely different traits can have a disproportionate impact on group dynamics. For example, in flocking birds and schooling fish (Sumpter 2010), individuals utilize local information, such as movement of a neighbor, to behave as a group. However, the individuals that comprise those groups can differ in their ability to perceive or respond to that local information. This variation can therefore influence how each collective behaves towards similar stimuli. In collectives, certain individuals may more strongly affect the behavior of those around it. Therefore, certain "keystone" individuals have nonlinear effects on the behavior of the group (Sih et al. 2009; Modlmeier et al. 2014). 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), such as the advantage the hybrid finches had in the case study (Grant and Grant 2002). 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 that are sometimes overlooked 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. The foundations of certain fields such as biomechanics and neuroscience are built on behavior, and would do well to maintain this perspective (Chen and Hong 2018). Some rare events may only occur under specific contexts, and these need to be considered in studies.

Statistical considerations and criteria

Another challenge is that we need sufficient data from a population to detect rare events. In the absence of large datasets, individuals that fall at the edge of a statistical distribution may be removed prior to analysis. Furthermore, when we set "criteria", we can eliminate important variation (Weitz 1961). One such study examined boredom and whether participants would self-administer electric shocks (Wilson et al. 2014). The authors of the study found that nearly 25% of the 55 participants did not find the shock aversive enough to pay money to prevent it. Yet, two participants gave themselves an inordinate number of shocks (119 and 190 in the 15-min period), whereas the rest of participants either administered none or only a handful (Wilson et al. 2014). In studies where such observations could be real rare events, we suggest that these excluded datapoints should be mentioned in publication for the purposes of future study (see below in "recommendations"). Reviewers should also encourage this reporting and journals should ask if any outliers have been excluded. Natural history notes are often a reasonable option, but publications from physics and medicine routinely publish $n = 1$ results.

Infrastructural challenges

If there is one thing that the Grants' work has demonstrated, it is the value of long-term support for studies that have the potential to reveal both the fundamental rules of life on Earth and are of the scope to identify rare events and track their influence. Although researchers that have earned previous grant funding are more likely to succeed in obtaining funding again (known as "the Matthew effect"; Bol et al. 2018), few mechanisms exist today to fund long-term population studies. The academic system is designed for projects that exist on a 3–5-year time scale, which is sufficient time for the completion of most federal grant funding, or for a student to complete a doctoral project. Yet, many behavioral processes, such as the speciation event in the case study (Grant and Grant 2009), can take longer to occur. One significant challenge to shifting science culture to reintegrate rare events is that we currently value certain types of science. In particular, if work tends to diverge from the status quo, is too variable, or is a "null result", we tend to discount findings from these studies. Part of this stems from what we value and fund through national and international funding agencies; we strive for "advancement" and "transformative" work, while replications, work aiming to confirm past findings, or work based on "messy" data is perceived as having lower merit. We posit that we need to rethink both what we fund and how we fund science in order to shift our merit conceptualization and to be able to obtain more information from the data that we have. Replication is important in identifying rare events, but failed replications are often shelved and unpublished, partly because these are seen as low-impact or due to some error. In extremes, some may turn to fraud to replicate previous findings. If "outlier" datasets are viewed as informative instead of problematic, then we can attempt to determine what conditions might have been the cause (e.g., Noah et al. 2018). In doing so, we can reduce the pressure to "recreate" findings exactly, reducing fraud, and improving returns on our investments overall.

Recommendations for change

Reintegrating rare events and individuals 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 biology, 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. This in itself requires intimate knowledge of a species and their ecology that laboratory scientists do not always possess.

Funding novel integrative approaches and teams

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, diversity, and outliers—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, certain scientists can themselves be considered outliers: they have disproportionate influence on the mean trajectory of the field of biology. Indeed, 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 2015).

To combat these trends that limit our science, granting agencies should play a larger role 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). Network-building can also be spread through newsletters and social media network platforms, such as VIVO (www. vivoweb.org/) and Profiles RNS (profiles.catalyst.harvard.edu/), which serve as match-making systems. Such changes could help to make connections more visible and to place more value on outliers and rare events in biological systems by demonstrating to researchers the importance of variation in their own study systems.

