Individuality in Behavioural Ecology

Personality, Persistence, and the Perplexing Uniqueness of Biological Individuals

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1 Introducing Individuality in Behavioural Ecology

Variation is rife in the natural world. This is especially so in biology. Broad categories like plants, predation, or prairies cover many more specific plant species, predator-prey relations, and habitat types. Even within a single species there is considerable variation. Some of this intraspecific variation can be further categorised: individuals can be of different developmental stages, sexes, or morphological types, or belong to different populations or generations. Other times the variation doesn't fall into readily identifiable categories. For instance, individuals may have variations in their genetic material, differences in size or colour patterns, or quirks in the kinds of food they consume or where they live. This less easily categorised intraspecific variation is called *individual differences*.

This book investigates individual differences in the context of research at the intersection of behavioural biology, ecology and evolutionary biology. In the last twenty years, researchers have studied how and why individuals differ from one another in key biological features such as behaviour, morphology, resource use and social interactions. Two closely related phenomena take centre stage in this research: animal personality and individual ecological specialisation (Araújo, Bolnick, and Layman 2011; Dall et al. 2012; Wolf and Weissing 2012; Trillmich et al. 2015). Biologists discover and characterise animal personalities and individual specialisation, the causal relations that connect them, and their ecological and evolutionary consequences.

The disciplinary backgrounds of researchers working on individual differences range from chemical ecology to animal welfare studies, behavioural biology to statistics. Bearing this diversity in mind, we can nevertheless situate research on phenomena such as animal personality and individual specialisation within behavioural ecology. Behavioural ecology is a decidedly interdisciplinary field that combines studies of behaviour, evolution and ecology to understand how behaviour evolves and plays out in the natural world (Davies, Krebs, and West 2012). In this book I speak of behavioural ecologists in a broad sense to cover researchers working on individual differences in behaviour and ecology, especially animal personality and individual specialisation, recognising that this may not always fit with scientists' own disciplinary affiliations.

There is much talk of *individuality* in behavioural ecology research on individual differences. Individuals are said to “demonstrate” or “portray” individuality (Barash 1997, 160); “individuality emerges over time” through individual development (Freund et al. 2013, 757); behavioural ecologists observe “indications of individuality” when recording differences in foraging behaviour (Fodrie et al. 2015, 81); social interactions that affect behavioural differentiation “promote the development of individuality” (Bierbach, Laskowski, and Wolf 2017, 2). This talk of individuality is seen across research into animal personality, individual specialisation, and other individual differences. I therefore call research on such topics *individuality research*.

This label reflects the way behavioural ecologists talk about their research on individual differences. However, it also raises a question. What exactly do individual differences have to do with individuality? This question is motivated from two sides. First, behavioural ecologists often use group-based methods in order to study individual differences, and these individual differences are often, strange as it may sound, differences between groups of individuals rather than between single individuals. Yet “individuality” sounds like it should be about single individuals, not groups. This leads to confusion amongst biologists about whether their group-based studies of individual differences really are related to individuality. Second, in philosophy the term “individuality” refers to what it is that makes something an individual. Philosophers of biology interested in individuality concentrate on figuring out how to demarcate single units in the messy, overlapping and interrelated world of biological entities. Questions about individual differences in behaviour or ecology seem secondary and perhaps even unrelated to these matters of counting biological individuals.

Motivated by biologists’ confusions on the one hand and the mismatch between behavioural ecology and philosophy on the other, I ask one central question in this thesis: what is individuality in behavioural ecology? Answering this question, it turns out, involves dividing it into three sub-questions. First, how do behavioural ecologists understand individuality? Second, how do they research individuality? And finally, how does what they research and understand under the heading of individuality relate to broader notions of individuality outside behavioural ecology? By answering these three questions, I develop an account of what individuality in behavioural ecology is. This account is practice-based, taking the cue from biologists' own practices of researching and thinking about individuality and individual differences. It is also distinctly philosophical, reconstructing and evaluating notions of individuality in behavioural ecology, and using these to sketch an integrated picture of individuality in biology more generally.

1.1 Differing Definitions

Behavioural ecologists working on individual differences often use the word "individuality," but they haven't explicitly defined the term. Moreover, they associate individuality with a variety of ideas which prove difficult to unite. This lack of clarity around the meaning of individuality leads to confusion and disagreements. To make way for resolving this confusion, in Part I, I distinguish a number of definitions of individuality in behavioural ecology.

The first definition is based on the objects studied in individuality research, such as animal personality and individual specialisation. I show that individuality covers phenotypic traits and ecological relations—relations to abiotic and biotic factors, including relations to conspecifics—for which individuals in a population vary. These are usually called *individual differences*. Specifically, individual differences include traits and relations for which there is variation within a population that cannot be attributed to obvious population subgroups such as sexes, age classes or morphs. In addition, the individual differences studied in individuality research are often required to be stable over time and consistent over contexts. I refer to this requirement of stability and consistency as *robustness* (distinct of course from the robustness of models, see Weisberg 2006; and from robustness in systems biology, see Hammerstein et al. 2006).

It is not coincidental that animal personalities and individual specialisation both fall under the banner of individuality research. Recent research in behavioural ecology has focused on how behavioural differences, and phenotypic differences more generally, determine the sorts of ecological relations in which individuals engage, and vice versa. This has, for instance, resulted in the development of the concept of the individualised niche (Müller et al. 2020; Trappes et al. under review; Elina Takola and Schielzeth 2021). An individualised niche is made up of the ecological relations in which an individual can or does engage. These relations are described as ranges along niche dimensions, where the dimensions include abiotic factors such as temperature or humidity as well as biotic factors, such as predation, inter- and intraspecific competition, population density, social relations, and so on. The ranges an individual occupies are based on the environments an individual can or does experience, as well as the individual's tolerances and requirements.

Based on the objects studied in behavioural ecology, individuality can be defined as *robust individual differences* in phenotypic properties and ecological relations. This definition is adequate to the phenomena investigated by behavioural ecologists. Yet it is not the whole story. Behavioural ecologists also associate individuality with other ideas less closely connected to their objects of research. Specifically, researchers frequently understand individuality in terms of *individual-level properties*, *individual-level processes*, and *phenotypic and ecological uniqueness*. The first two are more minor, referring to the ideas that individuality is either about any of an individual's properties or about properties that result from an individual's activities. The more dominant idea in behavioural ecologists' explanations and descriptions of individuality is phenotypic and ecological uniqueness, and I focus on this for most of the thesis.

Many individuality researchers believe that individuals have unique phenotypic properties or sets of phenotypic properties as well as unique individualised niches. They associate this uniqueness with individuality—with what it is that makes something an individual. This association suggests an additional definition of individuality as *phenotypic and ecological uniqueness*. The idea that individuality is about phenotypic and ecological uniqueness persists despite the fact that the objects of individuality research, robust individual differences, are themselves far from unique. Phenotypic properties and ecological relations exhibited by multiple individuals still count as robust individual differences, since the basic requirement is that they not be shared by the population or by recognisable population subgroups. Phenotypic and ecological uniqueness and robust individual differences are therefore distinct definitions of individuality.

Having multiple definitions of individuality is not in itself particularly problematic. But biologists are not clear on the differences and relations between the two major definitions, and this generates ongoing confusion. With thoughts of uniqueness in mind, biologists worry about how their research on between-group differences relates to individuality and even whether individuality is an appropriate object of research. Clarifying that there are two dominant but distinct individuality definitions, we will have made a first step towards resolving these confusions. But a second step is necessary. How do the two major definitions, robust individual differences and phenotypic and ecological uniqueness, relate? Is research on robust individual differences relevant to phenotypic and ecological uniqueness? To answer these questions, I look more closely at how behavioural ecologists study individuality.

1.2 Individual Differences and Group-Based Methods

Biologists themselves are not certain of the relation between phenotypic and ecological uniqueness and robust individual differences. But some do discuss how their research on group-level differences might relate to individuality via approximation and partial explanation. These explanations are suggestive of the idea that robust individual differences are an *operationalisation* of the more epistemologically troublesome phenotypic and ecological uniqueness. Making this argument takes up Part II of the thesis.

When biologists understand individuality in terms of phenotypic and ecological uniqueness, accurately measuring and causally explaining individuality looks extremely challenging. First, measuring a single individual is challenging due to the combination of measurement error, developmental and other changes in an individual over time, and the inability to repeatedly measure some properties such as internal organs. Second, developing causal explanations in biology invariably involves generalising over idiosyncrasies like unique properties; individuals are grouped in experimental treatments, and statistics are conducted on large data sets, not single individuals. Hence, phenotypic and ecological uniqueness is the origin of two distinct but related epistemological challenges: the problems of *measuring individuality* and *explaining individuality*.

The idea that individuality is about phenotypic and ecological uniqueness therefore provokes the worry that individuality cannot be studied scientifically. In contrast, when studying individual differences, which include between-group differences, these challenges largely disappear. Measuring groups overcomes issues with measurement error, and groups can be used to conduct experiments or apply standard statistical models. These group-based methods can be used to capture some but not all variation between individuals. Studying individual differences is therefore a way to make phenotypic and ecological uniqueness measurable and explainable.

In other words, robust individual differences are an operationalisation of phenotypic and ecological uniqueness. Operationalisation is often understood in terms of concrete applications of a concept, such as an experimental set-up or a set of survey questions (Feest 2010). Robust individual differences are not themselves concrete operations or tools. But there are established procedures for studying robust individual differences such as animal personalities and individual specialisation. Choosing to study individual differences therefore enables researchers to pursue their goals of measurement and explanation.

The idea that robust individual differences are an operationalisation of phenotypic and ecological uniqueness clears up the confusions that biologists have about individuality research. However, it leaves open the question of what uniqueness and individual differences have to do with individuality more generally. Why use the term “individuality” at all? To answer this question, I look at how philosophers have defined individuality in biology and how ideas about phenotypic and ecological uniqueness and robust individual differences relate to these philosophical accounts.

1.3 What is Biological Individuality?

Philosophers of biology have been asking for decades if not centuries about *biological individuality* (E. Clarke 2010; Guay and Pradeu 2016a; Lidgard and Nyhart 2017; R. A. Wilson and Barker 2019). Is a stand of genetically identical and functionally interconnected quaking aspen trees an individual, or a mere collection of individual trees? Is a Portuguese Man o’ War an organism, or just a collection of different organisms cooperating for survival? Are the microorganisms occupying the human body and ensuring its survival parts of the human individual, or are they rather elements of the human’s environment? When does a foetus cease to be a part of a gestating placental mammal? These sorts of questions prove rather difficult to answer. As a result, there has been an extensive debate about “the problem of biological individuality” (E. Clarke 2010; 2013; Olson 2021). Participants in the debate have sought to determine in a systematic way what counts as a biological individual. The debate covers biological individuals of all sorts, including populations, species, or ecosystems (e.g., Hull 1978; Millstein 2009; Lean 2018).

However, organisms are at the centre of attention, and I follow suit in this thesis by focusing on organisms as individuals.

Philosophers of biology have proposed various criteria for individuality derived from different biological disciplines as well as from intuitions or philosophical theories. For instance, Ellen Clarke (2013) has proposed that biological individuals are those objects that possess mechanisms inhibiting within-object selection and facilitating between-object selection. This definition of biological individuality helps evolutionary biologists count objects that can be assigned fitness and are subject to natural selection. As a contrasting case, Thomas Pradeu (2012) has looked at immunology. He argues that we can demarcate biological individuals by looking at the continuity of immunological reactions; whereas the immune system reacts at a continuous, medium-level intensity with “self” tissue, foreign objects generate strong discontinuous reactions. Many philosophers have developed their own definitions of individuality or debated whether existing definitions can function to count individuals across the extreme variation in the biological world (Lidgard and Nyhart 2017; R. A. Wilson and Barker 2019).

The philosophical debate on biological individuality purports to be highly general. It is about individuality *in biology*, which should presumably cover individuality in most or all biological disciplines. Yet the issues to do with individuality in behavioural ecology I outline in this thesis do not match up with the “problem of biological individuality” that philosophers find in other disciplines (Kaiser and Trappes 2021). Occasionally behavioural ecologists do need to figure out how to count individuals, especially when they are studying slime moulds or amoeba (Smith-Ferguson and Beekman 2019). But most behavioural ecologists deal with insects, birds, reptiles, fish or mammals. For most of these organisms, researchers have well-accepted and intuitive ways of counting individuals. There are of course tricky cases even amongst animals. Is an ant colony an individual? In clonally reproducing guppies, are genetically identical offspring new individuals? Are parasites parts of their hosts? What about microbiomes? Even in these cases, a decision had been reached about what to count as individuals, where to draw their boundaries and what to include as parts. Philosophers can debate all they like, but it seems most behavioural ecologists don’t need much theoretical reflection to meet their practical counting needs (Kovaka 2015).

Behavioural ecologists' interests in individuality seem different to that of philosophers. Rather than counting, topics like individual differences and uniqueness are the bread and butter of research on individuality in behavioural ecology. But this difference doesn't mean that individuality in behavioural ecology is irrelevant to the philosophy of biological individuality. Throughout this book, I will show how behavioural ecologists' concerns and concepts are continuous with philosophical conceptions of biological individuality. I demonstrate in Chapter 4 that behavioural ecologists discussing individuality mention criteria of biological individuality discussed by philosophers alongside notions such as robust individual differences and phenotypic and ecological uniqueness. In addition, as I elaborate in Chapter 7, philosophers have considered the possession of a unique identity to be an important aspect of individuality, which has received some marginal attention in the debate on biological individuality. Based on these connections as well as biologists' reasoning about uniqueness, I argue that phenotypic and ecological uniqueness is a necessary condition on biological individuality. Finally, in Chapter 8 I discuss the way behavioural ecologists' reidentification practices and their ideas about animal personality and individual specialisation accord with some philosophers' ideas about persistence and personal identity.

These continuities help to explain why behavioural ecologists take individuality to be a matter of individual differences and phenotypic and ecological uniqueness. Rather than just a discipline-own notion, individuality in behavioural ecology links up to broader understandings of biological individuality. In addition, behavioural ecologists' ideas about individuality can inform a more complete understanding of biological individuality. Both phenotypic and ecological uniqueness and phenotypic and dispositional persistence add further aspects to the concept of biological individuality, beyond what has typically been discussed in philosophy of biology. Philosophers can come away from a broader set of questions to ask, a conclusion which builds on preliminary work I have done with Marie I. Kaiser (Kaiser and Trappes 2021). In addition, philosophers can gain an expanded understanding of biological individuality that covers more disciplines and more biological features. I present this integrated picture of biological individuality in Chapter 9.

1.4 Perspectives on Individualised Research

The major aim of this thesis is to develop an understanding of individuality in behavioural ecology. Achieving this primary aim brings to light an important additional finding: what I call *individualised research*. The understanding of individualised research I develop highlights the methodological and technological novelties involved in recent behavioural ecological work on individual differences. It also has implications for understanding data-driven and individual-focused methods across the sciences.

Individualised research involves looking closer at variation within species. When they are studying individual differences, behavioural ecologists make increased use of repeated individual measurement and create a greater number of smaller groups to investigate a finer grain of variation between individuals. There are limits to the level of variation at which biologists can accurately measure and explain. Yet individualised research continually approaches these limits—getting closer to the individual and its unique properties.

Behavioural ecologists have always had some interest in intraspecific variation. For instance, game theory, historically one of the most dominant approaches in behavioural ecology, studies how heritable behavioural variation leads to the evolution of phenomena such as altruism or mate choice (Burkhardt 2010; Bolduc 2012; Potochnik 2017). In addition, ecologists in the 1970s were proposing models for how individual differences in resource use could affect interspecific competition (Roughgarden 1972). But behavioural ecology often neglected questions about the developmental and ecological causes of intraspecific variation, in favour of a focus on evolutionary history or ecological consequences. In addition, studies tended to involve modelling simplified differences, rather than the great variety of actually existing individual differences. With real organisms rather than models, it was often difficult enough to determine species averages for behaviour, resource use, dispersal, mate choice, and so on. Gaining further, finer-grained information about variation within a species—what I have called individualised research—was much more difficult.

Since the 1980s, however, there have been great improvements in tracking devices, tissue sampling techniques, genetic sequencing methods, video technology, data storage capacity and data processing software (Benson 2010; 2016). The increased power, lower cost, and greater availability and applicability of these technologies meant that researchers were able to get much more data on the animals they were studying. With more data, they could also gain a much more comprehensive understanding of the sheer amount of variation within populations, as well as an enhanced ability to track specific individuals and discover broader causal patterns. These technological advancements and the data they delivered fed an increasing recognition of the ubiquity of individual differences and a greater interest in the causes and consequences of such variation. The wider availability of increasingly individualised research techniques was therefore instrumental to the development of individuality research.

Individualised research in behavioural ecology is an example of how big data has affected scientific research. Big data refers to the increase in the size of datasets and the speed with which they can be generated and shared (Marx 2013). Philosophers have considered so-called data-driven science in model organism research (Leonelli 2016), epidemiology (Ratti 2015; Canali 2016), systems biology (Callebaut 2012; Gross, Kranke, and Meunier 2019), and phylogenetics (Gross, Kranke, and Meunier 2019). In addition, philosophers have reflected on personalised or precision medicine, in which data from genome sequencing technology and wearable health tracking devices provides a more detailed picture of individual patients, to be used for more targeted diagnosis and treatment (Nicholls et al. 2014; Giroux 2020; Vegter, Zwart, and van Gool 2021). Comparatively little attention has been given to the role of big data in field research on animals, with the exception of Etienne Benson's work on the history and current implications of animal movement tracking (Benson 2010; 2016; 2017).

Big data provides scientists access to more detailed information about complex and variable phenomena (Marx 2013; Leonelli 2016). In behavioural ecology, as well as in personalised medicine, this means the increasing ability to look closer at individuals. Interestingly, it seems that the availability of individualised research methods in turn raises the scientific interest in individuality. Examining how behavioural ecologists deal with the challenges and complexities of increasingly individualised research is therefore an instructive case study of how big data has affected the goals of scientific research. In addition, many of the epistemological constraints which I identify for individualised research in behavioural ecology likely also apply to fields such as personalised medicine (see Chapter 6).

In addition to data-driven science, individualised research in behavioural ecology can be compared with other individual-focused approaches in the sciences, including population thinking and methodological individualism. In Chapter 5, I contrast individualised research with population thinking, an approach that has received much attention in philosophy of biology. Ernst Mayr (2006) touted population thinking as Charles Darwin's revolutionary approach to biology. On Mayr's characterisation, population thinking involves emphasising unique individuals and the primacy of variation in populations, rather than conceiving of variation as the deviation from ideal types. Philosophers of biology have criticised Mayr's account of population on a number of points, including his unfair treatment of pre-Darwinian biology, his mixing of metaphysical and methodological points, and his obfuscation of the role of types in biology (Grene 1990; Morrison 2004; Sober 2006; Ariew 2008; Witteveen 2015).

A consensus has developed that population thinking is primarily interested variation for its effects on population-level phenomena. Evolutionary biologists want to explain and predict the changing frequency of phenotypes in a population due to natural selection. Accurately measuring or explaining a particular individual's unique phenotype is not necessary for studying these broader population-level processes. In contrast, behavioural ecologists researching individuality are precisely interested in measuring and explaining individuals' phenotypes, even if they can't always reach this goal. It is therefore in the aim for accurate measurement and explanation of individuals' properties that individualised research differs from population thinking. Of course, behavioural ecologists are also often interested in population-level phenomena. But they have an additional goal to do with studying individuality in its own right.

Acknowledging that individualised research differs from population thinking helps to understand how the trend to study individuality departs from existing approaches in evolutionary biology and ecology. A similar point can be made with respect to methodological individualism, an approach in the social sciences and more recently ecology. Methodological individualists deny the existence or explanatory usefulness of higher-level entities and processes in favour of the importance of individuals (Udehn 2002; Steel 2006; Justus 2014; Heath 2015). Individualised research is similar to methodological individualism in its focus on individuals and how they can be used to explain ecological phenomena. On the other hand, it tends to be non-reductionist, allowing for the existence and explanatory importance of population-level phenomena as well as still involving groups rather than only individuals (see Chapter 6).

In Chapter 9 I bring together many of the insights gained about individualised research and its relation to other approaches in the sciences that involve looking closer at individuals. This provides the beginnings of an interdisciplinary understanding of individualised research across the sciences. However, further research is needed to explore in detail the similarities and differences between approaches, especially between the social and natural sciences and between health sciences and animal biology.

1.5 An Empirical Practice-Based Approach

In examining how individuality is studied and discussed in behavioural ecology, I take a practice-based, engaged approach (Douglas 2010; Ankeny et al. 2011). As I spell out in Chapter 2, this means I pay attention to the ways behavioural ecologists study individuality, including their observational, experimental, and statistical methods, their presentation and interpretation of results, the way they talk and theorise about individuality, and various other contextualised activities that belong to scientific research. Practice-based approaches to philosophy of science obviously require some way to get information about scientific practices. In this project, I make use of qualitative empirical methods, including participation, a qualitative questionnaire and interviews. These methods provide deep and contextualised information on an interdisciplinary field in real time, including many details that escape publication (Mansnerus and Wagenknecht 2015; Osbeck and Nersessian 2015).

As a case study, I focus on the Collaborative Research Centre TRR-212 “A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance and Niche Construction (NC^3)”—hereafter the CRC. The group contains 17 projects with about 40 scientific members, including behavioural biologists, ecologists, evolutionary biologists, statisticians, and philosophers. As its title indicates, the CRC investigates individual differences in behaviour and ecology, including animal personality and individualised niches, with a special focus on applying a causal-mechanistic approach. As a member of this group throughout its first funding phase, I had access to a wealth of information and an enthusiastic body of researchers from whom to learn, as well as the opportunity to put my philosophical insights to work by providing input and collaborating on joint projects.

I make use of a variety of empirical resources. First, I draw on information about research methods and outputs gained from my participation in the group, internal documents, presentations, publications, and collaborative work. Second, I utilise material from a qualitative questionnaire and semi-structured interviews I conducted with members of the CRC (Trappes 2021). Finally, to broaden the scope beyond the CRC, I use key publications about individuality from behavioural biologists and ecologists at large. Together, these resources allow me to clarify how individuality is understood and studied by behavioural ecologists. They also provide insight into the epistemological challenges faced by biologists researching individuality and how these challenges can be solved.

My use of empirical material strikes a balance between descriptive adequacy and normativity. Representing how biologists talk about and study individuality is itself an important and challenging task. However, developing an account of individuality that is consistent and coherent requires critical contribution. Judgements are needed on the relative importance of and connections between different definitions of individuality, the validity and strength of justifications and arguments made by biologists, and the strengths and limitations of using particular methods to solve practical and epistemological problems. In the end, I make a normative claim about how individuality in behavioural ecology should be understood and where the limitations of individuality research lie.

1.6 Outline of the Book

The use of qualitative empirical methods is still fairly unusual in philosophy, so in Chapter 2 I discuss in more detail the methods and how they can be used to develop philosophical claims. The reader keen to find out more about individuality may skip the methods chapter, but they will likely want to return to parts later in order to evaluate the use of quotations and other empirical materials for philosophical ends.

Part I of the book is dedicated to distinguishing definitions of individuality in behavioural ecology. In Chapter 3 I concentrate on the phenomena studied by behavioural ecologists. Exploring definitions and examples of animal personality, individualised phenotypes, individual specialisation, and individualised niches, I develop a first major definition of individuality. On this definition, individuality is a matter of *robust individual differences*, differences between individuals in their phenotypic properties or ranges along niche dimensions, often with an additional requirement that these differences be stable over time and consistent across contexts. In Chapter 4 I lay out further ideas associated with individuality by behavioural ecologists. I ultimately focus on *phenotypic and ecological uniqueness*. Behavioural ecologists express the belief that individuals have unique phenotypic properties and unique niches, and strongly associate this uniqueness with what it is that makes the organisms they study individuals. Phenotypic and ecological uniqueness is therefore a second major definition of individuality in behavioural ecology.

By the end of Part I, we will have two dominant definitions of individuality in behavioural ecology. The next question is how these definitions are related. In Part II I provide the makings of an answer to this question. I do so through an analysis of the challenges which behavioural ecologists face when researching individuality. What becomes clear is that uniqueness is problematic for both measurement and developing causal explanations, the topics of Chapters 5 and 6 respectively. Measurement error, the need for generalisation, and the changing, hidden and complex nature of many biological phenomena, all make it extremely difficult or sometimes impossible to accurately measure individuals' unique properties or sets of properties and to identify their causes and consequences. Associating individuality with phenotypic and ecological uniqueness therefore leads some biologists to think that individuality cannot be studied scientifically. Robust individual differences, on the other hand, can be studied using standard group-based methods. In addition, the approaches to studying robust individual differences can be seen as ways to approximately or partially measure and explain unique properties or sets of properties. As a consequence, I suggest that robust individual differences are an operationalisation of phenotypic and ecological uniqueness. As well as linking the two major definitions of individuality, Part II introduces the concept of individualised research and compares and contrasts it with other individual-focused approaches in the sciences.

What remains is to explain why behavioural ecologists understand individuality in terms of phenotypic and ecological uniqueness and robust individual differences. This is the topic of Part III. In Chapter 7 I argue that unique sets of phenotypic properties and unique niches are necessary for something to be a biological individual. Phenotypic and ecological uniqueness can thus serve as an additional condition on biological individuality, alongside others that have been discussed in philosophy of biology. Chapter 8 tackles the remaining issue of what robustness has to do with individuality beyond behavioural ecology. I consider practices of reidentification in behavioural ecology and develop a dispositional analysis of animal personalities and individual specialisation, discussing what these might tell us about animal identity.

Part III has a special focus on linking robust individual differences and phenotypic and ecological uniqueness to individuality as it has traditionally been understood in metaphysics and philosophy of biology. Of course, it would also be possible to take phenotypic and ecological uniqueness as a discipline-own concept of individuality which is operationalised as robust individual differences. However, the important and interesting resonances between behavioural ecology and philosophy on the topic of individuality invite us to attempt a more unified account of individuality across the disciplines. I therefore end the thesis in Chapter 9 with a sketch of an integrative picture of biological individuality. I also gesture towards a future extended account of individuality and individualised research across biology, medicine and the social sciences.

2 Empirical, Engaged Philosophy of Biology

The methods I use in this thesis are motivated by a practice-based approach to philosophy of science. The practice turn in philosophy of science involves paying greater attention to science as it develops and is applied in context, rather than only to the products of science such as scientific theories and facts (Ankeny et al. 2011). Attending to scientific practice obviously requires a way to access this practice. Hence, the practice turn requires empirical methods. With greater use of empirical methods comes the question of how empirical information about scientific practice can inform philosophical accounts. Philosophical claims are often highly general, abstract, and normative. The challenge is to use empirical information about specific, concrete, and imperfect scientific practices to develop and support philosophical claims.

In this chapter I discuss these matters with specific reference to the methods I apply in this thesis. I focus especially on the qualitative methods of participant observation, a questionnaire with open ended questions, and semi-structured interviews. These methods are still relatively unusual in philosophy. Yet they offer a unique opportunity to gain rich and detailed insights into both concrete scientific practices and scientists' conceptualisations and theoretical understandings. As I explain in this chapter and demonstrate throughout the rest of the thesis, qualitative methods are especially appropriate for investigating a new interdisciplinary field where methods, concepts, and theory are still in early development.

I start in Section 2.1 by considering the arguments for the relevance of scientific practices for philosophy of science. I present the different methods for studying scientific practice in Section 2.2, arguing that empirical research methods adapted from the social sciences are particularly suitable for capturing scientific work in an emerging, interdisciplinary field. This leads me in Section 2.3 to consider what role empirical information about scientific practices can actually play in developing philosophical theories. I then detail the empirical methods used in the thesis, including participant observation (Section 2.4), a questionnaire (Section 2.5), and interviews (Section 2.6). Finally, in Section 2.7 I discuss how I use the empirical materials to make philosophical claims about individuality in behavioural ecology.

2.1 The Practice Turn in Philosophy of Science

The practice turn in philosophy of science is, like most turns, at once a turn towards and a turn away. It is a turn away from earlier approaches which tended to focus on the results of science, such as theories or facts, and which dealt in a heavily idealised understanding of scientific practice. It is a turn towards scientific practice, and in particular towards the rich, contextualised details of the processes leading to scientific results (Ankeny et al. 2011; Soler et al. 2014; Rouse 2014). Specifically for philosophy of biology, the practice turn involves looking at the "ways in which biologists think and act when carrying out their research" (Leonelli 2009, 189). Because it forms the background of my use of empirical methods, in this section I introduce the practice turn, without however any pretence to completeness.

Scientific practice includes a wide variety of activities and processes: material activities such as experimentation, instrument building, and field work, social or communicative activities such as recruitment, citation, and publication, and theoretical activities such as hypothesising, research design, modelling and data analysis (Kaiser 2015). These scientific activities are goal oriented. Science aims primarily at knowledge (Ankeny et al. 2011), but many scientific activities also pursue broader and more diverse goals, such as creating and extending skills, social relations, machines, instruments, facts and theories (Pickering 1995). Scientific goals are generally accompanied by rules and guidelines to ensure they are achieved (Chang 2011). In addition, practices are contextually situated in and between institutions, communication systems, disciplines, and application contexts (Soler et al. 2014).

The practice turn therefore involves paying greater attention to varied, goal-oriented and contextualised scientific activities. This increases the philosophical recognition of social, tacit, material, and practical or transformative aspects of science (Soler et al. 2014). It also places human and material agency at the heart of science, making it apparent that descriptive knowledge is just part of science (Pickering 1995; Rouse 2014). The practice-based approach is in addition generally "bottom-up," starting with the detailed examination of scientific practices and using the insights gained to generate general philosophical claims (Kaiser 2015).

A first argument for the practice turn is that it is more adequate to actual science (Ankeny et al. 2011; Soler et al. 2014; Rouse 2014). Early 20th century approaches to philosophy of science focused on scientific theories and facts; the process leading to scientific results was intentionally ignored or treated with plain disregard for historical accuracy (Kuhn 2012). Such idealisation distorted the understanding of science in a number of ways. First, focusing only on the products of science sidelines failures, plurality, and partial confidence in results (Rouse 2014; Soler et al. 2014). Second, many assumptions, methods, and material and social dimensions underlying scientific knowledge are overlooked (Ankeny et al. 2011; Rouse 2014). As a consequence, idealised approaches ignore many aspects of science that contribute to achieving results, making it unclear how exactly science is successful (Cartwright 1999, 72).

In addition to improving descriptive adequacy, looking at scientific practice is philosophically productive. It can help answer standard philosophical questions, as evident in the 1980s with philosophers like Nancy Cartwright and Ian Hacking arguing that scientific practices of experimentation tell us about causation and realism (Cartwright 1989; Hacking 1983). Similarly, in the 1990s several authors argued that philosophical questions about pluralism can be addressed by studying the limited scope of scientific models and theories (Dupré 1993; Cartwright 1999). These forerunners have been followed by a whole generation of philosophers looking at scientific practice to address traditional philosophy of science questions. The practice turn also brings up new philosophical questions (Rouse 2014). Attention to scientific practice raises questions about interdisciplinarity, scientific communication, hierarchies of evidence, instrumentation, statistics, modelling, policy advice, and many other issues. Often these are problems with which scientists themselves are struggling (Leonelli 2016; Feest 2017). Ignoring scientific practice, on the other hand, means largely neglecting these issues and denying their philosophical relevance.

Third, a proximity to practice facilitates what Heather Douglas calls “engaged philosophy of science,” collaborating with or advising scientists, policy makers, and other research-concerned communities (Douglas 2010). “Philosophy of science-in-practice” thus transforms naturally into “philosophy-of-science in practice” (Boumans and Leonelli 2013) or even “philosophy in science” (Pradeu et al. 2021). Engaged philosophy of science is especially valuable at points where scientists struggle with complex ethical, political, epistemological, or conceptual problems (Leonelli 2016; Laplane et al. 2019).

Finally, a practice-based approach is especially relevant when studying new scientific fields. In developing fields there are typically few established scientific products to be studied in an idealised, abstract fashion. By studying scientific practices, philosophers can gain access to these fields as theoretical consensus grows, witnessing how challenges are encountered and addressed, how debates are carried out, and so on. In addition, developing fields are often rife with conceptual and practical problems, providing ample material for an engaged philosophy of science.

The arguments from greater descriptive adequacy, philosophical productivity, scientific relevance, and access to developing fields all motivate taking a practice-based approach to studying individuality in behavioural ecology. Individuality research is still very much science in the making. Studying practices in individuality research reveals the multiplicity of ideas about individuality, the confusions these ideas generate, and the challenges and workarounds involved in individualised research. Such plurality and problem solving would have likely been missed by only studying the few existing products of behavioural ecological research on individuality. The insights gained from studying individuality research provide input to existing philosophical questions about biological individuality, as well as raising new questions about individualised research, uniqueness, and animal identity. Studying biologists' research practices in an embedded way (see Section 2.4) also enabled me to assist scientists to clarify concepts and develop their theoretical framework.

Before moving on to consider the methods that philosophers can use to find out about scientific practice, I want to briefly discuss the idea of a practice-based metaphysics of science. Many philosophers of science who argue for a practice-based approach concentrate on epistemology. Looking at how scientists actually develop and apply knowledge in context, on this view, can inform more better accounts of scientific knowledge (Ankeny et al. 2011). Some of the work I do in this thesis is epistemological, figuring out how behavioural ecologists develop knowledge about individuality and the challenges they face in doing so. But I also make claims about what individuality in behavioural ecology is, and more generally about the nature of biological individuality. These are metaphysical claims. More specifically, they belong to metaphysics of science—claims about the world studied by scientists. What can scientific practice tell us about the nature of the world?

Many metaphysicians pay attention to science, and some even argue for a fully scientific metaphysics (Hawley 2006; Kincaid 2013; Waters 2017; Guay and Pradeu 2020). Very roughly characterised, scientific metaphysics involves basing metaphysical claims about what exists in the world and what the world is like on science (Kincaid 2013; Chakravartty 2017; Reydon 2021). Often the focus is on scientific products, specifically facts and theories, and what they can tell us about the world. Studying scientific practice can feed into this more theory-oriented scientific metaphysics simply by providing the opportunity to learn more about scientific theories. In addition, information about scientific practice can contribute independently of scientific theory to developing metaphysical claims via transcendental, empiricist, or pragmatist arguments (Chakravartty 2017).

First, transcendental arguments identify metaphysical principles or positions as necessary conditions for scientific practices. For example, Hasok Chang argues that there are metaphysical principles that are conditions of the possibility of engaging in certain epistemic activities, such as the "principle of single value" assumed in making measurements (Chang 2004; 2008; 2009; see Chapter 5). Second, empiricists argue that certain metaphysical views are helpful, though not necessary, for engaging in certain scientific practices (Boucher 2019). For instance, philosophers like Matt Haber and Ellen Clarke argue for concepts or definitions of individuality because they enable making inferences or posing research questions (Haber 2015; E. Clarke 2021). Third, pragmatists argue for metaphysical principles as the best explanations of the success of scientific practices. Inspired by the pragmatist tradition, Ken Waters argues that successful scientific practices must be adapted to reality and can therefore tell us about the nature of reality (Waters 2014; 2017; 2018). Waters joins philosophers such as John Dupré and Nancy Cartwright in arguing that the plurality and limited scope of successful practices reveals that reality itself is messy, complex, or plural (Dupré 1993; Cartwright 1999; Waters 2017). Similarly, many philosophers have used scientific practices of experimentation, modelling and statistics to develop theories of causation (e.g., Cartwright 1989; Woodward 2004; B. Clarke and Russo 2016; Jiménez-Buedo and Russo 2017). And as I discuss in Chapter 8, scientific practices of individuation have been drawn on to develop accounts of biological individuality (e.g., contributions in Bueno, Chen, and Fagan 2018a).

In this thesis I draw on how behavioural ecologists study and understand individuality in two ways to develop claims about the nature of individuality in behavioural ecology. On the one hand, I use information about scientific practices to find out more about behavioural ecologists' explanations and understandings of individuality and the phenomena they study. I then construct metaphysical claims that reflect these theories and phenomena. On the other hand, I aim to make sense of the biologists' practices, such as their theoretical reasoning about phenotypic and ecological uniqueness, their worries about studying individuality, or their aims to study individuals more closely. The principles of individuality I discuss are not all amenable to broad-scale transcendental, empiricist, or pragmatist arguments. Nevertheless, they do play an important role in guiding and supporting behavioural ecologists' research into individual differences. In my thesis I combine these two ways of using scientific practice for metaphysics, taking the cue from scientific practice to develop metaphysical claims that are both based in scientific theory and able to make sense of biologists' practices.

