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Individual Differences, Uniqueness, and Individuality in Behavioural Ecology

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Abstract

In this paper I develop a concept of behavioural ecological individuality. Using findings from a case study which employed qualitative methods, I argue that individuality in behavioural ecology should be defined as phenotypic and ecological uniqueness, a concept that is operationalised in terms of individual differences such as animal personality and individual specialisation. This account make sense of how the term "individuality" is used in relation to intrapopulation variation in behavioural ecology. The concept of behavioural ecological individuality can sometimes be used to identify individuals. It also shapes research agendas and methodological choices in behavioural ecology, leading researchers to account for individuals as sources of variation. Overall, this paper draws attention to a field that has been largely overlooked in philosophical discussions of biological individuality and highlights the importance of individual differences and uniqueness for individuality in behavioural ecology.

Keywords: Individuality, Uniqueness, Animal personality, Individual specialisation, Individual differences, Operationalisation

1. Introduction

Behavioural ecologists studying individual differences often talk about individuality. Researchers investigating behavioural differences in genetically identical mice found that "individuality emerges over time" through development (Freund et al., 2013, p. 757). Similarly, social interactions in clonal guppies are said to "promote the development of individuality" by affecting behavioural differentiation (Bierbach et al., 2017, p. 2). And behavioural ecologists found "indications of individuality" when recording differences in otters' foraging behaviour (Fodrie et al., 2015, p. 81). What does "individuality" mean in this context? What is individuality in behavioural ecology? This is the question I ask in the present paper.

First appearances would suggest that the term "individuality" in behavioural ecology simply refers to individual differences, such as behavioural differences or differences in resource use.

However, equating individuality with individual differences leads to a problem. Individual differences include any sort of variation within a population that isn't associated with sex, age, or morphological type (Araújo et al., 2011; Bolnick et al., 2003; Dall et al., 2012; Sih et al., 2004; Violle et al., 2012). This means that some differences between groups count as individual differences; even bimodal intrapopulation variation in boldness, prey preference or feeding time is an individual difference if it is not associated with sex, age class or morphological type. But if individual differences can include such coarse-grained variation, what do they really have to do with individuality? Is "individuality" an appropriate term in this context?

To address these questions, I look at how behavioural ecologists discuss individuality. Specifically, I use findings from an ethnographic study involving participant observation, a questionnaire and interviews. I found that researchers do often talk about individual differences when discussing individuality. In addition, I found that many discussions about individuality involved another topic: the idea that individuals are phenotypically and ecologically unique. I ultimately argue that uniqueness offers a way to define individuality; individual differences in turn are an operationalisation of uniqueness because they offer partial empirical information about what makes individuals unique.

On my account, behavioural ecological individuality can be defined as phenotypic and ecological uniqueness, a concept which is operationalised as individual differences in behaviour and ecology. This concept can sometimes help us pick out individuals—often a primary question for philosophers and biologists when it comes to individuality (though see Kovaka, 2015). It also shapes the research agenda and methodological choices in behavioural ecology, encouraging researchers to look closer at how individuals differ. On this basis, I argue that behavioural ecological individuality is a new concept of biological individuality, joining other more well-studied concepts such as evolutionary individuality and immunological individuality in a broader "problem agenda" of biological individuality (Kaiser & Trappes, 2021; Lidgard & Nyhart, 2017).

I begin in Section 2 by briefly describing the case study and the methods used. I introduce research on individual differences, especially animal personality and individual specialisation, in Section 3. In Section 4, I present a first pass at defining individuality simply as individual differences. However, because individual differences include coarse intrapopulation variation, this definition doesn't seem to work. In Section 5, I argue that uniqueness can define individuality in behavioural ecology. I then situate the concept of behavioural ecological individuality in the broader debate on biological individuality in Section 6, and I discuss the various roles of this concept in Section 7. Finally, in Section 8 I summarise the account of behavioural ecological individuality and its implications and briefly consider similarities to other disciplines, suggesting avenues for future research.

2. Methods

From 2018 to 2021 I was a member of the interdisciplinary Collaborative Research Centre TRR-212 "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 40 scientific members, including behavioural biologists, ecologists, evolutionary biologists, and statisticians. It has been running since 2018 and is located at several universities in Germany. As its name suggests, the goal of the group is to investigate the phenomenon of individualisation (more on this below) across multiple disciplines or topics of research. The subtitle indicates the theoretical framework of individual-level mechanisms which unite and systematise disparate studies of organism-environment interactions (Kaiser & Trappes, 2022; Trappes et al., 2022).

During my time in the CRC I undertook an ethnographic study aimed at determining how researchers understand and work on individual differences and individuality. One element of the ethnographic study was participant observation, which involved attending regular talks, workshops and meetings, as well as collaborating more closely with a number of researchers and giving talks to the group. During this process I recorded findings and collected materials such as internal reports and photographs. The participant observation revealed the importance of individual differences and individuality in this field and delivered initial indications about how they are understood and studied. It also allowed me to later sound out my interpretations with researchers in the group.