Integrating field and lab studies

To shift how we think about and study outliers, we need to bring field and lab scientists together. 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 molecular biologists and neuroscientists, for example. We view the integration of field and lab studies as both necessary for and a benefit of reintegrating rare events into biology.

In addition to merging lab and field work, to assess how outliers 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 types *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, and/or epigenetics (e.g., Lim et al. 2004; Boonstra 2005; Simcox et. al 2005; Johnson et al. 2016; Vogel et al. 2018). Rarely, if ever, do we have sufficient information on how individuals have developed plasticity in all these systems in concert. Field studies that integrate over all these subdisciplines of biology are currently impossible due to methodological complications. Obviously, a single researcher or lab cannot observe all traits of an individual at all times and in all contexts, yet we often publish as if we have.

In the case of the Grants' work, rare individuals and events were under selective pressure, which led to the observation of speciation over the course of the study. In the absence of such long-term robust data, scientists should be encouraged to: (1) State clearly why certain criteria for exclusion were selected and (2) Discuss the potential ramifications of excluding such individuals from analysis. Including short discussions on these rare observed events is important to identify events that may have impacts that are only realized over the long-term (i.e., beyond the end of the study).

In summary, 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 and to maximize the potential of capturing rare events. To address current shortcomings, we should encourage translational scientists using animal models to work together with behavioral ecologists and ethologists to determine if experiments have relevance for naturally occurring behavior in ecologically-relevant contexts.

Potential impact

"Approaches to science": changing the way we think about data

One benefit of adopting an acceptance of data variance and these outliers is a shift in how we approach science and how we think about data. This includes a shift in culture where outliers or highly variable results are not seen as "problematic" (Greenwald 1975). Indeed, this historical type of view narrows the focus of science practice and can stifle diversity of thought. Much like the changes to include more diverse perspectives in our field, we need to reassess "problematic" datasets and move towards a more networked and integrative approach. An additional side effect may very well be the reduction of the motivation to falsify or selectively report data (Head et al. 2015) by encouraging researchers to publish their "messy" datasets, even if they do not fit within the paradigm of neat data. This shift is necessary and will have long-lasting impacts of what we consider "important" science.

Improved understanding of human health and behavioral disorders

Understanding variation and rare individuals in animal populations can shed light on the variation and plasticity that 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, but to realize the deep evolutionary roots of such rare events or individuals, a broader phylogenetic approach is required (Jourjine and Hoekstra 2021). Furthermore, 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' (Emery and Clayton 2004; Nissani 2004). Understanding variation may also shed light on the evolutionary roots of some diseases, such as autism, which has been studied using honeybees 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 we may be able to understand how genes for certain behaviors or plasticity may be conserved.

Conservation

By identifying rare individuals that excel or exhibit rare behaviors, 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 that 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

"Outlier" thinking might have broader impacts in addition to improving science. By rethinking how these unique contributions can impact our science, it is possible that we will start to better appreciate other unique perspectives in our collaborations.

Outliers in our teams

Research shows that diversity in teams can improve problem solving because members with unique information tend to share more in these diverse teams (Phillips et al. 2006). Furthermore, working with diverse views can alter both the cognitive effort people put into their work and also improve performance (Loyd et al. 2013). Therefore, one potential broader impact of changing how we think about outliers is a change in how we view "outliers" in our teams.

Open science, citizen science, and collaborations with local people

Identifying outliers 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 provided by outliers. 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 nonscientists 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 for educating the next generation of integrative biologists. Case-based instruction has been repeatedly demonstrated to build students' skills in analytical thinking, problem-solving, and cooperative learning (Herreid 1994; Duch et al. 2001; AAAS 2010; NRC 2011; Bonney 2015), and it 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, multifaceted 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

Our goal is to rethink how we currently deal with rare individuals and events in order to reintegrate them into biological science. This philosophy that rare individuals can give insight into biological processes has three themes in which we advocate for change: (1) We must change our scientific philosophy to allow for the discussion of "messy" data and rare individuals, (2) We must conduct our science and maximize our statistical power to expand our capacity to detect real rare events, and (3) We must have infrastructural supports that allow scientists to fully explore these unique events and individuals. By doing so we will improve our understanding of rare events, individuals, and evolution, which may lead to potential 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 and inclusive science will incorporate diverse teams, citizen scientists, and local naturalists, and change how we teach future students.

Data availability

No datasets were generated or analysed during the current study.

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