2.2 Which Methods for Engaging with Practice?

A practice-based philosophy of science requires some kind of access to scientific practice. Methods are needed for observing and analysing activities in context in a way that facilitates the development and justification of philosophical theories. This must clearly involve empirical methods, since scientific practice is a phenomenon in the world. Hence, a practice-based philosophy of science entails an empirical philosophy of science (Soler et al. 2014; Samuels and Wilkenfeld 2019). In this section I briefly introduce some of the different empirical methods that can be employed in philosophy of science and the considerations involved in selecting methods, before explaining my own choice of qualitative methods.

Various empirical methods have been adopted in recent philosophy of science. These can be grouped into at least four dominant categories: historical studies, qualitative methods drawn from the social sciences, experimental or survey-based approaches from psychology, and digital humanities techniques such as citation analysis or content analysis (Osbeck and Nersessian 2015; Machery 2016; Pence and Ramsey 2018). These methods can be applied with different levels of rigour. A historical study, for instance, could involve extensive archival and oral history research or evaluation of only published material. Qualitative methods can involve detailed and theoretically informed practices of embedding, interviewing, and recording, as often conducted in science studies, or it can involve sitting in on research seminars and casually interacting with scientists. And surveys can be short polls distributed to a select few, or standardised questionnaires delivered to large numbers of individuals from a target population, as in the behavioural sciences.

Different methods are appropriate for different research topics, afford different opportunities, and are accompanied by their own limitations and problems (Osbeck and Nersessian 2015). Results from digital humanities studies are typically more representative because they can include a very large number of publications within and between entire disciplines or topics of research, allowing the mapping of differences and patterns across fields and over time (Machery 2016; Pence and Ramsey 2018). In contrast, historical case studies provide rich details and permit reconstruction of the processes of innovation, theoretical development, hypothesis testing, and so on, often in the context of a particular research movement, institution, or historical period (Burian 2001). Similarly to historical studies, qualitative methods allow deep, detailed study of a particular case; but unlike historical studies, the case can be studied as it unfolds, allowing greater access to contextual and undocumented information such as social interactions or conceptual development, but also increasing the complexity and demandingness of the study (Mansnerus and Wagenknecht 2015). Experimental methods are typically more representative but less detailed than qualitative or historical studies, and they usually focus on cognitive aspects of scientific practice rather than contextual or social aspects (Stotz 2009; Machery 2016; Samuels and Wilkenfeld 2019).

In addition to choosing methods, it is necessary to determine the rigour with which to apply them. Some might think that philosophers should meet the high standards of natural and social science. On this line of thinking, philosophers should aim for well-motivated, planned and controlled use of empirical research methods, rather than their informal, haphazard, or partial application. However, philosophy is far more abstract and general than many sciences, and it is often engaged in making normative claims about science (see Section 2.3). Laborious, time-intensive empirical research needed for meeting the high methodological and evidential standards for the sciences may not pay off sufficiently in terms of philosophical insights. This is especially the case given that philosophers usually lack the resources and training to perform very rigorous empirical studies. Hence, philosophers must make a trade-off between philosophical productivity and empirical rigour. The choice of a particular level of rigour should therefore be motivated by reflection on its advantages and limitations.

In the present study, I primarily employed qualitative methods, including participant observation, a questionnaire with open-ended questions, and interviews. There were a number of reasons for this decision. First and foremost, individuality is a relatively new topic in behavioural ecology. My aim was to study this new concept as it is developed and operationalised in the context of an ongoing research consortium. Qualitative methods are especially appropriate for studying research practices in real time, enabling "a deeper understanding of how practicing scientists think and work, how they form collaborations and how they can produce good scientific knowledge." (Mansnerus and Wagenknecht 2015, 44) In addition, because individuality in behavioural ecology is a new topic, specific hypotheses and experiments could not be designed from the start of the study. Qualitative methods allow unexpected findings to arise out of the data in a way that is often difficult using quantitative methods (Osbeck and Nersessian 2015).

Qualitative methods were also crucial because much of the conceptual and theoretical work about individuality is not visible in published research articles. The interplay between different perspectives in interdisciplinary collaborations is often not made explicit in research products such as published articles. Interviews and participant observation are especially helpful in gaining access to such processes (MacLeod et al. 2019). In addition, researchers are more likely to express worries about conceptual and epistemological problems in conversation than in published articles. The qualitative methods I employed allowed me to identify these problems and work with the scientists to address them for future research.

I aimed for a moderate level of rigour in the application of qualitative methods. I employed formal interviewing and qualitative coding techniques and kept regular (though not daily) records of my participation in many different sorts of meetings. On the other hand, the questionnaire study and the participant observation were not extensively planned, and all methods engaged with only some activities and contexts of the CRC's research on individuality. The choice of moderate rigour was motivated by practically feasibility, with funds, time, and institutional setting in place for a small-scale ethnographic study. It was also based on the importance of fine conceptual distinctions and the presence of diversity amongst individuality researchers. Using more systematic tools like questionnaires, interviews, and qualitative coding enabled evaluating these distinctions, which would have been more difficult with casual participant observation and conversations. Later in the chapter I will describe the methods I employed in more detail. First, however, it is necessary to address the question of how empirical material can be used in philosophy.

2.3 Using Empirical Results for Philosophical Claims

Empirical information about scientific practice can play three different roles in philosophy: it can be used to develop or revise a philosophical theory (or claim, account, and so on), illustrate or exemplify a theory, or provide evidence to support or test a theory (Kinzel 2015; Mansnerus and Wagenknecht 2015; Woodward 2019). I call these three roles developmental, illustrative, and evidential. In practice-based philosophy of science, empirical information about scientific practice serves developmental or evidential roles, rather than only illustration. In this section I consider how empirical information plays these roles, given the highly general and often normative nature of philosophical claims.

Debates about the use of empirical information in philosophy of science have focused on the evidential role, and especially on the most common empirical approach: the use of historical case studies to justify or test philosophical theories (e.g., Burian 2001; Schickore 2011; Kinzel 2015). Philosophers using case studies face two major problems. First, philosophical claims are often highly general and abstract, whereas case studies are very specific and concrete. Philosophers of science risk overgeneralising from evidence about just one or a few episodes in the history of science. Second, the historical materials used to write a case study—like empirical data in general—must be selected and interpreted in order to identify philosophically relevant features. If the philosophical theory to be tested is used to perform this selection and interpretation, for instance by setting which features are relevant, then case studies do not provide independent evidence. Both of these problems are especially pressing because different selections and interpretations of the history of science have been made to support competing philosophical theories (Kinzel 2015). These problems also apply to other kinds of studies, such as ethnographic research, surveys, or citation analysis, both within philosophy and beyond. Any feasible empirical methods involve restricted scope or sampling as well as theoretical input in study design, implementation and data analysis.

The problem of generalisation can be partly addressed in a number of ways: combining different methods to get more wide-ranging evidence, restricting the generality of philosophical claims, arguing for the representativeness of a case, admitting to having only weak evidential support, or using cases only as counterexamples rather than as positive evidence. In addition, the problem of independence can be avoided when the theory used for interpretation is different from whatever philosophical claim is being justified (Kinzel 2015). However, none of these solutions is entirely satisfactory. Philosophers still tend to make highly general and abstract claims, and it is rare that study design and analysis is entirely independent of the claim to be tested or justified. Partly in response to the difficulties of using historical case studies to fulfil the evidential role, there is a growing consensus that we should focus instead on the developmental role of empirical information.

A number of authors have argued that philosophers should approach empirical information in a hermeneutic or interpretive way (Schickore 2011; Kinzel 2015; Mansnerus and Wagenknecht 2015; Leonelli 2016; Kaiser 2019). On this account, a philosophical theory is developed iteratively in communication with empirical data, which is itself sourced and interpreted based on preliminary versions of that theory. Interpretation of the data includes the ability to be critical. But avoiding confirmation bias requires taking seriously disagreements between data and theory (Mansnerus and Wagenknecht 2015). The ultimate aim is to reach reflective equilibrium, that is, to obtain a cogent account through a process of mutual adjustment between philosophical theory and empirical material (Schickore 2011; Kaiser 2019).

Developing and revising a theory in response to empirical data is slightly different to using empirical data as evidence. However, it does add some epistemic warrant to a theory. A philosophical account is likely more justified if it has been developed or adjusted in response to a case study, for instance, than if it hasn't (Kinzel 2015). Hence, empirical information that plays a developmental role can play an evidential role. Nevertheless, theories are often developed using a case study or limited sample, and theoretically informed selection and interpretation of the data remains central. Very general or controversial claims would benefit from further or independent evidence. Alternatively, approaches such as those discussed above could also be used to restrict the philosophical claims or expand the evidential base.

Philosophers of science make not only descriptive but also normative claims about science (Schickore 2011; Potochnik 2017; Kaiser 2019). For instance, practice-based philosophers of science describe scientific activities, products, contexts, and so on, but they also evaluate science or consider how it can be improved (Waters 2004; Kaiser 2019). Empirical information about scientific practice cannot serve as straightforward evidence for a normative theory without committing the is-ought fallacy. Actual science is not perfect, nor are scientists necessarily correct in their judgements about what is good science. Studying scientific practice therefore cannot play an evidential role for normative claims about science (Schickore 2011).

Nevertheless, empirical information can play a developmental role for normative theories. First, studying scientific practice can bring to light features of science that are relevant to normative judgements. For instance, in my research I found that scientists were expressing concerns about the concept of individuality. This encouraged me to consider what makes the concept problematic and how the problems could be solved, ideas which I developed in dialogue with scientists themselves. Second, information about scientific practices can be useful in revising a normative theory, for instance by indicating what changes might be possible or more likely to work (Woodward 2019). This is especially relevant if the aim is not to construct ideal theories of science but rather to help improve actual scientific practices, for instance through engaged philosophy of science (Section 2.1).

As I explain in more detail below, the empirical material in my project primarily plays a developmental role. In developing a philosophical account of individuality in behavioural ecology, I rely on and regularly return to the source material. I introduce distinctions to resolve apparent contradictions and identify assumptions and limitations underlying certain statements and practices. At the same time, I check for differences or inconsistencies with my interpretation and adjust my account in response. Through this mutual adjustment, I develop a coherent account of individuality in behavioural ecology. The empirical materials in turn support descriptive claims about individuality research, enhancing the epistemic warrant of my account though not supplying independent or complete evidence (see Section 2.7). I also use the empirical information to develop normative claims. Specifically, I use information about the conceptual confusions and epistemological problems, as well as the solutions that biologists explicitly propose or implicitly suggest, in making recommendations for how behavioural ecologists themselves could better understand the concept of individuality and its operationalisation.

2.4 Participant Observation

It remains to describe the qualitative methods I applied in this project and how I made use of the material I gained to make philosophical claims. In this section I explain the participant observation which I conducted as a member of the CRC.

Participation Roles

Participant observation is a technique used widely in the social sciences, especially in ethnographic studies in anthropology and sociology. It involves the researcher passively or actively participating in everyday situations together with their research subjects. This allows gaining highly detailed, contextualised and multifaceted information about people's experiences, activities and social interactions (Atkinson and Hammersley 1994; Jorgensen 2015). There is a long tradition of participant observation in scientific contexts, especially prominent in the laboratory studies that arose in the 1970s and 80s (Knorr-Cetina 1981; 1983; Latour and Woolgar 1986). The participant observation I conducted can be divided into three categories: attendance, collaboration, and input.

First, I attended various events as a regular CRC member. These included the fortnightly seminar series, "cloud" meetings (research meetings involving members of different projects), scientific workshops on topics such as meta-analysis, protein analysis, and research ethics, as well as yearly retreats. I also attended regular seminars in the biology faculty at Bielefeld University, including Animal Behaviour, Behaviour and Evolution, and Theoretical Ecology. In these seminars, local and visiting researchers present their findings and announcements are made about new staff or grants as well as practical matters such as animal housing and fieldwork.

Second, I undertook closer collaboration with the biologists in the CRC through the concepts cloud, in which philosophers and biologists worked together to develop a joint manuscript on definitions of major concepts in the CRC (Trappes et al. under review). As a student representative I also engaged closely with the PhD students and postdocs and took part in executive board meetings in which decisions were made about structural, financial and practical matters.

Finally, I was involved in providing philosophical input to the CRC. I presented my research at a number of CRC events, such as the seminar series and the retreat, as well as in local seminars of different research groups. In addition, I helped organise two philosophy workshops within the CRC, inviting international philosophers to provide input on CRC-related topics such as niches, ecological mechanisms and niche construction. Biologists in the CRC also attended these workshops and participated in a number of team exercises working on specific questions.

Throughout all of these participatory activities, I collected materials such as photographs of lab and field work settings, presentation slides, drafts of papers, and so on. I also took notes and kept a monthly journal recording observations and my initial interpretations.

Use of Participant Observation

The participant observation gave me first-hand insight into the daily research practices of biologists. I was witness to a vast range of activities, including presentations of results, discussions of methods, study design, statistics, or field trips, mentoring of younger scientists, theoretical debates, departmental politics, programmatic discussions about disciplines as a whole, and tactical decision making about publications and grant applications. Gaining this experience was crucial to discovering the issues faced by biologists in their working life and how they might be overcome. It was also important for keeping my work grounded in the biologists' practices. I was able to identify when certain philosophical problems, such as the problem of counting biological individuals, did not trouble biologists, and when other problems, such as the issue of measuring unique individuals, were most pressing. Contact with the biologists also prompted me to regularly check that my definitions were relevant to the way biologists use terms like "individuality" and "individualised niche."

In addition to gaining knowledge of scientific practices, the participation was also crucial for enabling philosophical input to and engagement with the biologists. Having a platform to present and discuss philosophical ideas with interested biologists and providing guidance and assistance in conceptual and theoretical matters was appreciated on all fronts. Not only was this fruitful for the CRC, but it also increased interest in and awareness of philosophy of biology amongst the biologists. Finally, my participation was crucial for the success of the other qualitative methods I employed, especially the interviews. As I discuss below, being seen as a familiar face and a fellow researcher was essential to establish the good rapport necessary for conducting short but informative expert interviews.

Limitations of the Participant Observation

There are a number of important limitations to the participant observation I conducted that are worth mentioning. It is well known that a participant observer cannot witness all moments and aspects of a certain context and can never provide a full description of everything going on in a group (Jorgensen 2015). In my case, I primarily witnessed public activities such as talks, discussions, training and mentoring. Though I got tours of facilities and talked informally to researchers about their experiences and daily schedules, I was not able to observe many everyday activities in the lab, field, or office. Hence, my knowledge of certain research practices remains second-hand, channelled and filtered through the interpretations of the biologists and what they were willing to share. Nevertheless, biologists were often happy to describe in detail how they go about conducting their research. These discussions, combined with the methodological information presented in talks and introduced in workshops, provided a fairly comprehensive window into the research practices of the scientists in the CRC.

2.5 Questionnaire

The second qualitative method I made use of is a questionnaire conducted together with other philosophers in the CRC. In this section I summarise the study. More detailed information, including copies of the questionnaire form and full results, can be found on the online project website (Trappes 2021).

Questionnaire Design

The questionnaire was designed to gauge the initial understandings within the CRC of four topics: individuality, fitness and functions, niches, and mechanisms. It included both short answer and multiple-choice questions. Questions involved asking for definitions, meanings or criteria of concepts like individuality, fitness, and population or individualised niches, asking for examples from participants' research of these phenomena or how they study them, and asking participants to evaluate statements about niches or provide reasons or explanations for statements about fitness and mechanisms. The questions that are especially relevant for the thesis are those concerning individuality and individualised phenotypes. Questions about individualised niches did not deliver particularly informative results and were therefore excluded from the analysis.

Questionnaire Delivery

All scientific members of the CRC were asked to fill in the questionnaire, including all principal investigators (PIs), postdoctoral researchers (postdocs), and PhD students. There was a total of 37 respondents, 90% of all scientific members of the CRC. The questionnaire was conducted in October 2018, just at the start of the first seminar series of the CRC. At the time of the questionnaire most PIs had worked together on conceptual development and experimental planning for several years. The postdocs and PhD students had joined three to six months before the questionnaire was conducted.

Questionnaire Analysis

The responses were analysed using semi-grounded qualitative coding. This involves developing codes for ideas or statements according to both their repetition or stress in the responses and whether they correspond to or contrast with theoretical preconceptions or philosophical positions. The codes were analysed for their frequency in the responses. There was no strong difference between the PI, postdoc and PhD groups in the codes used and their frequencies. In this case, then, there was no indication that the younger researchers were less competent in understanding and using the concepts under study. Groups were subsequently pooled for analysis. The results I make use from the questionnaire include code frequencies as well as quotations from responses.

Limitations of the Questionnaire

Throughout the analysis, a number of weaknesses were noted in the questionnaire. First, several of the questions contain leading or biased wording. For instance, one question asked, “When do you think individual differences are significant, and when are they just noise?” The words “significance” and “noise” are easily interpreted in statistical terms, and many respondents did in fact answer, sometimes in a puzzled way, by citing *p*-values and statistical significance. Another example of problematic wording is the way in which the questionnaire treats “individuality,” “individualisation” and “individual differences” as synonymous. While this wording largely reflects the use of terms in the CRC (see Chapter 4), it also means that the questionnaire cannot gauge whether there are any important differences between them.

Finally, the sample size of the questionnaire is quite small. On the other hand, given the size of the CRC the response rate was quite high. It is therefore a valid contribution to a study of the processes of conceptual formation in this particular research group and may extend to other research groups with similar goals or in similar research contexts.

2.6 Interviews

Following the questionnaire, I conducted interviews with CRC members on topics related to individuality. In this section I summarise the interview study. More information, including the interview guide, details on the coding, and a summary of the results, can be found on the online project website (Trappes 2021).

Interview Design

The interviews were semi-structured, using an interview guide containing sample questions but permitting asking further questions in the interview. The guide covered three topics: individualisation or individuality, individualised niches and phenotypes, and individualised research. Questions were about research practices, applications of concepts, and more theoretical discussions. The interviews were modelled on expert interviews, in which experts on a topic are interviewed by someone they see as a competent colleague (Bogner, Littig, and Menz 2009; Meuser and Nagel 2009). As both a philosopher and a PhD student I could have been seen as a critical outsider or a student to be taught. Nevertheless, I was an active CRC member, often engaging in discussion about CRC-related topics, and I was able to make use of background knowledge and vocabulary I gained in a bachelor’s degree in biology. All of this seemed to support the impression that I am a competent colleague.

Interviews involve the collaborative production of knowledge, as the interviewer guides the interviewee in producing statements, citing examples, and developing ideas (Kvale and Brinkmann 2015). This is especially important for philosophical interviews, since biologists are not always able to express conceptual and theoretical ideas clearly and sometimes get confused. In the interviews I used critical questioning and rephrasing to assist biologists to develop their views. However, I also exercised great caution in my input, attempting not to sway the biologists to one or another belief.

Interviewing and Transcription

Ten interviews were conducted, six with single interviewees and four with two interviewees at once. There were 14 participants, 34% percent of the total number of CRC members. Participants were selected to ensure a balance of genders, career stages, fields (behaviour, ecology, evolution), and target systems (insects, mammals, birds, amphibians, theory). Other factors used in choosing participants were their availability, and the inclusion of critical views (identified using the questionnaire).

I conducted the interviews in October and November 2019. This timing fell at the end of the second year of funding of the CRC, during which CRC members were cementing their conceptual framework, for instance by beginning to write concept papers and reviews. Each interview was 30-45 minutes long. The interview guide was usually followed fairly closely, with some additional questions for clarification or exploring new ideas. In some interviews (especially Interview 1) very few of the questions on the interview guide were asked, though information gathered from those interviews was still relevant to many of the questions in the guide. Interviews were recorded and transcribed for analysis.

Interview Analysis

Theory driven coding was used for analysing the interviews. An initial, detailed list of codes related to the research questions was developed after conducting the interviews. This list was modified and added to during coding. Subsequent analysis involved looking at the cooccurrence and frequencies of codes.

There were two reasons for using theory driven coding. First, using a semi-grounded approach for the questionnaire proved extremely difficult. Theory driven coding is much quicker, though it does require training to ensure codes are used in the same way by different coders, that is, to ensure inter-coder agreement. Second, the interviews were conducted with very specific goals in mind. Some of the issues, such as those to do with the uniqueness, universality, and causal and compositional structure of individualised phenotypes and niches, required very fine distinctions that could be anticipated from the outset. Starting with a list of codes facilitated more careful identification of these distinctions in the interviews.

The results I make use of from the interviews include code frequencies, indicating how often ideas came up across the interviews, code cooccurrences, indicating which ideas came up together in interviews, and illustrative quotations from the interview transcripts. In quotations, I indicate the interviewees with “S” (or “S1” and “S2” when there are two interviewees) and the interviewer with “R.” Quotations are anonymised except where interviewees agreed to being identifiable from quotes.

Limitations of the Interviews

The interviews also have a number of limitations. First, the sample size is relatively small. Although around a third of the CRC was covered and the sample was chosen to be representative, some diversity of opinions may have been lacking or misrepresented. Generalisations to biologists outside of the CRC must also be made with caution. Limitations in generalisations is a classic problem with qualitative research, where a compromise must be drawn between depth of analysis and generalisability.

Another concern is the risk of bias. As the primary researcher and the interviewer, I may have unconsciously directed biologists towards statements with which they might not actually agree or brought up issues that were not real problems for them. Sometimes this did become apparent in the interviews, for instance when researchers expressed confusion about the concept of individualised phenotype or the difference between individuality and individualisation. I reflect on some of these issues in Chapter 4. Nevertheless, an honest attempt was made to reduce bias and leading questioning in the interviews. The same can be said of the analysis, where utmost care was used in applying codes to ensure a faithful and not overly theoretical representation of participants’ views.

2.7 The Role of Results about Individuality Research

The participant observation, questionnaire and interviews I conducted provided a bounty of information about individuality research. I was able to learn about concrete examples of phenomena studied in the CRC. I found out about a wide variety of research methods and tools, as well as the thoughts that go on in designing experiments, analysing and interpreting results, and drawing conclusions. I also witnessed moments of wonder, confusion, excitement, frustration, passion, delight, and contemplation. As any researcher dealing with empirical information, the challenge is to sieve out relevant and important insights from the wealth of data at hand. In this section I describe the way I use the empirical material to develop philosophical claims.

First, I make descriptive claims about what phenomena biologists are researching and how they are doing so. Information about research objects and methods is especially important in Chapter 3. I use published papers as well as internal CRC documents and presentations to generate lists of examples of individualised phenotypes and niches, in order to develop a definition of individuality based on these examples. Descriptions of research methods also play a leading role in Part II, where I discuss how biologists circumvent challenges to do with measurement and explanation. Finally, in Chapter 8 I discuss methods for reidentifying animals, using insights I gained from attending presentations in the CRC, from the interviews, and from talking to CRC members and other scientists.

A second type of claim I make from the empirical material is also descriptive but concerns the ways biologists think and reason. This is especially important in Chapter 4, where I describe various ideas that the biologists in the CRC associate with individuality. It also plays an important role in Chapter 5, where I discuss the confusions that biologists have about whether and how their own research relates to individuality and the problems they face in researching individuality. And in Chapter 7 I make use of findings about the reasoning that CRC members employ in order to justify their beliefs about uniqueness. Although these are all descriptive claims about biologists' conceptual and reasoning practices, they do require interpretation of the empirical material. Biologists are not always entirely clear about what they think, and the conversational contexts of interviews or participation do not always provide the opportunity to develop detailed chains of reasoning. In addition, it is common for biologists to work with and talk about concrete examples to illustrate their points or think through topics. Drawing conclusions about how they think about abstract and general topics like individuality therefore sometimes required careful abstraction.

Third, I make normative judgements about how individuality and individualised research should be understood. I am convinced that biologists deserve to be taken seriously, even when discussing abstract philosophical topics. I therefore aim to remain largely consistent with how biologists think about and research individuality.

Nevertheless, I see an important role for philosophers in assisting biologists to gain greater clarity about what they think and where the limitations of their methods lie. The judgements I make about individuality and individualised research therefore aim to toe the line between faithfulness to biological practice and conceptual clarity and coherence.

I make use of the empirical material in developing normative claims in a number of ways. For example, the definitions individuality I develop in Part I are based on the descriptive claims about what biologists are researching and how they understand individuality. But they also involve judgements about what to count as conditions and what ideas and phenomena to focus on or ignore. As another example, in Part II I argue that there are certain limitations to individualised research. I do so in light of the limitations and solutions biologists discuss, while also arguing that some of the things they think of as limitations can actually be overcome. In Part II I also suggest that individual differences are an operationalisation of phenotypic and ecological uniqueness. This claim makes explicit and coherent the links that some biologists seemed to be implicitly making in discussing individuality, while reducing the conflict that they saw between individual differences and individuality. In addition, the information about biologists' reasoning practices that I describe in Chapter 7 is the basis for an argument for the necessity of phenotypic and ecological, but I introduce additional distinctions in order to make the argumentation more precise and convincing.

Before turning to the study, I should address the problem of generalisation mentioned in Chapter 2.3. Although I don't generalise to all of science, I do generalise from the particular group I study to individuality research as a whole. I believe the CRC can be considered exemplary of individuality research in general. This is supported by the way their work fits within the broader literature that I introduce in Chapter 3. In addition, through the participant observation I was able to witness talks from and interactions with prominent non-CRC researchers in the field, many of whom authored papers that are highly cited in individuality research. That their views were similar to those I found in the CRC provides further support for the generality of my account.

I also make suggestions about how the findings might apply to other fields in biology or the medical sciences and I do ultimately claim that the concept of individuality that I develop is quite general. These claims were developed through interpretive work with the empirical material, but they extend significantly beyond this material. In some cases, I was able to rely on studies performed by other philosophers combined with a structural similarity in our claims. However, it would be ideal to have further studies in other fields, to see how ideas about uniqueness, problems with measuring individuals, and so on, also occur in other disciplines. The findings from the present project could serve as a starting point for additional studies, especially broader quantitative surveys of multiple disciplines.

PART I

Defining Individuality in Behavioural Ecology

3 Individuals Differ!

There is no existing definition of the term "individuality" in behavioural ecology. Nevertheless, behavioural ecologists use the term to refer to a number of phenomena and associate it with several different ideas. In this part of the thesis, I investigate how individuality is understood and studied in behavioural ecology. The goal is largely descriptive. Based on empirical material from my work within the CRC, as well as published papers from the CRC and other researchers (see Chapter 2), I look at what phenomena are studied in individuality research (this chapter) and the ways behavioural ecologists themselves understand individuality (Chapter 4).

These analyses produce a plurality of definitions of individuality. These will not be definitions in the philosophical sense of necessary and sufficient conditions, but rather more like dictionary definitions (Gupta 2021) or pragmatic definitions (H. Taylor and Vickers 2017): characterisations that match up with how the word "individuality" is used and understood in the context of individuality research in behavioural ecology. The challenge in the remainder of the thesis is to figure out how these definitions are related and what they have to do with individuality beyond behavioural ecology.

Research on individuality in behavioural ecology covers two broad phenomena, what in the CRC are called *individualised phenotypes* and *individualised niches*. Individualised phenotypes and niches are in turn studied primarily in the form of animal personality and individual ecological specialisation. In this chapter I look at this collection of phenomena, including definitions, examples, and methods used to study them. On this basis, I develop an account of what it is that behavioural ecologists are studying when they study individuality. According to this definition, "individuality" is a term that refers to phenotypic traits and niche dimensions for which there are differences in a population that are not attributable to a recognisable population subgroup and, for many traits and dimensions, that are stable across time and consistent across contexts. Individuality, in other words, is a matter of *robust individual differences.*

This may seem like an odd way to define individuality. Surely individuality is about what makes something an individual. What do robust individual differences have to do with something being an individual? Can they tell us when something is an individual and when it is not, say because it is actually just a collection of individuals or a part of a larger individual? Can they help us pick out individuals and draw their boundaries? These are the usual sorts of questions that philosophers ask about individuality in biology (E. Clarke 2010; Pradeu 2016b; Lidgard and Nyhart 2017; Kaiser 2018; Kaiser and Trappes 2021). Later in the thesis (Part III), I consider how definitions of individuality in behavioural ecology relate to the philosophical understanding of biological individuality. For now, however, I concentrate on the descriptive project of drawing out definitions from the research practices of behavioural ecologists.

In this chapter I consider first individualised phenotypes, then individualised niches, and finally individuality in general. I begin in Section 3.1 by introducing the concept of phenotype more generally. In Section 3.2 I explore definitions, examples and methods for studying animal personality. Using the insights about animal personality, plus further examples, I develop a definition of individualised phenotypes in Section 3.3. I then turn to individualised niches, first introducing the concept of the ecological niche in Section 3.4. In Section 3.5 I discuss individual ecological specialisation, and in Section 3.6 I arrive at a definition of individualised niche dimensions and the individualised niche. I conclude in Section 3.7 with the general definition of individuality in terms of robust individual differences, closing with the question of what robust individual differences really have to do with individuality.

3.1 Defining Phenotypes

The term “phenotype” was first introduced at the turn of the twentieth century to refer to classes of organisms that share specific properties (P. J. Taylor and Lewontin 2017). However, the concept of phenotype that has become canonical concerns organisms’ properties, rather than classes of organisms. Specifying just which of an organism’s properties count as phenotypes is not an entirely straightforward task. I begin with some definitions from a variety of sources. Then I gradually develop the sense in which I will use terms such as “phenotypic property” and “phenotypic trait.”

According to a widely used biology textbook, a phenotype is “The observable physical and physiological traits of an organism, which are determined by its genetic makeup.” (Reece et al. 2011, G-26) The definition of phenotype in the Encyclopædia Britannica is similar, adding environmental as well as genetic causes: “all the observable characteristics of an organism that result from the interaction of its genotype (total genetic inheritance) with the environment. Examples of observable characteristics include behaviour, biochemical properties, colour, shape, and size." (The Editors of Encyclopædia Britannica 2016) In one of the few philosophical explorations of the term, phenotype is similarly defined as "the physical and behavioural traits of the organism, for example, size and shape, metabolic activities, and patterns of movement." (P. J. Taylor and Lewontin 2017) Finally, individuality researchers in behavioural ecology define a phenotype as such: "A character (or trait) can be considered as a characteristic of an organism shared by all or some of the individuals of a species that can vary, although not necessarily, among these individuals […] Measured individual values for that character are called phenotypes." (Réale et al. 2007, 293) In other words, a phenotype is an individual's value for a trait, where a trait is a variable characteristic exhibited by multiple individuals in a species.

These definitions share some common features but are also somewhat divergent. First, phenotypic properties are defined as distinct from genetic properties, such as chromosome number or heterozygosity for a certain gene. Both genetic and phenotypic properties are qualitative properties of organisms and not, say, relations between an organism and its environment, even if they can depend on such relations. Phenotypic properties are thus, minimally, non-genetic qualitative properties of organisms. I will remain neutral on whether all phenotypes are genetically determined, but this is a common assumption in many biological disciplines, including behavioural ecology (Davies, Krebs, and West 2012).

Second, the term "phenotype" can be used to refer to all of an organism's non-genetic properties, as in the first three of the definitions above. On the other hand, it can also refer to just one property, as in the quoted definition from the behavioural ecologists. Similarly, in modern day genetics, "the phenotype [is] the subset of an organism's traits associated with the genotype under given conditions." (P. J. Taylor and Lewontin 2017) For instance, when a pea plant has a "wrinkly seed" phenotype, this means it has the property of generating wrinkly seeds, but it doesn't tell us about other properties such as height or flower colour. The ambiguity between all properties and specific properties will become relevant in Chapter 4. For most of the thesis, I avoid the ambiguity by speaking of "phenotypic properties" and "sets of phenotypic properties."

A third distinction concerns the idea of values for traits, which arises in the definition from the behavioural ecologists. Often different phenotypic properties can be grouped together as variants of a common type of property, or a *trait*. For instance, pea plants have traits such as seed shape, height, and flower colour. The different phenotypic properties, short and tall, wrinkly and round, purple and white, are often called different "values" for the trait. The word "trait" is however also frequently used as a synonym for phenotypic properties, rather than only *types* of phenotypic properties. This is evident in the definition from the philosophers Peter Taylor and Richard Lewontin above, where "trait" is used instead of "property." In this thesis I use "trait" to refer to types of phenotypic property, for which individuals have different values, their phenotypic properties.

Finally, it is worth noting that phenotypic properties are observable only in a liberal sense of "observable." Some phenotypic properties, such as colour patterns or body shapes and sizes, can be observed with the unaided human senses. However, others require sophisticated tools, such as hormone levels or chemical profiles. In addition, while many phenotypic properties are concrete, some may be rather abstract. For instance, the reaction norm, the direction and degree of change in certain phenotypic properties in response to environmental changes, is itself considered to be a phenotypic trait. The historically important notion of phenotypes as observable—as distinct from unobservable genotypes—must therefore be taken with some lenience in modern biology (P. J. Taylor and Lewontin 2017).

More could be said about phenotypes at this point. Can "phenotype" really refer to the token level of individual organisms' properties given that it contains the word "type" (Grene 1990)? Could gene expression levels count as phenotypes (Nachtomy, Shavit, and Yakhini 2007)? What about epigenetic modifications? What exactly is the distinction between phenotype and genotype (P. J. Taylor and Lewontin 2017; P. J. Taylor 2018)? Are there phenotypic properties which can't be described as values for a certain trait? What about unique phenotypic properties? Some of these questions will be touched upon later. For now, I will settle on a characterisation of phenotype. Phenotypic properties are directly or indirectly observable, non-genetic qualitative properties of organisms. Phenotypic traits are types of phenotypic properties, where trait values are phenotypic properties. Finally, "phenotype" can refer to specific phenotypic properties or to all an organism's phenotypic properties. These distinctions are not conclusive, but they provide a common ground to pursue questions about individualised phenotypes and individuality.

3.2 Animal Personality

The past thirty years have seen a growing number of studies exploring the behaviour of individuals, rather than group or species behavioural norms. A major finding is that individual animals often exhibit different behaviours, and do so stably over time and consistently across contexts (Sih, Bell, and Johnson 2004; Bell, Hankison, and Laskowski 2009; Wolf and Weissing 2012; Trillmich et al. 2015). For instance, some individuals are bold, meaning they approach novel objects quickly or spend more time in open environments, and they do so both at multiple time points and in different contexts. Other individuals, in contrast, are shy: they tend to approach novel objects with hesitation and don't stay long out of shelter.

A number of terms exist for temporally stable and contextually consistent behavioural differences, including animal personality, behavioural repeatability, behavioural syndrome, behavioural specialisation, behavioural type, coping style and temperament (Sih, Bell, and Johnson 2004; Bergmüller and Taborsky 2007; Réale et al. 2007; Bell, Hankison, and Laskowski 2009; Dall et al. 2012; Wolf and Weissing 2012). I will use the term "animal personality." Despite its somewhat controversial status (to some, "personality" suggests psychological properties not studied by behavioural biologists) "animal personality" seems to be understood by most behavioural biologists without clarification (Sánchez-Tójar, Moiron, and Niemelä 2021).

Animal personalities are a prominent focus of the CRC, studied in almost every project (see Table 3.1, column "Behaviour"). For instance, Project A02 looks at optimism and pessimism in mice (*Mus musculus*). Researchers train mice to recognise positive and negative cues on a touch screen, and then observe the response to an ambiguous cue. Mice that repeatedly respond to the ambiguous cue as if it were positive, tapping on the screen and expecting a reward, are scored as more optimistic. Those that respond more often as if it were negative, not tapping the screen, to avoid a punishment (time out), are more pessimistic. Another example is Project C04, which studies predictability in steppe grasshoppers (*Chorthippus dorsatus*).

Researchers type individual grasshoppers according to whether they respond to a simulated predator by jumping with a consistent angle and distance or in very variable ways. This test is repeated multiple times on a day and over several days, to determine the repeatability of the behaviour. For all of the personalities studied in the CRC, individuals are typed according to repeated behaviour in a test or in an ongoing experimental or natural setting.

Marie I. Kaiser and Caroline Müller provide a philosophically informed definition of animal personality, distinguishing three conditions:

> For an individual animal to have a personality trait it must, first, behave differently than others (*Individual Differences*). Second, these behavioural differences must be stable over a certain time (*Temporal Stability*), and third, they must be consistent in different contexts (*Contextual Consistency*). (Kaiser and Müller 2021, 1)

Kaiser and Müller's definition matches those found in the behavioural ecology literature. For instance, Max Wolf and Franz Weissing define animal personality as "the phenomenon that individuals differ systematically in their behavioral tendencies" (Wolf and Weissing 2012, 452). Similarly, Denis Réale and colleagues propose that "temperament, personality and individuality describe the phenomenon that individual behavioural differences are consistent over time and/or across situations." (Réale et al. 2007, 294) It is helpful here to recall the distinction between traits and trait values. "Animal personality" is often used to refer to both traits and trait values. We can therefore distinguish between personality traits, such as aggressiveness, and personality trait values, such as high or low aggressiveness. This is parallel to the distinction drawn by Kaiser and Müller between personality traits and personality phenotypes (Kaiser and Müller 2021).