The second element of the ethnographic study was a questionnaire created together with Marie I. Kaiser, Ulrich Krohs, and Behzad Nematipour, the three other philosophers in the CRC (for full details, see Trappes, 2021a). The questionnaire was conducted at the start of the first funding phase of the CRC; we had 37 responses, a 90% response rate. Amongst other topics, we asked participants short-answer questions about individuality and individual differences. Together with Hanna Metzen, we analysed the responses using semi-grounded coding, which involves developing codes for ideas or themes that were identified while reading the responses (Mansnerus & Wagenknecht, 2015; Nersessian & MacLeod, 2022). Codes are categories or concepts (represented by words and phrases) that are used to mark the various themes, ideas, meanings, or characteristics that come up in different parts of a text (Corbin & Strauss, 2015, Chapter 12). Codes are assigned to text passages and can then be assessed for their frequency and cooccurrence, such as across questions or amongst participants. One major finding of the questionnaire was that participants frequently considered individuality in terms of individual differences, and sometimes also in terms of criteria of individuality discussed in evolutionary

biology, physiology and philosophy of biology, such as having boundaries or being a unit of selection (Kaiser & Trappes, 2021). Another finding was that uniqueness was sometimes mentioned in relation to individuality.

The third element of the ethnographic study was a series of semi-structured interviews with CRC members (for full details, see Trappes, 2021a). Interviews 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 CRC members. The sample was chosen to cover a range of disciplinary backgrounds, research topics, and career stages. Interviews included questions based on a prepared interview guide, as well as exploring topics that came up in the interview. Together with David Lambert I analysed interview transcripts using a primarily theory-driven approach, also known as deductive or hypothesis coding (Andow, 2016; Braun & Clarke, 2006; Saldaña, 2009). This involved preparing a detailed list of codes to capture themes and ideas based on my research questions, the questionnaire results, and my general impression having conducted all the interviews. The initial code list was then adjusted throughout the coding process to respond to emerging findings, such as new or unexpected ideas expressed by interviewees. Codes were analysed based on frequency of occurrence across interviews and cooccurrence with other codes. The interviews supported the associations between individuality and both individual differences and uniqueness. They also highlighted the worries of researchers in the CRC concerning the applicability of the term "individuality" to coarse-grained intrapopulation differences.

I want to note two things about the case study. First, these qualitative studies are co-creations between me as a researcher and members of the CRC as research subjects. CRC members expressed their ideas about individuality and discussed their research in particular contexts, often in response to my direct questions or prompts. These contextual factors shape what is said, how it is said, and what is left unsaid. This is especially apparent in interview studies, where a dialogue is clearly constructed by both researcher and subject (Kvale & Brinkmann, 2015). Similarly, philosophical interests shape thematic coding as well as the selection and interpretation of quotations. The findings I present and the account of individuality I develop should therefore be seen as a product of interdisciplinary interaction, rather than a pure representation of what biologists think and do.

Second, case studies provide a wealth of detail and access to research contexts that might otherwise be overlooked in broader historical or quantitative studies (Burian, 2001; MacLeod et al., 2019; Mansnerus & Wagenknecht, 2015; Osbeck & Nersessian, 2015). Yet their specificity and level of detail raise questions about generalisability. The CRC, for instance, is a group specifically funded to work on individuality, so they might be biased to think about individuality

in specific ways. Nevertheless, my observations suggest that visiting researchers and junior researchers arriving fresh from different institutes had similar views to longstanding CRC members. These similarities suggest that the CRC is likely to be representative of the broader field of behavioural ecological research on individual differences.

To support this generalisation, I also draw on definitions and examples from behavioural ecologists outside the CRC. These were gathered from a non-systematic survey of important literature on individual differences in behavioural ecology. Especially relevant were a number of key review and opinion papers that captured the emergence of the field in the early 2000s (Bolnick et al., 2003; Dall et al., 2004; Sih et al., 2004) and that cemented its status in the early 2010s (Araújo et al., 2011; Bolnick et al., 2011; Dall et al., 2012; Violle et al., 2012). These were supplemented with other texts discussing definitions of the relevant phenomena or methodological strategies and challenges.

3. Individual Differences

Behavioural ecologists use the term "individuality" in the context of research on individual differences. Before exploring the concept of individuality, in this section I introduce behavioural ecological research on individual differences.

Variation within a population has long been of interest for its role in evolution (Grene, 1974; Mayr, 2006; Sober, 2006). For instance, intraspecific variation is central to game theoretic models of the evolution of behavioural strategies, models which were instrumental in founding the discipline of behavioural ecology (Bolduc, 2012; Davies et al., 2012). In the past two decades, however, behavioural ecologists have paid increasing attention to variation in naturally occurring populations.

Several prominent reviews in the early 2000s highlighted the existence of unexplained variation in behaviour and resource use that may be ecologically and evolutionarily significant (Bolnick et al., 2003; Dall et al., 2004; Sih et al., 2004). These researchers called for more studies in a broader variety of species to better understand what differences there are, how they can be explained and what ecological and evolutionary consequences they might have. Behavioural ecologists took up the call and there is now a growing field of research into individual differences (Araújo et al., 2011; Bolnick et al., 2011; Dall et al., 2012; Violle et al., 2012). Studying individual differences is now seen as crucial for achieving the general goals of behavioural ecology and related fields, to describe and explain animal behaviour in ecological contexts and more generally to understand the causes and consequences of organism-environment interactions.

