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Studying Individuality in Behavioural Ecology: Overcoming Epistemic Challenges

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Abstract
Behavioural ecologists have recently begun to study individuality, that is, individual differences and uniqueness in phenotypic traits and in ecological relations. However, individuality is an unusual object of research. Using an ethnographic case study of individuality research in behavioural ecology, we analyse concerns that behavioural ecologists express about their ability to study individuality. We argue that these concerns stem from two epistemic challenges: the variation-noise challenge and the generalisation challenge. First, individuality is difficult to distinguish from noise, as standard practices lump variation between individuals together with noise. Second, individuality is difficult to capture in generalisations, as they typically involve ignoring idiosyncratic factors. We examine how these challenges shape research practices in behavioural ecology, leading to epistemic strategies for studying individuality via alternative approaches to measurement, experimentation, and generalisation.

Keywords: individuality; individual differences; variation; measurement; generalisation; varipraxis

1 Introduction

Biologists have long known that individuals differ from one another and even that they are unique. In behavioural ecology, this phenomenon is known as *individuality*, a concept which covers both individual uniqueness and more general variation between individuals in their phenotypic traits and ecological relations (Kaiser and Trappes 2021; Trappes 2022).[1] Individuality is an important phenomenon, being both widespread and ecologically and evolutionarily significant (see, e.g., Bolnick et al. 2003; Dall, Houston, and McNamara 2004; Sih, Bell, and Johnson 2004; Araújo, Bolnick, and Layman 2011; Dall et al. 2012; Layman, Newsome, and Gancos Crawford 2015). Nevertheless, some behavioural ecologists express concerns about individuality as an object of empirical research. Can group-based methods such as comparing treatment and control groups in experiments be used to capture individuality? How can we apply statistical methods to studying individuality if they require grouping individuals? Can the study of individuality deliver general knowledge or be subject to generalisations?

These sorts of questions were brought to our attention during an ethnographic study and ongoing collaboration with a large research consortium investigating behavioural, ecological and evolutionary aspects of individual differences and individuality. We found that some biologists in the consortium were concerned that standard methods and research goals make individuality difficult to capture. In this paper we analyse these concerns, arguing that they stem from two epistemic challenges: (i) the *variation-noise challenge*, the challenge of distinguishing individuality, as real and relevant variation, from noise; and (ii) the *generalisation challenge*, the challenge of developing generalisations about individuality, given that generalisation typically trades off with capturing idiosyncratic factors.

Behavioural ecologists do have strategies for studying individuality, including stratified sampling, repeated observation, factorial experimental design, replicate individual study design, limited-scope generalisations, and making multiple generalisations with varying levels of abstraction. These strategies are typically implicit and not conceived of as addressing the epistemic challenges. We make these strategies explicit and explain how they contribute to overcoming the challenges.

Our analysis brings to light and makes sense of behavioural ecologists' concerns about studying individuality and clarifies how and to what extent individuality can be investigated. In addition, our analysis contributes to a broader picture of how scientists deal

[1] This concept of individuality is distinct from but related to other concepts of biological individuality, such as immunological individuality or evolutionary individuality (Trappes 2022, 22). The latter concepts are relevant for questions about counting individuals or determining their boundaries. In contrast, uniqueness and individual differences are relevant for questions about distinguishing individuals from one another and defining their identity (Kaiser and Trappes 2021). These questions are closely related and together form a problem agenda of biological individuality (Kaiser and Trappes 2021).

with variation. Recently, James Lowe and David Ingram introduced the term "varipraxis", defined as "the set of practices involved in the apprehension, measurement, investigation and analysis of different forms of variation" (2023, 3). Lowe and Ingram developed this concept in the context of taxonomy. We suggest that the strategies that behavioural ecologists adopt to address the epistemic challenges of individuality constitute a distinctive varipraxis, one concerned with delimiting variation not between taxa but rather between individuals. Although distinctive, this varipraxis arises in response to tensions and trade-offs common across the sciences, especially the way that variation can disrupt scientists' efforts to develop reliable and general knowledge.

We begin in Section 2 by describing our methods. In Section 3 we introduce the field of individuality research in behavioural ecology, and in Section 4 we describe concerns expressed by behavioural ecologists studying individuality. Section 5 identifies the epistemic challenges underlying these concerns, and Section 6 analyses strategies for addressing the challenges. We conclude in Section 7.

2 Methods

From 2018 to the present, we have been members of the interdisciplinary research consortium "A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance, Niche Construction (NC^3)" (hereafter "the CRC"). The CRC has around 45 scientific members, including behavioural biologists, ecologists, evolutionary biologists, theoretical biologists, statisticians, and philosophers. It has been running since 2018 and is located at several universities in Germany. The CRC studies individuality and individual differences across a range of species, in the laboratory and in the field. Its general aim is to investigate individual differences and identify their causes and consequences (see Section 3).

As part of our role in the CRC, we conducted an ethnographic study from 2018 to 2021 (Trappes 2021). The study aimed to determine how researchers understand and study individual differences and individuality. One element of the study was participant observation, which involved attending meetings, collaborating with a number of researchers, and giving talks to the group. During this process we collected materials such as internal reports, photographs, and slide decks. Participant observation provided insights about how individuality is understood and studied within the group as well as amongst high-profile researchers in the field who were invited as guest researchers. These insights provided one source of material to develop our account, and also informed the design of the questionnaire and interviews.

The second element of the study was a qualitative questionnaire. The questionnaire was conducted in 2018, at the start of the first funding phase of the CRC. It had 37 responses, a 90% response rate. Amongst other topics, we asked participants short-answer questions about individuality, individualised phenotypes, and individualised niches. We analysed responses using semi-grounded coding. Coding is an approach that assigns codes—short words or phrases—to segments of text to pick out ideas, themes, meanings, or characteristics of the text (Corbin and Strauss 2015, chap. 12). Semi-grounded coding involves developing codes that allow latent meaning to emerge from the text, while still being loosely guided by the coders' research interests (Mansnerus and Wagenknecht 2015; Nersessian and MacLeod 2022). The codes we developed were guided by our interest in how individuality is understood and studied.