Following Kaiser and Müller, we can define animal personality. First, there must be variation for the trait in question, such that different individuals have different values for the trait. Specifically, it should not be the case that all members of a species, population or readily identifiable population subgroup such as age class, sex, or morphological type have the same trait value. This sort of variation is called *individual differences* (Sih, Bell, and Johnson 2004; Dall, Houston, and McNamara 2004; Dall et al. 2012).

"Individual differences" is a somewhat misleading term, since it can also include variation between groups of individuals. Many personality traits are scored bimodally or with just a handful of different values (Réale et al. 2007). This means multiple individuals can have the same value for a personality trait. For instance, many individuals could be typed as "bold," "very bold," "shy" or "very shy." Such differences still count as individual differences, so long as the groups identified using the personality trait are not recognisable population subgroups like sex, age class or morph.

Second, the individual differences in behaviour must be stable over time, such as in repeated behavioural tests, and consistent across contexts, such as in behavioural tests designed to replicate different functional or ecological scenarios (Sih, Bell, and Johnson 2004; Bell, Hankison, and Laskowski 2009; Stamps and Groothuis 2010). These two conditions of stability and consistency can also be grouped together as one condition, *robustness* (Goldie 2004; Banicki 2017), though this is not a term used in animal personality research.

Robustness is typically assessed by measuring within-individual correlation or repeatability (E. Takola et al. 2021; Sánchez-Tójar, Moiron, and Niemelä 2021). Within-individual correlation coefficients describe the correlation between an individual's performances at multiple times relative to other individuals' performances. Strong correlation indicates that the individual behaves in similar ways across multiple times relative to the behaviour of other individuals, meaning that the behavioural difference is temporally stable. If behaviour correlates across different contexts, such as tests representing different ecological scenarios, then the behavioural difference is contextually consistent (for more on contexts, see Chapter 8). Repeatability is similar but focuses on within- and between-individual variation rather than correlation. A trait has high repeatability when it has low variation within an individual over time (that is, there is little variation in an individual's performances in repeated tests) relative to the amount of variation between individuals in the population (Bell, Hankison, and Laskowski 2009). This means that individuals need not behave in exactly the same way for a trait to be repeatable (Stamps and Groothuis 2010). Instead, an individual can behave slightly differently in repeated tests, provided there are great enough differences between individuals.

The two conditions of individual differences and robustness define animal personality at the level of traits, that is, as a type of phenotypic property. Researchers are sometimes interested in animal personality at this level, especially when they investigate whether there are personality traits in a certain species. However, they often want to describe individuals' particular personality trait values. For instance, the researchers in Project A02 aim to determine how optimism affects risk-taking behaviour. To do so, they must first score the mice for optimism and then perform the risk-taking experiment; just knowing that there are stable and consistent individual differences for optimism in the group of mice would not suffice. To say that an individual animal has a personality is to say that it has a certain value for a personality trait. This means the individual's phenotypic property belongs to a type of behavioural property for which there are robust individual differences. Kaiser and Müller (2021, 9) suggest that the phenotypic properties in question are dispositions to certain behaviours, something I discuss in Chapter 8. For now, we can move on to individualised phenotypes more generally.

3.3 Individualised Phenotypes

Animal personalities are important instances of *individualised phenotypes*. "Individualised phenotype" is a term developed in the CRC. It so far lacks a definition, but it picks out a distinctive phenomenon. Drawing on examples of individualised phenotypes studied in the CRC and the definition of animal personality, I provide a minimal definition.

Individualised phenotypes in the CRC include animal personality as well as other sorts of phenotypic traits, such as colour patterns, morphology, life history traits, hormonal profiles, and immunity (see Table 3.1). For instance, Project A04 looks for boldness as well as differences in the colour patterns, skin chemicals, skin microbiome and immunocompetence of fire salamanders (*Salamandra salamandra*). Another example is Project B02, in which turnip sawflies (*Athalia rosae*) are typed according to their metabolic activity (metabotype), their level of immunity, and life history traits like the time it takes them to develop.

What unites such traits under the term "individualised phenotype"? As for animal personality, individual differences are key. Individual differences are central in the CRC, stressed in the initial funding application's opening catchcry, "Individuals differ!" Projects in the CRC therefore do not usually look at phenotypic properties exhibited by all members of a sex, age class, morphological type, or population (see Table 3.1). This was supported in the interviews, where differences, variation, individual differences, between-individual variation, and so on, were mentioned in relation to individualised phenotypes in at least 8 of the 10 interviews. For instance, the following researcher cited differences between individuals in a population as important for deciding that a phenotype is individualised (or, as this researcher preferred, an "individual phenotype," a terminological difference I discuss in Chapter 4).

> R: […] the individual phenotype, that's what you would call them [rather than individualised phenotype]. What makes you call it an individual phenotype then?
>
> S1: Because phenotypes are not only different between species or populations but also between individuals. So I would say this individual has its own phenotype, so it is an individual phenotype. (Interview 4)

The focus on individual differences is also reflected in methods used to identify individualised phenotypes. For instance, eight respondents to the questionnaire (20% of the total 37 respondents) indicated that comparing between individuals or in other ways identifying differences between individuals are important activities for identifying individualised phenotypes.

In addition to individual differences, many individualised phenotypes also involve robustness. Salamanders' colour patterns, for instance, are fixed after metamorphosis. As another example, researchers in Project B01 determine the endocrine profiles of guinea pigs (*Cavia porcellus*) by repeatedly measuring hormones such as cortisol. Endocrine profile is thus a trait that is stable over time and presumably consistent across the contexts that individuals experience. However, not all individualised phenotypes are required to be robust. For example, Project B04 takes single samples of the ejaculates of male zebra finches (*Taeniopygia guttata*) and in Project B05 fruit flies (*Drosophila melanogaster*) are dissected to measure reproductive morphology. Both of these are one-time measurements which do not permit determining robustness.

There is also disagreement amongst researchers about whether and why robustness is necessary for individualised phenotypes. The association between individualised phenotypes and robustness (or some variant, such as stability, consistency, or repeatability) was mentioned in 7 of the 10 interviews. Some researchers suggested that it was necessary.

> R: So, is the repeatability, is that important for it being an individual behavioral response? Or can you have just some individual that's really random in how it responds to things?
>
> S: These are the ones that serve as outliers usually! Scientists don't like this (laughing)… Yes, most individuals are repeatable when it comes to

> behavior and this is what made us say that individuals differ from a behavioral point of view, right. (Interview 6)

Another interviewee reasons from their experience with individualised phenotypes that all individualised phenotypes are theoretically repeatable, even if they cannot be measured repeatedly.

> R: So, would say that repeatability is also an important aspect of being an individualized phenotype […]? Or can you have an individualized phenotype that doesn't require that it's exhibited over time by an individual?
>
> S: So, are there phenotypes that are expressed once in a lifetime and you don't have, you can't measure any repeatability because you don't have repeated measures? So in this case you can't define repeatability, individual consistency, because all you can see is individual differences and you don't know… This is a good one actually. So, I would assume from my experience with repeatable phenotypes that they would be the same. In theory, as a thought experiment, I could run this individual through, and they would give similar, not identical but similar phenotypes and there would be some repeatability, I think. (Interview 8)

Other researchers thought that stability was necessary for calling a trait an animal personality but not for it being an individualised phenotype. For other individualised phenotypes, stability provides a test of experimental design.

> S2: So in that case [of personality] then you would need the stability but I think as a…for us it's even an important part that we see this stability because also then we are bit more sure that our experiment or design works. So that's why we also test the stability.
>
> […]
>
> S1: I would say that this [property], no matter if it's a trait or a state, is something that I would call a phenotype. But only if it's stable would I maybe call it personality in the biological sense. (Interview 4)

I explore the epistemological role of robustness, especially temporal stability, in Chapter 5. For now, we can identify two conditions for phenotypic traits to be individualised. First, individual differences are necessary. Second, robustness is usually, but not always, necessary. This provides us with a very minimal definition: individualised phenotypic traits are those traits with typically robust individual differences. More formally,

A phenotypic trait is individualised only if

> *Individual Differences (Phenotype)*. There are individual differences for the trait. That is, it is not the case that all members of a population, or

> recognisable population subgroup (sex, age class, morphological type) exhibit the same trait value.

In addition, most phenotypic traits are individualised only if

> *Robustness (Phenotype)*. The individual differences for the trait are robust. That is, each individual's trait values are similar or correlated over time and in different contexts, relative to other individuals' trait values.

Individualised phenotypic properties are in turn individuals' values for individualised phenotypic traits; they should differ from the trait values of some other individuals in the population, and they should be fairly stable and consistent relative to the amount of variation within the population.

The two criteria, individual differences and robustness, are not sufficient. There may be phenotypic traits for which there are robust individual differences that are not individualised phenotypes. For instance, endocrinological and immunological properties are sometimes investigated not as individualised phenotypes but rather as parts of the mechanisms that underlie or bring about individualised phenotypes. Furthermore, although transcriptomes are sometimes considered as phenotypic traits (Nachtomy, Shavit, and Yakhini 2007), and transcriptomes can show robust individual differences, researchers in the CRC did not seem to count transcriptomes as individualised phenotypes. In these cases, further conditions, such as the existence of causal relations to behavioural traits or the functional relevance of a trait for an organism's social or ecological interactions, seem to affect the decision whether to count traits as individualised phenotypes.

Such further conditions on individualised phenotypes would be important for a full definition of individualised phenotypes. Nevertheless, the conditions of individual differences and robustness are adequate for our purposes, highlighting the two central aspects of individualised phenotypes. In the next sections I turn to the second phenomenon of individuality, individualised niches. I begin with an account of ecological niches in general.

Table 3.1 Phenotypic Traits Studied in the CRC. Some traits are individualised phenotypes, especially behaviour. Others may be part of mechanisms underlying individualised phenotypes (e.g., hormones underlying behaviour), causes of individualised phenotypes (e.g., condition affects escape jumping behaviour), or related to fitness consequences of individual differences (e.g., life history traits are affected by social density). Details are derived from the CRC funding application, talks and publications.

Project	Species	Behaviour	Endocrinology	Immunology	Life history	Morphology	Other
A01	Antarctic fur seal *Arctocephalus gazella*	activity, aggression	testosterone, cortisol	innate immunity	growth		skin microbiome, transcriptomics
A02	House mouse *Mus musculus f. domestica*	optimism/pessimism	glucocorticoid metabolites		body weight		
A03	Steppe grasshopper *Chorthippus dorsatus*	predictability of escape jumping		immune status			condition
A04	Fire salamander *Salamandra salamandra*	boldness		immunocompetence			colour patterns, chemical phenotype, skin microbiome
B01	Guinea pig *Cavia aperea f. porcellus*	aggression, dominance, courtship	cortisol, testosterone, cortisol reactivity				
B02	Turnip sawfly *Athalia rosae*	activity, exploration, boldness, mating		immunocompetence	growth, development time, size		metabolism, transcriptomics
B04	Zebra finch *Taeniopygia guttata*	aggression, courtship, mating, parenting	testosterone, corticosterone			reproductive morphology	ejaculate traits, transcriptomics
B05	Fruit fly *Drosophila melanogaster*	aggression, courtship, resistance to mating			speed of aging	reproductive morphology	transcriptomics
C01	Red flour beetle *Tribolium castaneum*	activity, diurnal rhythmicity		immune priming		leg and eye morphology	quinone secretions, transcriptomics
C03	Common buzzard *Buteo buteo*	struggling behaviour	testosterone, corticosterone	expression of immunity genes	growth		

C04	Harvester ant *Pogonomyrmex californicus*	aggression	juvenile hormone (JH)		metabolism, transcriptomics

3.4 The Ecological Niche

Defining the ecological niche is if anything more complicated than the phenotype. Both terms were coined in the early part of the twentieth century. Yet in its short history the niche concept has been defined in disparate ways to cover different aspects of the relationship between organisms and their environments. I will not explore the rich history of the niche concept (Schoener 1989; Colwell 1992; Griesemer 1992; Pocheville 2015), nor will I do justice to the extensive debates about its proper definition and usefulness (Looijen 2000; McInerny and Etienne 2012; Justus 2013; Pocheville 2015). Instead, I develop a working definition based on textbooks, a theoretical standard, and common operationalisations of the concept (see also Trappes forthcoming). This definition will then serve to later specify the notion of an individualised niche.

One ecology textbook defines the niche as such: "the niche summarizes the environmental factors that influence the growth, survival, and reproduction of a species. In other words, a species' niche consists of all the factors necessary for its existence—approximately when, where, and how a species makes its living." (Molles 2015, 200) Another defines the niche in a similar way as "the conditions and resources needed by an individual or a species in order to practice its way of life." (Begon, Townsend, and Harper 2006, 31) These textbook definitions focus on the requirements for species, and perhaps also individuals, to live the way they typically do.

The textbook definitions are similar to the theoretical standard, G. Evelyn Hutchinson's niche concept (Hutchinson 1957; 1978; Holt 2009). Hutchinson defined the niche with respect to an abstract space of indefinitely many dimensions, each dimension being an abstract representation of an ecological factor, including both abiotic factors like temperature or illumination as well as biotic factors such as prey size or predator abundance. A species' niche is then represented as the region within this abstract space setting out the conditions under which the species could or actually does persist. Species' ecological niches are therefore defined in terms of the values for different ecological factors that permit population persistence.

Hutchinson distinguished between the fundamental and the realised niche. The fundamental niche of a species includes all conditions under which a species could possibly persist. The fundamental niche therefore depends crucially on the requirements and tolerances of a species. The realised niche is restricted to the ecological factors that permit the species' actual persistence. The realised niche is therefore usually a subset of the fundamental niche, limited by interspecific competition and restrictions on dispersal (Hutchinson 1957, 418–19).

Hutchinson's niche concept added precision to what had been a more qualitative notion for understanding community composition and species distributions (Schoener 1989; Griesemer 1992). However, its complexity makes it hard to apply. Not only is it difficult to measure all the ecological factors in the niche, it can even be challenging to determine which factors are present where a population persists (Schoener 1989, 93). The high level of detail also means that niches require species-specific studies (Sterelny and Griffiths 1999, chap. 11). To address these difficulties, operationalisations of the niche concept make significant simplifications.

One operationalisation is to study resource use, such as prey types and sizes (Feinsinger, Spears, and Poole 1981; E. P. Smith 1982; Schoener 1989; Pocheville 2015). Focusing on resource use dramatically reduces the number of dimensions to study and enables using standard methods like gut content analysis and stable isotope analysis. Another operationalisation of the niche is species distribution modelling, or ecological niche modelling. This approach looks at correlations between species occurrence and readily quantifiable abiotic factors, such as temperature, precipitation, or mineral abundance (Kearney 2006; Colwell and Rangel 2009; Elith and Leathwick 2009). Due to the relative ease of measuring abiotic factors and the availability of large climatic datasets, species distribution models can include many ecological factors. Yet they do not represent a species' whole niche because they exclude biotic interactions (Araújo and Guisan 2006; Elith and Leathwick 2009; McInerny and Etienne 2012). In addition, they are correlative, requiring further work to determine if factors are causally relevant to species persistence (Kearney 2006).

Resource use and species distribution models capture parts of a species' realised niche, since they look at the factors—biotic or abiotic—that permit a population's actual persistence. The fundamental niche is more difficult to study, requiring detailed and extensive experimentation and modelling beyond the limits of a species' current location. Nevertheless, there is a growing body of mechanistic niche models that combine physiological data and modelling to determine the full range of a species’ tolerances and requirements (Leibold 1995; Kearney 2006; Malishev, Bull, and Kearney 2018).

The fundamental and realised niche both depend crucially on the species’ phenotypic properties, which determine its resource use, distribution, and requirements and tolerances. Partly for this reason, some authors characterise the niche as a species’ property (Schoener 1989; Kearney 2006; Pocheville 2015). On this view, the niche would be a relational property, consisting of a species’ possible or actual relation to ecological conditions that permit its persistence. Alternatively, the niche could be understood as just the ecological conditions which sustain population persistence, dependent on but not actually consisting of the relations between species and ecological conditions. I will adopt the former approach, understanding niches to be relational properties of species (and correlatively, of individuals, see Section 3.6). I am confident that talk of niches as properties of organisms could also be replaced by talk of niches consisting solely of ecological conditions without dramatic consequences for understanding individuality (though other issues to do with identifying niches and their causal properties may of course arise).

As with phenotypes, many more questions could be asked about niches. What does talking about niches add to research on resource use, species distributions, and so on (McInerny and Etienne 2012; Justus 2019)? Can we define further niches, such as the establishment niche (Holt 2009), the social niche (Saltz et al. 2016) or the developmental niche (Stotz 2017)? Shouldn’t we also include a population’s effects on ecological factors, since these impacts are also relevant to its persistence (Leibold 1995; Chase and Leibold 2003; Chase 2011)? What might an individual’s niche look like (B. Smith and Varzi 1999; Kearney 2019)? To pursue a version of this last question, I will make use of a working definition of the niche. So, the ecological niche of a species or population is its relation to the ecological factors, both biotic and abiotic, that permit population persistence. It is determined by the requirements and the tolerances of the species and, for realised niches, by factors such as interspecific competition and dispersal limitations. Though this definition papers over several complications, it is sufficient for our purposes in exploring behavioural ecological studies of individuality.

3.5 Individual Specialisation

In recent years ecologists have shifted their attention from populations and communities to individuals (Justus 2014; Sarkar 2016). As part of this trend, a number of ecologists have drawn attention to *individual specialisation*, or *individual niche variation*, the phenomenon that individuals systematically differ in ecologically relevant traits, activities and relations (Bolnick et al. 2003; Araújo, Bolnick, and Layman 2011; Layman, Newsome, and Gancos Crawford 2015; Ingram, Costa-Pereira, and Araújo 2018). In this section I explore this phenomenon with a view to developing an account of individualised niches.

Although the study of interindividual variation in ecology stems back at least to the 1960s (Roughgarden 1972), interest stagnated until the late 1990s (see Bolnick et al. 2003). In a landmark revival, Daniel Bolnick, Richard Svanbäck, and a number of other prominent researchers argue that between-individual variation is both extremely prevalent and can have significant effects on population niches and thereby ecological and evolutionary processes (Bolnick et al. 2003). The authors catalogue evidence in a wide array of species for variation in features such as diet, foraging behaviour and efficiency, habitat and food preferences, habitat use, choice of host species, preference for oviposition sites, and parasite loads (Bolnick et al. 2003, 4–9). They sum this up in their definition, focusing especially on diet.

> We therefore define an "individual specialist" as an individual whose niche is substantially narrower than its population's niche for reasons not attributable to its sex, age, or discrete (a priori) morphological group. The phrase "individual specialization" can designate either the overall predominance of individual specialists in a population or the degree to which individuals' diets are restricted relative to their population. (Bolnick et al. 2003, 3)

A more recent review characterises individual specialisation similarly as the phenomenon "in which individuals use a small subset of the population's resource base" (Araújo, Bolnick, and Layman 2011, 948). Animal researchers study diets as well as traits that affect resource use, such as foraging behaviour and preferences (Araújo, Bolnick, and Layman 2011). Plant ecologists study variation in traits that affect nutrient uptake or photosynthesis, such as root depth or leaf area (Violle et al. 2012).

A key requirement for individual specialisation is that the trait or resource use be subject to *individual differences*. These individual differences can include variation between groups, such as discrete differences in foraging behaviour. In ecology it is sometimes difficult to ascertain that variation is not due to sex, age or morph (Layman, Newsome, and Gancos Crawford 2015, 3). Perhaps partly for these reasons, researchers have suggested that individual variation is continuous with or includes polymorphism between sexes, age classes and morphs (Bolnick et al. 2003, 3; Violle et al. 2012, 246). Nevertheless, individual differences are usually taken as the variation that remains after sex, age and morphological group have been factored into the analysis of variance for the trait or resource use. Moreover, if any group differences are identified (say, a strong bimodal difference in foraging behaviour), such groups should not be identifiable by another trait, such as a strongly bimodal size.

Having seen that individual differences are required for individual specialisation, as for animal personality, it is natural to inquire about *robustness*. Some traits, such as resource preferences or territory, are consistent across time and different experimental settings or ecological contexts (Bolnick et al. 2003). It indeed seems natural to think that individual specialisation requires temporal stability. Otherwise, observed differences could be due not to individuals but to sampling effects or resource patchiness. For this reason, several ecologists argue for repeated observation of resource use (Bolnick et al. 2003; Niemelä and Dingemanse 2018). Some methods already in use capture resource use over time. For instance, gut content analysis records the outcome of several feeding events, and stable isotope analysis measures the integration of material from the diet into an animal's tissues. Methods can also record resource use across functionally or ecologically relevant situations, that is, across contexts. For instance, animal movement studies track individuals across functional contexts such as grazing, resting and travelling (Project D06; see Chapter 8). These views and practices suggest that some level of robustness is relevant to individual specialisation.

Research on individual specialisation has however yet to reach a consensus about robustness. Some ecologists recommend distinguishing between short- and long-term specialists (Bolnick et al. 2003, 11). Others are interested in individual differences even when they result from transient environmental changes (Violle et al. 2012). This suggests that temporal stability (and by implication contextual consistency) is not necessary for all kinds of individual specialisation. To acknowledge such diversity, we can say that robustness is often a condition on individual specialisation. Individual specialisation is therefore the existence in a population of often robust individual differences in resource use, including diet, preferences, foraging behaviour, habitat use, and so on. Individual specialists are in turn members of a population whose resource use differs from some other individuals in the population, often in a fairly stable or consistent manner.

3.6 Individualised Niche Dimensions

Research on individual differences in ecology has recently extended from resource use to other ecological factors and relations. In this section I examine this research to develop a conceptualisation of the niches of individuals, or *individualised niches*. To do so, I introduce examples of individualised niche dimensions studied in the CRC as well as some recent proposals for defining the individualised niche.

The CRC studies individual differences in many ecological factors (see Table 3.2). These include the level of risk experienced by mice (Project A02), pond or stream environments of fire salamander larvae (A04), dominant or subdominant social positions in guinea pigs (B01), the flour microbiota surrounding red flour beetles (*Tribolium castaneum*, C01), the kinds and amount of greenery included in buzzard nests (*Buteo buteo*, C03), and collaborative or independent colony founding of harvester ants (*Pogonomyrmex californicus,* C04). There are individual differences for all of these factors: ponds and streams, greenery variety and abundance in nests, and the presence or absence (whether signalled or actual) of predators, microbiota, and competitors or collaborators.

A novel niche dimension not included in population niches is social group size or population density. For populations, population density is not a niche dimension but rather a response variable. However, at the level of the individual, density becomes a pertinent ecological factor. Individuals can differ in the number of conspecifics which they encounter or with which they interact, especially when the population has a patchy distribution. For instance, Project A01 studies two fur seal (*Arctocephalus gazella*) colonies, one high and the other low density. In an experimental context, Project B05 compares fruit flies raised in low, medium or high density.

Based on these examples, we can start to develop a definition of *individualised niche dimensions*. Individual differences are clearly important. This is evident in the

CRC's examples, all of which involve differences within the population other than sex, age class and morph (see Table 3.2). The importance of individual differences was also supported in the interviews; differences were mentioned in relation to individualised niches in 7 of the 10 interviews, all but one of the interviews in which individualised niches were discussed. Specifically, we can say that individuals occupy different ranges along an individualised niche dimension, such as a high or low level along the dimension of social density, or a pond or stream range along a bimodal dimension for larval environment.

As we have already seen, individual differences include between-group differences. Many of the projects investigating niches compare just two or three groups, such as high versus low competition or high versus low habitat complexity (see Table 3.2). Researchers in four of the interviews argued that the limited number of treatment levels represents a broader variety of conditions in the field (see Chapter 6). Yet even variation in the field is sometimes naturally grouped, such as ponds and streams. Because such between-group variation is not attributable to a recognisable population subgroup, it is still an instance of individual differences.

Robustness is sometimes relevant to individualised niche dimensions. Many of the differences in ecological factors are temporally stable. A minor fluctuation in population density, for instance when an individual temporarily leaves a group to forage, does not generate an individual difference in population density. Similarly, one or two losses in a fight does not shift an individual from a dominant to a subdominant position. These niche dimensions require more stability. In addition, some individualised niche dimensions involve differences that are consistent across contexts, that is, ecologically and functionally relevant scenarios. For instance, a pond or stream environment is present regardless of whether a salamander larva is feeding, escaping a predator, or interacting with conspecifics. Similarly, flour microbiota will persist whether red flour beetles are feeding, climbing, or interacting with conspecifics.

However, there are also individualised niche dimensions that are temporary and context specific, such as the risk level sensed by a mouse when foraging, but not in its home environment. Moreover, it is sometimes difficult to distinguish between contexts and niches, especially because some contextual factors may affect or be part of an individualised niche dimension. Robustness was also more peripheral to discussions of individualised niches in the interviews, where it was mentioned only once. This may be due to other pressing issues diverting attention away from robustness, such as the difficulty of identifying niche dimensions, how to distinguish between realised and fundamental niches, and the relation between population, group and individualised niches. The lack of explicit support in the interviews indicates that robustness is not central to defining individualised niches, though it may still be relevant.

So, in analogy to individualised phenotypes, an individualised niche dimension can be defined as a niche dimension for which individuals in a population vary, where the variation is not attributable to any recognisable population subgroup and, for some niche dimensions, where the variation is stable over time and consistent across contexts. More formally,

A niche dimension is individualised only if

> *Individual Differences (Niche)*. There are individual differences for the niche dimension. That is, it is not the case that all members of a population or recognisable population subgroup (sex, age class, morphological type) have the same range for the niche dimension.

In addition, some niche dimensions are individualised only if

> *Robustness (Niche)*. The individual differences for the niche dimension are robust. That is, each individual's ranges for the niche dimension are similar or corelated over time and in different contexts relative to other individuals' ranges for the niche dimension.

Defining individualised niche dimensions is often enough for empirical projects, which require the simplicity of one or a few dimensions. But for some tasks, such as forming hypotheses and explaining competition and population dynamics, a concept of the whole individualised niche is valuable.

The individualised niche has been defined by members of the CRC as a subset of the Hutchinsonian population niche (Müller et al. 2020; Elina Takola and Schielzeth 2021; Trappes et al. under review). Accordingly, the individualised niche involves the ecological conditions which an individual (rather than a species) can or does require or tolerate. The condition of population persistence is generally translated to the individual level as the condition that the individual can or does survive and successfully reproduce (Kearney 2019; Elina Takola and Schielzeth 2021; Trappes et al. under review). Importantly, the individualised niche is made up of an individual's ranges along various niche dimensions, including individualised niche dimensions as well as niche dimensions for which there are no individual differences.

The distinction between the realised and fundamental niche can also be made at the individual level. Generally, fundamental niches result from relatively robust traits such as experimentally determined preferences, performance variation, or morphological differences (Bolnick et al. 2003, 13) or limits set by physiology (Kearney 2019). Realised niches in turn include differentiation due to environmental fluctuations, intraspecific competition, and so on (Bolnick et al. 2003). This distinction does raise some questions, especially about how robust the traits should be and whether an individual can be defined outside of its social environment in order to make sense of the notion of a fundamental niche. Nevertheless, we can make a rough contrast between fairly robust traits determining where an individual could survive and reproduce, and differences that are more transitory based on where the individual actually lives.

Finally, as for population niches, individualised niches can be construed as relational properties. Individualised niches are like a person's diet or address. Diets and addresses are relational properties of people because they concern relations to food and houses. Similarly, individualised niches are relational properties of individuals, consisting of individuals' relations to ecological factors that support their survival and reproduction, which can be expressed as their ranges along certain niche dimensions. Nevertheless, I think individualised niches could also be redescribed as consisting only of the ecological factors themselves.

Table 3.2 Niche Dimensions Studied in the CRC. Many projects study social (intraspecific) niche dimensions, others look at niche dimensions that involve resources, habitat, or other interspecific interactions. In brackets is the treatments or variables used in the projects: many are bimodal variables, whereas some are continuous variables. Details are derived from the CRC funding application, talks and publications.

Project	Species	Social Dimensions	Resources and Habitat Dimensions
A01	Antarctic fur seal *Arctocephalus gazella*	social density at breeding site (high vs low)	
A02	House mouse *Mus musculus f. domestica*		risk level (high vs low), enrichment of developmental environment (enriched vs harsh)
A03	Steppe grasshopper *Chorthippus dorsatus*		habitat complexity (high vs low), colour (matching vs non-matching)
A04	Fire salamander *Salamandra salamandra*	assortative mating (stream vs pond)	larval habitat (stream vs pond), parasite load (continuous)
B01	Guinea pig *Cavia aperea f. porcellus*	social group size, social rank (dominant vs subdominant)	
B02	Turnip sawfly *Athalia rosae*		food availability as larvae (low vs high), access to clerodendrins (access vs no access)
B04	Zebra finch *Taeniopygia guttata*	male sexual competition (high vs low)	
B05	Fruit fly *Drosophila melanogaster*	larval population density (high, medium, low)	
C01	Red flour beetle *Tribolium castaneum*		microbiota in flour (species abundance and type)
C03	Common buzzard *Buteo buteo*		nest greenery (species type, quantity), parasite abundance (continuous), territory quality (continuous)
C04	Harvester ant *Pogonomyrmex californicus*	presence of other queens (present vs absent), colony type (mono- or polygynous)	
D03	Models	social density (emergence of heterogeneity across space)	

3.7 Robust Individual Differences

A number of articles have suggested combining research on animal personality and individual specialisation (Sih, Bell, and Johnson 2004; Bergmüller and Taborsky 2007; Dall et al. 2012; Toscano et al. 2016). The CRC describes itself as undertaking this very task; hence the title of the group, “A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution.” Given what we have seen in this chapter, this goal of synthesis is unsurprising. There are clear similarities between animal personality and individual specialisation, and individualised phenotypes and niches more generally. It thus makes sense to group these phenomena under a single heading.

To a certain extent, the term “individuality” already functions in this way. Animal personalities are often referred to with terms like “individuality” or “behavioural individuality” (e.g., Barash 1997; Réale et al. 2007; Freund et al. 2013; Vogt 2015; Bierbach, Laskowski, and Wolf 2017). Individual differences in various phenotypic traits have also been termed “non-genetic individuality” (Davidson and Surette 2008). Similarly, individual specialisation is sometimes referred to as an instance of “individuality” in ecology and evolution (Dall et al. 2012; Fodrie et al. 2015; Toscano et al. 2016; Niemelä and Dingemanse 2018). An alternative term is “individualisation,” as evident in the title of the CRC. Individualisation in this context appears to function synonymously with individuality, as I discuss in Chapter 4. Yet individuality is far more evident in the published literature. In addition, as will become clear later in the thesis, there are strong links between how biologists understand these phenomena (whether they are called individuality or individualisation) and philosophical understandings of individuality in biology. Hence, it makes sense to use the term “individuality.”

Both individualised phenotypes and individualised niche dimensions (and by extension individualised niches) are defined in terms of robust individual differences in either phenotypic traits or niche dimensions. So, individuality is a matter of robust individual differences. With this, we have our first definition of individuality in behavioural ecology.

> *Robust Individual Differences*. “Individuality” refers to types of properties (phenotypic traits and niche dimensions) for which there are robust individual differences, that is, differences in a population that are not

> attributable to a recognisable population subgroup and, for many traits and some dimensions, that are stable across time and consistent across contexts.

This definition accords with the way researchers categorise animal personality and individual specialisation, individualised phenotypes and individualised niches, as instances of individuality.

But what exactly do robust individual differences have to do with individuality? Individual differences include differences between groups. If researchers are often and sometimes even only studying differences between groups, why mention individuals and individuality at all? Robustness too is relative to the individual differences in a population, rather than tracking an individual's own stability or consistency (Sánchez-Tójar, Moiron, and Niemelä 2021). The objects of research captured by robust individual differences lack an obvious connection to individuality. It is thus unsurprising that researchers sometimes express perplexing statements about individuality, as one interviewee did when explaining how their project fits into the CRC.

> S: So, now that we identified individuals as groups I feel more comfortable with my project fitting in. Because we study two groups […] (Interview 3)

Researchers need additional elements to explain and justify their use of the term "individuality" for a phenomenon that has no apparent connection to individuals, or they risk emptying their talk of individuals and individuality of any of its usual significance and running into significant confusions. As I show in the next chapter, the necessary elements can be found in more theoretical and conversational contexts. After exploring a number of ideas that are associated with individuality, I focus on uniqueness. Phenotypic and ecological uniqueness is both a dominant idea amongst the biologists and, as will become evident in subsequent chapters, can help to explain the connection between robust individual differences and individuality.

4 Uniqueness and Other Notions

The previous chapter ended with a problem. What do robust individual differences have to do with individuality? Why do researchers talk about individuality when they are studying differences between groups? In this chapter we will encounter the beginnings of a solution to this problem.

As in the previous chapter, the goal of the present chapter is descriptive. In this case, however, I focus not on the objects of individuality research but more broadly on how individuality is discussed and understood in conversational and theoretical contexts. Through a detailed exploration of results from the questionnaire and interviews (see Chapter 2), I show that behavioural ecologists associate a number of different ideas with individuality. They cite factors such as agency, development, reproduction, innateness, discreteness, autonomy, individual-level properties, and uniqueness. Some of these, such as reproduction, discreteness, and autonomy, are in line with standard philosophical accounts of biological individuality. Others, such as individual-level properties and uniqueness, are less common in philosophy of biology. By considering these notions, it will become apparent that behavioural ecologists work with a far broader and more complex understanding of individuality than can be derived only from their objects of research.

One outcome of this chapter is a second major definition of individuality in behavioural ecology, *phenotypic and ecological uniqueness*. When discussing individuality, researchers talk about how individuals have unique sets of phenotypic properties and unique niches. Because of their prominence in discussions about individuality, I develop ideas about uniqueness into a definition of individuality. On this definition, the term "individuality" refers to the uniqueness of sets of phenotypic properties and individualised niches to single individuals. Phenotypic and ecological uniqueness at once complements and competes with the definition of individuality as robust individual differences, a relation I explore in Part II.

Another finding of this chapter concerns how individuality in behavioural ecology relates to philosophical understandings of biological individuality. Philosophers have mostly looked at individuality in evolutionary biology, immunology, physiology, and developmental biology (Guay and Pradeu 2016a; Pradeu 2016a; R. A. Wilson and Barker 2019). The criteria of individuality discussed have been based on features and processes such as fitness, natural selection, genetic homogeneity, reproduction, immunological interactions, physical or functional integration, or homeostasis (Lidgard and Nyhart 2017).

Many such criteria are also considered relevant by behavioural ecologists, as we will see in Section 4.1. Although there is continuity between fields, behavioural ecologists' understanding of individuality extends beyond what many philosophers have considered. As I explore in Part III, individuality in behavioural ecology provokes new questions (Kaiser and Trappes 2021) and new considerations about biological individuality.

I begin in Section 4.1 by outlining the various ideas that came up in association with individuality in the questionnaire and interviews. I then consider two lesser notions of individuality, the idea that individuality is about individual properties (Section 4.2) and that it relates to active organism-environment interactions (Section 4.3). The remainder of the chapter is dedicated to uniqueness. I introduce the topic in Section 4.4 and examine in detail how researchers in the CRC understand the uniqueness of niches and phenotypes in Section 4.5. On this basis, in Section 4.6 I present the second definition of individuality as phenotypic and ecological uniqueness. I conclude in Section 4.7 by surveying the various ideas of individuality found in this and the previous chapter.

4.1 Ideas of Individuality

The phenomena studied in individuality research can be united under the definition of individuality as robust individual differences. Yet behavioural ecologists describe and discuss individuality in many different and conflicting ways. In this section I introduce a variety of notions that arose in the questionnaire and interviews, some of which I explore in later sections (for full data, see Trappes 2021).

The first question in the questionnaire asked, "What about your research organisms makes them individuals?" This question can be understood as asking after criteria of individuality (i.e., criteria for being an individual). The diversity of responses was striking. Some answers accorded well with the definition of individuality in terms of robust individual differences. For instance, answers included "stable and persistent differences in behaviour" (PI 12), "Differences in development, behaviour, responses to external cues" (PI 2), or "Variation in Morphology, Physiology, Behaviour, Personality" (PhD 5). Other answers were somewhat different, though connected, to robust individual differences. For instance, development and experience was a common theme, seen in answers like "Prior experiences in their lives, leading to certain phenotypes or behaviours" (PI 5). Other answers were rather different, such as "Their Independent fate, like luck, experiences and death" (PI 8), "organism that reacts to its environment and has the potential to reproduce." (PD 3) or "Biologically speaking, I would say that an individual is a physically coherent bunch of cells (at least 1), each having almost the same genome." (PI 3)

We identified six major categories of answers to questions about individuality in the questionnaire: (i) individual differences, (ii) robustness (stability and consistency), (iii) phenotype, (iv) environment and experience, (v) uniqueness, and (vi) traditional criteria of biological individuality. The first two categories correspond to what we have seen in Chapter 3. The third and fourth categories were assigned whenever phenotypes, environments, niches, or experiences were mentioned in answers, including but not limited to answers talking about individual differences or robustness of these features. Because of their generality and overlap, these categories were not analysed further. The fifth category, uniqueness, was used when answers explicitly applied words like “unique” or “uniqueness” (though not when they were negating uniqueness), as well as when they spoke about individuals being different from any other member of the population (for examples, see Section 4.4). The final category groups various criteria that have been heavily discussed in the philosophy of biological individuality. These include functional or physical coherency, discreteness or having boundaries, distinctness in space and time, independence or autonomy, the ability to survive or reproduce, being a unit of selection, and being an organism.