Two phenomena take centre stage in this field: animal personality and individual specialisation. Animal personality—also known as temperament, behavioural syndrome,

behavioural specialisation, behavioural type, or coping style—is defined as behavioural differences between individuals that are stable across time and over contexts (Bell et al., 2009; Kaiser & Müller, 2021; Réale et al., 2007; Sih et al., 2004; Wolf & Weissing, 2012). Some examples of animal personality traits include boldness, aggression and exploration. Animals are scored according to their repeated performance on specific behavioural tests. For instance, an individual that in repeated tests spends more time in the centre of an open arena or more quickly begins exploring a new environment is scored as more explorative (or sometimes as bolder—there are debates about how exactly to individuate animal personality traits; Réale et al., 2007).

Behavioural biologists and ecologists aim to both describe animal personality in different species and determine animal personality's causes and consequences. For example, several studies in the CRC look at whether boldness correlates with risk levels or population density experienced during development. Other CRC researchers perform experiments to determine how aggression affects reproductive success or social group composition and dynamics.

The other sort of individual difference studied in behavioural ecology is individual specialisation, also known as individual niche variation. This is the phenomenon of differences between individuals in resource use or other ecologically relevant traits, activities and relations (Araújo et al., 2011; Bolnick et al., 2003; Ingram et al., 2018; Layman et al., 2015). For instance, individuals may differ in diet, habitat use, food preferences, nutrient uptake, host preference, or social hierarchy position. These differences imply that individuals can have different ecological niches, with the population niche being a broader sum of all the narrower individual niches (Bolnick et al., 2003; Takola & Schielzeth, 2022).

As with animal personality, researchers are involved in documenting individual specialisation and determining its causes and consequences. For example, several projects in the CRC work with populations in which parents systematically choose different sorts of developmental environment for their offspring, exposing them to different levels of risk for predation, parasitism, injury, or competition. As well as recording these differences, researchers correlate developmental environment with offspring phenotype, survival and reproductive success to determine the effects of these different developmental environments.

So far I have talked about individual differences, differences between individuals, and variation within a population, whether for behaviour (animal personality) or ecological relations (individual specialisation). But there are various sorts of intrapopulation variation. Differences between sexes, changes over ontogeny and distinct morphological types or morphs can all contribute to variation between individuals in a population. Researchers mark out their work on individual differences from that on sex differences, development, and polymorphism by defining individual differences as variation in a population that is not due to sex, age or morphological

type (Bolnick et al., 2003; Dall et al., 2004, 2012; Layman et al., 2015; Sih et al., 2004). Whereas sex, age and morph are already expected and often well-studied sources intraspecific variation, individual differences are those differences that are not explained by such standard analytic categories. One way to visualise this is that individual differences are the residual variation after factoring sex, age and morph into analysis of variance. Defining individual differences in this way highlights an overlooked, neglected, unexpected and unexplained kind of variation, thus delineating a new phenomenon to investigate (Bolnick et al., 2003, p. 3).

4. Defining Individuality as Individual Differences

In the previous section I introduced behavioural ecological research on individual differences, including animal personality and individual specialisation. In this section I consider how behavioural ecologists understand individuality in terms of individual differences and the worries and confusions this understanding generates.

In the questionnaire we asked participants "What about your research organisms makes them individuals?" and "What does individuality mean to you?" Individual differences came up very frequently in the responses (15 for the first question, 25 for the second; total responses for each question = 37). For instance, participants stated that what makes their research organisms individuals is "Stable and persistent differences in behaviour," "Variation in morphology, physiology, behaviour, personality," or "Differences in development, behaviour, responses to external cues." Similarly, participants characterised what individuality means to them with statements such as "For me individuality describes inter-individual differences in behaviour that are constant over at least certain time periods" or "Repeatable difference in attributes (behaviour in particular) of individuals."

Individual differences were not the only phenomena mentioned in relation to individuality. Traditional criteria of individuality were also frequently mentioned, such as having spatial boundaries or metabolic autonomy, being a unit of selection, or consisting of functionally or physically cohering parts (13 responses for the first question, 1 response for the second). The change in responses from the first to the second question is particularly interesting: the number of responses citing individual differences greatly increased, and the number of responses citing traditional criteria plummeted. Between the two questions on individuality, we asked about individualised phenotypes and individual differences. This may indicate that, when the context of research on individual differences is made more salient, individuality is more strongly associated with individual differences.

The questionnaire thus suggested that "individuality" refers to individual differences, such as animal personality and individual specialisation, at least in the context of behavioural ecological

research on individual differences. This picture was supported in the interviews. Interviewees were not asked explicitly what they mean by "individuality." However, when discussing their research projects interviewees used terms such as "individuality," "individualisation," "individual differences," and "individual variation" interchangeably. For instance, one interviewee characterised a motivating question for the CRC as a whole as "What makes animals special, each and every individual, [and] what are the consequences of that individuality?"

A similar picture is found in the broader behavioural ecology literature. Animal personalities are often referred to with terms like "individuality" or "behavioural individuality" (e.g., Barash, 1997; Bierbach et al., 2017; Freund et al., 2013; Réale et al., 2007; Vogt, 2015). Similarly, individual specialisation is sometimes called "individuality" (Dall et al., 2012; Fodrie et al., 2015; Niemelä & Dingemanse, 2018; Toscano et al., 2016).