The third element of the study was semi-structured interviews. Interviews were conducted in 2019 and were 30-45 minutes long, with either a single interviewee or two interviewees working on the same project. There was a total of 10 interviews and 14 participants, or 34% of all scientific members of the CRC. The sample was chosen to cover a range of disciplinary backgrounds, research topics, and career stages. Being semi-structured, interviews were loosely based on an interview guide, with space for adjusting the order of questions and asking follow-up questions. We analysed interview transcripts using deductive (also known as hypothesis) coding (Andow 2016; Braun and Clarke 2006; Saldaña 2009). Based on findings from participant observation, the questionnaire, and our reflections on the interviews, we developed a detailed list of codes in advance. During coding we adjusted the code list in response to emergent findings such as unexpected ideas and observed patterns. Full details about the ethnographic study can be found online (Trappes 2021).

Many of our findings are the result of biologists discussing with philosophers. We see this as a merit of our study: we provided the space for researchers to reflect on issues they might otherwise not explicitly discuss. This allows underlying concerns, such as those about studying individuality, to surface. We nevertheless aimed to minimise directing discussions, for instance by using open and general questions rather than leading questions (Kvale and Brinkmann 2015). In addition, we witnessed biologists voicing concerns about studying individuality when we were present as passive audience members (see Section 4). This supports the conclusion that our findings are valid beyond discussions with philosophers.

We generalise from CRC members to other researchers studying individuality in behavioural ecology and related fields (or "individuality researchers" for short). We believe the CRC is exemplary for research on individuality in behavioural ecology. It is a high-profile and large group, and outputs have been published in top journals. Some members of the consortium and its advisory board are recognised figures in the field, and the CRC is in continuous and supportive dialogue with other prominent behavioural ecologists studying individuality. This suggests that the research they are undertaking (Section 3) and the concerns they express about studying individuality (Section 4) are likely to be indicative of the field more generally.

3 Introducing Individuality Research

In this section, we introduce the field of individuality research in behavioural ecology, drawing on published literature and our case study.

3.1 Individuality as a Research Object in Behavioural Ecology

Research on individuality in behavioural ecology centres around two main phenomena: animal personality and individual specialisation. Animal personality, also known as behavioural type, temperament, or coping style, is defined as behavioural differences between individuals that are stable over time and consistent across contexts (Réale et al. 2007; Kaiser and Müller 2021). Examples of animal personality traits include boldness, such that animals are more or less risk averse, and aggressiveness, where some animals tend to display more aggressive behaviour towards conspecifics than others.

Individual specialisation, on the other hand, refers to stable differences between individuals in their ecological relations (Bolnick et al. 2003; Araújo, Bolnick, and Layman 2011; Layman, Newsome, and Gancos Crawford 2015). Examples include differences in foraging location or time of day, preferences for food types or sizes, or choice of host plant or breeding site. As well as differences in resource use, individual specialization also includes stable differences in social behaviour and social interactions, known as social niche specialization (Bergmüller and Taborsky 2010; Montiglio, Ferrari, and Réale 2013). A consequence of individual specialisation is that each individual has its own *individualised niche*, meaning that individuals differ in how they interact with different parts of the environment and which parts of the environment are relevant to them (Dall et al. 2012; Takola and Schielzeth 2022; Krüger et al. 2021).

What unites the study of animal personality and individual specialisation is that both concern *individual differences*. Animal personality studies focus on how individuals differ in behaviours that express personality traits, and individual specialisation studies focus on how individuals differ in ecological relations and ecologically relevant traits. As well as these two core phenomena, individuality researchers also investigate individual differences in other sorts of traits, such as physiological traits (e.g., hormone levels or immunological profile) or chemical traits (e.g., olfactory signalling chemicals) (e.g., Mutwill et al. 2020; C. Müller et al. 2020).

Individual differences in this context are defined as variation within a group or population not due to sex, age class, or discrete morphological type (Sih, Bell, and Johnson 2004; Dall, Houston, and McNamara 2004; Dall et al. 2012). Hence, individual differences are distinct from other kinds of intrapopulation variation, such as sexual dimorphism, developmental changes, or polymorphism. Another way of understanding this is that individual differences are the unexplained variation that remains once standard categories used to explain variation—sex, age class, and morph—have been applied in analysis.

When studying individual differences, researchers often talk about individuality (Réale et al. 2007; Dall et al. 2012; Freund et al. 2013; Fodrie et al. 2015; Toscano et al. 2016; Bierbach, Laskowski, and Wolf 2017). Individuality in behavioural ecology is defined as the *uniqueness* of single individuals in their phenotypic traits and ecological relation, such that individuals have unique *sets* of phenotypic traits and unique individualised niches (or unique *sets* of ecological relations) (Kaiser and Trappes 2021; Trappes 2022). Individuals are thus a locus of behavioural and ecological variation. Individual differences are in turn part of what makes individuals unique. Even when individuals don't have unique levels of aggression, unique food preferences or unique social interactions, variation across individuals in such traits contributes to each individual's overall uniqueness and thus to its individuality.