Overall, 13 participants mentioned a traditional criterion in answering the first question about individuality (“What about your research organisms makes them individuals?”; 35% of participants). A similar proportion of respondents referred to individual differences (15 participants, 40%). Interestingly, the distribution of answers changed in the second question about individuality (“What does individuality mean to you?”), which we asked after intervening questions about individualised phenotypes and individual differences. For this question, only one participant mentioned a traditional criterion. In contrast, 25 respondents mentioned individual differences (68%), and there were also more participants referring to robustness and uniqueness (Table 4.1). This shift in answers may indicate that in the context of discussions of individualised phenotypes and individual differences, biologists define individuality more in terms of individual differences, robustness, and uniqueness, rather than using traditional criteria of biological individuality.

Table 4.1. Ideas of Individuality in the Questionnaire. Different ideas were mentioned with different frequencies in response to the first and second questions about individuality. Two categories, phenotype and environment and experience, are not analysed because they confound with differences, uniqueness, and some traditional criteria. Note that some respondents mentioned several types of criteria in one answer. Total respondents = 37.

Ideas Mentioned	What makes your organisms individuals?	What does individuality mean to you?
Individual Differences	15	25
Robustness	3	7
Uniqueness	4	9
Traditional Criterion	13	1

Table 4.2 Ideas of Individualisation in the Interviews. Individualisation shows a similar pattern to individualised phenotypes and individualised niches in terms of the association with individual differences and, to a lesser extent, robustness. Some interviewees only talked about individualised phenotypes or individualised niches, but not both. As a result, the frequencies can be taken as a minimal estimate for the actual frequency with which these associations would be made. The association between individualisation and uniqueness was not evaluated. Numbers indicate how many interviews contained the association, but not how frequently it was made in each interview. Total interviews = 10.

Ideas Mentioned	Individualisation	Individualised Phenotype	Individualised Niche
Individual Differences	6	8	7
Robustness	1	7	1
Uniqueness	0	5	8

The same categories were applied in analysing the interviews (Table 4.2). There, however, traditional criteria were not cited at all. Instead, there was far more emphasis on individual differences, robustness, and uniqueness. One reason for this may be due to the fact that, rather than asking about individuality, the interviews used the term “individualisation.” This appears to function as a synonym for individuality in behavioural ecology, to describe individualised phenotypes and individualised niches (see Table 4.2). However, it may be that individualisation lacks the connection to traditional concepts of individuality. It should also be noted that, whereas interviewees were explicitly asked about uniqueness and robustness (especially but not only after they brought it up spontaneously), there were no questions in the interview guide asking about traditional criteria of individuality.

In the interviews there was a relatively consistent picture of individuality (or individualisation) as robust individual differences (see also Chapter 3) as well as a frequent discussion of uniqueness. Some alternative ideas also came up with lower frequency in the interviews. These included: being studied at the individual level (3 interviews), bearing a relation to an individual’s fitness function (for individualised niches; 2 interviews), having to do with individual-level processes such as birth, reproduction and death or internal physiological processes (2 interviews), being a product of an individual’s activities (1 interview), and being explicable or having consequences (1 interview).

This somewhat scattered list can by systematised into two major ideas. On the one hand is the idea that individuality has to do with individuals’ properties, properties that are studied by observing single individuals, such as individual fitness or an individual’s value for a phenotypic trait. On the other hand, individuality is associated with processes in which the individual is involved and especially in which it is actively involved, and properties which can be explained by or play a role in such processes. Both of these ideas find some resonance in the questionnaire, such as in references to individuals’ phenotypic properties or individual experience. In the next two sections I explore the minor but interesting ideas of individual-level properties and individual-level processes. The remainder of the chapter will then deal with the more prominent idea of uniqueness.

4.2 Individual Properties

Researchers occasionally characterise individualised phenotypes as just any phenotypic properties being expressed by individuals, not citing a need for variation. An interviewee, questioning the terminology, implied that an individualised phenotype is just a phenotypic property exhibited by an individual.

> S2: […] could there be non-individualized phenotypes? I always thought a phenotype belongs to an individual, that's how I regard it but I was surprised by the term here… (Interview 4)

In responding to a question about whether there can be individuals without individualised niches, another researcher suggested the individualised niche is just whatever niche an individual has as a consequence of its phenotypic properties and environmental interactions.

> S: […] I think you are an individual. I mean, even a generalist to me it is an individual phenotype and maybe just tells us something how broad something is or how narrow something is, a niche. But to me, not having a niche would mean to not exist at all because you must realize a phenotype and then you do interact with an environment, you do exist with an environment. So if we define the niche as it's the multitude of things that are around you, then I don't think you can be without a niche. (Interview 3)

The idea of individual-level properties therefore involves stressing the instantiation of phenotypic properties and niches by individuals.

In addition to talking about individual-level properties, many CRC members mention that studying properties like animal personalities and individual specialisation involves taking individuals as the units of analysis. Some questionnaire respondents explicitly stated that they identify individualised phenotypes by observing or testing single individuals (7 respondents, 19%). For instance, one questionnaire respondent stated that they identify individualised phenotypes simply by seeing which phenotypic properties are "Expressed by individual [organisms]." (PI 13) Individual-level methods are ways to find out about individuals' properties. They are also closely linked to the need to measure individual differences and robustness.

First, identifying individual differences often involves measuring individuals as opposed to groups. For instance, in order to analyse transcriptomic differences between individuals, samples from each individual must be analysed separately instead of the standard procedure of pooling samples from multiple individuals.

> S1: […] we make sure that all the measurements we take are on an individual level. For example, with the gene expression what happens a lot is that people pool samples when they want to compare groups. That is something that we explicitly chose not to do, to keep open the option of analyzing also the gene expression data on an individual level. So that is one way, one example, of how we try to connect to this individual level with this project. (Interview 1)

Another interviewee, when asked what makes them call a phenotype individualised, immediately cited both variation and individual measurements.

> R: Okay, and what is it that would make you decide to call something an individualized phenotype or individualized niche? […]
>
> S: So, well, yes. Every phenotype, unless there is no variation, which practically does not exist. I think the ability to put a number on each individual and to put different numbers on different individuals at any one time, this is, I think, in some sense individualization. (Interview 8)

When asked to elaborate, the researcher contrasted such individual measurements with group-based measurements.

> S: […] So it's opposed to having like a vial of Drosophila and measuring their biomass or measuring or their average climbing distances or whatever you can measure. So, this is what I mean [when talking about individualized phenotypes], like everything you could put a number on for individuals and not for groups. (Interview 8)

Hence, recording individual differences requires preserving individuals' data points rather than pooling samples to measure in groups.

A second reason for the importance of individual-level methods is that measuring robustness requires testing or observing the same individual multiple times and in different contexts. As a questionnaire respondent stated, they identify individualised phenotypes by doing repeated behavioural tests "to establish the behavioral phenotype of the focal animals." (PhD 8) Observing a group's behaviour over time would be insufficient, since individuals may change while the group average stays constant or, vice versa, some individuals may stay the same while the average changes. Individual-level observations are thus necessary to identify those individualised phenotypes and niche dimensions that require robustness.

Nevertheless, not all individualised phenotypes and niches must be studied at the individual level. As we saw in Chapter 3, some studies of individualised phenotypes and many of individualised niche dimensions look at differences between groups, rather than single individuals. This means that studies can determine and work with an average value of a certain phenotypic trait or niche dimension. In Part

II I explore how group-level approaches are seen as conflicting with the aims of individuality research. For now, we can conclude minimally that not all individualised phenotypes and niches are actually studied as individual-level properties, though this may be due to limitations on research methods.

4.3 Agentic Organism-Environment Interactions

In addition to individual-level properties, researchers also associate individuality with individual-level processes. These include birth, development, reproduction, and death. Most interesting, however, is the role which so-called NC^3 mechanisms are accorded in generating individuality.

Three researchers in the interviews drew a distinction between "individual" and "individualised" as descriptors of phenotypes or niches. In particular, one interviewee argued that individualised phenotypes, in contrast to individual phenotypes, must be produced by an active change of the individual in response to the environment.

> S: I'm probably more into individualized phenotypes, because we look at different aspects of a phenotype […] for which I think there is at least some kind of plasticity or a way actively to individualize that, in a way. Active is probably the wrong word. But for individuals to change that or to confor--… That is probably not the right wording.
>
> R: Individuals to differentiate?
>
> S: Yeah, but also to have a …because at least for me, if I think about "individualized" there is always this active process of the individual. At least that's how I understand it. Is it by conforming, by choosing or by constructing?
>
> […]
>
> S: I would think if I could find something that I can prove that an individual can actively develop or change it depending on the environment then I would call it an individualized phenotype (Interview 10)

This interviewee stood out by strongly associating individualisation with an individual's active change in response to the environment. Such active changes are captured in the mechanisms of niche choice, niche conformance and niche construction, or *NC^3 mechanisms*. These are individual-level ecological mechanisms, in which a focal individual responds to their environments by performing a focal activity: selecting a part of the environment in niche choice, altering the phenotype in response to the environment in niche conformance, or making changes to the environment in niche construction (Kaiser and Trappes forthcoming; Trappes et al. under review).

The researcher in Interview 10 was the only one who used the NC^3 mechanisms to define individualised phenotypes and individualisation. Nevertheless, seven interviewees agreed that NC^3 mechanisms are involved in producing individual differences, individualised phenotypes or individualised niches. The idea that NC^3 mechanisms lead to individualised niches is in fact a central part of the CRC's theoretical framework, inscribed into the funding application as well as project publications (Müller et al. 2020; Trappes et al. under review). In addition, NC^3 mechanisms are central to the way CRC members aim to explain both individualised niches and individualised phenotypes (Kaiser and Trappes forthcoming).

Most of the interviewees were explicitly asked about the connection between NC^3 mechanisms and individualised phenotypes or niches. The questionnaire offers some independent corroboration, since participants were not prompted to link individuality to NC^3 mechanisms. Three respondents mentioned NC^3 mechanisms when explaining what an individualised niche is, and five characterised the NC^3 mechanisms by stating that they produce individualised niches. In addition, individuals' experience and response to their environment, both closely related to the NC^3 mechanisms, arose in responses about individuality and individualised phenotypes. Of course, these associations may have occurred because researchers were explaining how individuality develops or what causal factors affect it, rather than providing a definition of individuality. In addition, researchers may have been providing details about the experiments or research program in which their study of individuality is situated.

Regardless, it is clear that several biologists in the CRC think individuals' activities are in some way central to individuality. The idea that individual-level processes, and in particular individuals' activities, are causally related to and should hence inform our understanding of individuality bears interesting connections to some literature on biological individuality in philosophy. For instance, agency has a long tradition in definitions of organismality and biological individuality (R. A. Wilson 2004). In addition, French philosophers of science Georges Canguilhem and Gilbert Simondon have both described how individuals interact with and gradually differentiate themselves from their physical environments and from other individuals

(Canguilhem 1989; Gayon 1998; Simondon 1992; 2005). Exploring these philosophical accounts and their relation to the behavioural ecological notion of individuality would be an interesting and likely fruitful task. However, doing so would require more extensive and conclusive evidence than I have available. For the remainder of this chapter, and indeed for much of the thesis, I will instead focus on an idea that is more prominent in discussions of individuality in behavioural ecology: phenotypic and ecological uniqueness.

4.4 Introducing Uniqueness

Researchers in the CRC strongly associate individuality with uniqueness, especially with respect to individualised niches. In this section I briefly introduce this association as it arose in the questionnaire and interviews. In the ensuing section I explore uniqueness with respect to individualised niches and individualised phenotypes.

In the questionnaire, uniqueness was explicitly mentioned a total of 13 times in response to the two questions about individuality (see Table 4.1). For instance, when asked what it is that makes their research organisms individuals, several researchers responded by referring to features such as "a combination of unique genotype and experiences" (PI 4) or "a unique colour pattern just like the human fingerprint" (PhD 2). And when asked what they mean by individuality, answers included "the unique composition of the traits of one individual" (PhD 13), "something that makes them unique or special" (PhD 6) and "how an organism will uniquely interact with its environment based on a set of pre-defined factors (e.g. genes)" (PD 3).

In addition to explicit references to uniqueness, related ideas such as differences between one individual and all other individuals or the population were also frequently cited (8 responses total for both questions). Furthermore, respondents in the questionnaire sometimes noted a distinction between a property being exhibited by multiple individuals and it being truly individualised. For instance, a researcher warned that statistically significant results about individualised phenotypes can be difficult to obtain since "if everything would be completely individual, they [the organisms] would have nothing in common, i.e., there would be no significant differences among [treatment] groups." (PI 5) I will return to this challenge of studying unique properties—properties that organisms do not have in common—in Part II.

The association between uniqueness and individuality was surprising. The phenotypic traits and niche dimensions investigated in the CRC are not unique to single individuals. Nor is it common that individuals have unique values or ranges for the phenotypic traits and niche dimensions being studied. Recalling Chapter 3, although individual differences imply that a property is not shared by a whole population or population subgroup, the property can still be shared by multiple individuals.

Because of its prominence and unexpectedness, I pursued the individuality-uniqueness association in the interviews. With some variation in formulation from interview to interview, I asked interviewees,

> We've been talking in the CRC about whether individualised niches and phenotypes are unique, whether they are really specific to single individuals. What do you think about this? Can individualised niches and phenotypes be shared between several individuals in a population? Or does each individual have its own specific phenotype or niche that no other individual totally shares? How do you see this in your research? (Interview Guide)

The interviews produced similar results supporting the association. Most interviewees talked about individualised phenotypes or niches being unique, many even without being prompted (8 interviews overall, 5 for phenotypes and 8 for niches). However, some interviewees also rejected the necessity of uniqueness, some of them in the same breath as stating that individuals are unique. In the next section I examine in more detail how interviewees discussed whether and in what sense individualised niches and phenotypes are unique. Researchers readily claim that individualised niches are unique, but the ambiguity of the term "phenotype" leads to a more ambivalent attitude to phenotypic uniqueness.

4.5 Niches are Unique, are Phenotypes Too?

Many researchers in the interviews stated or implied that individualised niches are unique to single individuals. Take for instance this interviewee, who argues that no two individuals could have the same individualised niche.

> S2: […] when we're really talking about individualized niche then we are talking about just one individual. Because I think that even if the situation is for our eyes completely the same, differences in the individual itself or, small-- or even how the individual is really seeing its environment can be different. So, I think that there will be never [i.e., it will never be the case that], coming out of an interaction of one individual and an environment,

> even it is the same for all eyes, it will be the same individualized niche. (Interview 2)

Similarly, responding to a question about whether all individuals have individualised niches, another researcher argued that all individuals have unique niches, whereas they can have non-unique phenotypic properties.

> S: So in this context like if we imagine this multi-dimensional niche containing also like the other two concepts of niche inside 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. So if I look at phenotypes in my project, I think they will share the same phenotype, they will have the same phenotype or present the same phenotype, but if you look in abstract niche in multi-dimensions they will be different for sure. (Interview 7)

As we will explore in more detail in Chapter 7, the complexity of individualised niches is an important feature of the biologists' beliefs about their uniqueness. The sheer improbability of exactly replicating the complex composition of ranges along niche dimensions that make up an individualised niche—replicating not only the combination ecological factors present in the environment but also the individual's relations to them—leads biologists to conclude that individualised niches must be unique.

One major exception to the consensus that individualised niches are unique was an interview with theoretical biologists. They pointed out that their models contain individuals with identical niches and suggested that exactly identical individualised niches are possible.

> S1: […] we are not requesting that all the individuals are unique in a sense. It could be still two individuals with the same individualized niche without the concept of the individualized niche collapsing, in my opinion.
>
> R: And would you say that's because you're dealing with theoretical models or would it also hold for people doing like the experimental work and the field work?
>
> S1: I think that's the same, yeah. I don't think they would expect […] to find differences or significant differences between any pair of individuals. There would be some that are very similar and others that are pretty different. (Interview 5)

It is interesting that only theoretical biologists made this statement, whereas the empirical biologists in the interviews seemed more inclined to reject the possibility of identical individualised niches. The sample size of the study doesn't permit drawing any firm conclusions about the existence of a disciplinary difference in beliefs about uniqueness. It is however worth pointing out that theoretical models typically use numerically distinct but non-unique individual units, even if researchers sometimes describe them as ways to study unique individuals (Grimm and Railsback 2005).

Three researchers in the interviews also mentioned epistemological constraints as a reason to define individualised niches as non-unique. Allowing individualised niches to be shared enables the use of standard group-based methods, an issue I explore in Part II. This compromise is expressed by the researcher who, in the first quote in this section, argued that individualised niches are unique.

> S2: […] The problem is that we cannot really do statistics or put any claims on that [the unique individualised niches], so what we do is kind of to… […] having a specific social situation, where we think 'okay there is not much of a range for this social situation' and we would call that the same individualized niche even, for example, there are five individuals in the same context… to make research possible. But for the concepts, I think, when we're really talking about individualization for me it's - as Oliver Krüger said also in his talk - it's really just one single point and no one else can touch this exact same point twice. But it's really hard. To get there we have to start a little bit broader but hopefully touching that in the end. (Interview 2)

As is evident in this quote, the idea that individualised niches are not unique was seen as an approximation or compromise. This indicates that the belief in unique individualised niches may be a strong theoretical belief, but its application in research is not clear.

There was more debate in the interviews about the uniqueness of individualised phenotypes. Some phenotypic properties might truly be unique. Recall the quote above from PhD 2 in the questionnaire, that their organisms are individuals because they have "a unique colour pattern just like the human fingerprint." Fingerprints and colour patterns are both properties that in many species are unique to individuals. For instance, monozygotic twins share a genetic code and are phenotypically very similar, but they differ in traits like fingerprints (Jain et al. 2002; Wong et al. 2005). Similarly, one interviewee (Interview 6) mentioned "more fine scaled morphological traits" that can make an individual unique. Of course, we can imagine two individuals sharing such purportedly unique properties, especially if we consider very long periods of time or allow for technological manipulation of organisms. But if we restrict our attention to natural populations in shorter timeframes then we can affirm that some phenotypic properties are unique.

Nevertheless, behavioural ecologists tend to study phenotypic properties that are not unique. For most of the phenotypic traits studied in the CRC, it is possible and even rather likely that two or more individuals will have the same trait value. Two fire salamander larvae, for instance, could both have the same boldness score or the same level of immunocompetence. Indeed, many projects in the CRC rely on trait values being shared by multiple individuals in their experimental set up and statistical tests. For example, the ants in Project C04 are grouped according to whether they are aggressive or prosocial, and the guinea pigs in Project B01 are grouped according to whether they are dominant or subdominant (see also Chapter 3, Table 3.1). Five respondents in the questionnaire explicitly stated that individualised phenotypes can be exhibited by multiple individuals. This belief was also echoed in the interviews, as we saw in the quote from Interview 7, where the interviewee contrasted unique niches with non-unique phenotypes.

Understanding individualised phenotypes as those phenotypic properties that are truly unique, not shared by any other individual in a population, would therefore conflict with the use of the term to refer to many non-unique properties, such as animal personalities or hormone levels. Nevertheless, some researchers insist on phenotypic uniqueness. Take for instance an interviewee responding to the question about whether individualised phenotypes and niches are unique.

> S: 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. (Interview 3)

This researcher initially mentions identical twins and then goes on to state that even they will show some “tiny” phenotypic differences. Another interviewee talked about the difficulty of creating phenotypically identical individuals in order to have replicates for studying phenotype by environment interactions.

> S2: 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. (Interview 1)

One way to make sense of this insistence on phenotypic uniqueness is to focus on phenotypes in their totality, as sets of phenotypic properties.

Recalling Chapter 3, “phenotype” is used to refer either to single phenotypic properties or to the set of all phenotypic properties exhibited by an individual. The latter is also called a phenome, in analogy to the genome (Scriver 2004). However, since “phenome” is not widely used outside human medicine and is not used at all within the CRC, I will refer to the set of all phenotypic properties as the *total phenotype*. It is primarily the total phenotype, and only occasionally single phenotypic properties, which the biologists in the CRC take to be unique. For instance, when the researcher in Interview 3 insists on the existence of some “tiny differences between individuals” even though the individuals “have an outwardly similar phenotype,” the interviewee must be using “phenotype” in the total phenotype sense of the term and hence thinking of unique sets of phenotypic properties.

Individuals can have unique total phenotypes although they exhibit the same phenotypic properties. Two guinea pigs, for example, could both have the same aggression level but differ in other traits, such as fur pattern or hormone levels. A single guinea pig could even share all of its phenotypic properties with other individuals and still have a unique total phenotype. This would be the case if each of the phenotypic properties were shared with different individuals; for instance, the guinea pig could share its aggression level with one conspecific, its colour pattern with another, and its hormone level with a third. In this case all the phenotypic properties are shared, but there is no other guinea pig with all the same phenotypic properties as this particular individual.

The uniqueness of total phenotypes can be defined more formally, such that a set of phenotypic properties exhibited by an individual is a unique total phenotype if and only if either of two conditions holds:

> *Unique single property.* At least one phenotypic property in the set is not exhibited by another member of the same population or species; or
>
> *Unique set of properties.* The entire set is not exhibited by any other member of the population or species, although no property is unique.

The idea that total phenotypes, and sometimes single phenotypic properties, are unique makes sense of the way researchers in the CRC talk about the uniqueness of phenotypes. It also matches the way individualised niches are thought to be unique. In the next section I therefore consider what these ideas about phenotypic and ecological uniqueness mean for understanding individuality as a whole.

4.6 Phenotypic and Ecological Uniqueness and Individuality

In a presentation in October 2018, towards the beginning of the CRC's first funding period, Oliver Krüger asked the question "What makes an individual?" (Krüger 2018). His proposed answer was that an individual occupies "a single position in multi-dimensional trait space" (Krüger 2018). In other words, each individual has a particular set of phenotypic trait values that can be depicted in graphical form as a point in a multidimensional space, in analogy to the multidimensional niche space. The talk was influential for the thinking of other CRC members; it was for example this talk which the interviewee in Interview 2 above (Section 4.5) cited in support of the idea that individualised niches are unique.

Krüger's proposal was at the time heavily debated. Some CRC members advocated including a temporal trajectory to account for the way an individual's properties change over time. Others argued that adding spatiotemporal dimensions would be necessary so that two individuals with the same position in the trait space could still be distinguished. This discussion indicates that biologists were looking for something that could pick out an individual uniquely and persistently over time. Krüger's proposal, interpreted as providing a complete definition of individuality, that is, of "what makes [something] an individual," was seen as problematic because it didn't ensure absolute uniqueness and persistence.

Although it was contested, Krüger's proposal conforms to what we have seen from the questionnaire and interviews in Sections 4.4 and 4.5. When discussing individuality, individualised niches and individualised phenotypes, researchers speak about uniqueness. They take individuals to have unique niches, composed of unique or non-unique ranges on many different niche dimensions, and unique total phenotypes, composed of unique or non-unique phenotypic properties. Combining these two ideas, individuals have unique sets of phenotypic and ecological properties (the latter being relations to ecological factors, one way of understanding the individualised niche—see Chapter 3), and this uniqueness is important for individuality. This way of understanding individuality can be formulated as a definition close to Krüger's proposal.

> *Phenotypic and Ecological Uniqueness*. "Individuality" refers to the uniqueness of individuals' total phenotypes and individualised niches.

Uniqueness is of course relative to a comparison class: an individual could be unique in a small group, but non-unique when compared to an entire population or over many generations. Many of the quotes above indicate a fairly broad comparison class for assessing uniqueness. Phrases like “there will be never” identical individualised niches (Interview 2), “there will be differences for sure” in multi-dimensional niches (Interview 7), “there will be tiny differences between individuals” (Interview 3), or “basically, it is impossible” to produce phenotypically identical individuals (Interview 1) all indicate a scope extending beyond the here and now, and in particular beyond the immediate groups with which biologists are working (see also Chapter 7).

The definition of individuality as phenotypic and ecological uniqueness tells us one meaning of individuality in the context of behavioural ecology. But it does not tell us whether phenotypic and ecological uniqueness is necessary or sufficient for something to be an individual. In Chapter 7 I will argue that phenotypic and ecological uniqueness is necessary but not sufficient for something to be an individual, and thus that it is part of individuality understood more broadly. For now, however, we need only recognise that behavioural ecologists tend to understand individuality in terms of phenotypic and ecological uniqueness.

4.7 Connecting Individuality Ideas

In this part of the thesis, I introduced two main definitions of individuality in behavioural ecology. The first is based on definitions and examples of, and methods for studying, the objects of individuality research. From these sources I proposed the dual conditions of individual differences and robustness, the latter being sometimes but not always necessary. Yet robust individual differences don’t have anything obvious to do with individuals and individuality. Phenotypic properties and ranges along niche dimensions can easily be shared by multiple individuals, and they are often studied at the level of groups sharing these properties.

The second major definition of individuality is derived largely from the questionnaire and interviews, as well as theoretical discussions and presentations within the CRC. These sources highlight that individuality is often understood in terms of the uniqueness of total phenotypes and individualised niches. The definition of individuality as phenotypic and ecological uniqueness salvages the relation to single individuals. Yet it seems relatively disconnected from behavioural ecologists’ research objects and empirical methods. Robust individual differences often include differences between groups and are rarely unique, and researchers use group-based methods, especially experiments involving treatment and control groups.

Distinguishing these two major definitions of individuality is already a positive contribution. As we will see in Part II, biologists themselves vacillate between talk of robust individual differences and phenotypic and ecological uniqueness in a way that generates confusion. However, just distinguishing these two definitions leaves several questions to be answered. First and foremost, how do these two definitions relate to one another? Do they just reflect two distinct ways to understand the same phenomena, or is there a more systematic connection between robust individual differences and phenotypic and ecological uniqueness? Second, what exactly do robust individual differences and phenotypic and ecological uniqueness have to do with individuality? How do they relate to ideas about individuality more generally, beyond behavioural ecology? These are the questions that we will deal with in the remainder of the thesis.

In this chapter we also encountered several other notions related to individuality, including the idea that individualised phenotypes and niches are properties of individuals, and the role of active organism-environment interactions and other individual-level processes. It remains an important question how other notions associated with individuality may compare with or complement robust individual differences or phenotypic and ecological uniqueness. Nevertheless, I concentrate on robust individual differences and phenotypic and ecological uniqueness because they are more prominent than notions surrounding individual properties and individual-level processes.

PART II

Individuality's Epistemological Discontents

5 Individualised Measurement

In Part I, I introduced two distinct but related definitions of individuality in behavioural ecology. First, individuality refers to *robust individual differences*. These are phenotypic traits and niche dimensions for which there are individual differences (not all members of a population or an obvious population subgroup like sex, age class or morph have the same trait value or niche dimension range) and often robustness (the differences are temporally stable and contextually consistent). Robust individual differences can also include differences between groups, raising the question of what they really have to do with individuality. Second, individuality is understood in terms of *phenotypic and ecological uniqueness*, the uniqueness of total phenotypes and niches to single individuals. Phenotypic and ecological uniqueness is more clearly related to individuals and individuality, yet researchers typically don't study unique sets of phenotypic properties or niches. So, how are the two major definitions of individuality related?

To answer this question, I look into the concerns that researchers in the CRC voice about studying individuality. They express uncertainty about how to study individuality, whether their own research employs the appropriate methods and study designs, and even whether scientifically studying individuality is possible at all. These are epistemological questions, concerning knowledge and how we acquire it. In this part of the thesis I consider the origins and nature of, and solutions to, the epistemological issues in individuality research. Doing so not only helps to understand how the two major definitions of individuality in behavioural ecology are related, but also highlights the possibilities and limitations of the scientific study of individuality.

I argue that the worries that behavioural ecologists have about studying individuality are due to the understanding of individuality as phenotypic and ecological uniqueness. First, uniqueness demands measuring single individuals, but observations of single individuals are plagued by measurement error. This leads to the problem of *measuring individuality.* Second, phenotypic and ecological uniqueness involves idiosyncratic causal histories, whereas causal explanation in biology requires generalisations. Individuality researchers therefore face the problem of *explaining individuality*. As I show in this and the next chapter, defining individuality as robust individual differences, including between-group differences, can be seen as a way to manage these problems. I argue that robust individual differences are used to gain epistemic purchase on uniqueness: they are an operationalisation of the unwieldy, more theoretical idea of phenotypic and ecological uniqueness.

This relation of operationalisation provides an answer to the question of what robust individual differences, which include group differences, have to do with individuality understood as phenotypic and ecological uniqueness. Recognising that robust individual differences are an operationalisation of phenotypic and ecological uniqueness will also assuage some of the biologists' worries about individuality research. Finally, it highlights the movement towards individualised research as well as the limitations on measuring and explaining individuality.

I begin this chapter in Section 5.1 by introducing and analysing the epistemological unease amongst CRC members. Then I focus on the first epistemological problem of measuring individuality. In Section 5.2 I canvas the general challenge of dealing with measurement error, which provides the context for the specific problem of measuring individuality, which I explain in Section 5.3. In Sections 5.4 and 5.5 examine the two ways in which biologists deal with this problem, individualised measurement and using groups as proxies. I conclude in Section 5.6 by considering how the epistemological goal of measurement has shaped the definition of individuality in behavioural ecology. The problem of explaining individuality and broader implications of the reflections on epistemology will be dealt with in Chapter 6.

5.1 Concerns about Studying Individuality with Groups

We can begin by examining how individuality researchers express the overall epistemological issues they are facing. To do so, I use material from the questionnaire, the interviews, and participant observation (Chapter 2). These empirical sources reveal resounding observations of a conflict between the goal of studying individuality and the means of group-based methods. In this section I present the conflict and analyse it into two separate issues, one to do with measurement and the other to do with causal explanation.

Many researchers voluntarily brought up the epistemological issues they were facing. For instance, one interviewee responded to a question about what phenomena they were studying with an observation about their use of group-based experiments.

> R: I was wondering if you would say that your project is related to either of these two phenomena [the individualized phenotype and the individualized niche] and, if so, how it is that your project is studying these things. […]
>
> S1: Yeah. So, I think it turns back a bit to what we said before, that in the end we have …
>
> R: Treatment groups.
>
> S1: Exactly, 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. (Interview 1)

The researcher clearly associates the study of individuality ("individual variation") with a methodological requirement. The use of an experimental design involving treatment and control groups is presented as in some way suboptimal, not permitting the researcher to "directly study" individuality. Note that the issue brought up in Interview 1 is not simply the problem of external validity, that is, the suitability of their chosen treatments for representing real-world variation and causal relations. Indeed, the interviewee appears to take this representativeness for granted. Instead, their focus is on whether such representative groups can provide information about *individual* variation.

Both subjects in Interview 1 were adamant that their project still indirectly studies individuality. In contrast, three interviewees reported that they do not study individuality partly because they employ group-based methods. One researcher explained their uncertainty about how their project fits into the CRC's study of individuality (or "individualisation," a rough synonym of "individuality," see Chapter 4).

> S: 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. (Interview 3)

The researcher in Interview 3, like two other interviewees, is hesitant to believe that their group-based approach to experimentation, measurement and statistics is capable of providing information about individuality. A similar tension was noted in the questionnaire, though less prominently. For instance, four respondents mentioned differences between groups when explaining and describing individuality and individualised phenotypes (11%, n=37). On the other hand, three respondents explicitly stated that comparison between or study of groups *doesn't* provide information about individualised phenotypes or individuality (8%).

Many of the researchers in the CRC are highly cognisant of the reasons for engaging in group-based experiments or analysis. Practicality and the demands of statistics are often cited.

> S: 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)

In addition, some researchers cite the need to explain or develop generalisations as a reason for the employment of group-based approaches.

> S: And perhaps, I mean, again, one idea would be to say, okay, in a population, or where you have, I don't know, a very variable environment, you have more individualization compared to environment where you have very stable environmental conditions. But would that be individual based studies? You would need the individuals to see the variance differences. And that might be valuable. But then again you're generalizing based on these group differences.
>
> R: Because one group is more individualized and the other is less.
>
> S: Exactly. (Interview 10)

Interviewees in seven of the ten interviews mentioned their aims for explanation and causal knowledge as relevant for their use of group-based approaches. Three interviewees also mentioned the epistemic goal of categorising as a reason to use group-based approaches. Further justifications included simplicity (3 interviews) and practicality (2 interviews). In general, it seems that certain epistemic aims were seen both as crucial elements in the scientific study of a phenomenon and as entailing the use of group-based methods.

Researchers also stress the importance of clarity about the relation between group-based approaches and the study of individuality. This concern was lucidly thematized by one interviewee.

> S: That also has been bothering me, like whether we are talking about groups of individuals or individuals themselves. I think for the sake of science we should be talking about groups of individuals but in a theoretical level [*sic*] you could use individuals as your unit.
>
> R: But when it comes to doing experiments then things get tricky.
>
> S: Another thing that I find very tricky is that prior to starting a discussion we have always to agree on the scale that we are talking at. Like are we talking about cells, are we talking about organs, tissues or are we talking about individuals or groups of individuals? These are different scales that can mess up a lot our process of thinking.
>
> R: If they are not clear?
>
> S: Yeah. (Interview 6)

Without clarity about the level of analysis, communication between researchers, interpretation of results, and design of further experiments will be undertaken without sensitivity to differences introduced by changes in scale.

In summary, the researchers in the CRC express concerns about their use of group-based approaches. Group-based approaches seem necessary for achieving certain scientific goals. Yet they also seem to involve ignoring or misrepresenting some aspects individuality. Researchers consequently express doubts about the ability of their research to provide information about individuality. To better understand this tension between studying individuality and using group-based methods, it will help to distinguish two epistemological goals that provide distinct reasons to use group-based approaches: measurement and causal explanation.

An important task in individuality research is the measurement, description, and classification of individualised phenotypes and niche dimensions (Bolnick et al. 2003; Toscano et al. 2016). For instance, in the CRC Project A03 documents individual differences in the escape jump predictability of steppe grasshoppers, and Project A02 tests mice for differences in their level of optimism or pessimism. In addition, more recent research has moved from describing to explaining and understanding individuality (Bolnick et al. 2011; Wolf and Weissing 2012; Forsman and Wennersten 2016; Costa-Pereira et al. 2018). Most projects in the CRC seek to determine the causes of individuality phenomena and what consequences they have for evolutionary and ecological processes (Kaiser and Trappes 2021). For example, Project A01 looks for explanations of why fur seal mothers choose different beaches on which to raise their pups, and Project C01 studies how the immune experiences of individual red flour beetles affect the evolution of their social group (see also Chapter 6).

Both measurement and explanation typically require group-based approaches. As I explain in this chapter, a common way to deal with measurement error is to measure multiple individuals and take the average as the real value. On the other hand, as I explore in Chapter 6, picking out causally relevant factors from the many factors in each individual case usually involves experiments or statistics that generalise over multiple individuals. Group-based approaches are used to address different issues for measurement and explanation. Hence, we can divide the tension that researchers feel between group-based approaches and researching individuality into two separate concerns.

> *Measuring Individuality*. How can we measure individuality if measurement is usually performed on groups?
>
> *Explaining Individuality*. How can we develop causal explanations of individuality if identifying causal factors usually involves generalisation?

These questions can be read in two voices. One is despairing, "How on earth can we…?!" or "How can we presume to…?" This voice assumes the impossibility of the scientific study of individuality based on the assumption that group-based approaches can't tell us about individuality. The other is curious, "Let's find out how we can…" or "What are the ways to…?" This voice is optimistic about the possibility of scientifically studying individuality but isn't quite clear what this would look like or how it could be justified. Both of these voices are evident amongst the interviewees.

Having distinguished these concerns about measuring and explaining individuality, we can ask more pointed questions. On the one hand, why are group-based approaches important for measurement and explanation, and are they really necessary? On the other, why might group-based approaches pose problems for studying individuality and how can these problems be addressed? In this chapter I concentrate on measurement, reserving explanation for Chapter 6. I look first at why group-based approaches are important for measurement, and then at how the tension with individuality arises and can be partly resolved.