All the evidence thus seems to point to the conclusion that the term "individuality" in behavioural ecology means "individual differences in behaviour and ecology, especially animal personality and individual specialisation." This definition accords with and extends the concept of behavioural individuality proposed by behavioural ecologists Jules Smith-Ferguson and Madeleine Beekman (2019). In behavioural experiments on slime moulds and eusocial insects, replicate individuals are identified by looking for behavioural differences. As Smith-Ferguson and Beekman explain, "Even though the individuals used in the studies above originally came from the same genetic individual, they behave differently and are thus considered to be different individuals." (Smith-Ferguson & Beekman, 2019, p. 5) In this context, individuality is defined comparatively by differences.

Yet there is something peculiar about this definition. Note that individual differences include any sort of intrapopulation variation not due to sex, age or morph. This means differences between groups of individuals can also count as individual differences. For instance, a bimodal difference in personality or food preference can count as an individual difference, as long as the difference does not track sex, age or morph. In fact, researchers often study individual differences at this coarse level, using two or a handful of categories (Réale et al., 2007). This is also seen in other disciplines such as psychology, where individual differences can also include bimodal differences (Ward, 2020). But what does such coarse-grained intrapopulation variation have to do with individuality?

This question was a source of major discomfort for several of the biologists I interviewed. A quote from one of the interviewees highlights the problem:

> So, individualization for me was... to 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.

Other interviewees voiced similar concerns. Terms like "individuality," "individualisation," and even "individual differences" seem to imply something about single individuals. Yet behavioural ecologists studying individual differences almost always work with multiple individuals—with treatment groups in experiments, with samples for measurement and statistics, with bimodal or trimodal variation in a population, and so on. Coarse intrapopulation variation such as bimodal or trimodal differences might fall under the definition of individuality as individual differences. But should it? Shouldn't individuality be reserved for single individuals? These sorts of questions arose very frequently in my observations of the biologists in the CRC, both in interviews and in public contexts such as research talks and group discussions.

Defining individuality in terms of individual differences fits the way "individuality" is used to refer to phenomena like animal personality and individual specialisation. But it falls foul of the intuition that individuality should concern single individuals. One option at this point is to replace "individuality" with a more neutral term, such as "unexplained intraspecific variation." But this would be premature. As I discuss in the next section, the concept of uniqueness can help make sense of the link that behavioural ecologists make between individuality and individual differences.

5. Phenotypic and Ecological Uniqueness

In the questionnaire, several researchers mentioned uniqueness in relation to individuality (4 in response to the first question on individuality; 9 for the second question). For instance, they explained individuality in terms of "a unique colour pattern just like the human fingerprint," "the unique composition of the traits of one individual," "something that makes them unique or special" or "how an organism will uniquely interact with its environment based on a set of pre-defined factors (e.g., genes)." Similarly, several participants mentioned the idea of individuals being different from all other individuals in a population.

Following up on the questionnaire results, in the interviews I asked interviewees if they think there can be two individuals with exactly the same set of phenotypic traits or exactly the same ecological niches. Even before asking this question, many interviewees characterised individuals as phenotypically or ecologically unique—as different from all other individuals in their phenotypic properties or ecological relations. Upon being asked the question, most researchers insisted on uniqueness (8 of 10 interviews); in one interview the question was not asked, and in another interview the interviewees argued that individuals need not be unique, as discussed below.

One researcher discussed ecological uniqueness: "if we imagine this multi-dimensional niche […], you will see that it's very difficult then for individuals to have the same… to share absolutely the same niche, because some part in one dimension they will be different." Another interviewee spoke about phenotypic uniqueness: "That's a trick question only a philosopher can ask. Because there's twins and they can at least have an outwardly similar phenotype, maybe also very much inward. But I still believe there will be tiny differences between individuals." Phenotypic uniqueness also creates practical difficulties for experimental researchers, as this interviewee pointed out: "It's easier [to replicate] with genotypes. Because genotype by environment interactions, you just produce a lot of clones, then, that's easy. But it is so uneasy [*sic*] to produce identical individuals. Basically, it is impossible."

What these and similar statements have in common is the idea that individuals are unique because they are complex. Individuals are both compositionally and dynamically complex (see Elliott-Graves, 2018; Mitchell, 2003). They have very many phenotypic properties and ecological relations that exist in non-simple interrelations—compositional complexity. In addition, many phenotypic properties and ecological relations are characterised by feedback loops, nonlinear dynamics and sensitivity to initial conditions—dynamic complexity. Together, these forms of complexity make an exactly identical individual so unlikely as to be virtually impossible. One interviewee summed this idea up: "I think there is so much variation there in the environment then… I don't know. From atom level on there is so much variation that each complex individual is somehow a bit different than the other one."

Interestingly, the only interviewees who insisted that individuals need not be unique were theoretical biologists. Discussing how their models allow for individuals with exactly identical positions along a number of niche dimensions, they stated "We are not requesting that all the individuals are unique in a sense. It could be still two individuals with the same individualised niche without the concept of the individualised niche collapsing, in my opinion." These biologists work with models of simplified individuals having only a handful of traits, and simulations can be repeated many times. This means that identical individuals are to be expected. In contrast, experimental and field biologists are faced with great complexity and limited numbers of individuals, so can essentially rule out the existence of identical individuals as impossible (as the experimental biologist above concluded).

The belief that individuals are unique doesn't necessarily imply that individuality *is* uniqueness. Some CRC members did characterise individuality in terms of phenotypic and ecological uniqueness in response to the questionnaire. But perhaps they really meant individual differences (in line with their colleagues' responses) and were just exaggerating. Although this is a live option, I favour an alternative interpretation. Specifically, I argue that an implicit belief that

individuality is uniqueness underlies the way behavioural ecologists explain how their research on individual differences relates to individuality.

