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INDIVIDUAL-LEVEL MECHANISMS IN ECOLOGY AND EVOLUTION

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PHILOSOPHERS HAVE STUDIED MECHANISMS in many fields in biology. The focus has often been on molecular mechanisms in disciplines such as neuroscience, genetics, and molecular biology, with some work on population-level mechanisms in ecology and evolution. We present a novel philosophical case study of individual-level mechanisms, mechanisms in ecology and evolution that concern the interactions between an individual and its environment. The mechanisms we analyze are called niche choice, niche conformance, and niche construction (NC^3) mechanisms. Based on a detailed analysis of biologists' research practices, we develop metaphysical claims about the components and organization of NC^3 mechanisms, the phenomena they bring about, and how these phenomena relate to individual differences, a major explanatory target in the field. We provide reasons for why processes of niche choice, conformance, and construction are mechanisms and how they differ from molecular mechanisms underlying individual differences. Finally, we demonstrate that a general representation of NC^3 mechanisms is highly abstract, such that more specific types of NC^3 mechanisms in particular study systems exhibit more complex components organized in more complex ways. Our case study highlights some distinctive features of individual-level mechanisms in ecology and evolution, such as complex and heterogeneous organization and multiple phenomena.

1. INTRODUCTION

How do zebra finch males react to different levels of competition? Why do different buzzards use different kinds of greenery in their nests? What makes a female fire salamander deposit its larvae in a pond or a stream? These are typical sorts of questions asked by behavioral and evolutionary ecologists. To address such topics, behavioral and evolutionary ecologists study individual-level ecological-evolutionary mechanisms. In this chapter, we present a philosophical case study of a paradigmatic example of individual-level mechanisms, so-called niche choice, niche conformance, and niche construction (NC^3) mechanisms.

NC^3 mechanisms reveal how individual organisms interact with their environment, that is, in which activities an individual engages and which acting entities constitute the individual's environment. Specifically, NC^3 mechanisms reveal how individuals change their phenotype–environment match and fitness and, as a result, their individualized niches. Due to their focus on individual organisms rather than populations or sub-organismal entities, NC^3 mechanisms are an instance of "individual-level" (Pâslaru 2018, 349) ecological-evolutionary mechanisms.

The goal of our case study is to contribute to a better understanding of individual-level mechanisms in ecology and evolution. Much of the philosophical work on mechanisms has focused on fields such as cell biology, molecular genetics, and neuroscience (e.g., Machamer, Darden, and Craver 2000; Bechtel 2006; Craver 2007; Craver and Darden 2013). This chapter falls in line with the few philosophical analyses that have been conducted on higher-level biological mechanisms in ecology and evolutionary biology (Baker 2005; Skipper and Millstein 2005; Barros 2008; Pâslaru 2009; 2014; 2018; Raerinne 2011; Havstad 2011; DesAutels 2016; 2018).

Unlike much of this literature, however, our aim is not primarily to consider the extent to which niche choice, conformance, and construction fit into the framework of the New Mechanists (e.g., Machamer, Darden, and Craver 2000; Bechtel 2006; Craver 2007; Craver and Darden 2013; Glennan 2017). Rather, we use this framework to analyze the investigative and explanatory practices of studying NC^3 mechanisms in order to get a deeper understanding of what NC^3 mechanisms are. What makes NC^3 mechanisms special and distinguishes them from, for instance, molecular mechanisms? Which phenomena are explained by describing NC^3 mechanisms, and how do they relate to other kinds of phenomena to be explained in this research field? What components do NC^3 mechanisms have, and how are the components organized?

We begin in section 2 by characterizing our analysis as an instance of "metaphysics of biological practice" (Kaiser 2018b, 29) and by explicating our philosophical methodology. In section 3, we introduce the NC^3 mechanisms, looking at how they involve a focal individual and a focal activity and why biologists refer to them as mechanisms. We then go on to investigate the phenomena that NC^3 mechanisms explain. In section 4, we examine how they explain changes in phenotype–environment match and fitness. Since individual differences are a key topic in the research field that we analyze, in section 5 we consider how individual differences figure in to the NC^3 mechanisms. We argue that NC^3 mechanisms explain a second type of phenomenon, namely changes in individualized niches. Finally, in section 6, we point out how concrete cases of NC^3 mechanisms are far more complex than their initial abstract representation, indicating that simplification is necessary for understanding the commonalities between NC^3 mechanisms.