5.2 Observation, Measurement and Error

In the philosophy of science, measurement and observation have often featured in the debate about realism, that is, whether the entities being studied by scientists are real and independent of scientific study (Chang and Cartwright 2008). My aim here is to analyse and address the problems which biologists themselves are facing, so I follow them in adopting a largely realist stance. This means I take it for granted that measurement is about determining the actual values of real phenomena. Yet even measurement and observation from a realist perspective generate a number of different problems for scientists (Chang and Cartwright 2008; Feest 2017). One of these problems is the difficulty of dealing with measurement error. Because this problem forms the background to the concerns about measuring individuality, in this section I consider in some detail the origins and solutions to the challenge of measurement error.

Following James Bogen and James Woodward (1988), we can distinguish between observation and measurement. Roughly, observation involves recording some value, such as checking a thermometer or reading off a value on a measuring tape. Measurement then involves taking one or more observations as the true value of the observed phenomenon. This distinction is important, because repeated observation of a single phenomenon usually produces not a single value but rather a scatter of values (Bogen and Woodward 1988). One reason for this scatter is that instruments, humans, environmental fluctuations, and so on can introduce *error*, both systematic and random, into the values that are recorded when making observations (Woodward 2010). This error alters an observation so that it is not a one-to-one match with the thing being observed in the world: the observation doesn't accurately represent reality. Measuring—taking the observed value as the real value of the phenomenon—must therefore deal with measurement error. Methods for managing measurement error are needed so that true values can still be estimated from the scatter of observed data.

Because measuring organisms introduces extra complexity, it will help to start with a somewhat contrived everyday example of dealing with measurement error. Imagine a shop assistant measures and cuts a metre of fabric for me at the store. I take it home and measure it, only to find it to be 95 centimetres. I measure the fabric again, just to be sure. Now I find that it is 93 centimetres! That can't be right. After a few more takes, trying to spread out the fabric and place the tape measure straight, I have a scatter of length data that centres around 95 centimetres. Convinced that I have been swindled, I return to the store. Before a refund, the shop assistant checks the fabric at their measuring table. To my surprise, it is one metre! Perhaps, then, my measuring tape is faulty. Indeed, when I compare it to a brand-new measuring tape, each centimetre on my tape is slightly longer, making it measure one metre on the new tape as 95 centimetres. I buy the new measuring tape, apologise to the shop assistant for my mistrust, and take my metre of fabric back home.

Both systematic and random error are present in this story. First, a systematic error was introduced by my faulty measuring tape: the tape consistently reported values that were lower than the real value. Second, random error was introduced when I measured the fabric and found it to be slightly longer or shorter than 95 centimetres: the recorded values fluctuated around a central point due to things like wrinkles in the fabric or not placing the tape measure straight. The wrinkles in the fabric and crookedness of the measurement tape could also have been systematic errors if they were not symmetrically distributed.

Both forms of error become apparent when multiple observations of a single object are found to conflict. Since an object cannot have multiple lengths, any apparent observation of it having multiple lengths must be mistaken. Hasok Chang argues that this reasoning relies on what he calls the principle of single value, according to which “a real physical property can have no more than one definite value in a given situation.” (Chang 2004, 90) According to Chang, this is an ontological principle that is necessary for the activity of measurement. It is this principle which underlies our conclusion that differing observations of the fabric length indicate error. Another way of putting this idea is that we require the phenomena we measure to be stable, that is, to have characteristics we can repeatedly observe using different techniques, and often in various contexts (Bogen and Woodward 1988; Woodward 2010; Feest 2011; 2017).

The vignette also illustrates how we usually cope with error. One key strategy for reducing measurement error is *eliminating or controlling* identifiable sources of variation. Systematic error can be identified by comparing measuring instruments (Chang 2004, chap. 2). To remove systematic error, the instrument that doesn’t agree with others is adjusted or replaced by instruments that do agree, as when I purchased the new tape measure. Sources of random measurement error can also sometimes be eliminated, as when I tried to flatten out wrinkles and place the measuring tape straight. Another strategy is *quantifying and correcting for* identified causes of variation (Chang 2004, 52). However, sources of error are not always readily identifiable or quantifiable. To deal with these unknown or unquantifiable sources of variation, I made multiple observations and took the average to be the true value, what we could call the strategy of *repeated observation*.

Repeated observation is a standard way to cope with random measurement error. Since the error is random, the error introduced is sometimes great, sometimes small, sometimes positive, sometimes negative, but it should in the end form a standard curve around zero. Hence, making multiple observations and taking the average will give us the point at which random error is approximately zero, assuming that the error is symmetrically distributed and additive. The average of the data points can then be taken as the true value (give or take a margin of error based on the variation in the data and hence the likelihood of having under- or overestimated the true value). The true value is therefore estimated or inferred from the scatter of data on the basis of a theory of statistical inference and other assumptions about the spread of error (Bogen and Woodward 1988).

Another strategy to cope with random measurement error is *sampling*. Chemists and physicists often observe different samples of a chemical substance or instances of a physical phenomenon. Similarly, in molecular and cell biology, measurements are generated using multiple samples of a solution, tissue, cell type, or so on. In all these cases, observations are made on multiple different objects, rather than repeatedly on the same object. In turn, the average is taken to be the true value for the phenomenon or substance from which the sample was taken, rather than for the specific objects that were observed. Sampling allows researchers to eliminate random error generated both when making an observation and through sample isolation or preparation. It involves the same principles of statistical inference as repeated observation, as well as additional assumptions about the representativeness of the sample and the homogeneity of the phenomenon being sampled.

In summary, measurement error is typically recognised when conflicting observations of the same phenomenon are made, assuming the principle of single value. When sources of error can be identified, they can be eliminated or quantified and corrected for. Unknown random error is dealt with by repeated observation or sampling: making multiple observations of the same or different objects and taking the average as the real value. In the next section I return to individuality research, considering how standard ways of dealing with measurement error in behavioural ecology generate the problem of measuring individuality.

5.3 The Problem of Measuring Individuality

We now have one element needed to understand the problem of measuring individuality. Recall the problem.

> *Measuring Individuality*. How can we measure individuality if measurement is usually performed on groups?

The reason why measurement is usually performed on groups is that this allows researchers to deal with measurement error via the strategy of sampling. Observations are made of different individuals or groups of individuals, each individual (or group) observation is a point in the scatter of data, and the average of the individual observations is taken to be the true value of the phenomenon being studied (Barash 1997; Bolnick et al. 2003). Of course, we saw in the previous section that there are alternatives to the group-based approach of sampling. I will return to one of these alternatives, repeated observation, in the next section. First, however, we should address the other half of the problem of measuring individuality: why are group-based approaches seen as problematic for measuring individuality?

One reason for the perceived conflict is the standard *typological* approach to sampling in behavioural ecology. It is common to take individuals as representatives of a species or other phylogenetic group, so that the phenomena measured are characteristic properties of that taxon. For instance, a plant ecologist might measure the temperature tolerance of a particular plant variety; to do so, they observe different individuals or small groups of individuals (such as plots or sampling sites) growing under different temperature regimes and inferring on that basis the temperature range for the variety. Or a behavioural biologist might look at the mating behaviour of a certain species by observing how individuals and pairs behave and inferring from those behavioural data the behaviour that is characteristic of the species.

Some biologists in the CRC see this typological approach as conflicting with individuality. For instance, one interviewee doubted that individuality was worth studying because it does not provide information about general characteristics of a species.

> S: […] 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 experiments 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 researcher explained their doubts about scientific research on individuality.

> S: Yes I could and I do measure individuals, but I cannot make any quant-- I cannot really take that any further, I could just say individual A is something or individual B is something but then I'm stuck with that and I cannot come up with a broader conclusion. (Interview 3)

In total, four interviewees mentioned generalisation or general knowledge as a goal of their research that demands the use of group-based studies and may conflict with individuality research.

The typological approach of using individuals to measure species-typical properties contrasts with the "population thinking" more dominant in evolutionary biology (Grene 1990; Mayr 2006; Sober 2006; Ariew 2008). Whereas population thinking recognises individual variation, typological projects ignore individual differences in favour of type-level properties and processes. By averaging over individuals to determine species-typical properties, typological approaches shift individual differences into the variation around a species-typical mean. For this reason, the typological approach has been criticised in individuality research (Barash 1997; Violle et al. 2012; Layman, Newsome, and Gancos Crawford 2015). For instance, Sasha Dall and colleagues conclude their synthesis of research on animal personality and individual specialisation by invoking Ernst Mayr's metaphysical take on typological thinking: "Could it be that an emergent evolutionary ecology of individual differences will allow organismal biology to finally shake off the last vestiges of the Platonic typological approach to describing the natural world?" (Dall et al. 2012, 1196)

One reason for individuality researchers to be concerned about group-based approaches to measurement, then, is because they are associated with typological projects. However, it is possible to reject the typological approach without abandoning group-based measurement. This is just what researchers studying individual differences often do, working with groups of individuals that share common phenotypic properties or ecological relations. This means that group-based approaches are perfectly appropriate for measuring individuality when individuality is defined in terms of robust individual differences. So, typology aside, why do biologists worry about using groups to measure individuality?

Researchers in the CRC often brought up the idea that measuring individuality should involve measuring the properties of single individuals, so-called *individual-level* or *individualised measurement*. For instance, one interviewee cited measurements of single individuals when explaining what counts as an individualised phenotype.

> S: [An individualized phenotype is] Everything that I can measure I can take an individual or watch an individual and give it a number essentially or a score or assign it a class by looking, measuring, whatever on this. (Interview 8)

In total, individualised measurement was mentioned in 8 of the 10 interviews. Interviewees themselves weren't certain why they feel the need for individualised measurement. But we can make sense of the need for individualised measurement.

In particular, the idea that individuality is about phenotypic and ecological uniqueness can explain the need for individualised measurement. Measuring unique properties requires measuring single individuals; otherwise, any unique individual trait values are combined with measurement error in the variation around the group mean. Even accurately measuring an individual's unique set of properties requires individualised measurement, since many of an individual's properties may deviate from the group average, even if some of them do not. Therefore, if we understand individuality in terms of phenotypic and ecological uniqueness, as the biologists in the CRC are wont to do, we ought to be measuring not groups but single individuals.

Similar reasoning might seem to result when individuality is understood in terms of individual-level properties, another idea associated with individuality that we saw Chapter 4. If individuality is about individuals' properties, then surely biologists should be measuring these properties, not average properties of groups. However, the aim to measure individuals' properties does not itself directly mandate the use of individual-level measurement. It is quite common to infer what properties an individual has from group-level measurements—to infer the temperature tolerance of a plant or the mating behaviour of an animal from measurements of a genotype or a particular population, for instance. Such inferences only become problematic when we expect individuals to vary, and in particular when we expect each individual to be different from the next. In other words, it is ultimately uniqueness that confounds the use of group-based measurements to infer individuals' properties.

So, the problem of measuring individuality is generated by two factors: the common use of sampling to deal with measurement error, and the perceived need for individualised measurement due to the idea that individuality is about phenotypic and ecological uniqueness. In the next two sections I consider how researchers address this problem and where the limits on measuring individuality lie.

5.4 Repeated Observation and Real Traits

The obvious solution to the problem of measuring individuality is to use the strategy of repeated observation. Averaging across the observations allows us to eliminate random measurement error and thereby obtain an accurate measurement of an individual's properties, even when they are unique. In this section I consider the possibilities and limitations of using repeated observation in behavioural ecology.

Many studies of individuality in behavioural ecology make use of repeated observation to measure single individuals. For instance, animal personality is typically measured by recording an individual's performance at least twice (Bell, Hankison, and Laskowski 2009; Stamps 2016). Assessing ecological specialisation also often involves making multiple independent observations of individuals, for instance by observing foraging events or analysing gut contents at several time points (Araújo, Bolnick, and Layman 2011; Fodrie et al. 2015). Repeated observation is also undertaken in many of the projects in the CRC, especially for behavioural and hormonal analyses.

There however are a number of limitations on repeated observation. First, multiple observations of a single individual are sometimes not possible. Sometimes an organism must be dissected to observe physiological and morphological parameters. For instance, in Project B05, fruit flies are dissected to measure the length of the female seminal receptacle. Of course, a dissected organ can be observed multiple times to deal with some measurement error, such as error arising from how the organ was positioned during observation. However, other sources of measurement error remain, such as how the animal was killed or how the tissue was prepared. Field studies are also limited to single measurements when individuals cannot be tracked or recaptured for testing. For instance, in Project C03 common buzzard chicks are tested just once for a whole host of different physiological and behavioural traits. Recapturing the buzzards for measuring physiological and behavioural traits is not feasible, especially after fledging.

A second limitation on individualised measurement is that repeated observation can affect an individual. This is especially important for behavioural studies, in which organisms can habituate to a stimulus and, as a result, show different behavioural responses in later tests (Réale et al. 2007; E. Takola et al. 2021). Although sometimes habituation can be corrected for, this is challenging at the individual level because individuals may vary in how quickly or to what extent they become habituated to a particular test.

The final limitation on individualised measurement is that organisms' properties can change over time (Montévil 2019). An individual can be disinterested one moment and attack aggressively the next, consume a small prey item one day and four large items another day, and its hormones, immune status and gene expression can fluctuate widely over the course of a single hour. Changes can occur haphazardly or regularly as cycles or progressive development, and can be due to environmental, temporal, or internal fluctuations. Behavioural ecologists refer to variation of an individual's properties over time as the variation "within" an individual, or within-individual variation (Bolnick et al. 2003; Bell, Hankison, and Laskowski 2009). When within-individual variation is very high, the individual's measured trait value would be an average of very divergent observations. In such cases, the principle of single value (see Section 5.2) doesn't seem to hold, because there are real changes in the property being measured.

There are three ways to cope with high within-individual variation. First, researchers can employ the strategies of eliminating or quantifying and correcting for sources of variation. Within-individual variation can be reduced by choosing a timeframe for repeated observation that limits developmental and circadian, lunar or seasonal changes (Bell, Hankison, and Laskowski 2009; Stamps and Groothuis

2010; Araújo, Bolnick, and Layman 2011; Fodrie et al. 2015). For instance, researchers found that observing resource use in sea otters (*Enhydra lutris nereis*) in different seasons increases within-individual variation compared to observations within a season or in the same season over multiple years, likely due to seasonal diet variation (Novak and Tinker 2015). Measuring individuals' resource use can account for cycles in resource use by either restricting observations to the same point in the relevant cycle or quantifying and correcting for temporal variation (Novak and Tinker 2015, 70).

Another way to deal with traits showing high within-individual variation is to exclude them from the definition of individuality. The temporal stability condition in the definition of individuality as robust individual differences achieves something similar to this. Recalling Chapter 3, temporal stability requires that within-individual differences are smaller than between-individual differences. When within-individual differences for a trait are greater than between individuals, that is, when individuals' trait values are wildly fluctuating, the trait does not count as an instance of individuality.

A third way to cope with traits with high within-individual variation is to deny that they are traits at all. This may sound drastic, but it does make some sense from the perspective of a researcher developing or applying a particular test or phenotyping procedure. In the interviews a researcher explained why they stopped using a behavioural test.

> S: So we have them [the organisms] in a bag and when we measure their weight we try to measure how much they struggle. It's not repeatable! So it's just measurement error, the variation we see. […] You can't replicate it, it's just stochasticity and measurement error. So sometimes you get these kinds of measurements and then you think whether it's useful or not to include them and with the replication we thought it's just no rep-- it's just stochasticity.
>
> R: Okay. So because it wasn't repeatable--
>
> S: Yep, it wasn't.
>
> R: …it seemed to be mostly measurement error that you were recording…
>
> S: …exactly… […] It doesn't really describe anything real about the phenotype of the animal. (Interview 9)

When a test does not produce stable values over repeated observations for a single individual, it is discarded as unsuitable for measuring an individual's trait value. Indeed, it doesn't seem to measure a real trait at all. The inference from the nonrepeatability of the struggle behaviour to the conclusion that struggle behaviour is not a phenotypic trait assumes that phenotypic properties must be stable. This raises interesting questions for how to define phenotypic properties (see Chapters 3 and 8). At least in the case of behaviour, low within-individual variation is seen as important for ascribing a phenotypic property to an individual.

To sum up, repeated observation can sometimes be used to accurately measure individuals' properties, even unique ones. However, there are many properties that cannot be repeatedly observed or that change over time. Sometimes sources of variation can be identified and eliminated or controlled for, and some labile properties are excluded from the definition of individuality or rejected as not real phenotypic properties. However, robustness or the ability to be repeatedly observed is not required of all individualised phenotypes and niches (see Chapter 3). For these properties, the problem of measuring individuality returns: how do biologists measure individuality (taken as phenotypic and ecological uniqueness) if they can't use repeated observation?

5.5 Approximating Individuality by Measuring Groups

When repeated observation of single individuals is not available, researchers usually revert to the sampling strategy. In this section I consider how group-level measurements are used to study individuality and whether this overcomes the problem of measuring individuality.

Group-based approaches are especially common in measuring individualised niche dimensions. Although resource use can be and often is measured at the individual level, other niche dimensions are easier to study by grouping individuals according to their relation to a specific ecological factor (see Table 3.2). For instance, Project A01 groups fur seals according to whether they breed on a densely or sparsely populated beach, Project A04 groups fire salamanders according to whether they are deposited into a pond or a stream, and Project C04 groups harvester ant queens according to whether they found a colony alone or with other queens. Some individualised phenotypes are also measured using groups, especially when they can't be observed twice. For example, observations of internal organs from different individuals are used to measure the average organ size for a group of individuals. In addition, some phenotypes are even *observed* at the group level. With molecular phenotypes, samples from several individuals can be pooled before observation;

depending on the sensitivity of the test, pooling may even be necessary to obtain sufficient quantity.

Many researchers in the CRC see the sampling strategy as providing only approximate or partial information about individuality. In seven of the ten interviews, interviewees brought up the idea that group-level approaches to measurement are a way of getting closer to individuals or approximating individuality in some way. For instance, one interviewee introduced the idea that between-group differences are “proxies” for individuality.

> S: Because you can’t make a census all the time, like measuring every individual of all the populations or everything; it’s not always possible unfortunately. So you have to use again, let’s say proxies for individualization: traits that can vary a lot but also allow you for some grouping. (Interview 6)

A similar idea was voiced in Interview 1, cited in Section 5.1, where the researchers justify their use of two treatment groups because they “should be representative of, well, at least some more extreme parts of the variation that we can find in a real natural population.” Group-level measurement cannot directly measure individuals’ unique properties and sets of properties, but they can provide some approximate and partial information.

First, group-based measurements can provide *approximate* information about how individuals from different groups differ. For instance, taking a fur seal pup from a sparsely populated beach and another pup from a densely populated beach, we would know that they experience a different social density. Individual pups on the same beach can still experience different densities (for instance, if they are on the outside of the colony compared to the inside), but we have at least an estimate of the density they experience and how it differs from pups on other beaches. Group-level measurement can fulfil this approximation role even if individuals have unique values for the particular trait or niche dimension being considered.

Second, group-level measurement can provide *partial* information about individuals’ unique sets of properties. Specifically, they can inform us about particular properties that compose more complex total phenotypes and niches. Group-level measurements of many different phenotypes or niche dimensions can then help us to build up a picture of a single individual’s total phenotype or niche. Of course, the knowledge of individuals’ properties will only ever be approximate and partial. It will exclude any variation at the individual level not captured by group measurements, meaning that an individual's actual trait values or niche dimension ranges may not be entirely accurately represented. Nevertheless, group-level measurements and the between-group differences they capture can provide some descriptive knowledge of individuals' unique total phenotypes and niches.

We can now respond to the problem of measuring individuality. How can we measure individuality if measurement is usually performed on groups? First, researchers sometimes can measure single individuals, using repeated observation to deal with measurement error. Second, group-based approaches to measurement can still tell us about individuality, since between-group differences providing approximate and partial information about individuals' unique properties and sets of properties. These are the very approaches to measuring individuality already in use. The work I have accomplished in this chapter contributes to assuaging the biologists' worries by revealing both the justifications and the limitations of their own methodological solutions. And judging from the positive responses I received, biologists value this minimal philosophical service.

5.6 Towards Individualised Research

In this chapter I identified two epistemological problems facing individuality researchers in behavioural ecology. As we saw, the problem of measuring individuality has its origins in the association between uniqueness and individuality coupled with the necessity of dealing with measurement error. One approach to overcoming this problem is to use repeated observation of single individuals, which works for some properties, even when they are unique to single individuals. However, individualised measurement is limited to stable traits which can be observed repeatedly without habituation. The other approach is therefore to measure between-group differences to gain approximate and partial information about individuality.

The problem of measuring individuality does not arise when individuality is defined as robust individual differences. Robust individual differences can be measured using repeated observation, and between-group differences with group-level measurement. And both of these approaches can provide some partial and approximate information about unique total phenotypes and niches. This suggests that defining individuality as robust individual differences could be understood as a way to make individuality measurable by circumventing the epistemological troubles brought up by phenotypic and ecological uniqueness. In other words, robust individual differences could be understood as an operationalisation of phenotypic and ecological uniqueness. I substantiate this claim at the end of Chapter 6.

Aside from starting us in the direction of a clearer understanding of individuality in behavioural ecology, this chapter also highlighted a novel mode of research, which I will call *individualised research*. Individuality researchers intentionally shift away from typological thinking, since they are not interested in the properties of species, population, or definable types in populations like sexes, age classes or morphs. Yet individuality researchers don't use population thinking. Population thinking only requires an overview of the level of variation in the population, not accurate measurements of individuals' properties (Morrison 2004). In contrast, individuality researchers are explicitly interested in measuring individuals' properties. This calls for a new methodological tack, not only looking beyond population-level averages, but also taking up the challenge of dealing with measurement error at the individual level.

A key goal in individuality research is therefore increased *individualisation* of research practices. This idea was expressed by an interviewee contemplating what individualisation means.

> S: For me it's not sure what is meant with individualization. […] So is individualization like this process of starting to look at the individuals? Or what is individualization? Because this is what I understand.
>
> R: So you understand it as a process for starting to look at individuals rather than groups?
>
> S: Yes.
>
> R: And would you say then that the research into individualized phenotypes and niches is part of this process of starting to look more at individuals?
>
> S: Yeah, I think with the projects that we have we'll have several looks on how looking at the individual is important. (Interview 7)

Individuality researchers aim to increase the number and decrease the size of groups in order to more closely approximate individuality. Increased individualisation is also evident in the continuous development of technology that permits individualised measurement, such as portable movement tracking technology and statistical tools for analysing individual data (e.g., D. D. Brown et al. 2013; Benson 2016; Stoffel, Nakagawa, and Schielzeth 2017). These technological developments are prised by biologists because they enable greater sensitivity to individual differences and thereby proximity to individuality.

On the other hand, some limitations on individualised measurement will likely remain. Researchers will continue to grapple with within-individual variation and the fact that some traits cannot be repeatedly observed. Hence, biologists should not expect a wholesale transformation of their discipline to individualised measurement. Instead, they need a careful articulation of how measuring individuality is possible, and in which circumstances individualised measurement and group-based measurement can and should be applied. The analysis in this chapter provides an outline for such advice. One promising avenue for developing a more comprehensive account of the possibilities and limits of individualised measurement would be to consider similar issues in the social and medical sciences, where research on individuals is more established. I return to this point briefly in the next chapter.

6 Explaining Individuality

The previous chapter introduced the two problems of measuring and explaining individuality. We saw that the problem of measuring individuality results from the association between individuality and uniqueness combined with the difficulty of individualised measurement. In this chapter I turn to the problem of explaining individuality, where we see a similar structure.

Explanation involves answering questions such as why something exists, what causes it, or how it works. In biology there are several sorts of explanation, including causal, mechanistic, and evolutionary explanations, as well as explanation based on law-like generalisations (Schaffner 1993; Keller 2000; Longino 2000; Mitchell 2003). All of these forms of explanation have a place in behavioural ecology. I focus on causal explanation, both because it is the dominant explanatory framework of the CRC and because of the special problems that individuality poses for developing causal knowledge. Many of the findings will also extend to other sorts of explanation where causation plays a role, such as mechanistic or evolutionary explanation.

In this chapter I argue that developing causal explanations in behavioural ecology involves generalisation. Through experiments and statistical modelling, researchers identify causal relations by comparing multiple individuals to identify common factors. Researchers also often generalise their findings to whole populations or species, draw on knowledge from other species, and develop explanations that apply to many species at once. Given the importance of generalisation for developing causal explanations, researchers face the problem of explaining individuality (see Section 5.1).

> *Explaining Individuality*. How can we develop causal explanations of individuality if identifying causal factors usually involves generalisation?

Like the problem of measuring individuality, this problem arises because of the association between individuality and uniqueness, since unique properties and sets of properties cannot be subject to generalisation and are therefore usually ignored in developing causal knowledge.

As I show in this chapter, alternative methods for generating causal knowledge in single cases are not suitable in behavioural ecology. On the other hand, there are two approaches that can be used to generate partial causal knowledge about unique properties and sets of properties: decomposing unique (sets of) properties into non-unique properties, as well as developing quantitative scales. Explanation by decomposition and quantification are already used by behavioural ecologists. Clarifying their suitability helps to address the biologists' concerns about how their research relates to individuality, as well as identifying limitations on causal research into individuality.

I begin in Section 6.1 by explaining why generalisations are important for developing causal knowledge. In Section 6.2 I show that the problem with explaining individuality only arises when individuality is understood as phenotypic and ecological uniqueness. In Section 6.3 I ask whether causal knowledge can be developed about single instances at all, finding that options that might exist in other fields are not suitable for behavioural ecology. Nevertheless, in Section 6.4 I show that there are two ways to develop causal knowledge about unique properties or sets of properties, decomposition and quantification. I conclude in Section 6.5 by considering what the reflections on explanation and measurement tell us about how the two dominant definitions of individuality in behavioural ecology, robust individual differences and phenotypic and ecological uniqueness, are related.

6.1 The Need for Generalisation

Generalisations identify commonalities across multiple instances, individuals, locations, and so on (Cartwright 1989; Elliott-Graves 2018). In this section I use examples from the CRC to consider how developing causal knowledge involves generalisation at various levels: within studies (local generalisation), from studies to populations (statistical or typological generalisation), from species to species (extrapolation), and across many species (general explanations).

A single case almost always has some factors which are causes of a phenomenon of interest, and many factors that are either causally irrelevant or themselves caused by the phenomenon or its causes. A bold individual might have developed in a good patch, be well-fed, have no siblings, be white, have a parasite, be aggressive, prefer smaller prey, choose certain mates, and so on. However, it is not evident from the one case which of these factors explains boldness, which factors are explained by boldness or a common cause, and which are irrelevant. To solve this problem, behavioural ecologists rely on experimentation or statistics to identify causal relations across multiple individuals.

In experiments, scientists identify a regular association between cause and effect by intervening on a potential cause and observing the outcome in the putative effect (Schaffner 1993; Woodward 2004). The outcome in the treatment group is compared to a control group, in which the intervention was not performed. Because the only difference between treatment and control groups should be the intervention, any difference in the outcome must be due to the intervention on the putative cause. Assuming the absence of confounding factors, scientists conclude that there is a causal relation between the two factors.

Experimentation therefore involves what I call *local generalisation*. In comparing the response of the treatment group to the control group, the focus is on the causal factors and responses common in each group, not on the idiosyncrasies of each member of the group. Many projects in the CRC employ experiments and thus local generalisation. For example, Project A02 tests the effects of the developmental environment on the optimism level of mice by comparing mice in a treatment group, having access to a special playground, with a control group (Bračič et al. 2021). Another example is Project B02, which looks at how early nutrition levels affect morphology and life-history traits of turnip sawflies by exposing groups of larvae to different starvation treatments and comparing their traits as adults (Paul, Putra, and Müller 2019).

Scientists often suggest that only experiments can demonstrate causation. Yet practical, ethical, and financial constraints mean that experiments are not always possible, and there are also limitations on what inferences can be made from experiments to complex real-world situations. As a consequence, behavioural ecologists frequently use statistical models to investigate data from observational or field studies.

Sometimes the data permit a group comparison. There are several examples of this in the CRC. For instance, Project C04 aims to explain why some harvester ant queens found a colony in cooperation with other queens, known as polygyny. To do so, they compare genomic data from queens of different founding types to identify genetic regions that may contribute to polygyny (Errbii et al. 2021). As another example, Project A01 looks at how population density affects fur seal pups, including their behaviour and microbiomes. Because experiments on fur seals are neither feasible nor ethically permissible, researchers compare pups from a high and low density beach (Grosser et al. 2019; Nagel et al. 2021). In both these cases, there are natural groupings that permit comparison, a sort of "natural experiment." As for experiments, group-based statistics involve local generalisations: values for many individuals are compared in order to identify common factors that differ between the groups.

Continuous variables can also be treated like groups, by creating segments or windows along the continuum. Alternatively, they can be correlated using linear regression and other statistical models. For example, researchers in Project A01 also compare how pup activity correlates with hormonal levels as well as with factors such as time of day and time since the mother left to forage. These continuous variables can be correlated in a statistical model (Nagel 2021). As another example, Project C03 aims to explain why common buzzards have different amounts of greenery in their nests. One hypothesis was that the greenery protects chicks from parasites. However, researchers did not find a correlation between the amount of greenery and the parasite load, so they inferred that greenery does not affect parasites (Ottensmann 2020). Correlational statistics, too, involve local generalisation. In the case of regression, a coefficient of variation is determined based on the values of many individuals, in a way that minimises the variation between the regression equation and individual values. The regression line is therefore a generalisation across these many individuals.

So, experiments and statistics involve local generalisation because researchers focus on common factors to identify possible causal factors. Variation between individuals in groups or around the regression line is elided, even when this variation might be causally relevant (Steel 2007, 93). Another way generalisation enters biological research is via the aim for general knowledge. In particular, biologists develop generalisations about populations, species, communities, and so on (Mitchell 2003, chap. 5; Rosenberg and McSchea 2007, chap. 3; Lange 2008). They do so by *statistical generalisation*, generalising from samples to populations, and *typological generalisation*, generalising from tokens to types. In behavioural ecology, experiments and statistics are usually taken to provide knowledge of causal relations beyond the sample in the study itself to a particular population or species or higher-level taxon.

It is also common to *extrapolate* knowledge gained in one population or species to other populations or species (Steel 2007). This is especially evident in the way biologists deal with the gap between observed correlation and causal knowledge. Correlation does not indicate a direction of causation and could result from a common cause, and absence of correlation could be due to a confounding variable. To support the inference from an observed correlation to a causal relationship, scientists use mechanistic knowledge or extrapolate knowledge derived from similar systems (Woodward 2004, 342). In behavioural ecology, this often takes the form of extrapolating knowledge from other species to the species of interest.

Finally, behavioural ecologists use computational models, meta-analysis, and theory to develop explanations that apply to many species. Project D03, for example, uses modelling to explain how differences in population density and phenotypic traits arise. They show that density dependent selection can over time lead to spatial variation in density and traits within a population (Van Benthem and Wittmann 2020). Another example is Project D05, which included a meta-analysis investigating how nutritional condition affects risk taking in many different species (Moran et al. 2021). Finally, the NC^3 mechanisms (see Chapter 4) are general or abstract mechanisms used to explain changes in phenotype-environment match, fitness, and individualised niches in many different species (Kaiser and Trappes forthcoming; Trappes et al. under review). They are described by identifying entities, activities and phenomena in the different species in which the mechanism occurs, regardless of species-typical nuances (Kaiser and Trappes forthcoming).

To sum up, developing causal explanations in behavioural ecology involves a number of types of generalisation: local generalisation about the groups of individuals being studied, statistical or typological generalisation to populations and species, extrapolation to other populations or species, and generalisations about many species. In the remainder of the chapter I consider what this means for explaining individuality.

6.2 Explaining Individuality

The researchers in the CRC are well aware that generalisations are typically necessary for generating causal explanations. They are less certain about whether individuality can be the object of generalisation. In this section I examine how the problem of explaining individuality arises for individuality researchers.

As we saw in Chapter 5, some researchers express doubts about explaining individuality. Some hesitation may derive from the problem of measuring individuality, since causal studies rely on accurate measurement. In addition, many researchers cite the need for generalisation, experimentation and statistics as limiting the study of individuality. In the questionnaire, one respondent spontaneously brought up the need for generalisation (identifying properties that individuals have in common).

> […] this can only be measured for experimental treatment groups, i.e., if everything would be completely individual, they would have nothing in common, i.e., there would be no significant differences among groups. (PI 5)

Similar ideas were expressed more frequently in the interviews, where the issue of group-based studies of individuality was also explicitly addressed in the interview guide. For example, two interviewees discussed why they focus on a bimodal grouping along a niche dimension, ignoring the way different individuals in each group have slightly different ranges along the niche dimension.

> S1: I have [individuals] that are [in group X and in group Y]. But not all [X individuals] act the same way: they have their own ways of [being X]. […] So, there are a lot of different individualized ways to [be X and Y] but nevertheless it's the same [group].
>
> R: Yeah. And so you are studying them at that level, the level of [group X and group Y] rather in an individual way of...
>
> S2: 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. But I think the problem is also, if, I mean, when we are talking about that each individualized niche is not the same to each- I mean, it's really hard to come up with an idea of how to study that. (Interview 2)

Similarly, another two interviewees pointed out that causal studies were important for their aim of explaining variation.

> S2: Of course, it is not really a new thing to measure between individual variation in natural environments. I think the aim is clearly to explain that variation.
>
> S1: Yeah
>
> S2: And therefore I think we have to go experimental and causal. (Interview 1)

They later explained that the need for experimentation required grouping natural variation into broad treatment and control groups.

> S2: It's more or less a matter of experimental feasibility that we restrict our experiment to just two points on this axis of [a niche dimension], but of course the ambition of the project is to explain when you go out into natural [populations], part of this between individual variation and traits we look at. So, it would have been nice to have more treatment levels that accurately simulate other [points on the niche dimension] but we are restricted to some degree. But conceptually, clearly this is the individualization angle. (Interview 1)

Seven of the ten interviews included statements that experimentation or group-based studies were necessary in order to gain causal knowledge or explanations of individuality. In addition, as the quotes demonstrate, there was often a felt tension between the use of group-based approaches and the goal of studying individuality. Six interviews mentioned limitations on explaining individuality due to the existence of further variation between individuals that isn't captured by experimental groups; four interviews included the idea that comparison between groups is meant to represent wider variation in nature.

Issues to do with causal explanation and experimentation are also sometimes discussed in publications on individuality in behavioural ecology. For instance, Judy Stamps and Ton Groothuis (2010) highlight the complexity of developmental influences affecting animal personality. They suggest that genetically identical individuals from the same litter can serve as "approximations of 'replicate individuals'" (Stamps and Groothuis 2010, 312). By eliminating many of the existing sources of variation between individuals, multiple individuals can stand in for a single individual. These 'replicates' can then be distributed into treatment and control conditions. Nevertheless, the authors note that genetically identical littermates are still only approximations of replicate individuals, because variation between individuals is reduced but not eliminated (Stamps and Groothuis 2010, 313). In the end, explaining animal personality still requires generalisations across individuals.

Experiments, statistics, and modelling are powerful means to develop causal explanations, but they involve generalisation. Generalisation in turn is seen to conflict with individuality. This is the problem of explaining individuality.

> *Explaining Individuality*. How can we develop causal explanations of individuality if identifying causal factors usually involves generalisation?

This problem does not arise if individuality is understood in terms of robust individual differences. Robust individual differences are in fact prime targets for causal explanation. Causal relations are often identified by looking for "actual difference makers," that is, factors which differ that can explain other factors which differ in a sample or population (Waters 2007). In addition, individual differences can serve as "variation explananda," demanding an explanation of why there are differences rather than uniformity (Ward 2020; manuscript). Moreover, robust individual differences are suited to experimentation and group-based statistics, since individual differences include between-group differences (see Chapter 3).

It is only when individuality is associated with uniqueness that generalisation becomes a problem. Something that is unique to a single individual is by definition not common with other individuals, so it cannot be subject to generalisation. The problem of explaining individuality therefore results from the idea that individuality is to do with unique properties and sets of properties, combined with the need for generalisation to develop causal explanations.

The problem of explaining individuality in behavioural ecology has a correlate in *personalised* or *precision medicine*. Personalised medicine is based on the insight that diagnostic criteria and treatments often do not apply equally well to all patients, because individuals differ in genetic makeup, comorbidities, gender, ethnicity, cultural background and lifestyle (Nicholls et al. 2014; B. Clarke and Russo 2016; Vegter, Zwart, and van Gool 2021). Ideally, clinicians would be able to deliver diagnoses and treatments tailored to each unique individual. However, evidence about causes of symptoms and treatment effectiveness requires experiments such as randomized control trials (RCTs), or extrapolating mechanistic knowledge from experiments or basic science (B. Clarke et al. 2014). Hence, healthcare practitioners face the challenge of diagnosing and treating unique individuals when only general information is available. Partly as a consequence of this dilemma, personalised or precision medicine actually only provides diagnosis and treatment for particular population subgroups or strata (Nicholls et al. 2014; Giroux 2020).