3.2 Research Questions and Goals in Individuality Research

Many behavioural ecologists have become interested in better understanding individuality and how it arises and changes; that is, they seek to *capture individuality* (see Box 1). This epistemic aim is motivated by accuracy, but also by the growing awareness that individuality matters. Individual variation can have drastic impacts on key ecological and evolutionary phenomena, including dispersal and colonisation, predation pressure, community composition, intra- and interspecific cooperation and competition, the spread of diseases and invasive species, and population-level responses to climate change (Wolf and Weissing 2012; Toscano et al. 2016; Chang et al. 2017; Spiegel et al. 2017; Des Roches et al. 2018; Moran et al. 2022). Individual differences are also increasingly recognised as important for conservation (Buchholz 2007; Sih 2013; de Azevedo and Young 2021; Hunter et al. 2022; Martínez-Abraín, Quevedo, and Serrano 2022) and animal welfare (Richter and Hintze 2019; Feige-Diller et al. 2021).

Box 1: Capturing Individuality

Definition of Individuality in Behavioural Ecology: Individuality is defined as an individual being different from others and thus as the phenotypic and ecological uniqueness of individuals. Individuality researchers study individuality by focusing on individual differences in phenotypic traits (e.g., behavioural traits) and ecological relations (e.g., resource use). *Uniqueness* means that individuals have unique sets of phenotypic traits and ecological relations.

Epistemic Aim of Capturing Individuality: Research on individuality must *capture* the phenomenon of individuality as defined above. That is, research must represent the phenotypic and ecological uniqueness of individuals when addressing the three main research questions, (i) which individual differences exist, (ii) how do individual differences arise or change, and (iii) what consequences do individual differences have. Capturing individuality is not binary; studies can capture individuality to various degrees, depending on how and to what extent they represent the phenotypic and ecological uniqueness of individuals.

Individuality researchers ask three main research questions. First, they aim to reveal individual differences in different populations or taxonomic groups. This is a largely descriptive project, involving measuring or testing for individual differences in a trait or ecological relation. An important issue in this context is the stability of individual differences. For example, when biologists study individual differences in behavioural traits of mustard leaf beetles (e.g., moving, staying at the wall, and turning with an angle smaller than

90°) they investigate whether individuals rank consistently across behavioural traits and over their lifetime (T. Müller and Müller 2015). Another issue is the relation or correlation between different types or levels of individual differences, such as the reported positive relationship between social rank (e.g., dominance) and baseline testosterone concentration in guinea pigs (Mutwill et al. 2021).

A second research question concerns how individual differences arise and change over time. This process is referred to as *individualisation* since it leads to the emergence, increase, or change of individual differences and thus of individuality (Kaiser et al. 2024). Individuality researchers study three subtypes of individualisation processes or mechanisms: niche choice, niche conformance and niche construction, known as NC^3 mechanisms. The NC^3 mechanisms reveal how a (type of) individual interacts with its environment to bring about changes in how an individual's phenotype matches its environment, thereby altering its individualised niche (Trappes et al. 2022; Kaiser and Trappes 2023). For example, biologists found out that fire salamander larvae adjust their behaviour differently, becoming more risk prone or less risk prone, depending on the size and type of habitat they live in (Oswald et al. 2020). This is an example of individual differences in niche conformance, where the individual adjusts its phenotype to conform to the environment. As another example, there are individual differences in how red flour beetles perform niche construction, in which they release quinone-rich stink gland secretions into the flour and thereby influence microbial growth (Lo et al. 2023).

Finally, researchers ask about the consequences of individual differences for broader ecological and evolutionary processes. For instance, one study reports that individual differences in microhabitat choice of grasshoppers is relevant to the maintenance of the green-brown polymorphisms in grasshopper populations (Heinze et al. 2022). In addition, a systematic review found that individual differences, for instance in foraging tactics or in social behaviour, can influence whether inter- and intraspecific ecological interactions are more cooperative or more antagonistic (Moran et al. 2022). These sorts of studies reveal the importance of variation amongst individuals for larger-scale phenomena, giving biologists additional reasons to study individual differences.

4 Concerns about Studying Individuality

Although they see individuality as important and are already studying it, some biologists express concerns about studying individuality. In this section we introduce these concerns as evidenced in our ethnographic study.

We first encountered concerns about studying individuality through participant observation. For instance, in discussions after talks we witnessed debates about whether and to what extent individuality can be studied using standard methods that compare groups of animals, such as experiments comparing treatment and control groups. In addition, in the questionnaire, three responses to questions about individualised phenotypes stated that individual differences cannot be studied by comparing groups.

Following these initial observations, we included a question about using group-based methods for studying individuality in the interview guide. In fact, most interviewees brought up the topic themselves, often directly upon being asked how their research fits into the CRC. For example, one researcher discussed how using groups is important for tractability and statistical power:

> I mean, again, we group them in morphs, which is a simplification. So I think quite often individual variation is simplified into cohorts, into groups, into treatments, of course. Which is something that we find better to handle, and it also increases the statistical power when you do analysis. So we do ignore some element of individuality if we find it suitable or meaningful. (Interview 9)

As this quote shows, the use of groups is seen as necessary for but also limiting the ability to capture individuality. Similar ideas were expressed by another biologist:

> We are definitely thinking a lot about processes at the individual level, although that does not necessarily mean, like [my colleague] said, that every individual does something completely different, in our models they are simplified. But I think, yeah, often we have some types, like genotypes, and sometimes like if you have multiple loci, say you have ten loci and at each locus you have two alleles, so there is already many combinations so that lots of individuals are doing something different. Although we don't have for every individual that they are really unique unique [sic] in what they are doing. (Interview 5)

Here the use of groups is described as a simplification that limits the ability to capture the uniqueness of individuals.

Three interviewees even voiced strong doubts that they were studying individuality at all because they use group-based methods. For example:

> [T]o me in the beginning it was said that we look at the individual and I don't look at an individual. I always manipulate groups and then, I measure members of that group. And then in biology we do statistics and I do statistics on a mean of that

> group. I mean, I take the individual variation and I can look at whether they vary more strongly or less strongly, I could do all of that, but I still work with the group and I define the group and I don't define the individual. (Interview 3)

This researcher, like two others we interviewed, is hesitant to believe that their group-based approach is capable of providing information about individuality at all.