2. METAPHYSICS OF BIOLOGICAL PRACTICE

Our analysis of NC^3 mechanisms as paradigmatic cases of ecological-evolutionary mechanisms is an instance of "metaphysics of biological practice" (Kaiser 2018b, 29). We develop metaphysical claims about what NC^3 mechanisms are, that is, their ontology. We do so on the basis of careful analysis of scientific practices: how biologists investigate, reason about, and use NC^3 mechanisms to explain certain phenomena. In this section, we specify the metaphysical and the practice-based character of our analysis in turn.

First, we make more than epistemic claims about how biologists represent, study, and explain NC^3 mechanisms. Our analysis involves developing *metaphysical claims* about what NC^3 mechanisms are, which phenomena they bring about, what their components are, how their components are organized, and what distinguishes them from other kinds of biological mechanisms. These are metaphysical (or, more precisely, ontological) claims because they concern what the world is like, which kinds of entities exist in the world, and what these entities are like. Since we draw these metaphysical claims about NC^3 mechanisms from epistemic practices in biology, they can only be "provisional" (Kaiser 2018b, 30). Our metaphysical claims depend on a realistic interpretation of these epistemic practices. That is, we presuppose that the scientific claims made in these practices (or that the practices rely on) are true and that the theoretical terms that they include (e.g., "NC^3 mechanism," "fitness," "environment," or "phenotype") refer to entities that exist in the world independently of scientific investigation. The provisional nature of our claims, however, does not run contrary to their metaphysical character.

Second, we adopt the approach of *practice-based* or "broad-practice-centered" (Waters 2019) philosophy of science. This means that we pay special attention to how biologists investigate NC^3 mechanisms, which research questions they pose, how they report about and draw conclusions from their empirical findings, which explanatory strategies they pursue when investigating NC^3 mechanisms, and how they individuate these mechanisms and their components.

To do so, we draw on our work as members of a large biological Collaborative Research Centre (CRC) investigating NC^3 mechanisms. Being members of the CRC allows us to take into account a broad variety of empirical sources when philosophically analyzing the research practices of the biologists. We analyze the project plans and experimental designs described in the grant application and research talks as well as how the biologists report about the empirical results of their projects in research talks and publications. Where possible, we cite publications, but the ongoing nature of this case study means that many projects are still awaiting final results.

We also gain fruitful insights by directly collaborating with the biologists to refine their central concepts and theoretical assumptions. For instance, we have collaborated with CRC members on a paper for biologists setting out the theoretical framework of the NC^3 mechanisms (Trappes et al. 2022). Our approach is thus not only practice-based and "reflective" but also an example of "*embedded* interdisciplinarity" (Kaiser et al. 2014, 66, our emphasis) or what has been called "philosophy-of-science in practice" (Boumans and Leonelli 2013) and "philosophy in science" (Pradeu et al. 2021). Most claims in this chapter, however, result from a reflection about the CRC's research practices and extend beyond our collaborative work with the biologists.

In line with "*empirical* philosophy of science" (Wagenknecht et al. 2015, our emphasis), we also use two qualitative empirical methods to gain more information about the biologists' practices: a questionnaire and interviews. We conducted the questionnaire in October 2018, toward the beginning of the first funding period. Among other topics, we asked members of the CRC open-ended questions about the mechanisms they were researching and how they understood the NC^3 mechanisms. There were thirty-seven participants, 90 percent of all scientific CRC members including PhD students, postdocs, and principal investigators (PIs). Responses were analyzed using hypothesis-driven coding, starting with an extensive list of codes as well as grounded and semi-grounded qualitative coding, generating codes while reading responses.

The interviews were conducted in October 2019 with fourteen members of the CRC on their research in the CRC. Interviews were semi-structured with single or paired interviewees. Transcripts were analyzed using hypothesis-driven coding. NC^3 mechanisms were discussed in many of the interviews, both spontaneously and in response to direct questions. In this chapter, we present some results from the questionnaire and interviews and use them in our analysis of the CRC's investigative and explanatory strategies for studying NC^3 mechanisms. For a full description of the empirical methods and further results, see Trappes (2021a; 2021b).