Both the problem of explaining individuality and the challenge of truly personalised medicine can be understood as instances of what Zina Ward calls the *Uniformity/Uniqueness Dilemma* (Ward 2020). Ward investigates this dilemma in the context of psychological modelling, in which

> Models that impose uniformity on the population can elide significant, theoretically meaningful differences between individuals. But modeling every individual completely independently is incompatible with scientific generalization and does not do justice to what we have in common. (Ward 2020, 40)

As we have seen, this dilemma extends from theoretical modelling in psychology to other disciplines and practices, such as empirical research in behavioural ecology and diagnosis and treatment in medicine. Ward suggests that a middle ground must be found between absolute uniformity and complete uniqueness. I draw a similar conclusion later in the chapter. First, though, I consider whether the dilemma might be circumvented by directly developing causal knowledge in individual cases.

6.3 Singular Causation and Individual Causal Knowledge

Can causal knowledge be developed without generalisations? Answering this question involves considering singular or token causation, an instance of one entity causing another. In this section I consider whether knowledge of singular causation is possible independently of general causal knowledge.

Many philosophers believe that causal knowledge must involve generalisation. This is because they define causation as something that at least could happen in multiple instances, and as what is common across these instances. For instance, causation has been defined as regular association between events (Hume 1975; Morris and Brown 2020) or counterfactual dependence holding in many possible instances (Woodward 2004; Menzies and Beebee 2020). On these models, causal knowledge, including knowledge about a single instance of causation, involves generalisations about connections between (possible) events.

One prominent dissenter to this view is Nancy Cartwright. For Cartwright, associations are useful tools to find out causal laws, but they are secondary to instances of singular causation; general causal relations depend on singular causation, both epistemically and ontologically (Cartwright 1989; 2000). Cartwright takes inspiration from G.E.M. Anscombe, who argued that singular causation is both ontologically and observationally primary to causation (Anscombe 1981). Anscombe argued that we can directly observe instances of causation, such as a cat lapping up milk (causing milk to leave the bowl) or a dog making a funny noise. Cartwright agrees with Anscombe in viewing singular causation as primary to regular associations. As she puts it, “There may well be a regularity corresponding to each singular [causal] fact, but the regularity does not constitute the truth of the singular claim, nor is it necessary for its confirmation. We can, after all, *see* that the cat is lapping up the milk." (Cartwright 2000, 47)

However, Cartwright notes that many instances of causation in science are not directly observable like a cat lapping up milk. Causal processes like molecular interactions, tectonic plate movement, or photon transmission cannot be directly observed due to spatial or temporal scale, or because they must first be produced or isolated by scientists. One way to uncover causal relations is to look for regularities using the methods we saw in Section 6.1. In contrast to many scientists and philosophers, Cartwright insists that it is also possible to establish causal claims by studying single cases, even in science. Her two examples are single-shot experiments and case studies.

Many experiments in physics, Cartwright argues, need not be repeated to demonstrate a causal relation: a single instance is enough to establish that the cause brought about the effect. The success of such single-shot experiments lies in the ability to isolate the causal sequence of interest by eliminating or controlling for any other relevant causal factor. Physicists are able to do so for three reasons: they have sufficient knowledge of other causally relevant factors, they can construct instruments to control and measure these factors, and they are able to precisely define the effect before the experiment starts (Cartwright 2000). Given that the causal sequence of interest has been isolated from any other relevant causal factors, a single instance is enough to show that the cause brought about the effect. Any repetition, Cartwright suggests, is merely to demonstrate that the instruments were working or that the causal sequence was appropriately isolated, not to establish a regular association between cause and effect (2000, n. 7).

A second method to establish singular causation in science is that of case studies. Both Anscombe and Cartwright mention Claude Bernard's insistence on case studies to discover what caused a patient's condition (Anscombe 1981, 139; Cartwright 2000). Case studies remain a common practice in medicine today (Ankeny 2014). They are also common in other fields, especially in the social sciences and history (Burian 2001; Morgan 2012). When case studies are used to develop explanatory knowledge, researchers engage in deep, detailed study of the case and use background theoretical information to pick out causally relevant factors from the myriad of factors present.

According to Cartwright, the successes of single-shot experiments and case studies demonstrate that we can make singular causal claims in science. Some general causal knowledge is still necessary to establish singular causation. For example, single-shot experiments require knowledge about other causal factors obtained from other experiments, causal laws, and so on. Nevertheless, the general causal knowledge need not be about the sequence under study, allowing us to "bootstrap" to the new sequence of interest (Cartwright 2000, 57).

However, these methods are usually intended to establish that the causal relation would apply in other relevantly similar situations (Woodward 2004, 70–74). Cartwright herself argues that single-shot experiments demonstrate the existence of causal capacities, universal (not singular) tendencies of entities that are exercised in singular causation (Cartwright 1989, 136). In addition, Rachel Ankeny discusses how case studies are used in medicine to develop general causal knowledge to facilitate diagnosis and treatment in other similar cases (Ankeny 2010; 2014). As James Woodward points out, "it is hard to think of realistic examples of such claims [i.e., singular causal claims with no general implications] and, if there are such examples, they appear to play little role in science." (Woodward 2004, 70) Hence, even methods for making singular causal claims in science usually aim at developing general causal knowledge.

Nevertheless, single-shot experiments and case studies, as well as direct observation in non-scientific contexts, might at least establish singular causal claims without starting with a generalisation about the causal relation in question. Unfortunately, none of these three methods for establishing singular causal claims are suitable for individuality research behavioural ecology. First, single-shot experiments are not feasible in biology. Single-shot experiments require a large amount of background knowledge to identify other causally relevant factors, as well as the ability to control those factors to isolate the causal sequence of interest. Such is not the epistemic position of a behavioural ecologist today or any time in the near future.

Second, although case studies can be employed in biology, their use for developing causal knowledge of phenotypic or ecological properties of single individuals seems unlikely to be fruitful. Many organisms live for only a short while, many causal processes go on within the organism and cannot be observed without invasive or lethal procedures, and there is often a great degree of complexity in the causal processes that lead to a particular phenotypic or ecological property. Case studies, in contrast, require detailed and deep engagement with the study object, typically only possible when there is a great amount of data about the object and the relevant causal processes. Some behavioural ecologists do express interest in undertaking case studies on single animals to determine the causes of their personalities or individual specialisation (Norbert Sachser, personal communication). This may sometimes be possible with long-lived organisms kept in captivity. However, it will not be possible for most studies in behavioural ecology.

Finally, the causation involved in phenotypic and ecological properties is not directly observable, being too complex, indirect, and often hidden within organisms. Of course, researchers can observe animals and infer, for instance, that a certain stimulus in the environment caused the animal to show a certain response. However, such inferences usually require repeated observation, since it can’t at first be ruled out that the animal was responding to something else or displaying an internally driven behaviour. It is for such reasons that ethology as a science developed only out of careful, prolonged observation of animals (Burkhardt 2010; Bolduc 2012).

Hence, although there may be methods for developing knowledge of singular causation, these are not appropriate for research in behavioural ecology. Generalisation is necessary for causal studies of individuality, and the problem of explaining individuality remains.

6.4 Causal Knowledge via Decomposition and Quantification

Are there other ways to circumvent the problem of explaining individuality? Recall that the problem was about how to generate causal explanations of individuality given that individuality is understood as phenotypic and ecological uniqueness. Here I consider two ways biologists can and already do develop causal explanations about unique properties and sets of properties: decomposition and quantification.

First, unique total phenotypes and niches can be decomposed into many non-unique phenotypic or ecological properties. Causal knowledge about non-unique properties can be obtained using standard experimental or statistical methods. The causal relations identified in the experiments or statistics can then be used to provide causal explanations for the non-unique elements of an individual's unique set of properties. Hence, decomposing a unique set and explaining elements of that set can contribute to explaining the set as a whole. I call this strategy *explanation by decomposition*. The interviews contained several examples of explanation by decomposition.

> S: I think [a group-based approach] is something that tells you something about individual differences, although you lump them [the differences]. I mean, no one would deny there are differences between the sexes, but in doing so I have lumped all the billion individuals on the planet into two categories. And I would think that is okay to do. […] And I can then divide them into more specific groups, I could go to different countries and compare the sexes. Again, I would say, I don't know, German women are different from German men and again German men are different from British men and so on. I find no problem in that. I mean, it lets you break down a larger entity into smaller entities and yes you are not talking at the level of the individual, but you are still contributing to individual differences.
>
> R: To an understanding of individual differences?
>
> S. Absolutely. By grouping things into meaningful or workable units. (Interview 9)

As the interviewee implies, a complex set of properties can be decomposed into many different properties which can be grouped into meaningful categories. These grouped properties can be studied using experimentation or statistics to determine their causes or consequences. Doing this for many elements of a unique set of properties would contribute to an understanding of the complex set itself. CRC researchers have also made this claim explicitly about the individualised niche (Elina Takola and Schielzeth 2021). This means that projects investigating robust individual differences enable us to explain unique total phenotypes and niches by decomposition, connecting the two definitions of individuality.

There are however limitations to explanation by decomposition. First, if there is interaction between causes or properties, then general causal knowledge may not apply to the particular individual with their unique combination of properties. Second, even non-unique properties are often grouped in a way that does not capture all existing variation. For instance, several experiments in the CRC use two or three levels of population density or nutrition, where variation would be more gradual in the wild (see Table 3.2). Relying on broad groupings may limit the causal picture to categorical causes and effects, obscuring finer grained causal relations. Similar limitations have been identified with stratification in medicine, which captures some but not all sources of variation (Nicholls et al. 2014; B. Clarke and Russo 2016).

Researchers in the CRC often recognise these limitations on decomposition. For instance, one interviewee pointed out that they cannot model unique individuals, even if they include more variables in their models.

> S1: We are definitely thinking a lot about processes at the individual level, although that does not necessarily mean, like S2 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" in what they are doing. (Interview 5)

As the interviewee mentions, their models are simplifications of more complex individuals and are therefore not unique.

The second way to approach unique properties or sets of properties is *explanation by quantification*. Variation in a quantitative trait across multiple individuals can be correlated with putative causal factors, for instance using linear regression, even when individuals have unique trait values. Provided that researchers have some knowledge about likely causal factors, an observed correlation can support inferences about the causal relation at play. For instance, one interviewee described how hormone levels can be correlated with personality trait values to determine their effect on personality, even if each individual has a unique personality trait value. Hence, when traits are quantitative, it may be still possible to develop causal knowledge about unique properties.

Some qualitative traits can be decomposed into quantitative traits, combining explanation by decomposition and by quantification. For instance, fire salamanders' distinctive colour pattern can be decomposed into quantitative traits such as the proportion of yellow or the number of dots (Caspers et al. 2020). Similar examples can be found in human biometrics, such as fingerprint analysis using ridge counts and other measures (Wong, Gottesman, and Petronis 2005). The lower-level quantitative properties composing a qualitative property can then be studied using experimentation or statistics to develop causal knowledge.

There are also limitations on explanation by quantification. There may be aspects of unique qualitative traits that cannot be captured in quantitative traits. As a consequence, it might not be possible to fully explain unique qualitative traits. In addition, researchers are often uninterested in explaining unique qualitative traits. For instance,

> S: Every individual has its individual color pattern. […] But does it matter? I mean, I see they're all different, yes, and there are probably reasons why one has more [of a certain color] than the other. But to assume that this color pattern itself is of any benefit to recognise from a scientific point of view that it is different, I don't know whether that is the case. (Interview 10)

The researcher goes on to argue that the unique pattern is biologically irrelevant, having no consequences for conspecific recognition or predation. Hence, although it is possible to explain such properties, it may not always be interesting for biologists to do so.

What remains of the problem of explaining individuality? It did not arise at all for robust individual differences. In addition, the combined techniques of decomposition and quantification mean that at least some causal knowledge can be gained about individuals' unique properties or sets of properties. However, this knowledge will be limited due to the possibility (or even likeliness) of causal interactions, due to grouping methods that obscure gradual variation, and due to the inability to fully capture qualitative traits using quantitative variables. In addition, there may very well be properties that are not interesting for biologists to study, because they lack biological significance or do not contribute enough to biologists' general knowledge. This means that complete causal knowledge of unique properties or sets of properties is unlikely.

6.5 Operationalisation to Overcome Epistemological Challenges

In this part of the thesis, I have considered the epistemological challenges encountered in studying individuality. Researchers are aware of something problematic, often bringing up a conflict between their use of group-based approaches and the goal of studying individuality. As we saw, this tension can be resolved into the problems of measuring and explaining individuality.

Measuring individuality is a problem of trying to make accurate measurements of single individuals. Measurement error can be eliminated using repeated observations of single individuals. However, repeated observation does not work for labile traits or traits that can only be observed once. Observations of multiple individuals can also be used to measure phenotypic properties or niche dimension ranges. This can capture some subpopulation variation, but any remaining variation within the groups being measured will disappear into the deviation around the group mean.

The problem of explaining individuality is a consequence of the need to make generalisations in order to develop causal explanations. Experiments and statistical models, combined with statistical generalisation, extrapolation, and so on, work well for explaining robust individual differences. In contrast, unique properties or sets of properties cannot be subject directly to generalisation. Techniques for discovering singular causation, including direct observation, single-shot experiments, and case studies, are not suitable for the complex, hidden, and fleeting causal processes occurring in individual organisms. On the other hand, explanation by decomposition and quantification can be used to generate partial explanations of unique properties and sets of properties. Some limitations will however remain due to causal interactions, gradual variation, and non-quantifiable properties.

The perhaps surprising outcome of this part of the thesis is that the epistemological challenges are not as threatening as they seem. There are many ways to gain partial and approximate descriptive and causal knowledge of individuals' unique properties and sets of properties. The problems of measuring and explaining individuality do persist as limits on gaining complete and exact knowledge, setting restrictions on what scientists can measure and explain. Yet there are many individualised phenotypes and niche dimensions which can be subject to scientific investigation, and such investigation can provide partial and approximate knowledge about unique individuals.

If the problems are only seldom insoluble, why do they seem so pressing to individuality researchers? Why do so many biologists in the CRC express scepticism or concern about their study of individuality? A major reason is the confusion between phenotypic and ecological uniqueness and robust individual differences. When individuality is understood in terms of phenotypic and ecological uniqueness, things become more difficult for researchers. Measurement must be performed on single individuals, requiring repeated observation, or must be partial and approximate using groups. Causal knowledge must be gained in an indirect and limited way via decomposition or quantification. Biologists who associate individuality with uniqueness would thus think that these sorts of limits should accompany any study of individuality. Moreover, if they are uncertain of the justifications for approaches like decomposition and quantification, they may think that studying individuality is impossible altogether. Hence the confusion about whether studying individuality is possible.

In contrast, understanding individuality in terms of robust individual differences facilitates biologists' research. Specifically, the robustness condition means that repeated observation is often possible, and the inclusion of between-group differences under individual differences allows for group-based approaches for measurement and causal studies. At the end of the previous chapter, I briefly suggested that robust individual differences could be considered a kind of operationalisation of individuality understood as phenotypic and ecological uniqueness. Uljana Feest defines operationalisations or "operational definitions" as descriptions of the paradigmatic conditions of application of a concept, especially descriptions of an experimental set-up that is understood to test for the phenomenon of interest (Feest 2010, 178). This is important when the concept is difficult to apply in a straightforward way, for instance because the phenomenon it picks out is in complex interactions with other phenomena. Operationalisations are practical tools for researchers that enable them to study phenomena. They are therefore bound up with and directed by researchers' explanatory goals and practices.

The definition of individuality as robust individual differences does set out broad conditions for application. For instance, there are fairly well-established tests and measures for animal personality and individual specialisation. More generally, the definition of individuality as robust individual differences enables practices such as measurement, experimentation and statistical modelling, making it possible for biologists to pursue diverse research questions involving descriptive and explanatory goals. This is in stark contrast to phenotypic and ecological uniqueness, which primarily causes problems for biologists. As well as being well-suited to empirical study, robust individual differences can inform us about phenotypic and ecological uniqueness, albeit often only partially and approximately. This supports the idea that robust individual differences are a way to gain some knowledge about phenotypic and ecological uniqueness, a concept that is itself difficult to directly apply in scientific research. The definition of individuality in terms of robust individual differences is admittedly still quite general, not specifying detailed empirical procedures as in more classical operational definitions. Nevertheless, it does seem to fit Feest's account of operationalisations: setting out how to apply a concept that lacks obvious application conditions, in a way that enables research on that topic.

With that, we can answer the question that arose in Part I. How do the two major definitions of individuality in behavioural ecology relate? One answer is that the definition of individuality as robust individual differences is an operationalisation of the less readily applicable definition of individuality as phenotypic and ecological uniqueness. There are of course other possible relations between ideas of robust individual differences and uniqueness. For instance, biologists might start by observing robust individual differences in behaviour and ecology and subsequently infer that all individuals are phenotypically and ecologically unique. I consider some examples of this sort of inference in Chapter 7. There may even be a cycle of inferences from empirical examples of individual variation to concepts of uniqueness, and subsequent applications of concepts of uniqueness to empirical examples via the operationalisation robust individual differences. Regardless, the findings from the interviews I conducted suggest that the relation of operationalisation is an important link between uniqueness and robust individual differences. What remains is to link this all back to individuality more broadly, not just the concept as it is understood and applied in individuality research in behavioural ecology. This is the task for the final part of the thesis.

Before this, however, I want to note two things. First, the epistemological challenges of individuality are not the mere products of confused definitions, to be cleared away and forgotten once greater clarity is achieved. Rather, these problems, and their origins in the uniqueness-individuality association, are part and parcel of a general momentum towards more individualised research. Technological advancements that facilitate individualised measurement, combined with study designs using a larger number of smaller groups, mean researchers can increasingly satisfy their curiosity about individuality. Yet there are limitations on the descriptive and causal study of individuality imposed by the dual challenges of measuring individuals and explaining their idiosyncratic properties. How far the momentum of individualisation can lead and what it really means to do individual-based research in behavioural ecology are important topics for future investigation.

Second, we can use the insights gained in this part of the thesis to distinguish individualised research from a related approach to studying individuals: methodological individualism. In sociology, economics and psychology, methodological individualists focus on single individuals rather than groups or institutions as the primary units to analyse and explain social or economic processes (Udehn 2002; Steel 2006; Heath 2015). Methodological individualism also occurs in ecology, when processes like community formation or succession are explained by referring to interactions between individuals (Justus 2014; Sarkar 2016). Methodological individualism is often ontologically reductionist, denying the existence of higher-level entities, such as institutions or communities, or higher-level causal processes. Alternatively, it may be explanatorily reductionist, denying the usefulness or possibility of explanations at higher levels (Kincaid 1986; Dupré 1994; Steel 2006; Heath 2015). Some philosophers criticise this reductionism (Kincaid 1986; Dupré 1994) and others praise it (Steel 2006; Justus 2014).

Individualised research is very similar to methodological individualism, since it also encourages looking closer at individuals and using individuals' properties to explain processes like intra- and interspecific competition, migration or invasion. On the other hand, individualised research need not exclude higher-level entities or explanations. For instance, predation could be set as a population-wide force that affects differentiation between individuals, or individual variation may be used to demarcate a species niche to be used for studying interspecific competition at the species level. Such non-reductionist tendencies mark a distinction between individualised research and methodological individualism. In addition, we saw that behavioural ecologists often rely on groups to undertake descriptive and causal studies. Reducing everything to individuals, as in methodological individualism, would greatly limit the scope of research in behavioural ecology. Instead, individualised research involves capitalising on the inferential relations between knowledge of individuals and group-level studies, as well as recognising the interaction between individual- and group-level properties and processes. I return to these ideas about individualised research in Chapter 9, where I briefly lay out how individualised research relates to other similar approaches across the sciences and suggest avenues for future research.

PART III

Metaphysics of Individuality

7 The Uniqueness of Biological Individuals

In Part I, I developed two major definitions of individuality in behavioural ecology: robust individual differences, and phenotypic and ecological uniqueness. I argued in Part II that the former is an operationalisation of the latter. With that, we have the means to answer the question with which we began. What is individuality in behavioural ecology? It is phenotypic and ecological uniqueness, which is then defined operationally as robust individual differences.

We could stop here, taking phenotypic and ecological uniqueness and its operationalisation as discipline-specific definitions of individuality. This would however leave unexplained why behavioural ecologists use the term “individuality” in the first place. I therefore use this final part of the thesis to investigate the relations between uniqueness, robustness, and individuality understood more generally. In this chapter, I argue that phenotypic and ecological uniqueness is a necessary condition for biological individuality. In the next chapter I consider how robustness is related to individuality. Together, these chapters explain why behavioural ecologists define individuality in terms of phenotypic and ecological uniqueness and robust individual differences. They also contribute to a broader philosophical account of biological individuality.

In metaphysics, individuality—what it is to be an individual—is defined as having two aspects, countability and identity (Lowe 2003; Krause and Arenhart 2016). Identity, in turn, must be unique. This already suggests that some sort of uniqueness is relevant to individuality, though just which sorts of properties should be unique is subject to debate. Philosophers of biology have also occasionally talked about different sorts of unique properties that are relevant to defining individuality, such as genetic uniqueness (see Table 7.1). Based on biologists’ reasoning practices, I reconstruct an argument that phenotypic and ecological uniqueness is what I call a *biologically necessary* condition of biological individuality. Specifically, I argue that the compositional and dynamic complexity of biological systems and the limited number of individuals that can exist under similar conditions imply that exactly identical individuals will not exist in the realm of possibility with which biologists are concerned. The question of whether identical biological individuals could exist in our imagination or some distant possible world, their *metaphysical* possibility, is in contrast irrelevant for practising biologists.

Elaborating the biologically necessary condition of phenotypic and ecological uniqueness helps to understand and justify the uniqueness-individuality association in behavioural ecology. This reconstructive work corresponds to the practice-based approach to metaphysics of science that I introduced in Chapter 2, which aims at reflecting and making sense of scientists' ways of investigating and understanding the world. As well as explaining biologists' beliefs, the phenotypic and ecological uniqueness condition contributes to the philosophical debate on biological individuality, affecting what sorts of biological individuals are countenanced as possible and bringing to light new questions.

I begin in Sections 7.1 and 7.2 by discussing how uniqueness and individuality are treated in metaphysics and the philosophy of biology, drawing out the distinctions that will help us to reconstruct biologists' views on uniqueness. In Section 7.3 I consider whether phenotypic and ecological uniqueness might just be a contingent empirical fact. I argue that, although biologists in the CRC often refer to experiences or experiments, their views on uniqueness are too general to be supported with empirical evidence. In Section 7.4 I therefore employ the distinctions and concepts derived from the philosophical debates to reconstruct a justification for behavioural ecologists' views on uniqueness. Based on an argument from complexity, I conclude that phenotypic and ecological uniqueness are biologically necessary for biological individuality. I finish in Section 7.5 by pointing out consequences for the philosophical debate on biological individuality.

7.1 Uniqueness and Identity in the Metaphysics of Individuality

Many metaphysicians associate individuality with uniqueness. Ronald De Sousa, for instance, notes with little justification that "Individuals are *particular*, *specific*, and often *unique*." (De Sousa 2005, 197, emphasis in original) Here I focus on how metaphysicians connect individuality with uniqueness via identity. The debates on individuality and identity are extensive and contain many conflicting positions. I concentrate on the relation between uniqueness and individuality and the different ways in which individuals can be unique.

Metaphysicians often define individuality, what it is to be an individual or what makes something an individual, as involving two aspects. For instance, Jonathon

Lowe writes that "what individuates, in the metaphysical sense, is whatever it is that makes an entity *one* entity, distinct from others, and *the very entity that it is*, as opposed to any other." (Lowe 2003, 78) As another example, Décio Krause and Jonas Arenhart state that an individual is "something that is considered as *one*, distinct from any other individual, and which at least in principle can be reidentified [...] as being *that* same item." (Krause and Arenhart 2016, 62) Both of these definitions highlight two dimensions, features or aspects of individuality: *countability* and *identity* (Lowe 2003, 78). On the one hand, individuals should be countable. An individual is a single thing rather than merely a collection of many things or a mass. Butter, for instance, is not an individual since I can't count "a single butter." In contrast, the pat of butter in my fridge is a single thing. Second, individuality involves identity, something that makes an individual "the very entity it is, as opposed to any other," or that allows it to be reidentified in different circumstances. The pat of butter in my fridge is that pat of butter, not the pat of butter in my neighbour's fridge nor the pat of butter I finished last week. Both aspects, countability and identity, are important for individuality.

Through the long debate about identity, one thing is clear: whatever it is that determines identity must be unique to an object, picking it out rather than any other object. Take for instance Leibniz's Principle of the Identity of Indiscernibles, or Leibniz's Law (Forrest 2020). This principle states that two things that bear all the same properties—that are "indiscernible" in a strong sense—must actually be one and the same thing. This means that two distinct objects cannot have all the same properties: each entity is unique. Leibniz's Law can be applied *synchronically*, such that each entity is unique compared to all other objects at a time. It can also—more controversially—be applied *diachronically*, such that two indiscernible entities at different times are actually identical. In Chapter 8 I consider diachronic identity and its relation to practices of reidentification. For now, I focus on synchronic identity. To get an overview of different ideas about uniqueness and identity in metaphysics, and how they might differ from biologists' ideas about the uniqueness of individuals, it will help to use a series of distinctions introduced by Katherine Hawley (2009).

First, what kinds of entities are in question: concrete particulars, abstract particulars, universals, or tropes? Both biologists and metaphysicians tend to focus on concrete particulars when discussing the identity of individuals (Hawley 2009).

At least for biologists the reason for this focus is clear: individual organisms exist concretely in the world. For metaphysicians, it may be a historical contingency that much debate revolves around concrete objects such as organisms and artefacts (Lowe 2003, 77).

Second, what sort of necessity is needed? Do we require metaphysical necessity, so that an individual is unique in all possible worlds or all conceivable situations? Do we claim physical necessity, so that there are no other physically possible situations in which another object has all the same properties? Or do we only require contingency, so that an object is unique contingent on the way the world actually is? Amongst metaphysicians the focus is almost exclusively on metaphysical necessity. Later in the chapter I will argue that a different sort of necessity, what I call biological necessity, is relevant for understanding biologists' beliefs about phenotypic and ecological uniqueness.

Third, what kinds of properties are relevant to identity: intrinsic, qualitative or relational? Amongst philosophers it is common to exclude the relational property "being identical with" since that makes defining identity trivial (Noonan and Curtis 2018). Apart from this restriction, there is considerable debate about which sorts of properties can define identity. Most metaphysicians agree that qualitative properties do not suffice (Strawson 1959; Lowe 2003; Hawley 2009; Forrest 2020; Noonan and Curtis 2018). Some philosophers think that qualitatively identical individuals actually exist (Gracia 1988), but most just argue that they are metaphysically possible; we can for instance imagine two exactly identical loaves of bread, even if real loaves are always slightly different. Some metaphysicians argue that relational properties such as spatiotemporal position can define identity (e.g., Strawson 1959). Other philosophers use thought experiments about a symmetrical universe with only two qualitatively identical objects to challenge the suitability of relational properties (Lowe 2003; Noonan and Curtis 2018). Finally, some metaphysicians opt for intrinsic, non-qualitative properties such as haecceities or essences as the properties which determine identity (Gracia 1988; Cross 2014). In contrast, the biologists in the CRC are interested in the uniqueness of phenotypes, which are qualitative properties, and niches, which are relational properties (see Chapter 3).

So, some metaphysicians take identity, alongside countability, as an important aspect of individuality. Moreover, identity requires some sort of uniqueness with some degree of necessity. There are important differences amongst metaphysicians' theories of individuality and identity, as well as between metaphysical theories and behavioural ecologists' individuality-uniqueness association. Nevertheless, the very fact that some metaphysicians take uniqueness to be important for individuality in general provides support for a similar relation in the particular case of behavioural ecology (Kaiser and Trappes 2021). I will return to this idea in Section 7.4, using the distinctions about types of necessity and types of properties to reconstruct biologists' views about uniqueness. First, however, we should look at how philosophers of biology have regarded the relation between uniqueness and biological individuality.

7.2 Contesting the Uniqueness of Biological Individuals

The philosophical discussion of biological individuality has focused on how to pick out biological entities as single things, that is, on countability. In this section I briefly characterise the debate on biological individuality before turning to consider how philosophers have understood the uniqueness of biological individuals. I show that there has been some interest in the uniqueness of a variety of biological properties and highlight the relative disinterest in metaphysical necessity. This will set the stage for returning to behavioural ecologists' ideas about uniqueness.

Looking at the living world, we are faced with an abundance of questions about what biological entities count as individuals and how to determine their boundaries, parts, and unity (Lidgard and Nyhart 2017; Kaiser 2018; R. A. Wilson and Barker 2019). What makes something an individual in biology? When is something part of an individual, and when is it external to the individual? How can we distinguish between reproduction, which creates a new individual, and growth of the same individual? Does very tight cooperation in a group mean that the group counts as individual? These questions have proved difficult to answer due to the utter complexity and variety of life forms, the way such life forms conflict with our intuitions about individuality built from non-pregnant adult mammals, and the sheer difficulty of selecting suitable criteria for distinguishing individuals from non-individuals (Kaiser and Trappes 2021).

The profusion of problem cases and the difficulty of selecting suitable criteria have fed a protracted debate, often conducted under the title of "the problem of biological individuality" (E. Clarke 2010). The aim is to develop one or perhaps several definitions of biological individuality. These definitions should allow us to count individuals either in accordance with our intuitions or for the purposes of scientific practices like assigning fitness in evolutionary theory or distinguishing self and other in immunology (E. Clarke 2010; Pradeu 2012). To develop these definitions, philosophers have focused on common functional and structural properties of biological individuals, such as metabolic autonomy, life cycles, or immunological reactivity (for a complete list of proposed criteria of biological individuality, see Lidgard and Nyhart 2017).

Despite its purported generality, the debate on biological individuality has centred around just *some* questions about biological individuality, sidelining other questions to do with uniqueness and to some extent temporality (Kaiser and Trappes 2021). This is not to say that uniqueness is entirely absent from the debate on biological individuality. Genetic uniqueness has received considerable attention (see Table 7.1), sometimes confusingly called genetic homogeneity, that is, homogeneity of genetic material within an organism and genetic distinctness between organisms. There are several reasons for this genetic focus. First, genetic uniqueness may be relevant for evolutionary theory, which is thought to require genetically distinct individuals as the units of selection (Janzen 1977; Godfrey-Smith 2009, 81; E. Clarke 2012; Herron et al. 2013; Lidgard and Nyhart 2017). Second, genetic uniqueness is very common among familiar organisms, especially mammals, birds, and many fish and reptiles (so-called "paradigmatic individuals"; J. A. Wilson 1999). Finally, the proximity of genetic properties to intrinsic properties or essences (Hauskeller 2004; Oyama 2010) perhaps invites the idea that genetic uniqueness is the "translation" of metaphysical principles of identity into the biological realm (Chauvier 2017, 8).

Though often discussed, genetic uniqueness is also usually dismissed as unsuitable for defining individuality. One problem is the existence of metaphysically possible genetically identical entities. More pressingly for philosophers of biology, genetic properties cannot distinguish *actual* genetically identical living beings (Santelices 1999; Hauskeller 2004; De Sousa 2005; Folse III and Roughgarden 2010; Boniolo and Testa 2012; E. Clarke 2012; Elwick 2017). Organisms that reproduce asexually, including bacteria and archaea as well as many plants, fungi, and animals, are often not genetically unique. In addition, monozygotic twins and artificially produced clones usually share all their genetic material. Some people are willing to conclude that such genetically identical beings actually form one individual (Janzen

1977). However, most people believe that at least twins and clones, and potentially also the offspring of asexually reproducing organisms, should be counted as separate individuals. Genetic uniqueness is therefore not necessary for individuality.

Organisms are more than their genes, and there is some scattered interest in non-genetic properties of biological individuals as potential sources of uniqueness. This includes epigenetic, immunological, neurological, morphological, and general phenotypic uniqueness, as well as development, experiences and spatiotemporal position (see Table 7.1). For instance, Alexandre Guay and Thomas Pradeu note that, in contrast to physics, "in biology, even individuals that are said to be 'identical' express, most of the time, some significant differences and, at the very least, can usually be distinguished one from the other from a spatial point of view." (Guay and Pradeu 2016a, 10) Similarly, Lynn Nyhart and Scott Lidgard point out that a combination of qualitative and relational properties can distinguish between genetically identical individuals: "for a single sterile worker bee in a colony, its identity [...] may be given by unique nuances of form, functional duties, spatial and temporal boundedness, and so on, that distinguish it from all other bees." (Nyhart and Lidgard 2017, 30) Nyhart and Lidgard also clarify that identity, what distinguishes individuals from one another, is one important aspect or "mode" of individuality, alongside what they call *unity* (similar to what I have called countability), which holds together an individual's parts and demarcates them from the environment (Nyhart and Lidgard 2017, 30).

Observations about the ubiquity of non-genetic uniqueness are not trivial. After finding that biological individuals on the whole are not genetically unique, many philosophers conclude that individuals are not unique at all (J. A. Wilson 1999; Folse III and Roughgarden 2010; E. Clarke 2012; Herron et al. 2013; Chauvier 2017; Love and Brigandt 2017). In both metaphysics and philosophy of biology it is especially common to assume that clones and monozygotic twins, being genetically identical, have no other differences in their qualitative properties. For instance, David Hull states that "Identical twins do not become one organism simply because they are phenotypically indistinguishable." (Hull 1978, 345) Hull argues instead that biological individuals are historically unique, that is, they have a unique beginning and end (Hull 1978, 349). On the other hand, we could observe with Guay and Pradeu that identical twins are not in fact phenotypically indistinguishable, even if they might look very similar at first sight (see also Hauskeller 2004). Such marginal debates suggest that uniqueness questions might deserve philosophers' attention, something I argue for more strongly in Section 7.5.

The reasoning about uniqueness also shows that some philosophers of biology are not concerned with metaphysical necessity. Instead, they are content to observe what is true of actual biological individuals. It is the actual existence of genetically identical biological individuals, rather than their mere metaphysical possibility, which shows that genetic uniqueness is not necessary for biological individuality. In turn, if there is strong evidence that all biological individuals share a certain feature, such as homeostasis or reproduction, then philosophers of biology may take this as an important or even defining feature of biological individuality. They do so without asking if there might be some metaphysically possible individual that lacks the feature common to real biological individuals. There is thus some precedent for restricting the notion of necessity required in a definition of biological individuality to something closer to the possibilities that are realised in the actual world, something I explore in more detail below.

Despite some forerunners, the discussion of uniqueness has not produced any widespread consensus and remains limited and scattered. In another paper, Marie I. Kaiser and I argue that this marginal status is undeserved: uniqueness should be recognised as central to the problem agenda of biological individuality (Kaiser and Trappes 2021). In the rest of the chapter, I argue for a uniqueness condition that can contribute to the debate on biological individuality.

Table 7.1. Types of unique properties mentioned in philosophy of biology as relevant to biological individuality. The list was generated by searching for "unique*" in a comprehensive set of publications on biological individuality, mostly publications from 1990 onwards but including some from 1950 to 1990. Only searchable texts were included. Citations are in chronological order.

Metaphysical Type	**Biological Type (Broad)**	**Biological Type (Narrow)**	**References**
Qualitative	Genetic	Genotype/Genome	(Medawar 1957; Janzen 1977; J. A. Wilson 1999; Santelices 1999; Hauskeller 2004; De Sousa 2005; Pepper and Herron 2008; Godfrey-Smith 2009; West and Kiers 2009; E. Clarke 2010; 2012; 2013; Folse III and Roughgarden 2010; Michod 2011; Minelli 2011; 2020; Boniolo and Testa 2012; Gorelick 2012; Pradeu 2012; 2016a; E. Clarke and Okasha 2013; Herron et al. 2013; Booth 2014; Chauvier 2017; Elwick 2017; Love and Brigandt 2017; Gerber 2018; DiFrisco 2019; Smith-Ferguson and Beekman 2019)
Qualitative	Epigenetic	Epigenetic markers	(Boniolo and Testa 2012; Gorelick 2012; Elwick 2017; Nyhart and Lidgard 2017)
Qualitative	Phenotypic	All traits	(Burgio 1990; Hauskeller 2004; De Sousa 2005; Godfrey-Smith 2009; E. Clarke 2016; Guay and Pradeu 2016a; Elwick 2017; Nyhart and Lidgard 2017)
		Neurological traits	(Boniolo 2005; Pradeu 2012)
		Immunological traits	(Medawar 1957; Burgio 1990; Pradeu 2012; 2016a; Ferner and Pradeu 2017; Nyhart and Lidgard 2017; Minelli 2020)
		Morphological traits	(Pradeu 2012; Elwick 2017; Lidgard and Nyhart 2017)
		Behavioural traits	(Nyhart and Lidgard 2017)
Relational?	Ontogenetic	Development	(Pradeu 2012; Elwick 2017)
		Experiences	(Ruiz-Mirazo, Etxeberria, and Moreno 2000; De Sousa 2005)
Relational	Spatiotemporal	Location, origin	(Hull 1978; Guay and Pradeu 2016a; Lidgard and Nyhart 2017)

7.3 Is Uniqueness Just an Empirical Fact?

The sorts of properties biologists in the CRC consider to be unique have been rejected by metaphysicians as irrelevant for identity and have received scant attention in philosophy of biology. Are biologists poor metaphysicians? Or are they perhaps just stating a contingent matter of fact when they claim that all biological individuals have unique total phenotypes and niches? In this section I consider this latter option.