Let's look again at the worries about studying individuality. One interviewee expressed their uncertainty about the relevance of their experiments:

> in the end we have […] treatment groups, that should be representative of, well, at least some more extreme parts of the variation that we can find in a real natural population. And in that sense, we don't directly study this individual variation.

Similarly, another interviewee said that

> 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.

In studying groups, these researchers state, they are only indirectly or partially studying individual variation or individuality. This implies that true individuality is not to be found at the level of groups exposed to the same experimental treatment or cohorts with similar phenotypic properties—contrary to the definition of individuality as individual differences including coarse intrapopulation variation. On the other hand, the researchers also imply that studying such coarse variation can deliver some partial, indirect knowledge of individuality.

This way of characterising the relation between differences and individuality makes sense if we take "individuality" to refer to uniqueness. Coarse variation such as that between a few personality types or foraging styles is obviously not everything about what makes an individual unique—it does not enable us to directly study individuality. But variation in a niche dimension or phenotypic trait can contribute to a more complex set of properties being unique to a single individual. For instance, part of an individual's unique niche could involve a bimodal variation for habitat use or prey preference. When we record this variation, we have some knowledge about what makes the individual's niche unique. Full knowledge of an individual's ecological uniqueness would of course require looking at variation in many other niche dimensions, though such detailed studies are generally neither feasible nor interesting enough for a biologist to undertake. Nevertheless, studying variation between groups still provides some partial information about individuals' phenotypic and ecological uniqueness.

Taking the cue from the way biologists explain how their work relates to individuality, I therefore argue that individuality in behavioural ecology is defined as the phenotypic and ecological uniqueness of single individuals. In line with the ideas about complexity discussed above, what makes an individual phenotypically unique is generally not a single phenotypic property, but rather a whole set of phenotypic properties (or the "phenome", in analogy to the genome; Scriver, 2004). Each individual has a unique set of phenotypic traits when no other

individual has the exact same set of phenotypic properties. Similarly, an individual is ecologically unique when no other entity has all the same ecological relations, even if some of the relations are shared across several individuals, such as particular abiotic tolerances or the use of certain resources. Ecological uniqueness can also be understood in terms of the individual having a unique multi-dimensional individualized niche (Takola & Schielzeth, 2022; Trappes et al., 2022).

In turn, individual differences are related to individuality by providing partial knowledge about uniqueness. Uniqueness and unique phenomena are notoriously difficult to account for fully in empirical research, especially in the life sciences where many phenomena are short-lived and hidden (Cartwright, 2017; B. Clarke & Russo, 2016; Woodward, 2010). Using groups circumvents such problems, allowing researchers to study repeatable phenomena and sample sizes larger than one while still gaining some information about the variation between individuals (see also Trappes, 2021b; Trappes et al., draft). The importance of studying groups has already been recognised for fields such as medicine and psychology, where cohorts are used as ways to approximate the greater variation between unique individuals (Nicholls et al., 2014; Ward, 2020). As in these fields, coarse differences in behavioural ecology provide a means to study unique individuals, if only partially and approximately. Defining individuality in terms of individual differences can thus be understood loosely as an operationalisation—as a practical translation of a concept that is difficult to apply directly in empirical research (see Feest, 2010).

Why should behavioural ecologists care about uniqueness at all? Uniqueness is not itself a target of description or explanation in behavioural ecology. Researchers don't generally ask "what makes this organism unique?" or "why does this animal have this unique set of traits?". Even if it were possible to answer such questions, doing so would involve describing highly specific, idiosyncratic properties and causal histories of little general interest. Instead, the focus is on the implications of individuals' uniqueness. Behavioural ecologists care about uniqueness to the extent that it can change the course of ecological and evolutionary processes and thus disrupt the descriptive adequacy of their descriptions and models. Better accounting for individuality is therefore central for pursuing the more general goal of understanding organism-environment interactions.

6. Uniqueness and Biological Individuality

So far I have argued that individuality in behavioural ecology is phenotypic and ecological uniqueness, operationalised as individual differences like animal personality and individual specialisation. This accords with the way behavioural ecologists discuss individuality. But it is quite different to existing definitions of individuality in other biological disciplines. In this section I introduce some of the recent discussions about individuality in philosophy of biology,

highlighting where individuality has been linked to uniqueness. I suggest that behavioural ecological individuality is a new concept to add to a plurality of existing individuality concepts, a suggestion which I develop further in the Section 7.

Philosophical debates about biological individuality have concentrated on questions about identifying individuals, as well as their parts, boundaries and what holds the parts together (Kaiser, 2018; Kaiser & Trappes, 2021; Lidgard & Nyhart, 2017). These questions are important: picking out individuals is no mean feat in the messy world of living beings, but being able to do so is necessary in order to do things like determine population size, distinguish growth from reproduction, or figure out what belongs in an organism and what can or should be eliminated (E. Clarke, 2010; Lidgard & Nyhart, 2017; Pradeu, 2016; R. A. Wilson & Barker, 2019). Philosophers of biology and biologists alike have therefore discussed at length what sorts of criteria can be applied in order to systematically answer these questions about identifying and demarcating biological individuals (for a comprehensive historical summary, see Lidgard & Nyhart, 2017).