We agree with philosophers such as Ken Waters (2004) that directly asking scientists what they mean by a certain concept is often not the best way to philosophically analyze this concept. At least it should not be the only kind of empirical information that philosophers rely on. Questionnaires and interviews, however, can also be used to analyze what scientists say and how they use a certain concept without directly asking how they understand or define this concept. Waters too acknowledges that empirical methods, such as polls, questionnaires, and interviews, provide a "kind of information [that] could be valuable for the critical analysis of scientific concepts" (2004, 31–32). We think that the philosophical use of empirical methods is particularly fruitful for philosophy *in* science, that is, when philosophers and scientists are members of the same research group and collaborate to pursue the same or closely related research goals. In this case, analyzing the research practices of the scientists by, for instance, examining their research plans and publications, listening to their research talks and discussions, and speaking with scientists is complemented by more structured interactions, such as semi-structured interviews and questionnaires. We therefore use the data gathered from our qualitative empirical methods as one among many resources to develop a broad picture of the biologists' research practices and to generate metaphysical claims about the NC^3 mechanisms.

3. INTRODUCING NC^3 MECHANISMS

3.1 Individual-Level Ecological Mechanisms

Often when we think of mechanisms in biology, we think of things like protein synthesis, gene expression, or neuronal transmission. This is reflected in the literature on mechanisms in philosophy of biology, which has by and large focused on examples of *molecular and genetic mechanisms* in fields such as cell biology, molecular genetics, and neuroscience (e.g., Machamer, Darden, and Craver 2000; Bechtel 2006; Craver 2007; Craver and Darden 2013). This is not to say that biological mechanisms on higher levels and from other biological areas have been ignored. Philosophical work has also been done, for example, on the mechanism of natural selection (Baker 2005; Skipper and Millstein 2005; Barros 2008; Havstad 2011; DesAutels 2016; 2018) and on mechanisms in ecology (Pâslaru 2009; 2014; 2018; Raerinne 2011). Nevertheless, molecular and genetic mechanisms play a dominant role when philosophers think about biological mechanisms.

Interestingly, biologists also tend to associate the concept of mechanism with molecular or genetic mechanisms. In our case study, for instance, the biologists frequently use the term "mechanism" to refer to genetic, epigenetic, transcriptomic, physiological, or hormonal mechanisms that underlie individual differences in behavior or other phenotypic traits. On the other hand, however, they also talk about niche choice, niche conformance, and niche construction as mechanisms. They therefore seem to recognize the existence of mechanisms at higher levels than the molecular.

NC^3 mechanisms can be characterized as "*individual-level mechanisms*" (Pâslaru 2018, 359, our emphasis) because they operate at the level of individual organisms and their abiotic and biotic environment. Usually, descriptions of NC^3 mechanisms identify one (type of)[1] individual as the so-called *focal individual*. It is the individual that takes center stage in the study of an NC^3 mechanism and that engages in the *focal activity* that determines whether the mechanism is one of niche choice, niche conformance, or niche construction. In line with how the concept of an activity is understood in the mechanism debate (Illari and Williamson 2013; Kaiser 2018a), focal activities can be specified as what individual organisms do. They are temporally extended and actualized, and they produce changes (Kaiser 2018a, 120). Besides the focal individual, which is actively involved in a focal activity, there are other entities (passively and actively) involved in a focal activity. In terms of interactions, one can say that all focal activities require that the focal individual interacts with different parts of its abiotic and biotic environment.[2]

In mechanisms of niche choice, conformance, and construction, these individual–environment interactions differ in characteristic ways from each other. As part of our interdisciplinary work in the CRC, we collaborated with the biologists on formulating precise and practically useful definitions of the NC^3 mechanisms (Trappes et al. 2022). According to these definitions, the three focal activities involved in NC^3 mechanisms are specified as follows: in niche construction, the focal individual makes changes to its environment; in niche choice, it selects an environment; and in niche conformance, it adjusts its phenotype.

First, in niche construction mechanisms, the focal individual *makes changes to its environment*. This means that the change is happening primarily in the environment rather than in the individual or only in the individual–environment relation. In addition, the individual is actively involved in making these changes (rather than playing a passive role in this activity; Kaiser 2018a, 120). Niche construction mechanisms can involve changes of any abiotic and biotic environmental conditions. This includes altering the presence or abundance of other species, such as when red flour beetles (*Tribolium castaneum*) release quinones, which in turn shapes which microbiota grow in the flour where they live (Project C01; Schulz et al. 2019). Changes to the biotic environment also include changes made to the social environment, such as conspecific behavior or social group size. An example of social niche construction is when harvester ant (*Pogonomyrmex californicus*) queens interact either aggressively or sociably with other queens, which affects the other queens' aggression and sociability and ultimately determines whether they will form a colony together (Project C04; Overson et al. 2014).