Biologists in the CRC often appeal to their everyday experience working with or observing animals to justify their belief that individuals are unique. The interviews provide a number of illustrative examples of this form of reasoning. For instance, one researcher answered a question about how individualised phenotypes and niches develop by describing their experiences with their animals.

> S1: [When I first see them] I have the impression that some individuals are more curious than others or some are more jumpy than others. […] I'm not sure if they are born already different but probably I would argue that, yes, we are all born already different. (Interview 4)

Though the interviewee didn't mention uniqueness explicitly, they did go on to insist that the organisms always show behavioural and morphological differences, even when they have the same genotype and developmental environment. Another noteworthy example comes from a researcher who does field research on the common buzzard.

> S: Each buzzard looks slightly different. You know, in the old days, when there were fewer around I would take photographs and draw them, and I was able to recognize individuals by the drawings. I mean, these feather patterns [indicates taxidermy buzzards on shelf], they stay the same throughout their life, and life can be 25 years. So it is very clear these are individuals, you can recognize they are so, they do behave differently. (Interview 9)

Such anecdotal remarks are commonplace in conversations with scientists. They are distinct from scientific claims; although they are based on empirical evidence, they involve more unsystematic evidential relations.

Some biologists also cite experimental evidence that differences develop despite organisms having an identical genotype and experiencing near-identical environmental conditions (e.g., Freund et al. 2013; Bierbach, Laskowski, and Wolf 2017). They take this as evidence that phenotypic and ecological uniqueness is ubiquitous amongst biological individuals. One example comes from a researcher discussing whether all individuals have unique niches.

> S2: One thing that also some researchers started to do is trying to control for every single thing they could, taking clonal individuals so there is no genetically different background and giving them the exact same experiences. And still, the individuals do differ and they do differ from the beginning. I mean, these are hints but to prove that, it's really hard to tell. (Interview 2)

The researcher emphasised that such experiments provide hints, but not proofs, that all individuals have unique niches.

In addition to experimental evidence, we can have very strong observational support for the belief that individuals are unique, even without checking all the individuals in a population. For instance, one reason we believe that all humans have unique fingerprints is that no two humans have ever been found with exactly identical fingerprints, and we have examined the fingerprints of very many humans. Similar inductive arguments can be made for many phenotypic properties, such as skin colour patterns, antibodies, and chemical phenotypes: after studying many individuals, no identical individuals have been found, so each individual is unique. However, for many species it is not feasible to study a sufficient number of individuals to have a strong inductive argument for uniqueness. This is one reason why researchers grant importance to experiments showing that differences develop despite identical genotypes and near-identical environments. These experiments provide evidence that differences arise even from great uniformity, suggesting that phenotypic and ecological uniqueness is to be expected in non-experimental contexts where genetic and environmental heterogeneity abound. This lends some support to the belief that *all* biological individuals, not just all individuals in a particular experiment, are unique.

Since biologists are far more used to empirical reasoning, they are inclined to cite whatever empirical evidence they have. However, as is also obvious to the biologists, anecdotal evidence and a small number of experiments is not a very reliable source of information about reality. The number of studies may increase, especially with improved technical capacity to uniform the environment. However, they will be limited to species for which genetically identical offspring are possible; extrapolations from these species to others may not be valid. In addition, the number of studies might remain low; they will only be performed if they can answer a biological research question, and uniqueness doesn't usually feature in biologists' research questions (see Chapter 6). Hence, there will likely be persistent limitations on empirical justification for the belief that all biological individuals are unique.

If the biologists are stating a contingent matter of fact about the uniqueness of individuals, their evidence is quite limited. In addition, as discussed in Chapter 4, a number of responses to the questionnaire indicate that uniqueness is at least partly what makes organisms individuals or that uniqueness is part of the definition of individuality, and statements in the interviews often implied that uniqueness holds very broadly, not restricted to local investigative contexts. These are much stronger claims than that individuals just happen to be unique. Given such generality and connections to defining individuality, the belief that all biological individuals are phenotypically and ecologically unique seems to be more than a mere empirical claim. Of course, some biologists really might hold the uniqueness of individuals to be a (weakly supported and overly general) contingent empirical fact. But the materials I gathered suggest that many biologists in the CRC associate phenotypic and ecological uniqueness with individuality in a much stronger sense. In the next section I consider how biologists' theoretical reasoning can support uniqueness as a necessary condition on biological individuality, shifting biologists from contingent matters of fact to a distinctly biological metaphysics.

7.4 The Complexity Argument for Uniqueness

In this section I argue that the biologists' views can be interpreted in terms of a uniqueness condition, which states that biological individuals necessarily bear unique sets of phenotypic and ecological properties. I support the phenotypic and ecological uniqueness condition with an argument from complexity, clarifying in the process in what sense phenotypic and ecological uniqueness is necessary.

We saw in Chapter 4 that many biologists in the CRC believe that all biological individuals have unique total phenotypes and niches. I propose that this belief expresses a condition of biological individuality, what I call the *phenotypic and ecological uniqueness condition*. According to this condition, having a unique total phenotype and a unique niche is necessary for being a biological individual. Using the distinctions derived from metaphysics, the condition states that all biological individuals necessarily bear unique sets of qualitative (phenotypic) and relational (niche) properties.

The Phenotypic and Ecological Uniqueness Condition. Something is a biological individual only if

(i) it bears a set A of phenotypic properties,
(ii) it bears a set B of niche-dimensional properties, and
(iii) no other entity bears A or B.

This condition conforms to the biologists' belief in the uniqueness of all biological individuals and their insistence on each of the property types as a source of uniqueness. It does however remain vague on the size of the sets of properties to be considered. Complete sets that include all phenotypic properties or all ranges along niche dimensions are hard to specify due to the difficulty of determining what counts as a phenotypic trait or a niche dimension (see Chapter 3). We can therefore only say that the relevant sets should be fairly comprehensive, approaching something like a complete set.

Biologists are often unfamiliar with the metaphysical implications of their beliefs and how to express those implications. As a consequence, explicit statements that all individuals are (or aren't) necessarily phenotypically and ecologically unique might result from confusion or misunderstanding. Nevertheless, the way biologists in the CRC explain and defend their views about uniqueness implies that they do think phenotypic and ecological uniqueness is necessary for biological individuality. In the interviews I asked subjects whether they think individuals have unique phenotypes or niches or whether there could be different individuals with exactly the same individualised phenotypes or niches (see Chapter 4). A representative answer is the following.

> S2: 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. (Interview 4)

This is an example of what I call the *complexity argument*, invoking the complexity of biological systems to argue that each individual must be unique.

The complexity argument can be elaborated by distinguishing two types of complexity in biology: *structure* or *compositional complexity* and *process* or *dynamic complexity* (Mitchell 2003). Compositional complexity refers to the way biological systems are composed of multiple parts in non-simple relations, where a system can be composed in dramatically different ways while remaining the same kind of system

(Mitchell 2003, 5; see also Elliott-Graves 2018). Dynamic complexity adds another layer, highlighting the prevalence of feedback loops, recursion, nonlinear dynamics, and saltation, as well as the sensitivity of causal processes to initial conditions (Mitchell 2003, 6–7). The complexity argument appeals to both kinds of complexity.

First, phenotypes and niches are compositionally complex. Take this example about the niche.

> S: So in this context like 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. (Interview 7)

The individualised niche is composed of many different dimensions—relations not just to abiotic conditions such as temperature or rainfall but also to biotic conditions such as food resources, population density, and conspecifics (see Chapter 3). There are many different ways to compose such a niche, with many different relations between different ecological factors and how individuals relate to them. The same goes for total phenotypes, which are similarly composed of many parts in complex relations (Nijhout 2001).

In addition to their compositional complexity, total phenotypes and niches have high dynamical complexity. For instance, the causal structures that produce phenotypic properties include feedback loops and nonlinear dynamics. An example from the interviews illustrates a biologist's reasoning about this dynamic complexity.

> S2: I mean, in the past it was rather, okay, we are coming with a specific genotype and the environment is coming and of course that can like make some trajectories for the individual. But we now know that it is much more complex and that also not only the genotype can affect the behavior but also the behavior of an individual is showing after a cue in the environment. This can also backwards influence the genotype and be also presented in the next generation. So, I personally think that from the beginning to the end it's not only what cues you receive but it's also how you decide upon that and how you also perceive these cues is completely different. So, I would say that from the beginning based on these interactions that cannot be the same for two individuals. That would be what I think. (Interview 2)

This researcher refers to the many different causal factors involved in the production of a behavioural phenotype: past history, current environmental cues, genes, perception, and even the behaviour itself. They also mention feedback loops ("backwards influence") between the behaviour, environment, and genotype. This complexity means that the exact replication of a causal sequence leading to a behavioural phenotype is extremely unlikely. The same goes for other phenotypic properties as well as niches.

Further complexity is added by causal relations between phenotypic properties and ranges along niche dimensions, as explored by researchers under the framework of NC^3 mechanisms (see Chapter 4). These relations mean that differences in one type of property generally produce differences in the other. Different phenotypic properties usually lead to different niches since they alter the way individuals relate to their environments, for instance by changing their requirements, how they explore space or how they interact with other organisms. In return, a difference in the niche due to relating to different environmental stimuli often causes an organism to plastically adjust its phenotypic properties. Hence, a unique set of properties of one type is expected to generate a unique set of properties of the other type.

The compositional and dynamic complexity of total phenotypes and individualised niches and their interrelations make exactly identical individuals very unlikely. In addition, there are obvious limitations on how many organisms of a species can exist under similar enough conditions that their total phenotypes or niches might be even vaguely similar. These limitations compound the improbability of exactly identical individuals. This combination of compositional and dynamic complexity as well as limited numbers of individuals is the core of the complexity argument.

Extremely unlikely scenarios are of course still metaphysically possible. That means phenotypic and ecological uniqueness is not metaphysically necessary for individuality. In addition, phenotypic and ecological uniqueness is not physically necessary. Physical or natural necessity concerns when something follows from scientific laws (Fine 2002; Lange 2008; Kment 2017). The existence of two identical biological individuals does not contradict any scientific law; indeed, laws are very difficult to find in biology (Mitchell 2003; Lange 2008). However, metaphysical and physical necessity are not the only sorts of necessity that phenotypic and ecological uniqueness could carry.

First, we can look at statistical necessity. Stochastic processes generate stable, predictable and consistent system behaviour, described for instance in the laws of thermodynamics and the laws of probability. Some have argued that these laws involve a sort of statistical necessity, rather than physical necessity (Filomeno 2019).

Similarly, the generation of uniqueness by complex systems, where only a limited number of systems can be instantiated at once, might also be attributable to a law of probability. On this view, phenotypic and ecological uniqueness would be statistically necessary.

This idea of statistical necessity could be combined with something like practical necessity. Practising biologists aren't concerned with a very wide sphere of possibilities that would encompass the extremely improbable occurrence of phenotypically or ecologically identical individuals. Instead, like many philosophers of biology (see Section 7.2), they are interested in possibilities that are fairly close to the actual world. Given the complexity argument, individuals should be phenotypically and ecologically unique in practically any situation which a biologist might study. Since phenotypic and ecological uniqueness will hold across the board in scenarios relevant to practising biologists, it makes sense for biologists to hold that uniqueness is necessary. Another way of putting this is to say that uniqueness is necessary within the realm of possibilities that is relevant to biologists.

I call this kind of modality *biological necessity*, that is, necessity for practising biologists given their epistemic goals as well as the nature of biological systems. Hence, phenotypic and ecological uniqueness is biologically necessary due to the interests of biologists in a restricted sphere of possible situations as well as the complex nature of total phenotypes and niches and the limited numbers of organisms that can exist under similar conditions. But why call this biological *necessity*, given that there is still a large element of contingency on things like biologists' research interests and the nature of biological systems?

An answer can be found by comparing generalisations in biology to laws in physics. Sandra Mitchell (2003) argues that all scientific laws are contingent in a logical sense, since they do not describe all logically possible worlds. Physical necessity is therefore only necessity given certain conditions that make the relevant law hold. Similarly, biological generalisations describe how certain outcomes are necessary given the conditions that make the generalisation valid (for a similar idea, see Kment 2017). The difference between physical laws and biological generalisations, Mitchell argues, is not that one involves necessity and the other doesn't. Rather, biological generalisations are contingent on conditions that are relatively unstable and complex in comparison to the stable and simple conditions of physical laws. For instance, many biological generalisations apply to a limited spatiotemporal range or rely on evolution having taken a particular course. Despite this instability and complexity, biological generalisations can still be used to predict and explain phenomena as necessary given that the right conditions are in place.

Applying Mitchell's scheme, the phenotypic and ecological uniqueness condition states that biological individuals are necessarily unique *given some specific conditions*. These conditions include the compositional and dynamic complexity of biological systems, the limited numbers of biological individuals that can exist under similar conditions, and biologists' interests in only a restricted sphere of possibilities. These are more restricted, unstable conditions than those involved in physical laws. But they are also more general and stable than the conditions involved in many biological generalisations about particular species or ecological communities. This relative generality and stability supports the idea that phenotypic and ecological uniqueness is *biologically* necessary, not just necessary for some specific research project or species.

To summarise, there is a strong theoretical argument for the necessity of phenotypic and ecological uniqueness, based on the complexity of total phenotypes and niches, the limited numbers of individuals that can exist under similar conditions, and biologists' research interests. Phenotypic and ecological uniqueness may not be metaphysically or physically necessary, but it is biologically necessary: within the sphere of possibility relevant to practising biologists, all biological individuals are and will be unique in their total phenotypes and individualised niches.

7.5 Understanding Biological Individuality with Uniqueness

The phenotypic and ecological uniqueness condition directs philosophers' attention towards an overlooked aspect of the living world. It may seem obvious that everything is unique in biology (Guay and Pradeu 2016a). Nevertheless, this seemingly trivial fact has been overlooked by a number of philosophers of biology and metaphysicians, as we saw in Sections 7.1 and 7.2. Recognising the phenotypic and ecological uniqueness condition corrects this tendency, making it apparent that such biological individuals, though perhaps metaphysically possible, are biologically impossible.

A typical response to the phenotypic and ecological uniqueness condition is that it begs the question. Comparing individuals to establish whether they are unique requires individuals that are countable as single things. Hence, goes the objection, uniqueness requires individuality, not the other way around. This objection trades on the conflation between individuality and countability. It is indeed necessary to count things to determine if they are unique. However, as we saw in Section 7.1, being counted as a single object is at least on some metaphysicians' definitions only one aspect of individuality. That uniqueness requires countability is therefore compatible with it being an additional condition on individuality.

The phenotypic and ecological uniqueness condition is not sufficient for biological individuality. Some entities might bear unique total phenotypes and niches but not qualify for biological individuality for other reasons. For instance, unique niches and sets of phenotypic properties can be assigned to groups of organisms, including populations and species. Although some authors argue that populations and species are individuals (Hull 1978; Millstein 2009; Haber 2016), others would disagree since species and populations don't or only barely meet other requirements for individuality, such as being bearers of fitness or having tight enough functional integration (Godfrey-Smith 2009). On the other end of the organisational scale, it might be possible to assign phenotypic properties and niches to cells or groups of cells, raising the possibility that they too might satisfy the phenotypic and ecological uniqueness condition. Yet cells and tissues that are parts of multicellular individuals are not usually considered individuals in their own right, for instance because they are not autonomous.

Although it is only a necessary condition, considering uniqueness does highlight overlooked questions in the debate on biological individuality (Kaiser and Trappes 2021). The uniqueness condition I presented here makes both unique phenotypic properties and unique niches necessary for individuality. In contrast, we saw that philosophers of biology tend to focus on genetic uniqueness, and to a lesser extent other sorts of uniqueness. Is there a reason for this difference? What sorts of properties are most relevant in defining individuality, and why? Looking at the differences between how philosophers and behavioural ecologists discuss uniqueness helps to both reveal assumptions in philosophical discussions of biological individuality and highlight implications of the phenotypic and ecological uniqueness condition.

First, philosophers of biology have largely focused on genetic uniqueness. The relative stability of individuals' genomes means genetic properties may help to resolve questions about diachronic identity. Phenotypes and niches, in contrast, seem too flexible and contingent to tell us what makes something the very individual it is over multiple time points. In the next chapter, I suggest that some robust phenotypic properties are also suitable for defining diachronic identity. On the other hand, we should recall that diachronic identity is just one way to think about identity. It may be that phenotypes and niches are enough to define individuals' synchronic identity.

Second, philosophers and behavioural ecologists focus on different sorts of phenotypic traits. Philosophers of biology have paid more attention to immunological properties (see Table 7.1), which are relevant to defining the boundary between an organism and other organisms or foreign objects (Medawar 1957; Pradeu 2012). Behavioural ecologists, in contrast, talk more about behavioural, morphological, and chemical phenotypes. For instance, they consider animal personality, skin colour patterns, or chemical signals like pheromones, as important to individuality. These are properties which help conspecifics or humans recognise different individuals (see Chapter 8), or which make it important to include individuals in understanding organism-environment interactions (see Chapter 6). Hence, behavioural, morphological and chemical phenotypes are related to different problems and questions about individuality, beyond the question of defining an individual's boundaries (Kaiser and Trappes 2021).

Third, the inclusion of niches is particularly novel for a condition of individuality. A few philosophers have considered individuals' unique experiences or spatiotemporal position (see Table 7.1). But neither of these explicitly concerns organisms' relations to ecological conditions. The phenotypic and ecological uniqueness condition means that social interactions, resource use, migration routes or mate choice are relevant to individuality. An important question is whether such relations are equally as important as genetic or phenotypic properties, or whether qualitative properties are more central to defining individuality. In addition, we can ask what it means for an individual to be defined in part by its surroundings.

Fourth, acknowledging the phenotypic and ecological uniqueness condition brings new biological sciences into the debate on biological individuality, broadening the scope beyond evolutionary biology and physiology. It also encourages reconsidering the genetic and molecular focus in many discussions of biological individuality, shifting away from the reductionism that many philosophers elsewhere declaim (Dupré 1993; Mitchell 2003; Waters 2008; Nicholson 2014). On the other hand, it is worth noting that individuality in behavioural ecology may harbour its own reductionist tendencies due to its proximity to methodological individualism (see Chapter 6).

Finally, considering the phenotypic and ecological uniqueness condition brings to light a new practical role for the concept of individuality. Recently, practice-based philosophers have looked at how individuals are identified or "individuated" by practising biologists. They find that we usually individuate organisms through spatial boundaries, functional integration, and so on (see, e.g., the contributions in Bueno, Chen, and Fagan 2018a). It may be that individual differences in phenotypes are relevant to telling individuals apart (Smith-Ferguson and Beekman 2019) or reidentifying them (see Chapter 8). But the phenotypic and ecological uniqueness condition does not typically guide behavioural ecologists' practices of picking out single individuals from a group.

Instead, the phenotypic and ecological uniqueness condition plays a different sort of role. As we saw in Part II, phenotypic and ecological uniqueness is a theoretical concept that is operationalised as robust individual differences. Believing that each individual is unique encourages biologists to look closer at the differences between individuals, analyse variation in their samples rather than only averages, and make use of individualised methods such as repeated observation. Hence, the phenotypic and ecological uniqueness condition plays the heuristic role of facilitating the choice of phenomena to study and methods by which to study them. Therefore, alongside meeting individuation needs, another practical role for a condition of individuality is to encourage and facilitate individualised research.

In conclusion, I maintain that phenotypic and ecological uniqueness is a biologically necessary condition of biological individuality, supported by the complexity argument and biologists' research interests. Given the compositional and dynamic complexity of phenotypes and niches, the limited number of biological individuals that can exist, and biologists’ interests only in possibilities that are close to reality, all biological individuals will have unique phenotypes and niches. The phenotypic and ecological uniqueness condition guides biologists’ choice of research objects and methods, and it can lead to new questions and insights about biological individuality.

8 Understanding Animal Identity

In Chapter 7 I explored the strong ties between phenotypic and ecological uniqueness and individuality more generally, beyond its definitions in behavioural ecology. These ties help to explain why behavioural ecologists associate individuality with phenotypic and ecological uniqueness. They also suggest that individuality in behavioural ecology is more than a discipline-specific definition irrelevant to other individuality concepts. In this chapter I follow this argumentative line further, focusing on the conditions of temporal stability and contextual consistency, or *robustness* (Goldie 2004; Banicki 2017). Why require individual differences to be robust? What does robustness have to do with individuality?

Following recent practice-based philosophy of biological individuality, I first examine the role that robustness plays in behavioural ecologists' identification practices. In behavioural ecology, reidentification of individuals relies on phenotypic properties like colour patterns or body shape, as well as devices like identification tags and trackers. Properties used for reidentification must sufficiently distinguish individuals from one another and remain the same over time and across contexts. These reidentification practices suggest a principle of identity, according to which robust differentiating properties are sufficient for individuals' identity over time. I argue that this principle must be established empirically for particular species. I then consider the importance of robustness for animal personality and individual specialisation. I argue that understanding these phenomena as dispositions helps make sense of the requirement for robustness. The dispositional analysis also permits an analogy to human personality, which I use to argue that behavioural ecological dispositions are relevant to animal identity.

Given that identity is one important aspect of individuality, as I suggested in Chapter 7, these reflections on robustness and identity help to explain why behavioural ecologists take robustness to be relevant to individuality. This complements the epistemological explanation of the temporal stability requirement as a way to enable repeated observation, which I discussed in Chapter 5. It also offers the missing explanation for contextual consistency.

I begin in Section 8.1 by introducing behavioural ecologists' reidentification practices. In Section 8.2 I consider a potential identity principle underlying these practices. I find that, although the practices themselves do not justify a general principle of identity, more specific empirical findings may be able to support more local, restricted principles of identity. The rest of the chapter develops and employs a dispositional analysis of animal personality and individual specialisation. I prepare the way by summarising the robustness condition in Section 8.3 and developing a brief account of dispositions in Section 8.4. In Section 8.5 I argue that animal personality and individual specialisation can be understood as extrinsic, multi-track dispositions. This allows me in Section 8.6 to draw an analogy to human personality, which I employ to argue that animal personality and individual specialisation could serve as conditions of animal identity. I conclude in Section 8.7 by highlighting implications of these reflections on identity for debates about persistence and personal identity.

8.1 Reidentification Practices in Animal Research

Philosophers of biology have recently proposed shifting the debate on biological individuality towards scientific practices of individuation. On this practice-based approach, philosophers should ask "How do scientists individuate the things they investigate and thus count them as individuals?" (Bueno, Chen, and Fagan 2018b, 1). In other words, "the question 'What *is* X, fundamentally?' is replaced by the question 'How should I *follow* X through time?'" (Guay and Pradeu 2016b, 318). In this and the next section I consider to what extent conclusions about individuality can be drawn from individuation practices in behavioural ecology. In line with the philosophical literature on individuation practices, I focus on individuation over time, or *reidentification* (see the contributions in Bueno, Chen, and Fagan 2018a; Meincke and Dupré 2021). Reidentification involves determining that an individual observed at some time is identical to an individual observed at a later time. It therefore concerns identity over time, also known as diachronic identity or persistence.

Reidentification is an everyday activity. We typically rely on properties for reidentification: we recognise people by their faces or voices, cars by their make and colour, television shows by their opening credits or characters, and so on. In general, the properties that we look for are those that are both different for distinct objects and the same for one object over time. Reidentification practices in animal research rely on similar principles. Behavioural ecologists reidentify individuals using properties that pick out one individual from its fellows and that are stable for an individual over time and consistent in different contexts. The ability to reidentify animals is in turn critical for individualised research (see Part II) and for studying many other topics in behavioural ecology, such as life history, mate choice, and migration patterns.

Various traits are used for reidentifying animals. Sometimes, individualised phenotypes can play this role. In Chapter 7 I quoted a researcher talking about how they could recognise buzzards by their unique feather patterns. The same researcher continued on to talk about recognising by behaviour.

> S: […] Some of our individuals we do recognize by behavior. We have an animal that is called Crazy White, because it goes crazy when you go to the nest. I mean if you are close by he is just going to make mock charges, dive down on to you and then sweeps over your head at a meter or two meters distance. Most other animals do not. So there it is very clear we're dealing with individuals here. (Interview 9)

Similar stories were told by other interviewees, especially those working with reasonably small numbers of animals where the animals are large enough to have readily detectable differences colour patterns or body shape.

Reidentification using phenotypic traits is especially prominent in primate studies, where small groups of individuals are studied intensively. One researcher recounted working at a primate research centre; by the end of their time there, they could recognise an individual from a hunched over shoulder (personal communication). Such skilled reidentification practices are necessary, the researcher explained, because primates cannot ethically be tagged with physical identifiers. The guinea pigs studied in the CRC (Project B01) are also recognised by distinctive fur patterns (personal communication). In addition, colour patterns and other morphological traits are used to identify large animals protected under conservation laws. For instance, tigers are reidentified based on unique stripe patterns and whales are identified from photographs of their dorsal fins (Benson 2010).

When phenotypic differences between individuals are not easily recognised, researchers rely on artificial identifiers. The buzzards mentioned above, for instance, are now given identification rings as chicks, allowing easy reidentification of a large number of individuals as they fledge and disperse. Bird ringing or banding has a century long history and has been valued for the increased ability to follow particular individuals and understand their life histories (Benson 2017). Identification tags have also been used in wildlife management of large mammals such as bears (Benson 2010). In lab studies of insects, researchers may paint unique colour codes on each insect. Alternatively, individuals that are not kept in groups can be identified by a number assigned to a cage or container. Finally, researchers can use devices such as radio transmitters, GPS trackers, and accelerometers to track large numbers of individuals in the field, with each device uniquely reidentifying a particular individual (Benson 2010; 2016; H. J. Williams et al. 2020).

These examples highlight several distinctive features of reidentification practices in animal research. First, reidentification requires properties that distinguish an individual from other individuals in an area or population, that is, properties that are unique over a restricted region. Second, reidentification requires properties that are stable over time and, for animals in the field or experimental animals subject to tests, consistent across contexts. We can call this robustness, noting that we are talking about the robustness of an individual's properties, not the robustness of individual differences (see Section 8.3). Finally, the properties must be readily observable, whether in situ, in a photograph or video, or in the readout of a tracking device. Chemical profiles or pheromones—although potentially relevant for conspecific recognition—are often not especially useful for researchers' reidentification purposes. Notably, while individualised phenotypes are sometimes used for reidentification, it is more common to use artificial identifiers such as tags, painted colour codes, or tracking devices.

In general, then, reidentification practices in behavioural ecology rely on robust, observable differentiating properties. Encouragingly, a complementary analysis of behavioural ecological practices of individuation at one time point (synchronic individuation) finds a similar reliance on individual differences, though less attention is granted to robustness (Smith-Ferguson and Beekman 2019). In the next section I consider what reidentification practices can tell us about identity.

8.2 Practical Principles of Animal Identity

In Chapter 2 I discussed transcendental, empiricist, and pragmatist approaches to drawing out metaphysical claims from successful scientific practices. On these approaches, metaphysical principles are necessary for, helpful for, or can explain successful scientific practices. Can these approaches be applied to derive principles of identity from reidentification practices in behavioural ecology?

Behavioural ecologists' reidentification practices do assume that robust differentiating properties do indeed lead to true assessments of identity over time. This assumption is not entirely self-evident. For instance, we can imagine that an animal could change all its properties—that a tiger changes its stripes, say. And it is metaphysically possible that another individual could arise with the same properties. Both of these cases would lead to misjudgements about identity, either failing to reidentify an individual or mistakenly identifying a different individual as the one seen earlier. Yet biologists still rely on these robust differentiating properties for reidentification.

A principle that would support the practice of reidentification is that robust, differentiating properties are sufficient for animals' diachronic identity (identity across time, or persistence). This principle could be formalised as follows:

> *Principle of robust differentiating properties.* An individual a at time t_x or in context C_1 is identical to an individual b at t_{x+1} or in context C_2 if
>
> 1. *Same Properties*. There is some set of observable properties P which both a and b have; and
> 2. *Differentiation*. No other individual in the relevant group or population at either t_x or t_{x+1} or with respect to context C_1 or C_2 has P; and
> 3. *Robustness*. The properties in P are stable over time and consistent across contexts.

The relevant types of properties are often artificial identifiers added by humans, like identification tags, radio transmitters or painted colours. But they can also be naturally occurring (that is, not created by humans), such as colour patterns or body shape. The principle of robust differentiating properties can support reidentification: given two individuals at consecutive time points with the same robust differentiating properties, we can infer that the two individuals are identical.

The principle of robust differentiating properties would strike many metaphysicians as poorly misguided. Properties like stripes and shoulders, identification tags or radio transmitters, are only contingently robust and differentiating. They could have changed or been lost or duplicated. Identity, in contrast, should hold necessarily and universally (see Chapter 7). To respond, we can emphasise the practical nature of the principle of robust differentiating properties. If these robust differentiating properties weren't sufficient for identity, the practice of using them for reidentification wouldn't make sense. Researchers require the principle of robust differentiating properties to hold in order for their practices of reidentification to work. This would make the principle of robust differentiating properties *practically necessary*.

However, the argument from practical necessity faces a problem: it assumes that robust differentiating properties must always lead to successful reidentification. Yet reidentification practices don't have to always succeed. Researchers only need to know that the properties they use are for the most part robust and differentiating, leading with high probability to successful reidentification. Failures in reidentification should of course be eliminated as best as possible. But they need not be eliminated entirely. It is for the permissibility of failure that I think reidentification practices in behavioural ecology do not permit us to infer a general principle of identity.

On the other hand, most biologists would agree that there are only very dim prospects of radical alterations or duplications of properties known to be robust and differentiating, such as colour patterns or body shape. Perhaps such properties are robust and differentiating with what I called in Chapter 7 *biological necessity*. That is, their change or replication in another individual might be so unlikely as to be considered impossible for practising biologists. This would make robust differentiating properties sufficient for the diachronic identity of animals in contexts relevant to biological research. Unlike in the case of phenotypic and ecological uniqueness (Chapter 7) there does not seem to be a general theoretical argument for the robustness of properties like colour patterns or body shape. Instead, establishing the robustness of morphological properties requires detailed examination on a case-by-case basis, especially because morphology can vary greatly across taxa.

Nevertheless, given sufficient evidence, it could be that specific principles could be drawn up for identity in particular species or even higher-level taxa. For instance, given our evidence about human fingerprints, we take having the same fingerprints to be sufficient for identity of human individuals (not necessary, though, since fingerprints can be removed, or digits lost). Importantly, information about the robustness of types of properties such as colour patterns or fingerprints can be readily generalised from some individuals to all individuals in a species, each with their specific colour patterns or fingerprints. This makes it is easier to provide empirical evidence for species- or taxon-specific claims about robustness than for claims of uniqueness (see Chapter 7).

Such species- or taxon-level principles of identity would lack the generality that we usually expect of metaphysics. For instance, they do not support behavioural ecologists' reidentification practices across the board, in the way that practice-based metaphysics of science might incline us to expect of metaphysical principles. Nevertheless, I think they could be considered principles of identity, albeit of a relatively local sort. Such local principles of identity can help explain why behavioural ecologists take robustness as relevant to individuality, given the connection from identity to individuality.

8.3 Recap of Robustness

In the previous two sections we looked at robustness of properties used for reidentification. For the remainder of the chapter, I turn to the robustness of animal personality and individual ecological specialisation. Why is robustness taken as necessary for animal personality and individual specialisation? And what does this tell us about individuality? To answer these questions, I argue that animal personality and individual specialisation are dispositional properties and suggest that such dispositions are relevant to identity. In this section, I prepare by summarising robustness (see also Chapters 3 and 5) and briefly outlining what constitutes a context.

We can start with animal personality, defined as stable and consistent individual differences in behaviour (Carere and Eens 2005; Wolf and Weissing 2012; Dall et al. 2012). *Temporal stability* is the similarity of an individual's behaviour at different time points, relative to the behaviour of other individuals (Bell, Hankison, and Laskowski 2009; E. Takola et al. 2021). The temporal stability requirement is reflected in the use of repeated testing or observation to identify animal personalities. For instance, Project A02 scores mice for optimism levels using repeated cognitive judgement bias tests, and Project A03 uses repeated jumping trials to determine grasshoppers' predictability.

Contextual consistency is the repetition of similar behaviours in different contexts. Contexts are functionally or ecologically relevant scenarios, which can be represented in test set-ups (Sih, Bell, and Johnson 2004). They consist of external stimuli, both abiotic and biotic, present when an individual exhibits a certain behaviour (Stamps and Groothuis 2010). For instance, a bold individual performs in similar ways (ways indicating boldness) in a number of different tests, such as a novel object test and an open arena test (Réale et al. 2007). The individual should (repeatedly) contact a novel object sooner and also (repeatedly) spend more time in an open arena.

Note that different contexts usually involve different behaviours. Contacting a novel object slowly or rapidly, for instance, is not exactly the same behaviour as spending more or less time in an open arena. To measure consistency, biologists group together behaviours that exhibit a similar form, motivational basis, or functional significance (Sih, Bell, and Johnson 2004; Réale et al. 2007; Stamps and Groothuis 2010). In the boldness case, contacting a novel object and remaining in an open arena are both risky activities for many species, so their performance indicates an individual's boldness. Contextual consistency therefore describes the relative invariance of similar behaviours across a number of contexts.

Definitions of individual specialisation focus on individual differences in resource use, rarely making robustness explicit (Bolnick et al. 2003; Dall et al. 2012). Nevertheless, in Chapter 3 I argued that temporal stability is often relevant to identifying and measuring individual specialisation (Bolnick et al. 2003; Fodrie et al. 2015; Novak and Tinker 2015; Niemelä and Dingemanse 2018). In addition, individual specialisation is often tracked across functional contexts, as in animal movement studies (Project D06) or experimental research on resource preferences or performance on a certain resource (Bolnick et al. 2003). Hence, individual specialisation too involves robustness.

As I discussed in Chapter 3, robustness is measured by within-individual correlation or repeatability. Both measures involve comparing individual differences to so-called within-individual differences. To count as robust, an individual must behave (or use a resource) in a way that differs more from other individuals than it differs over time and contexts. In other words, an individual's behaviour or resource use is fairly similar over time or across contexts, relative to the behaviour or resource use of other individuals. As a consequence, robustness depends on an individual's own behaviour or resource use as well as the behaviour or resource use of other individuals.

Why should animal personality and individual specialisation require robustness? In Chapter 5 I suggested an epistemological reason for temporal stability: it makes it possible to measure these properties at the individual level. But what about contextual consistency? I think the robustness requirement can be explained by understanding animal personality and individual specialisation as *dispositions*. To make this argument, I start by looking more generally at how we tell when something is a disposition.

8.4 Diagnosing Dispositions

Roughly put, dispositions are properties that tell us what entities do under certain circumstances. For instance, if a glass is fragile it will break when struck, sugar cubes are soluble because they dissolve in liquids, and a lethal poison is one that will kill those exposed to it. Much ink has been spilled over how exactly to understand dispositions and what distinguishes them from categorical properties like shape, colour, or position (Choi and Fara 2018). Rather than looking at what dispositions are, in this section I focus on features that indicate that a property is dispositional, what Jennifer McKitrick calls “marks of dispositionality” (2003, 156). These diagnostic features will then help to argue that animal personality and individual specialisation involve dispositions.

First, dispositions have characteristic manifestations. For fragility, the manifestation is the entity breaking, and for solubility it is dissolving. In particular, dispositions permit a distinction between the instantiation of a property and its manifestation, since an entity can have a disposition without manifesting it (Hüttemann and Kaiser 2018). Dispositions are thus ontologically independent of their manifestations (Alvarez 2017). In contrast, having a categorical property necessarily implies that the property is manifest. For instance, a glass can be fragile even if it never breaks, whereas its being cylindrical involves actually exhibiting that shape. So, being able to distinguish between having and exhibiting a property is an indicator of dispositionality.

Second, dispositions have characteristic stimulus conditions, circumstances needed for the manifestation to occur. Again, a fragile entity must be struck in order to manifest fragility by breaking. Similarly, a soluble entity must be immersed in liquid to dissolve. Without the right conditions, the entity will not manifest the disposition. On the other hand, the occurrence of the stimulus conditions should lead to the disposition's manifestation, either necessarily (for "surefire" dispositions) or with a certain probability (for probabilistic dispositions). A tendency to take certain conditions as necessary for a property to be exhibited is another diagnostic feature of dispositions.