Recently, many philosophers have come to accept pluralism about biological individuality (Bueno et al., 2018; Dupré, 2012; Ereshefsky & Pedroso, 2015; Lidgard & Nyhart, 2017; Love & Brigandt, 2017; McConwell, 2017; Pradeu, 2016; Şencan, 2019; Waters, 2018). Not only are there multiple criteria vying for attention, it seems that different criteria are relevant in different scientific contexts and for different purposes (Godfrey-Smith, 2013; Lidgard & Nyhart, 2017; Pradeu, 2016; R. A. Wilson & Barker, 2019). And if different criteria are more or less relevant for picking out individuals in different contexts, then we may have multiple concepts of individuality, such as evolutionary, developmental, physiological, immunological, or ecological individuality (Lidgard & Nyhart, 2017; Pradeu, 2016; R. A. Wilson & Barker, 2019). For instance, Ellen Clarke's concept of evolutionary individuality requires the existence of mechanisms to limit intraindividual selection and promote interindividual selection (E. Clarke, 2012, 2016). In contrast, Thomas Pradeu's concept of immunological individuality requires that the immune system react at a continuous, medium-level intensity to parts of the individual and discontinuously with high intensity to external objects (Pradeu, 2010, 2012).

On this pluralist model, I argue that behavioural ecology has its own concept of individuality that requires the possession of unique sets of phenotypic traits and unique sets of ecological relations. Behavioural ecological individuality can thus join other individuality concepts in the problem agenda of biological individuality (Kaiser & Trappes, 2021; Lidgard & Nyhart, 2017). This is not the first time that philosophers have considered uniqueness in relation to biological individuality. I therefore briefly review existing references to uniqueness in the literature, highlighting the novelty of the concept of individuality in behavioural ecology.

Genetic uniqueness is frequently mentioned in discussions of biological individuality, in part due to the importance of genetic variation for evolution (Chauvier, 2017; E. Clarke, 2012; Godfrey-Smith, 2009, p. 81; Herron et al., 2013; e.g., Janzen, 1977; Lidgard & Nyhart, 2017; J. A. Wilson, 1999). However, many organisms exist that are not genetically unique, including monozygotic twins and the vast number of asexually reproducing organisms. Most people agree that twins, and perhaps also the offspring of asexually reproducing organisms, should be counted as separate individuals. As a consequence, genetic uniqueness is usually rejected as unnecessary for biological individuality (Boniolo, 2005; E. Clarke, 2012; De Sousa, 2005; Elwick, 2017; Folse III & Roughgarden, 2010; Hauskeller, 2004; Santelices, 1999).

Upon finding that genetic uniqueness is not necessary for biological individuality, many philosophers conclude that other sorts of uniqueness are unnecessary too (Chauvier, 2017; E. Clarke, 2012; Folse III & Roughgarden, 2010; Herron et al., 2013; Love & Brigandt, 2017; J. A. Wilson, 1999). This may rest on a mistaken assumption that clones and monozygotic twins, being genetically identical, are identical in other properties like phenotype or ecological relations. In contrast, Alexandre Guay and Thomas Pradeu note that "in biology, even individuals that are said to be 'identical' express, most of the time, some significant differences" (Guay & Pradeu, 2016, p. 10). Similarly, Christine Hauskeller points out that in humans "Twin studies have shown that even the same genome does not always produce the same phenotype." (Hauskeller, 2004, p. 296) The existence of genetically identical individuals therefore does not allow us to conclude that phenotypic or ecological uniqueness is unsuitable for defining biological individuality.

There have in fact been some scattered discussions of phenotypic uniqueness with respect to individuality (Burgio, 1990; E. Clarke, 2016; De Sousa, 2005; Elwick, 2017; Godfrey-Smith, 2009; Guay & Pradeu, 2016; Hauskeller, 2004; Hull, 1978; Nyhart & Lidgard, 2017). Uniqueness of specific kinds of phenotypic traits has also been considered, including immunological traits (Burgio, 1990; Ferner & Pradeu, 2017; Medawar, 1957; Minelli, 2020; Nyhart & Lidgard, 2017; Pradeu, 2012), morphological traits (Elwick, 2017; Lidgard & Nyhart, 2017; Pradeu, 2012), neurological traits (Boniolo, 2005; Pradeu, 2012), and behavioural traits (Nyhart & Lidgard, 2017). Although ecological relations themselves are prominent in concepts of ecological individuality (Huneman, 2014a, 2014b; Millstein, 2018), I have not found authors who have discussed the uniqueness of ecological relations. However, there have been minor discussions of unique experiences as relevant to individuality (De Sousa, 2005; Ruiz-Mirazo et al., 2000). In addition, unique spatiotemporal position or historical origin is frequently considered as a condition on individuality (Guay & Pradeu, 2016; Hull, 1978; Nyhart & Lidgard, 2017; Strawson, 1959).

Phenotypic and ecological uniqueness has therefore received scant attention in recent philosophical discussions about biological individuality. In addition, only a few philosophers have explicitly come down in favour of phenotypic uniqueness (of certain kinds or in general) as a criterion of individuality in disciplines such as immunology and neurology (Boniolo & Testa, 2012; e.g., Burgio, 1990; Lidgard & Nyhart, 2017; Nyhart & Lidgard, 2017). In contrast, many have been more circumspect, arguing either that phenotypic uniqueness is not strictly necessary, or that it is not helpful for identifying individuals and therefore not relevant for individuality (E. Clarke, 2012; Elwick, 2017; Folse III & Roughgarden, 2010; e.g., Hull, 1978; Pradeu, 2012; Santelices, 1999). In the next section I therefore substantiate my claim that phenotypic and ecological uniqueness introduces a new concept of individuality.