The interviews also brought to light an additional concern about studying individuality. Amongst 4 of the 14 interviewees, there was a sense that studying individuality might conflict with making generalisations or developing general knowledge. For instance:

> Again, I don't see the benefit looking at 96 individuals and then if I can say, okay, individual 98 [*sic*] is so different. I mean, they are probably all different from each other. But it's hard for me to generalise, to have the idea. Because when I do science I always want to do this generalisation, saying something like, okay, I do my experiment is based on 100 individuals and due to these results I can say [organisms of a certain species] in general do that. At least I do not have in my head saying something like, okay, because I see individual 68 is doing something different, what does it tell us about [individuals of that species] or individual differences or... That's my problem. (Interview 10)

Similarly, another interviewee referred to the role of generalisation in hypothesis generation:

> Because the only way you could do that is descriptively. So, you could just like have a graph with single lines of each individual and say 'okay, it's visible there, the differences' but we kind of have to make some groups of individuals based on specific factors to come to, first, some general assumptions and then maybe we can test them further. (Interview 2)

As these quotes indicate, there was a sense that studying individuality doesn't fit with the aim to develop and test generalisations.

Overall, limitations in the ability to develop knowledge about individuality were brought up in 9 of the 10 interviews, and in each of these 9 interviews they were brought up more than once. We identified two broad types of concern. First, standard methods for measurement, experimentation, and analysis make use of groups of individuals, but this limits the ability to capture individuality. Second, the goal of generalisation is seen as conflicting with that of capturing individuality. Discussions of these concerns were often accompanied by expressions of confusion, apprehension, or discomfort. They were associated with a range of epistemic practices: measurement, categorisation, approximation, experimentation, statistics, generalisation, and explanation. They were also associated with several different epistemic values: generality, simplicity, accuracy, and tractability. Finally, they were associated with several other factors, including measurement error, causal complexity, and uniqueness, topics we elaborate on below.

Discussions of concerns about studying individuality were surprising and intriguing for us. Why would scientists who are working in a consortium on individuality discuss so frequently whether, how and to what extent their research methods and goals fit with their aim of capturing individuality? In the next section we identify two general epistemic challenges of individuality research that explain individuality researchers' concerns. In Section 6 we then discuss the different strategies for addressing the two challenges.

5 The Epistemic Challenges of Individuality

In this section we identify two epistemic challenges of individuality: the variation-noise challenge (Section 5.1) and the generalisation challenge (Section 5.2). These challenges underly and explain individuality researchers' concerns about group-based methods and generalisation.

5.1 Variation, Noise and Error

Variation within a dataset is often viewed with suspicion, and with good reason. In some systems, especially those with low levels of complexity, variation is most likely to be the result of error, such as measurement error. Error can enter into datasets in many different ways, despite scientists' best efforts. In ecology, for example, data for seemingly simple and straightforward variables, such as population size, can be extremely difficult to collect, and even state-of-the-art methods often yield patchy or biased datasets (Akamatsu et al. 2001; Tyne et al. 2016; Boakes et al. 2016). In this context of almost ubiquitous error, data points that diverge from the norm are likely to be erroneous. Thus, scientists tend to treat them as *noise* (see Box 2) and ignore them in their experiments or models.

Box 2: Key Terms

Individuality. Being different from others; the phenotypic and ecological uniqueness of single individuals.

Individual Differences. Variation within a group or population not due to sex, age class, or discrete morphological type. Examples include differences in personality traits (e.g., boldness-shyness) and differences in resource use.

Noise. Variation that is due to errors or that is deemed to be irrelevant to the phenomenon under study.

Idiosyncratic Factors. Factors that differ across individuals or systems and that are therefore typically ignored in generalisations.

Group-based methods are perfect examples of this approach to variation. For example, in many sciences it is common to take the average across samples or replicates to indicate the value for a phenomenon of interest, with the variation around the mean used to determine a margin of error. The inference from the scatter of observed values to a phenomenon is based on assumptions about the representativeness of the samples, the spread of error, and a general theory of statistical inference (Bogen and Woodward 1988). As another example, data points that differ radically from the average are often discarded as *outliers*, leaving them out of the sample because they are likely due to some idiosyncratic factor (see Box 2) that is not relevant to the research question at hand. These are common, successful, and often well-justified practices. However, one consequence is that real variation—that is, variation that is not due to error—is lumped together with error as noise and is subsequently ignored or discarded.

To illustrate this point, consider a fictionalised example that is not about individuality research: a scientist studying the fecundity of a butterfly species. The scientist observes that most butterflies across all fields lay between 20 and 40 eggs in clutches. By comparing the average number of eggs and clutches from different fields, the scientist aims to determine whether and how fecundity changes according to different environmental conditions. In the process, they treat variation around the averages as noise, disregarding it as irrelevant for the causal relationship in question. Imagine further that the scientist found two clutches with only one or two eggs. The typical response would be to classify these clutches as outliers; for instance, perhaps a dog on a walk disturbed the two clutches, or perhaps the scientist made a mistake when writing the number of eggs down.

As biological systems become more complex, the status of variation becomes more uncertain. Often, this is because scientists are not able to determine whether the variation is the result of error or, rather, a reflection of genuine differences in causal factors, properties, or dynamics within a system. Even when scientists can distinguish errors from genuine variation, these differences are not always directly relevant for a particular investigation. Moreover, incorporating additional factors and variables into a scientific investigation increases the likelihood of error. So, scientists have to think very carefully about whether to try to incorporate or ignore variation in their investigations.