A third feature of dispositions is that they often permit inferring counterfactual conditionals. When an entity has a disposition, we can frequently infer that if the right stimulus conditions were to come about then the manifestation would occur. Knowing that a glass is fragile, we expect it would break if we were to drop it on tiles; knowing that sugar is soluble, we predict it to dissolve when we stir it into tea. There is considerable debate about using dispositions to make counterfactual inferences. Interfering factors (known as finks, maskers or antidotes, and mimics) can change the instantiation of a disposition, block a disposition's manifestation, or make it look like a disposition is manifesting without the right stimulus conditions (Martin 1994; Choi and Fara 2018). When interfering factors are present, the formula of inferring a disposition's manifestation from the presence of the stimulus conditions breaks down. Despite these problems, there remains an important, if "clumsy" (Martin 1994), connection between dispositions and counterfactual conditionals. Dispositions are generally about what entities would do and thus what we can expect them to do under certain conditions. As such, counterfactual conditionals about what an entity would do under certain circumstances serve as marks that a disposition might be involved.

A final feature of dispositions is that they can often be described using a canonical dispositional statement: a disposition to produce a manifestation *M* under stimulus conditions *C* (Choi and Fara 2018; Hüttemann and Kaiser 2018). Specifying manifestations and stimulus conditions is often challenging. For instance, fragility is manifested when a glass shatters, chips, cracks, or splinters, and these manifestations can occur upon being dropped, scratched, struck, pressed, twisted, or heated. Are these all examples of one stimulus condition, and if so how should we specify this condition? Such questions have for instance led to a debate about whether and when dispositions are "multi-track," that is, whether they have multiple stimulus conditions and manifestations and therefore cannot be described by simple canonical dispositional statements (Vetter 2013). Regardless of this debate, the tendency to describe properties in terms of characteristic manifestations and stimulus conditions is often indicative of dispositionality (McKitrick 2003).

We now have four diagnostic characteristics of dispositions: dispositions have characteristic manifestations and stimulus conditions, they typically license counterfactual conditionals, and they are often formulated in canonical dispositional terms. Diagnostic criteria in hand, we can turn to consider whether animal personality and individual specialisation are dispositions.

8.5 Behavioural Ecological Dispositions

In this section I argue that animal personality and individual specialisation carry marks of dispositionality. Taking these phenomena to be dispositions helps to make sense of why biologists take them to be single properties of individuals and why they require robustness. I start with animal personality.

Animal personalities have characteristic manifestations: the behaviours typed as bold, shy, aggressive, optimistic, and so on. In addition, these behaviours are exhibited given certain stimulus conditions, whether natural contexts or behavioural tests. Identifying animal personality also enables researchers to make inferences about how an individual will behave in certain contexts. For instance, they expect that an individual typed as bold using a novel object test and an open arena test will also behave in bold ways in future tests of the same type or in other, relevantly similar contexts, such as in a new enclosure or when exposed to a predator scent. Biologists often refer to animal personality in dispositional terms, for instance as a “behavioral tendency” (Wolf and Weissing 2012, 452) or “inherent disposition” (Réale et al. 2007, 294). Reflecting this use amongst biologists, Marie I. Kaiser and Caroline Müller have introduced a canonical formulation of animal personality as the disposition to perform certain types of behaviours in particular contexts (Kaiser and Müller 2021).

Behavioural ecologists sometimes worry about introducing disposition talk. For instance, Denis Réale and his colleagues argue against characterising personality as a disposition since behavioural ecologists do not investigate underlying psychological mechanisms (Réale et al. 2007, 294). This worry may be based on the common thought that studying a disposition requires investigating an underlying causal basis that links the stimulus conditions to the manifestation. Yet this thought has been disputed in philosophical circles; we can for instance talk about a fragile glass without determining its molecular structure (McKitrick 2003; Choi and Fara 2018). Similarly, it is possible to talk about a disposition for a behaviour without knowing anything about underlying psychological mechanisms. But the scepticism of dispositions may stem from another source. Animal personality is measured with the behaviour of individuals. Why not just settle with characterising animal personalities as robust individual differences in behaviour?

Apart from meeting the diagnostic criteria for dispositionality, a major reason to take animal personalities as dispositions is that it fits with the way animal personality is ascribed to individuals. Animal personality is a property that persists through periods when individuals do not engage in the relevant behaviour. An exploratory individual, for instance, maintains its exploratory disposition even when it is in other contexts where it doesn't engage in exploration, such as in a home cage or when resting. This makes sense once we distinguish between the instantiation and the manifestation of the personality, making the manifestation conditional on certain stimulus conditions.

We can extend the dispositional analysis of animal personality to individual specialisation. Individual specialisation covers phenomena like differences in resource preferences or performance on a certain resource. A preference for a food resource, for instance, can be understood as a disposition to use that resource more frequently than other individuals (a manifestation) in contexts of foraging, perhaps distinguishing foraging with and without competition (stimulus conditions). Similarly, performance can be seen as a disposition to perform better, that is, to be healthier, in better condition, or have higher fitness than others (a manifestation) given a particular resource (stimulus condition). Researchers can and often do formulate counterfactual conditionals about how individuals with certain preferences or performances would behave, survive, or thrive had their environment realised different competition levels or resource abundance.

So, both animal personality and individual specialisation can be understood as dispositions. Collectively, we can call these dispositions for certain sorts of behaviours, resource use and so on *behavioural ecological dispositions*. Behavioural ecological dispositions are manifested under different conditions, namely functionally or ecologically relevant scenarios, and are the source of observed individual differences in behaviour and ecological relations. They also support counterfactual conditionals and at least animal personality has been formulated in relatively canonical terms.

Behavioural ecological dispositions have two interesting features. First, contextual consistency means that they can be manifested in multiple ways and in multiple contexts. For example, as I mentioned earlier, boldness is manifested in approaching a novel object sooner and in spending more time in an open arena or out of shelter—two slightly different stimulus conditions and two slightly different manifestations. This means behavioural ecological dispositions could be characterised as multi-track dispositions, like many other dispositions in biology (Hüttemann and Kaiser 2018). Second, behavioural ecological dispositions depend on more than just the individual with the disposition. Animal personality and individual specialisation are defined in terms of individual differences. In addition, as I discussed earlier, the robustness condition means that an individual must be more similar to itself over time and contexts than it is similar to other individuals. So an individual can only have a behavioural ecological disposition if other individuals are different to it. As a consequence, behavioural ecological dispositions could be understood as *extrinsic* dispositions, requiring conditions outside the individual. It seems many common dispositions such as vulnerability and visibility also have implicit extrinsic conditions (McKitrick 2003).

Characterising animal personality and individual specialisation as multi-track, extrinsic dispositions can explain the requirement for robustness. Requiring that individuals exhibit fairly similar behaviour, resource use, and so on at different time points and in different contexts can be seen as a way to look for repeated manifestations of a multi-track disposition. Given the occurrence of the right stimulus conditions, repeated manifestation indicates that the individual has the disposition. On the other hand, a failure to exhibit the same manifestation over time or in the right contexts would indicate that the individual does not have the disposition. Robustness, in other words, is important for identifying multi-track dispositions. This is in contrast to categorical properties, such as colour pattern or body shape. Accurately measuring categorical properties may require repeated observation (Chapter 5), but a combination of temporal stability and contextual consistency would be superfluous. In contrast, the dispositional analysis can explain why robustness in its full scope is required for animal personality and individual specialisation.

8.6 Personality and Animal Identity

As well as making sense of the robustness requirement, the idea of behavioural ecological dispositions suggests a route to link robustness to identity. In this section I develop an analogy between behavioural ecological dispositions and human personality and consider how the analogy may help us to understand animal identity.

Human personality is generally understood to involve dispositions to certain sorts of behaviour, preferences, emotions, and so on in particular contexts (Goldie 2004; Banicki 2017). An extraverted person is friendly and open when meeting new people, say, but prone to loneliness if isolated, whereas an introvert acts in shy ways in groups of people and will prefer to be alone. Human personalities have characteristic manifestations, including behaviours and emotions, as well as stimulus conditions, such as social contexts. In addition, we often infer counterfactual conditionals from personalities, predicting what people will do on the basis of their personality. For instance, I rely on my generous friends to help me in situations like buying a birthday present for a mutual friend; I don't expect my miserly friend to contribute, and if they do, I am suspicious that they have ulterior motives. The predictive role of personality is however not straightforward. Psychological research indicates that contextual factors often predict behaviour better than personality (Goldie 2004, Chap. 3). For some, these results indicate that personalities are not real behavioural dispositions (Banicki 2017). Others argue that personalities are dispositions with a weak influence on behaviour such as narrowing down a range of likely actions (Goldie 2004, 69). This view tempers the predictive power of personality, while still allowing that personalities are behavioural dispositions that support imprecise counterfactual conditionals.

Behavioural ecological dispositions are similar to human personality. In the human case, the relevant dispositions are for certain types of behaviours, preferences, emotions, and so on, in certain often interpersonal contexts. In behavioural ecology, the dispositions are for behaviours, resource use rates, survival, and so on in certain functional or ecological scenarios. There are of course differences in the manifestations and stimulus conditions; animal biologists by and large avoid talk of emotions, for instance, and psychologists of course do not consider factors like how well humans survive and reproduce at different temperatures or humidity levels. Nevertheless, there is considerable overlap in the manifestations (e.g., behaviours, preferences) and contexts (e.g., social groups of different sizes, risky situations). In addition, both behavioural ecological dispositions and human personality seem to be extrinsic, multi-track dispositions. Both are characterised by multiple types of manifestations and multiple sorts of stimulus conditions. And they share the condition of individual differences: like animal personality, human personality dimensions are defined in a way to capture variation between individuals' behaviour, choices, emotions, and so on.

A possible disanalogy between human personality and behavioural ecological dispositions is that character traits might not be dispositions (Alvarez 2017)—where character is roughly synonymous with personality (Goldie 2004; Banicki 2017). Paradigmatic dispositions are truly ontologically independent of their manifestations: a vase can be fragile even if it never breaks. In contrast, Maria Alvarez argues that character must be manifested before it exists (Alvarez 2017). A person cannot have a character trait, she reasons, if they never exhibited any of the expected manifestations, even if they were never exposed to the right stimulus conditions. As a consequence, characters are different to paradigmatic dispositions because they fail to be independent of their manifestations. Instead, they are *tendencies*, properties that have to be manifested to be instantiated (Dinges and Zakkou 2021).

Are behavioural ecological dispositions also tendencies? It is true that you don't usually find a behavioural ecological disposition that hasn't been manifested, in contrast to fragile vases that have never broken. There are two reasons for this. First, unlike for vases, an individual's behavioural ecological disposition cannot be inferred from what type of individual they are. This is because individual differences are precisely those differences that are not due to recognisable population subgroups. As a result, we can only identify behavioural ecological dispositions when we have observed manifestations. Second, the stimulus conditions for behavioural ecological dispositions are often ubiquitous. Animals in the field usually encounter conspecifics to which they react aggressively or sociably, new objects or locations that they can approach boldly or timidly or different prey items they can consume with greater or lower frequency. Yet this is different for lab animals. For instance, researchers in

Project B01 test aggression in male guinea pigs by exposing them to another male. Males raised in pairs with females haven't faced the right stimulus conditions before. But as soon as they are exposed to a male, they manifest their disposition to aggression. Lab animals can therefore have a behavioural ecological disposition without having ever manifested it, and researchers discover such dispositions when they expose lab animals to the right conditions. Behavioural ecological dispositions therefore don't seem to be tendencies.

I think a similar case can be made for human personality. Humans are usually faced with a range of social environments, risks and challenges that provoke different feelings, behaviours, and so on—if not in reality, then through fiction and imagination. Hence, they basically always have manifested their personalities. But deprivation of the means to exercise charity, for instance, should not imply that a person is not charitable. Arguing for this point would however take us beyond the scope of this chapter. Instead, I will take it on credit that human personality and behavioural ecological dispositions are analogous dispositions and turn to the matter of identity.

Human personality is often thought to bear a special relation to identity. For instance, Peter Goldie cites the definition of personality in the Oxford English Dictionary, "that quality or assemblage of qualities which makes a person what he is, as distinct from other persons." (Oxford English Dictionary 2002; cited in Goldie 2004, 1) This sounds much like identity, what makes something the very thing it is, as opposed to any other thing (Chapter 7). Indeed, personality is generally seen as *characteristic* of a person, in the sense that it is both typical of a person and serves to identify them. In discussions of identity, "personality" is sometimes used to refer to memories and other psychological properties (B. A. O. Williams 1957; Wilkes 1981; Lizza 1993; M. T. Brown 2001). But even when we restrict personality to dispositions for behaviours, emotions, and so on, it seems natural to think of personality as what makes someone who they are, as what makes me *me* and you *you*. Hence, we might conclude that personality determines identity in persons. Then, by analogy to human personality and personal identity, behavioural ecological dispositions could be characteristic of particular individuals, determining animal identity.

Yet philosophers usually argue that human personality doesn't work as an identity condition. For example, although we might say that someone whose personality changed has “become a new person,” most philosophers would argue this is only metaphorical (Lizza 1993). Underlying superficial personality changes is the same person, persisting based on features such as bodily identity, psychological continuity, or autobiographical narratives (Olson 2019). As Eric Olson (2019) argues, personality or character is only a temporary and contingent property. As such, it cannot provide a necessary and sufficient condition for identity. The same argument could apply to behavioural ecological dispositions: as contingent and temporary, such dispositions cannot define animal identity.

To respond to this argument, we should first recall the distinction between synchronic and diachronic identity. Something that is characteristic of an individual might be relevant to synchronic but not diachronic identity. For instance, an individual’s characteristic resource preference might distinguish it from its fellows at a particular time, but not identify the individual over time. Hence, behavioural ecological dispositions could be temporary but still serve as conditions of synchronic identity, like phenotypic and ecological uniqueness (Chapter 7).

Second, we can recognise that behavioural ecological dispositions are not actually as temporary as they might seem. The requirement of robustness means that behavioural ecological dispositions persist across many observations and multiple different contexts, and often over entire life stages. This means behavioural ecological dispositions could be used for determining identity across reasonable time frames and realistic ecological contexts. Of course, behavioural ecological dispositions are still somewhat temporary: they often take time to develop, and they can and do change. Other features discussed by philosophers of biology as candidate persistence conditions, such as continuity of immunological or metabolic reactions, are more constant and long-lived (Guay and Pradeu 2016b; Pradeu 2018; Meincke 2019; 2021). Nevertheless, behavioural ecological dispositions could be relevant to diachronic identity within and potentially even across life stages.

Third, behavioural ecological dispositions are not as contingent as they may seem. Researchers investigate developmental, ecological and evolutionary causes of animal personalities and individual specialisation. Hence, although behavioural ecological dispositions are contingent in the sense that they could have been otherwise, they are also a product of a particular causal history: the individual’s maternal environment, birth order, nutritional status when developing, and so on.

This dependence on particular causal histories, combined with empirical evidence that at least animal personalities are often robust within developmental stages, suggests that it is very unlikely that behavioural ecological dispositions will change radically in a particular individual in a particular life stage. Similarly, it will be very unlikely that the dispositions would be duplicated in another individual, given the difficulty of replicating the relevant causal histories. We might even be able to apply the idea of biological necessity again: the chance of change or duplication in a life stage could be so slim as to be considered impossible by practising biologists, falling outside the space of relevant possibilities.

I cannot provide a full argument that behavioural ecological dispositions are robust and differentiating with biological necessity. More evidence would be needed to show that different causal histories do bring about differences in behavioural ecological dispositions, and to further support the robustness of these properties. Instead, I will settle with the claim that behavioural ecological dispositions could perhaps serve as a condition of identity for particular life stages. This matches the principle of robust differentiating properties discussed in Section 8.2. And as was the case with this principle, the suggestion is enough for the present purposes, helping to explain the link that behavioural ecologists make from robustness to identity and suggesting new topics for the philosophy of biological individuality.

8.7 From Robustness to Individuality

Biologists wanting to reidentify individuals use properties that are robust over the timescale they are interested in. And properties like behavioural dispositions that are robust over life stages can define an animal's identity for that period. But for a property to serve as a truly necessary and sufficient condition of identity, it would have to be perfectly robust, over the entire period of the animal's existence, as well as perfectly differentiating, that is, unique. None of the properties I looked at here are perfectly robust. But more local, restricted principles of animal identity can be derived from empirical research.

First, reidentification practices involve using natural or artificial properties which are robust and differentiating. Although reidentification practices cannot justify a practically necessary principle of identity, empirical research on the robustness and differentiation of biological properties may allow us to develop more restricted, biologically necessary principles of animal identity. Second, a dispositional analysis of animal personality and individual specialisation and an analogy to human personality supports a connection to identity. Both human personality and behavioural ecological dispositions can be considered characteristic of an individual. In addition, behavioural ecological dispositions are less temporary and contingent than often thought, meaning they might, provided further argumentation, be able to provide a biologically necessary condition of animal identity within certain timeframes.

The idea that behavioural ecological dispositions could be conditions on animal identity has implications for the debate on personal identity, especially the position known as animalism. Animalists argue that human persons are nothing but animals, and hence that personal identity depends only on the identity conditions of animals (Meincke 2021; Snowdon 2021). This position is usually taken to imply that psychological properties are irrelevant to defining persistence over time. Instead, the focus is on metabolism, homeostasis, immunological reactions, development, functional integration, and so on (Meincke 2019; 2021; Newman 2021; Snowdon 2021). Such properties and processes, animalists argue, can be used to answer questions about personal identity, such as whether a person persists in a vegetative state.

The analogy between human personality and behavioural ecological dispositions supports the animalist argument for continuity between animal and human identity. Yet it does so in a way that blurs the distinctiveness of the animalist position. If animalists think personal identity is determined solely by the identity conditions of animals, then they ought to include behavioural properties such as personality as at least candidate conditions. Taking behavioural dispositions as relevant to identity therefore broadens philosophical attention to behavioural and ecological conditions of animal identity.

As well as bearing implications for animalism, the potential of properties like colour patterns, body shapes, or animal personalities to define identity complicates arguments for a process ontology of biology. Advocates of process ontology argue that animals persist not by being stable but by changing, for instance by performing metabolic processes such as respiration and digestion (Nicholson and Dupré 2018; Meincke 2019; 2021). In this chapter we saw that stability, such as the possession of robust properties, may also be part of animal persistence. Whether the role of robustness in identity is compatible with a process ontology is an interesting question for future research.

Finally, we can return to the questions that prompted this chapter. Why do behavioural ecologists take robustness to be relevant to individuality? Robustness is important for practices of reidentification and for behavioural ecological dispositions, and it is at least potentially relevant to defining identity. Given that identity is one aspect of individuality (Chapter 7), it therefore makes sense that behavioural ecologists include robustness as part of their understanding of individuality. In this sense, robustness is like phenotypic and ecological uniqueness. Of course, neither phenotypic and ecological uniqueness nor robustness represent the entirety of individuality. As I discussed in Chapter 7, it is generally necessary to first be able to count individuals before determining whether they have unique or robust properties. But merely being countable does not make something an individual. Based on my analysis of individuality research in behavioural ecology, exhibiting robust individual differences, being identifiable, and being unique are all important additional aspects of being an individual animal.

9 An Integrated Account of Individuality

I began this thesis with one central question and three sub-questions. What is individuality in behavioural ecology? How do behavioural ecologists understand individuality? How do they study individuality? And what can individuality in behavioural ecology tell us about biological individuality more generally? We now have the materials to answer these questions. In this final chapter I draw up a picture of individuality in behavioural ecology, summarising some of the key insights and highlighting directions for future research.

Research on individuality in behavioural ecology covers a number of interrelated phenomena. On the one hand, behavioural biologists study animal personality and other phenotypic traits such as colour patterns, chemical phenotypes and hormone profiles. These are all *individualised phenotypes*, defined as phenotypic traits for which there are individual differences, often with the extra requirement that the individual differences are robust. On the other hand, ecologists study individual specialisation, as well as individual differences in ecological factors such as population density or developmental environment. These phenomena can be understood in the framework of *individualised niches*, which are composed of niche dimensions for which there are individual differences that are sometimes robust. As a term which is used to cover individualised phenotypes and individualised niches, "individuality" can therefore be defined as a matter of *robust individual differences* in phenotypic and ecological properties.

However, robust individual differences include differences between groups of individuals, not only differences between single individuals. So, what do robust individual differences have to do with individuality? Behavioural ecologists bring up a number of other ideas when discussing individuality, including *individual-level properties*, *individual-level processes*, and *phenotypic and ecological uniqueness*. Phenotypic and ecological uniqueness, the idea that individuals have unique niches and unique sets of phenotypic properties, is most dominant. Based on how biologists in the CRC associate individuality with uniqueness, we arrived at a second definition of individuality as phenotypic and ecological uniqueness. This definition is evident in individuality researchers' concerns that their research on group-level differences do not relate to individuality—such a worry only makes sense if they understand individuality in terms of phenotypic and ecological uniqueness rather than just robust individual differences.

The way biologists discuss their methods for measuring, experimenting and doing statistics when studying individuality provides clues to how the two definitions of individuality relate to one another. Measuring and explaining unique properties or sets of properties is very difficult in biology. In contrast, including between-group differences in robust individual differences enables the use of group-based approaches for measurement and generating causal explanations. Between-group differences are in turn approximations or partial elements of individuals' more complex unique sets of properties. Studying between-group differences can therefore be used to develop an approximate and partial picture of individuals and their unique sets of properties. In view of these relations of approximation and decomposition, robust individual differences serve as an *operationalisation* of phenotypic and ecological uniqueness.

Why do biologists understand individuality in terms of phenotypic and ecological uniqueness at all? The topic of uniqueness has been sidelined in the recent philosophical debate about biological individuality. Nevertheless, some metaphysicians think that uniqueness is an important aspect of individuality. They argue that something is an individual when it is a single, countable entity, and when it is the same as itself and distinct from other similar entities. These two features are called *countability* and *identity*. Philosophers of biology have focused mostly on countability, for instance when they investigate what determines an organism's boundary or the unity of its parts. In contrast, phenotypic and ecological uniqueness is most relevant to identity, since identity requires that individuals are unique. Metaphysicians usually ignore phenotypic traits or niches because it is metaphysically possible that there could be two individuals with identical total phenotypes or niches. Although this is true, I argued that exactly identical total phenotypes or niches will not come about within the sphere of possibility which interests biologists, due to the sheer level of compositional and dynamic complexity involved and the limitations on the number of individuals that can exist under similar conditions. Having unique phenotypic and ecological properties is therefore *biologically necessary* for something to be a biological individual.

Phenotypic and ecological uniqueness might determine an individual's identity at one time point. But many of an organisms' phenotypic and ecological properties change throughout its life, sometimes very dramatically. Total phenotypes and niches therefore cannot define an individual's identity over time. Looking at how biologists reidentify individuals, we saw that they rely on robust differentiating properties such as natural colour patterns or artificially added tags. Reidentification practices do not themselves require that properties are necessarily and universally robust and differentiating. However, empirical evidence can indicate that for a particular species there are some properties, such as colour patterns, which are necessarily robust and differentiating and can therefore define identity over time. Adding to this, a dispositional analysis of animal personality and individual specialisation suggest that some sorts of robust differentiating properties can be seen as "characteristic" of animal individuals. This blurs the distinction between animal and personal identity, as well as suggesting ways in which questions about identity could be settled using behavioural ecological dispositions.

Figure 9.1 depicts the steps from the phenomena studied in individuality research, through definitions of individuality and principles of identity in behavioural ecology, to broader notions of biological individuality. The first parts of this chart are already a significant achievement. Identifying individuality phenomena and distinguishing the two major definitions of individuality in behavioural ecology is important for the field of individuality research in behavioural ecology, where such clear definitions and distinctions are still lacking. In addition, recognising robust individual differences as an operationalisation of phenotypic and ecological uniqueness is essential for assuaging some of the worries that biologists themselves have as well as determining the possibilities and limitations of scientific research into individuality. Clarifying the links between individuality phenomena, robust individual differences, and phenotypic and ecological uniqueness also helps philosophers. We can now make sense of some of the perplexing statements made by some biologists, such as that individuals can be identified with groups for the purposes of experimentation (see Chapter 3), or the contradictions between biologists who equate animal personality with unique behaviour and others who say they they're not studying unique behaviour, even if they do study animal personality.

We might be inclined to leave it at that: individuality in behavioural ecology is just the uniqueness of phenotypic and ecological properties, which is studied by decomposition and approximation using robust individual differences. However, the links from the behavioural ecologists' understandings of individuality to broader accounts of individuality are equally important.

First and foremost, the links to philosophical accounts of individuality allow us to understand why biologists take uniqueness to be relevant to individuality. Ignoring these links would mean prematurely surrendering the opportunity to make better sense of biologists' practices. Why do biologists use the term "individuality" for phenotypic and ecological uniqueness and robust individual differences? They just do, we would have to answer. Overlooking the links from uniqueness through identity to individuality could even invite the interpretation that behavioural ecologists are mistaken in their use of the term "individuality," since it doesn't match with how the term is used in other biological disciplines.

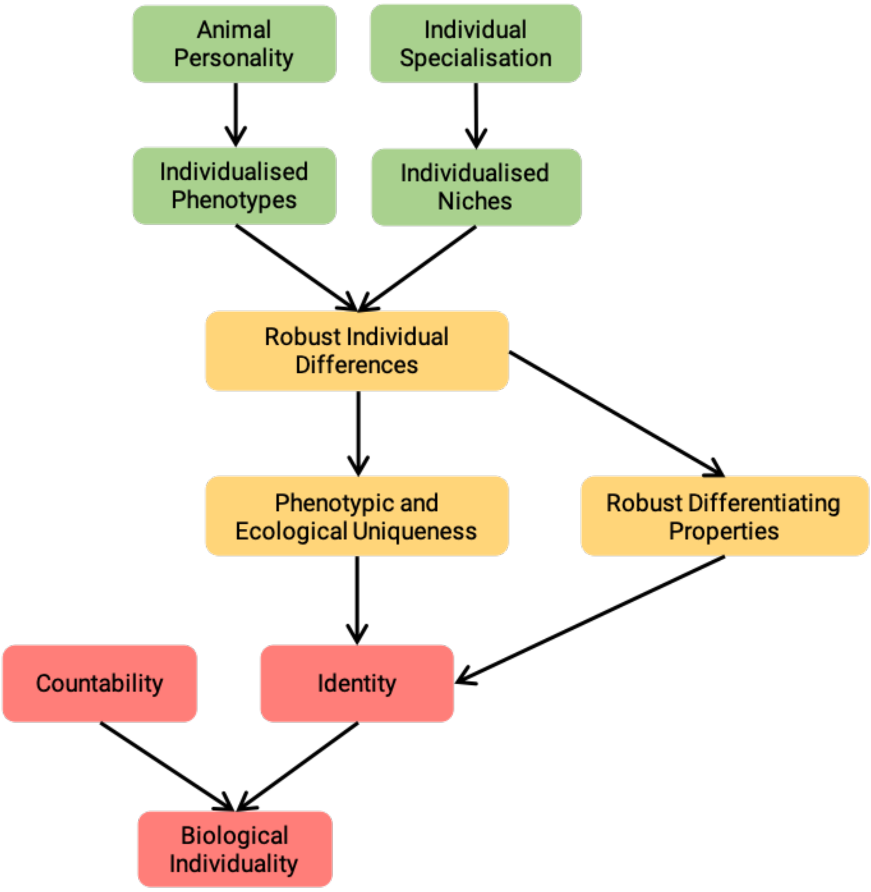

Figure 9.1. Exploring Individuality in Behavioural Ecology. Starting with the phenomena studied in behavioural ecology, we developed a first definition of individuality in behavioural ecology as robust individual differences. Based on biologists' discussions of individuality and their epistemological troubles, we identified robust individual differences as an operational definition of phenotypic and ecological uniqueness. Finally, we saw that phenotypic and ecological uniqueness and robust differentiating properties are relevant for defining synchronic and diachronic identity. Identity and countability are two important aspects of individuality in biology more broadly, defining what it is for something to be a biological individual.

It is of course possible to ultimately reject the connections between individuality concepts in behavioural ecology and in other biological disciplines and in metaphysics more broadly. On this view, behavioural ecologists have their own distinctive concept of individuality, unrelated to other concepts but sharing the same term. But justifying this view demands serious consideration of the plausible relations between individuality concepts and the explanations of behavioural ecologists' practices that these relations suggest.

A second reason to take seriously the links to broader philosophical accounts of individuality is that they bring new insights to the philosophical debate on biological individuality. When identity is recognised alongside countability as important for individuality, philosophers gain a broader set of questions to ask about biological individuality (Kaiser and Trappes 2021). More than just counting and corollary issues like drawing boundaries or determining parthood, philosophers can investigate different sorts of uniqueness or how various sorts of biological features might determine identity over time. I have already made a first step in this direction with my arguments for the biological necessity of phenotypic and ecological uniqueness and the relevance of robust differentiating properties for identity. Such ideas extend our understanding of what it is that makes something a biological individual to encompass more features and more disciplinary perspectives.

On this basis, I will sketch an integrative understanding of biological individuality, depicted in Figure 9.2. For something to be an individual it must be a single entity, demarcated from its environment, including from other individuals, made up of parts organised or working together in a certain way, and so on. These are all insights we can gather from recent philosophical work on biological individuality, even if there are different accounts for just what determines boundaries, parthood, or unity (Kaiser 2018). In addition to countability, an individual must be itself, distinct from other individuals, both at one time point and across time. Identity can be determined by various sorts of properties and processes, including but by no means limited to the ones I discussed: total phenotypes, individualised niches, robust differentiating properties, and behavioural ecological dispositions.

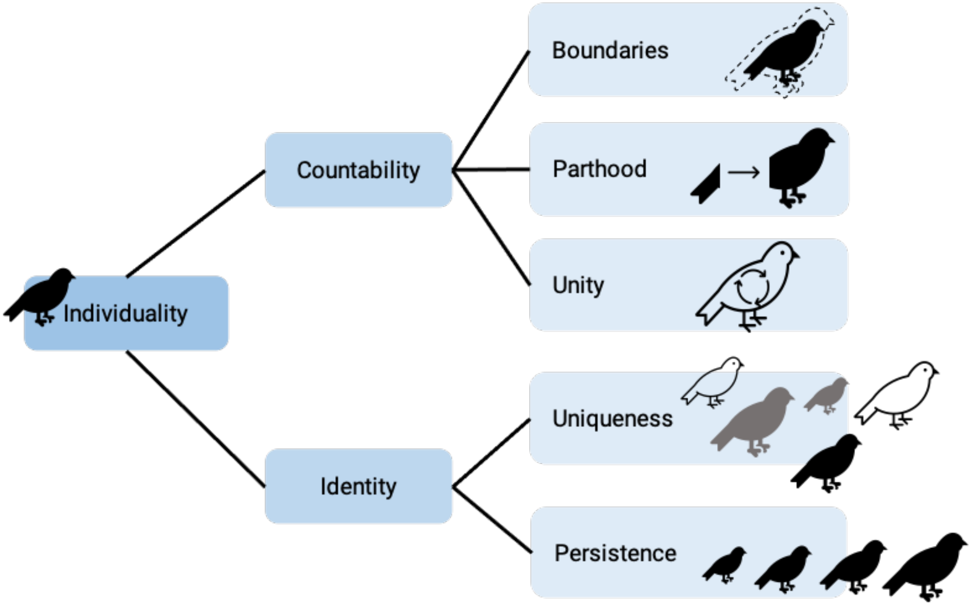

Figure 9.2. An Integrated Understanding of Biological Individuality. Individuality involves both countability and identity. The philosophical debate has largely focused on countability, and thereby on issues like boundaries, parthood, and unity (Kaiser 2018; Kaiser and Trappes 2021). Looking at behavioural ecology draws greater attention to issues of identity, such as uniqueness and persistence, which are often marginal in debates on biological individuality. The concepts depicted here are delineated largely based on how they feature in the debates on biological individuality and identity, despite some very important connections between them. For instance, many authors ask about what makes an individual hang together (unity) or where to draw its boundaries; sometimes these questions concern unity over time or temporal boundaries and thus are questions about persistence, too (Kaiser and Trappes 2021). Nevertheless, the focus in the literature has largely been on determining what counts as a single unit across time, and thus on countability, and less on preservation of identity as that which makes something the very thing it is.

In developing this integrated account of biological individuality, we encountered the idea of *individualised research*. Researchers strive to move beyond broad, species- or population-level approaches in order to investigate individuals and their properties. However, actually reaching the point of measuring and understanding individuals is not always directly possible. Instead, researchers use a larger number of smaller groups to gain information about the individuals they study. This information can be used to describe and explain individuals' properties, but it will always be approximate and partial. Individualised research involves moving towards but never entirely reaching the point of studying individuals' unique sets of properties.

Individualised research in behavioural ecology has escaped the attention of philosophers. However, it bears some similarities to methodological approaches in other disciplines that have been discussed in philosophy. Finding out about the possibilities and limitations of researching unique individuals in behavioural ecology sheds greater light for instance on why population thinking in evolutionary biology doesn't actually involve looking at unique individuals (Mayr 2006; Ariew 2008). Individualised research in behavioural ecology also contrasts with methodological individualism in the social sciences (Steel 2006; Heath 2015). Sociologists and psychologists are often able to focus on single individuals. In contrast, behavioural ecologists rely on groups for making measurements and gaining causal knowledge and continue to recognise group-level causal processes. Finally, the challenges involved in individualised research turn out to be quite similar to those in personalised medicine (Nicholls et al. 2014; Walker, Bourke, and Hutchison 2019; Vegter, Zwart, and van Gool 2021). In both behavioural ecology and health sciences, the aim for more precise, individually tailored descriptions, explanations and interventions conflicts with the requirements of accurate measurement and generating causal knowledge. Further investigation into the similarities and differences between individualised research in behavioural ecology and other individual-focused approaches could help to develop these initial coarse findings into a comprehensive account of individualisation in scientific research.

A study of the interdisciplinary nature of individualised research could also extend from methodology to the level of content. Sociologists, for instance, argue that social, economic and cultural changes since the end of the middle ages have generated increasing *individualisation* (Simmel 1971; Beck 2002; Junge 2002; Cortois and Laermans 2018). Individualisation, also called individualism (distinct, however, from methodological individualism), denotes phenomena such as the increasing localisation of responsibility with individuals, the availability of more varied social roles, or the demand on individuals to develop their own authentic, often unique, self-expression (Honneth 2004; Cortois and Laermans 2018). This investigation into social processes that affect differentiation between individuals is strikingly similar to behavioural ecology research into mechanisms producing individualised niches.

Another connection is between animal personality and human personality. Acknowledging animal personality increases awareness of the great complexity of animal behaviour and the striking similarities between human and non-human animals. Some have even argued that this raises non-human animals in our ethical estimation (Birke 1994). At the minimum, taking animal personality into account is crucial for improving the treatment of captive animals, for instance through improved diagnosis of behavioural problems or provision of conditions that suit animals of particular personalities (Tetley and O'Hara 2012; Richter and Hintze 2019). The insights from and debates about personality psychology could in turn prove relevant for animal welfare interventions based on animal personality.

The interconnections between individuality research in behavioural ecology and similar topics in the human sciences deserve more attention than can be given here. On the one hand, the disciplines seem to face parallel, though not identical, methodological challenges. A comparison of the various solutions on offer in the different fields would likely generate both new possibilities for different fields as well as a greater understanding of the differences in the epistemic position of the different disciplines. On the other hand, there are commonalities in the topics of research, such as individuality, personality, uniqueness, and mechanisms or processes affecting individual differences. Yet there are also differences: it is questionable, for instance, whether non-human animals should be assigned responsibility or selfhood, and many behavioural biologists are wary of psychological interpretations of animal behaviour. A comparison between these phenomena would likely provide a clearer vision of individuality in both non-human animals and humans, serving the basis for a more interdisciplinary account of individuality beyond biology.

Finally, I want to take a moment to reflect on the methodology I used in this thesis. Qualitative methods are still unusual in philosophy, especially the use of semi-structured interviews and coding. Using these methods has been essential to developing an account of individuality in behavioural ecology. Together with other philosophers, I believe that such methods can productively be employed in many philosophical projects investigating scientific practices in real time, above and beyond published or archived materials (Mansnerus and Wagenknecht 2015; Osbeck and Nersessian 2015). These methods provide deep, contextualised insights which are suitable for developing detailed and reflective philosophical accounts of science in the making. On the other hand, qualitative methods can be supplemented by broad scale or quantitative methods to strengthen generalising findings beyond the case study to entire research fields or disciplines. The qualitative results obtained in this study provide a perfect basis for such future work on individuality in behavioural ecology.

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