7. The Makings of an Individuality Concept

The concept of individuality in behavioural ecology serves a number of purposes. As some behavioural ecologists have discussed, phenotypic and sometimes ecological differences are sometimes used to identify individuals (Smith-Ferguson & Beekman, 2019). In addition, I argue that the concept of behavioural ecological individuality shapes behavioural ecologists' research agenda and methodological choices. Before discussing these conceptual roles, however, I deal with a common objection to the idea that phenotypic uniqueness can define individuality.

Some philosophers have argued against including phenotypic uniqueness in concepts of individuality because individuals are not necessarily phenotypically unique. Specifically, phenotypic uniqueness is neither logically nor metaphysically necessary; we can imagine, for instance, two phenotypically identical human babies born at different times in history, or an exact physical duplicate of ourselves in another part of the universe (De Sousa, 2005; Hull, 1978, p. 349; Strawson, 1959, Chapter 1). There is also no law of nature demanding that all individuals be phenotypically unique, so phenotypic uniqueness is not physically necessary. For many philosophers this lack of necessity is enough to conclude that phenotypic uniqueness cannot be used to define individuality. The concept of behavioural ecological individuality would therefore be defective, because it falsely assumes that the individuals studied in behavioural ecology are necessarily unique.

However, many other concepts of biological individuality do not satisfy such a strong notion of necessity. Most criteria of individuality considered by philosophers of biology, such as Clarke's mechanisms for supressing intraindividual selection or Pradeu's continuity of immunological reactions, are neither logically, metaphysically, nor physically necessary. The metaphysical or physical possibility of an organism without these mechanisms or processes is simply not relevant to philosophers of biology interested in identifying individuals in the actual world with respect to

particular disciplines. Instead, concepts of biological individuality typically only need justification that the relevant feature is universal amongst biological individuals of the relevant type.

There is in fact good evidence that all individuals in behavioural ecology are phenotypically and ecologically unique. As I discussed in Section 5, the complexity of biological systems gives reason to think that all individuals are unique. In addition, experiments with genetically identical individuals raised in uniform environments are yet to produce phenotypically identical individuals (Bierbach et al., 2017; Laskowski et al., 2016). Finally, we have strong inductive evidence for the uniqueness of biometric traits in humans and other animals. In fact, biologists often capitalise on the existence of unique traits for reidentification, such as using tigers' stripes, whales' dorsal fins and salamanders' colour patterns to reidentify animals for research and conservation (Benson, 2010; Faul et al., 2022). Less direct empirical evidence exists for ecological uniqueness, likely due to the difficulty of measuring multiple ecological relations for single individuals. Territorial animals and social animals frequently occupy distinct locations or positions in social networks, with their accompanying relations to different conspecifics, resources, and environmental conditions. More generally, ecological uniqueness is often easy to infer from the sheer number and complexity of ecological factors to which individuals relate through the course of their lives. We therefore have reason to think that phenotypic and ecological uniqueness is universal amongst individuals in behavioural ecology; necessity, on the other hand, is not required.

A concept of individuality should also fulfil certain purposes in the relevant discipline (Kovaka, 2015; Love & Brigandt, 2017). As I mentioned above, questions about picking out individuals have been central to philosophical discussions of biological individuality. It might seem that uniqueness can't help with this problem. Comparing individuals to establish whether they are unique would typically require that we've already identified the individuals to compare. In addition, speaking of phenotypic properties and ecological relations implies that we have already individuated the entity that bears these properties. On this basis, for example, Pradeu characterises "The question of biological individuality" as "What counts as *one* living thing?" and concludes that "Individuality is not the same thing as uniqueness, or even more generally as the description of the individual." (Pradeu, 2012, p. 222, emphasis in original)

Yet some phenotypic differences can actually assist researchers to tell individuals apart. I already mentioned the use of unique properties like fingerprints, tiger stripes and dorsal fins to reidentify individuals. In this case, phenotypic uniqueness is used to individuate an individual over time. In addition, in less conventional organisms like slime moulds, eusocial insects, and perhaps even some plants, behavioural differences can be instrumental for distinguishing individuals at one time point (Smith-Ferguson & Beekman, 2019). Ecological differences may

play a similar role, such as identifying an individual by its territory or its position in a social hierarchy, though in most cases this seems less reliable than phenotypic identification.

The concept of behavioural ecological individuality also plays other roles than enabling the identification of individuals. In behavioural ecology, as in many fields interested in characterising organisms' phenotypic traits and ecological relations, individuals are not just countable units; they are also sources of variation. In classic statistical representations such as box and whisker plots or regressions, individuals appear as variation around a mean. Behavioural ecologists are increasingly interested in understanding this variation, especially since individuals' uniqueness can disrupt biologists' generalisations and predictions about ecological and evolutionary processes (see Section 5). When individuals are seen as phenotypically and ecologically unique, individual variation is something that requires attention, rather than an error or bug to be ignored in favour of studying species averages. The concept of behavioural ecological individuality thus facilitates the choice of phenomena to study, encouraging biologists to look closer at the differences between individuals.