Going back to the butterfly example, consider the possibility that the two outlier clutches contained one or two eggs because of factors that were directly relevant to the investigation. For example, the small clutches may have been located on a north-facing, steep slope with less snow and vegetation cover. Individuals developing there would have depleted energy reserves and less food available, so when it came time for them to reproduce they may have only had the resources to lay one or two eggs. In this version of events, the small clutches manifest genuine variation in fecundity due to a difference in environmental conditions, exactly the relationship the scientist was interested in; *not* including the outliers therefore skews the data, introducing the error of biased sampling.

The difficulties surrounding variation also manifest for other epistemic practices, such as modelling and meta-analysis. In the debate about optimal model complexity, the worry is that complex models which include many variables or dynamics risk 'overfitting' the data: they may fail to distinguish between accurate data points and noise, and so yield inaccurate explanations and predictions (Hitchcock and Sober 2004; Schindler and Hilborn 2015; Ward et al. 2014). On the other hand, in contexts with extensive variation, simple models that leave out data points and variables can obscure or misrepresent genuine and relevant causal factors (Travis et al. 2014; Elliott-Graves 2019). In the case of meta-analysis, the difficulty in distinguishing between variation and noise is due to the fact that the primary studies on which a meta-analysis is based often use different methods. It is thus difficult to know when variation between studies reflects genuine variation between systems and when it is merely an artefact of the different methods (Whittaker 2010).

To summarise, variation presents a challenge for researchers studying complex systems because of its uncertain status: sometimes it is a result of error or is irrelevant, but sometimes it reflects genuine and relevant differences in the causal structure or dynamics of a system. A common way to deal with variation is to treat it as noise, for instance through applying group-based methods. But doing so can introduce new errors, such as biased sampling or obscuring important causal factors.

With this background, we can now return to individuality research. Individuality researchers aim to capture variation between individuals (see Box 1). But they cannot study *all* variation; some variation *is* the result of error or is irrelevant for the purposes of the study. For example, two individuals may have different measures for a behaviour due to a slight difference when handling the animals prior to the behavioural test or a difference in auditory or olfactory cues present during the test. The challenge then is to distinguish what of the observed variation is due to real and biologically relevant variation between individuals, rather than due to error or irrelevant variation. In short, individuality researchers face what we call *the variation-noise challenge*: the challenge of distinguishing individuality (one type of real and relevant variation) from noise.

The variation-noise challenge is particularly acute for individuality researchers due to the presence of multiple interacting sources of behavioural variation. In addition to factors introduced by researchers, such as sampling, handling, and testing procedures, a wide variety of other factors can lead to variation in observed behaviour. In particular, it is well known that behaviour is affected by factors that can vary over comparatively short time-scales, such as hunger, hormonal levels, recent experiences, local environment, and diurnal and seasonal cues (Dingemanse and Dochtermann 2013; Brommer 2013; D. J. Mitchell et al. 2020). Animals also learn, habituate, and otherwise plastically adjust to their environments, including test apparatuses and experimental handling, and there can be individual differences in the consistency or plasticity of behaviour (Biro and Adriaenssens 2013; Stamps 2016; Takola et al. 2021). As a consequence, variation in a behavioural dataset may be due to many different factors: differences in handling or test environment, fluctuations in individuals' internal state or environment, different rates of habituation and plastic adjustment by individuals, as well as genuine individual differences in behaviour. The challenge is to determine whether and to what extent the observed variation can be attributed to individual differences.

This means that the variation-noise challenge is not only about distinguishing variation from noise, but also about distinguishing different sources of variation. In particular, the variation-noise challenge underlies discussions in individuality research about the difficulty of accounting for what are known as "within-individual differences", that is, variation in an individual's behaviour due to short-term fluctuations, plasticity, and so on. Individuality researchers need to distinguish within-individual differences from genuine ("between-" or "amongst-") individual differences (Laskowski et al. 2022). But within-individual differences are also different from measurement error. First, within-individual differences are not always (or even often) randomly distributed, so lumping them together with random measurement error can lead to biases and mistakes in data analysis and statistical modelling (Dingemanse and Dochtermann 2013; Brommer 2013). Second, within-individual differences reflect real and potentially relevant sources of behavioural variation, since factors such as physiology, plasticity, or environmental change may be important for fully understanding the causes and consequences of individuality. For these two reasons, individuality researchers often want not only to distinguish individual differences from noise, but also to parse out different sources of variation. We return to this point in Section 6.

The variation-noise challenge arises in relation to all three of the main research questions in individuality research (see Box 1). Researchers aiming to identify and describe individual differences in phenotypic traits and ecological relations certainly need to distinguish these individual differences from noise due to measurement error, short-term fluctuations in individuals' state, and so on. But the variation-noise challenge also arises when studying the causes and consequences of individual differences. For instance, researchers need to distinguish individual differences from noise in order to determine if experimental interventions have affected individual differences.

We can close this subsection by returning to the concerns raised by scientists in our case study (Section 4). There we found some researchers who were concerned that group-based methods do not work for capturing individuality. The variation-noise challenge helps to explain this concern. Standard group-based methods are little help in addressing the variation-noise challenge because, rather than allowing researchers to distinguish individuality from noise, they tend to lump individuality under noise. It is for this reason that some individuality researchers in our case study were concerned about their ability to study individuality using group-based methods. Fortunately, individuality researchers are well aware of the variation-noise challenge, and they have developed alternative practices to address it. Recognising these strategies as responses to the variation-noise challenge helps to make sense of their role in individuality research, and pinpoints specific limitations in the ability to study individuality. We discuss these strategies in Section 6. First, however, we consider an additional epistemic challenge of individuality, one that explains individuality researchers' concerns about generalisation.

5.2 Generalisation and Idiosyncrasies

Scientists are routinely interested in extending their knowledge to cover entire populations, species, regions, and so on (S. D. Mitchell 2003; Steel 2007; Lange 2008). They do so by generalisation: identifying patterns in how events, phenomena or causal factors repeat across space, time, or taxonomies (Potochnik 2017). Examples include statistical generalisation, generalising from samples to populations; typological generalisation, generalising from tokens to types; and extrapolation, generalising from one population or species to other populations or species. Being able to generalise is valuable because it allows scientists to gain insights that go beyond their current investigation and to transfer knowledge across contexts (Elliott-Graves 2023).

Generalising typically involves ignoring idiosyncratic factors, factors that differ across groups or systems (see Box 2; Cartwright 1989; Strevens 2004). Going back to the butterfly example, the scientist aims to make claims about the butterfly species based on the samples they have collected. Making claims about one or two clutches will be neither particularly interesting nor informative in a broader context. The goal of generalisation thus provides an additional reason to ignore variation.

However, generalising is not the only epistemic aim in scientific practice; indeed it often trades off with other goals, such as the realistic and accurate representation of phenomena for the purposes of explanation and prediction (Levins 1966; Matthewson and Weisberg 2009). The more realistic a representation or explanation of a phenomenon or system is, the more real-world factors it will include. Yet, as stated above, study systems (individuals, populations, geographical areas, and so on) differ; even when patterns repeat, they are not identical across systems. This means that the more accurate a description or explanation of a phenomenon or system is, the less this description will capture how exactly the phenomenon occurs in another system. Indeed, the more extensive the generalisation aims to be, the more factors need to be left out.

This leaves scientists with a dilemma: either generalise extensively but then face the danger of the generalisations breaking down (or being erroneous to start off with) or constrain the scope of the generalisations in order to take into account all the relevant factors, but then have generalisations that only encompass a few systems or even just a single system (Elliott-Graves 2023; S. D. Mitchell 2003; Steel 2007). To return to the butterflies, if the two small clutches reflect genuine and relevant variation, then leaving them out gives us a picture of the overall population fecundity that really only applies to a subset of the population, namely those from fields that are neither north facing nor steep. If the scientist aims to develop accurate representations or precise predictions, they should therefore limit the scope of their generalisation to some fields—but then they are no longer achieving their goal of developing a generalisation about the species as a whole.

In the case of individuality research, this trade-off is particularly severe. Individual variation and uniqueness are idiosyncratic factors, as they are not common across populations but specific to particular individuals. Ignoring individual variation allows scientists to find patterns and generalise their results. The goal of generalisation therefore provides a second motivation for ignoring individual variation. Individuality researchers, like other scientists, aim to generalise their findings from single studies to entire populations or species, as well as across different taxa, habitats, geographic areas, years, and so on. Individuality researchers therefore face what we call the *generalisation challenge*: the challenge of developing generalisations about individuality, given that generalisations trade off with capturing idiosyncrasies and thus capturing individuality (see Box 1).

A special form of the generalisation challenge is the difficulty of extrapolating insights about individual differences in behaviour across contexts, especially from lab to field, and from experimental studies to natural populations. As mentioned in Section 5.1, many of the traits being studied in individuality research are highly labile and context-sensitive. Despite careful attempts to control for confounding factors, lab-based experiments, field-based experiments, and natural settings can differ in key factors relevant to behaviour. For instance, a lab-based and a field-based test for exploratory tendency in great tits produced different measurements for the same individuals; the authors reasoned that the different environmental cues present in the lab versus the field may have changed individuals' behaviour, and may even mean that individuals were exhibiting entirely different behavioural traits in each test (Mouchet and Dingemanse 2021). These sorts of cases illustrate the difficulty of generalising about individuality across contexts, given that the expression of individual differences depends on specificities of the environmental context. This difficulty also compounds the difficulty of generalising about individuality across species, since even closely related species may be tested using slightly different assays and under slightly different conditions (White, Pascall, and Wilson 2020).

The generalisation challenge accounts for the second sort of concern about studying individuality voiced by some of our interviewees. As we discussed in Section 4, some individuality researchers expressed the view that the goal of capturing individuality conflicts with that of generalising, such as making descriptive generalisations or generating hypotheses. We can now see that this concern arises because generalising involves ignoring idiosyncrasies. If generalising is a central epistemic goal, then sacrificing this goal in order to capture individuality may be seen as inappropriate.

Of course, capturing individuality does not require abandoning generalisation altogether. In fact, the trade-off generates a spectrum of degrees of generality and degrees of capturing individuality: The more general a hypothesis or claim is, the less individuality it captures, that is, the less it accounts for idiosyncratic factors. Vice versa, less generality allows for better capturing individuality. For instance, a causal claim made at the level of a species identifies size and developmental environment as causes of a specific animal personality trait: "[W]e showed that size as well as the larval habitat influences risk-taking behaviour in fire salamander larvae." (Oswald et al. 2020, 919) In contrast, in a study of guinea pigs reacting to social niche transition, the researchers made the causal claim that adaptive adjustment of the behavioural and hormonal phenotype occurs during adulthood (Mutwill et al. 2020). This is a much broader generalisation that is, however, less detailed about the specific behavioural or hormonal traits and about how individuals differ in these traits; it therefore does not capture individuality to the same extent as the more specific claim about fire salamander larvae. As we discuss in the next section, individuality researchers have negotiated the trade-off between generalisation and capturing individuality, developing strategies for studying individuality by revising expectations and norms surrounding generalisation.