It also specifies which sorts of methods are needed. Researchers should at least use methods that are sensitive to individual differences and analyse variation in their samples rather than only averages. Ideally, they would use methods that can capture fine-grained variation rather than only very coarse group-based differences, thus getting closer to accounting for individuals' uniqueness. For instance, researchers are beginning to design experiments with a greater number of smaller treatment and control groups and to split data into more differentiated cohorts for analysis, approaches that are also becoming common in biomedical studies (Nicholls et al., 2014). The concept of individuality as uniqueness may also affect decisions about what counts as a replicate individual for experimentation (Smith-Ferguson & Beekman, 2019).

In addition to more refined experimental design and analysis, accounting for individual's uniqueness requires individual-based measurement. Accurately measuring individuals' behaviour and resource use requires repeated observation of individuals (Bell et al., 2009; Fodrie et al., 2015; Réale et al., 2007; Takola et al., 2021). For instance, the study of individual differences in movement and behaviour is enabled by animal movement tracking devices that allow single individuals to be reliably tracked over time (Nathan et al., 2008; Spiegel et al., 2017). The increasing availability of tracking and recording technology, as well as software for analysing such data, are instrumental both for more directly studying individuality. They are also important for accounting for individual variation in the search for more general patterns in behavioural and ecological phenomena.

Defining individuality can therefore involve more than just asking "How do scientists individuate the things they investigate and thus count them as individuals?" (Bueno et al., 2018, p.

1) Instead, we can also look at what makes individuals interesting to behavioural ecologists, how individuals appear in behavioural ecological research, why researchers aim to study individuals, or what prompts behavioural ecologists to adopt more individual-based methods. And these questions point us in the direction of uniqueness and individual differences. What makes something an individual in behavioural ecological research is its phenotypic and ecological uniqueness, that is, the way it is a source of variation to be accounted for or studied using fine-grained or individual-level observational, experimental or statistical methods.

To sum up, we have good reasons to think that all individuals in behavioural ecology are phenotypically and ecologically unique, this uniqueness can assist in identifying individuals, and it also supports other conceptual roles, such as affecting the choice of research objects and methods. Of course, individuality is more than just phenotypic and ecological uniqueness. Like concepts of evolutionary and immunological individuality, then, I propose that phenotypic and ecological uniqueness is a definition of individuality in the specific context of behavioural ecology, that is, a definition of behavioural ecological individuality.

8. Individuality in Behavioural Ecology and Beyond

Behavioural ecologists work with a concept of individuality as phenotypic and ecological uniqueness, which they operationalise using individual differences like animal personality and individual specialisation. This concept is different from many individuality concepts that have been investigated in philosophy of biology, such as evolutionary individuality or immunological individuality. Nevertheless, phenotypic and ecological uniqueness is likely universal amongst individuals, it can enable identifying or reidentifying individuals, and it can fulfil other roles such as shaping the research agenda and methodological choices.

There are of course many remaining questions. Are phenotypic uniqueness and ecological uniqueness equally important for behavioural ecological individuality? If ecological uniqueness is part of behavioural ecological individuality, does this mean an individual is defined in part by its surroundings? Does behavioural ecological individuality have a temporal dimension, and if so, how is it defined? Are there degrees of behavioural ecological individuality and how would these look? How does behavioural ecological individuality relate to other kinds of individuality? For instance, does it depend on evolutionary or physiological individuality, or is it entirely independent? Answering these questions is a task for future work. For now, I will point out some consequences of my account of individuality in behavioural ecology.

Recognising behavioural ecological individuality adds to the array of discipline-specific individuality concepts already recognised in philosophy of biology. It also elevates phenotypic properties and ecological relations in the estimation of philosophers. Some philosophers have a

tendency to dismiss phenotypes and ecological relations as superficial and thus irrelevant to the nature of things. But in disciplines like behavioural ecology, features like behaviour, habitat use, feeding preference, social relations, and so on, are core to what makes something an individual. Taking these phenomena seriously is thus part of shifting away from the reductionistic and theory-centric focus that philosophers of biology elsewhere declaim (Dupré, 1993; Mitchell, 2003; Nicholson, 2014; Pradeu, 2016; Waters, 2008).

Discussions around individuality in behavioural ecology bear distinct similarities to issues in the social sciences concerning individualisation and individualism (Beck, 2002; Cortois & Laermans, 2018; Heath, 2015; Honneth, 2004; Junge, 2002) and in the health sciences with personalised medicine (Lillie et al., 2011; Nicholls et al., 2014; Walker et al., 2019). There, too, the focus is on uniqueness, individual differences, and what intrapopulation variation can tell us about individuals. Behavioural ecological individuality could thus provide a starting point for broadening discussions of individuality in philosophy of biology towards other scientific disciplines.

Finally, sorting out the nature of individuality in behavioural ecology helps to resolve the concerns of working behavioural ecologists. Their research on individual differences does relate to individuality, just not in the direct way that some might have expected. Instead, studying coarse-grained variation is a way to gain empirical information about some dimensions of the variation between individuals. The limitations on being able to study unique individuals, familiar from personalised medicine, mean that a full understanding of individuality is unlikely at best. Nevertheless, the more variation we study, the better we can understand what makes individuals behave the way they do and how this affects ecological and evolutionary processes.

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Conflict of Interest
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