6 The Varipraxis of Individuality Research

The two epistemic challenges have given rise to epistemic strategies or "compensatory tactics" (Love 2010, 685) to promote observation of variation that is typically ignored in standard research practice. Together, these strategies form a distinctive varipraxis (Lowe and Ingram 2023). That is, they make up a set of practices that researchers engage in to delineate, characterise and investigate what they deem relevant variation. Like the varipraxis of DNA barcoding in taxonomy (Lowe and Ingram 2023), the varipraxis of individuality research in behavioural ecology involves a combination of methodological, epistemological and ontological aspects. For example, the epistemic strategies used to study individuality shape the ways in which individuality researchers define and operationalise the concept of individuality (Trappes 2022).

There are likely additional practices comprising the individuality research varipraxis. For instance, long-term primatological studies, bird banding, animal tracking technology, and the use of unique markings such as tiger stripes and whale dorsal fins are examples of practices that allow researchers to identify, observe and compare individuals, thus facilitating the study of individual differences (Benson 2010; 2016; 2017; Longino 2013; Trappes 2023). In this section, we focus on identifying some of the main epistemic strategies that address the two epistemic challenges, as evidenced in our case study. Our goal is to make these strategies explicit and to discuss the extent to which they address the two epistemic challenges. In the process, we reveal how the epistemic challenges have shaped practices in individuality research, and what limitations remain in studying individuality.

6.1 Strategies for Distinguishing Individuality from Noise

One strategy for addressing the variation-noise challenge is *repeated observation*. Standard group-based methods treat each individual as a replicate, such that averaging over the individuals gives you the value for the group and variation amongst individuals is noise around that value. Repeated observation builds on this practice, but instead of having individuals as replicates, the replicates are different observations of the same individual. Researchers can then separate out individuals' behavioural traits from the noise of each observation. As a result, they can distinguish between individual differences and other sources of variation in the observed behaviour such as measurement error, short-term fluctuations in individuals' state, and so on (see Section 5.1).This is expressed using the statistical quantity of repeatability (*R*), which is the proportion of total observed phenotypic variance that is explained by or attributable to differences between individuals; or formally, $R=V_I/V_P$ (where, for some trait of interest, V_I is the among-individual variance and V_P is the total phenotypic variance) (Bell, Hankison, and Laskowski 2009; Nakagawa and Schielzeth 2010; for a discussion of different concepts of repeatability see, e.g., Wilson 2018).

Repeated observation is a common practice for measuring animal personality (Réale et al. 2007; Bell, Hankison, and Laskowski 2009; Niemelä and Dingemanse 2018; Kaiser and Müller 2021; Takola et al. 2021). Animal personality traits such as boldness, sociability, or aggressiveness are studied by measuring the behaviour of an individual at different times and in different experimental contexts (Kaiser and Müller 2021). The boldness of mustard leaf beetles, for instance, is studied by measuring five behaviours in different contexts, assuming that all these behaviours express the same personality trait: contacting a novel object, moving in the inner area of a petri dish, emerging from a refugee, staying at the wall of a petri dish, and feigning death (Tremmel and Müller 2013). Observing behaviour both over time and in different behavioural assays addresses the variation-noise challenge, as it helps distinguish real and relevant behavioural variation from variation that may be due to chance and uncontrolled factors in the experimental context.

The variation-noise challenge shapes the epistemic strategy of repeated observation in further distinctive ways, especially relating to the study design and the statistical models used. Recall from Section 5.1 that the variation-noise challenge includes the challenge of distinguishing individual differences from other sources of variation, including measurement error but also within-individual differences, i.e., variation due to fluctuations and differences in individuals' internal state, local environment, plastic response, and so on. Repeated observation therefore requires distinctive study designs, such as an observation frequency that allows internal and external processes or factors to change over observations, or the inclusion of habituation periods when conducting behavioural assays (Biro and Adriaenssens 2013; Stamps 2016; Niemelä and Dingemanse 2018; Takola et al. 2021). Others recommend using more complex statistical models that separate out and model within-individual differences as a function of a physiological or environmental parameter, such as modelling within-individual differences in activity as a function of ambient temperature (Dingemanse and Dochtermann 2013; Brommer 2013; D. J. Mitchell et al. 2020).

Repeated observation is widely applicable, but it has some fairly obvious limitations. First, the trait has to actually be observable multiple times. Practical and ethical restrictions often limit repeated observation, and some traits, such as time to fledge or time to first reproduce, only occur once for a given individual. Second, the trait of interest must be sufficiently stable across observations. Repeated observation doesn't work when trait values change irregularly or unpredictably across observations.

A second strategy for addressing the variation-noise challenge is *stratified sampling*, i.e., partitioning a population into subpopulation groups from which to sample. For instance, using stratified sampling researchers can characterise different foraging strategies (Fodrie et al. 2015). Stratified sampling addresses the variation-noise challenge by distinguishing the mean value for each subpopulation group (or 'stratum') from the noise of individual observations. However, stratification is unable to capture very fine-grained variation. In addition, identifying relevant subpopulation groups requires prior knowledge about variation in the population. Both limitations are familiar from personalised medicine (Nicholls et al. 2014).

Stratified sampling can also be used in *factorial experimental design*, where multiple potential causal factors are studied at once by splitting an experiment into several "mini-experiments" (Shaw et al. 2002; von Kortzfleisch et al. 2020; Karp and Fry 2021). Factorial design can help to incorporate real variation into experiments (Piotrowska 2023). For example, it can allow researchers to determine how individual differences affect or mediate responses to the environment or social interactions. Again, this allows researchers to capture coarse-grained variation amongst individuals. A similar experimental approach to studying individual differences is *replicate individual study design*, where individuals with the same genotype and prior experiences are used as replicates (Stamps 2016, 545). This experimental design allows researchers to study variation in phenomena that are not repeatably observable for a single individual, such as ontogenetic plasticity and once-in-a-lifetime events. Variation amongst replicate individuals, on this study design, is attributed to noise, with the average value for the replicate individuals being treated as the value for the trait of interest. However, these study designs are limited: in many species it is not possible to rear genetically and environmentally homogenous individuals; moreover, individual differences such as animal personality can still develop despite genetic and environmental homogeneity (Stamps 2016; Bierbach, Laskowski, and Wolf 2017).

Strategies like repeated observation, stratified sampling, factorial experimental design, and replicate individual study design are useful because they enable researchers to capture individuality by distinguishing some genuine variation from noise. However, the limitations of the different strategies mean that individuality researchers can often capture individuality only to certain degrees.

6.2 Strategies for Making Generalisations about Individuality

Individuality researchers have also developed strategies for addressing the generalisation challenge. One strategy is to concentrate on making *limited-scope generalisations*. Take for instance a study of individual specialisation in Galápagos sea lions (Schwarz et al. 2021). Researchers used animal tracking devices to observe foraging behaviour of a sample of adult females, distinguishing three foraging strategies. They then generalised this pattern from the sample of tracked animals to other adult female Galápagos sea lions. The scope of this generalisation is limited: researchers expect the three foraging strategies to recur in different colonies and across different years, but they restrict the claim to adult females rather than also generalising to juveniles, adult males, or indeed to other species. This limited-scope generalisation allows researchers to capture individuality to some degree, though it still obscures some idiosyncrasies, such as slightly different locations or timings of each individual's foraging trips.

Limited-scope generalisation has also been proposed as a response to the reproducibility crisis, because it accounts for the ways that local factors can strongly affect research findings (Leonelli 2022; Yarkoni 2022; Elliott-Graves 2023). This strategy can also be accompanied by explicit attention to and study of the conditions under which generalisations hold or break down. This can for instance be done by conducting additional experiments or observations with different apparatuses, under different conditions, or with different species (Mouchet and Dingemanse 2021). Researchers are also developing specific statistical tools for making well-informed restricted-scope generalisations about individual differences, such as multivariate models for cross-species comparison of individual differences (White, Pascall, and Wilson 2020).

A second strategy is to *make several generalisations with varying levels of abstraction*. For example, researchers studying the animal personality trait of boldness in mustard leaf beetles made the quite detailed generalisation that "Beetles feeding low-quality diet were bolder than animals reared on high-quality food" (Tremmel and Müller 2013, 390). From this finding of a cause of individual differences in a particular behavioural trait in a particular species, the authors developed various generalisations with different taxonomic scopes: beetles, non-social insects, specialist insect pests, insects more generally, herbivores, and even all animals. Some of these generalisations remain relatively close to the study findings, but most abstract away from the details of the causal relation in order to extrapolate the observed pattern to other species. For instance, the authors drew a much broader generalisation about the potential causes of behaviour, stating that "Our results demonstrate that the environment does not only affect life-history traits but has also a consistent impact on an individual's behavior" (Tremmel and Müller 2013, 386). This generalisation abstracts away from the particular causal relationship between diet quality and boldness in mustard leaf beetles, to a more abstract relation amongst environment and behaviour in insects or even animals more broadly.

This example shows how more general claims about causes and consequences of individuality are more abstract and therefore less detailed about the variation being studied, and vice versa. By making generalisations of various sorts, researchers can at once capture individuality and make generalisations. It is important to note, however, that different generalisations play different roles in research. More detailed and local generalisations about study species are typically ways of reporting research findings and their immediate implications. In contrast, more abstract generalisations serve for generating further hypotheses about other taxa, synthesising results of many studies, and developing broader theoretical frameworks.

7 Conclusion

In this paper, we analysed the challenges that behavioural ecologists face when studying individuality. These researchers aim to capture individuality when identifying and describing individual differences and studying their causes and consequences. However, they are also concerned about their ability to capture individuality. We analysed these concerns and argued that they arise from two epistemic challenges: First, individuality researchers face the variation-noise challenge, the difficulty of distinguishing real and relevant variation from noise. Second, they face the generalisation challenge, the difficulty of making generalisations about individuality given that generalising trades off with capturing idiosyncrasies.

Researchers have adapted their research practices when studying individuality. We argued that these adapted practices serve as epistemic strategies to address both epistemic challenges of individuality, enabling researchers to distinguish some real and relevant variation from noise and to balance the goal of generalisation with that of capturing individuality. We discussed repeated observation, stratified sampling, factorial experimental design, replicate individual study design, limited-scope generalisations, and making multiple generalisations with varying levels of abstraction. These practices constitute a distinctive varipraxis that helps to transform individuality from an elusive target into an accessible object of research. Each of these strategies has limitations in terms of the amount and kinds of variation that can be studied. Nevertheless, the varipraxis still enables researchers to capture individuality to a greater degree than otherwise possible.

The challenges we identified have their roots in broader issues to do with variation and its role in scientific practices. Individuality research thus brings to the fore trade-offs and tensions that are present for all researchers but are often less apparent due to the entrenchment of standard goals, values, and methods. The varipraxis we identified may also be applicable across the sciences, especially in fields such as personalised medicine and personality psychology that also consider individual differences and uniqueness.

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Competing Interests

The authors have no competing interests to declare that are relevant to the content of this article.

Ethics Approval

The interview study was approved as ethically appropriate by the Ethics Review Board of Bielefeld University (Application No. 2019-210, 12th September 2019).

Data Availability

Questionnaire results and interview transcripts from the project cannot be sufficiently anonymised and are therefore not published. Other materials and data from the project such as questionnaire and interview instruments, participant summaries, lists of codes and code co-occurrences are published as an OSF project under https://doi.org/10.17605/OSF.IO/RKU47.

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Rose Trappes: Conceptualization, Methodology, Investigation, Analysis, Writing – original draft, Writing – review & editing, Project administration

Alkistis Elliott-Graves: Conceptualization, Writing – original draft, Funding acquisition

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Rights Retention

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