Second, the focal individual in niche choice mechanisms *selects an environment* and thereby changes its relation to the environment. Selecting an environment can be understood fairly broadly here, including the individual changing its location, its resource use, or its (social) interactions. For example, in forests in central Germany, female fire salamanders (*Salamandra salamandra*) choose whether to deposit their eggs in free-flowing streams or in standing ponds; this is selection of the reproductive environment, which determines the environment experienced by the offspring (Project A04; Krause and Caspers 2015; Oswald et al. 2020). As another example, researchers tested how cognitive differences affect whether mice (*Mus musculus*) choose to forage in a dangerous environment that has a high reward or in a benign environment that has a low reward (Project A02).

Finally, niche conformance mechanisms involve the focal individual *adjusting its phenotype* in response to certain environmental conditions. Niche conformance therefore involves phenotypic plasticity, the ability to develop different phenotypes, including behavioral, morphological, or physiological traits, in different environments. For instance, one project in the CRC studies how male zebra finches (*Taeniopygia guttata*) alter their levels of aggressive and courtship behavior as well as their ejaculate traits in response to the presence of a male competitor; in this case, the environment to which the focal individual responds is the level of reproductive competition, created by the extra-pair male (Project B04). Another example of a niche conformance mechanism studied in the CRC is the way Antarctic fur seal (*Arctocephalus gazella*) pups (are hypothesized to) change their behavior, hormones, and immune profile in response to the social density of the colony in which they develop; here the environment to which the pups conform is the social density as well as the corresponding parasite load, infection risk, and predation risk (Project A01; Grosser et al. 2019).

In sum, an NC^3 mechanism reveals how a focal individual interacts with its abiotic and biotic environment by either making changes to its environment (niche construction), selecting an environment (niche choice), or adjusting its phenotype (niche conformance). Other authors have grouped these activities together as various kinds of niche construction (Aaby and Ramsey 2019; Chiu 2019). The CRC, however, suggests reserving the term "niche construction" for the more specific mechanism of making changes to the environment, distinguishing as separate mechanisms the other two ways in which individuals interact with their environments (Trappes et al. 2022).

3.2 Why Mechanisms?

As individual-level mechanisms, NC^3 mechanisms are distinct from the lower-level molecular (i.e., genetic, epigenetic, transcriptomic, physiological, or hormonal) mechanisms that underlie individual differences. Given this distinction and the status of molecular mechanisms as paradigmatic biological mechanisms, one might wonder why organism–environment interactions should be described in terms of mechanisms at all. Biologists in the CRC use the term "mechanism" to refer to niche choice, conformance, and construction. This fact alone, however, does not take us very far. In this section, we uncover the biologists' *reasons* for referring to NC^3 as mechanisms. We argue that these reasons are in line with the framework of the New Mechanists (e.g., Machamer, Darden, and Craver 2000; Bechtel 2006; Craver 2007; Craver and Darden 2013, Glennan 2017).

In the questionnaire, we asked participants what makes niche choice, conformance, and construction mechanisms. Various reasons were provided, and the answers were often quite illustrative. For instance, one respondent stated that "all three processes are ways by which individuals can either adjust or adapt to environments. Therefore, they are all tools for an individual to match its phenotype with the environment." Another wrote, "I think of a mechanism very basically as something that describes how a pattern or phenomenon comes to exist/occur. I think all three are potential mechanisms as each describes how individual niches variance can arise within and between organisms."

In total, twenty-three (of thirty-seven) respondents provided reasons for characterizing niche choice, conformance, and construction as mechanisms. A total of twelve respondents stated that NC^3 are mechanisms because they have a specific outcome (five respondents) or because they lead to, result in, or aim at a specific phenomenon (eleven), such as the maximization of fitness, a change in phenotype, or individualized niches. Seven respondents stated that they are mechanisms because they specify how or the way in which a phenomenon is produced (see sections 4 and 5). Two respondents explicitly mentioned explanation in relation to NC^3 mechanisms. In addition, seven respondents mentioned that niche choice, construction, and conformance are processes. One respondent added that they are processes with complex organization, and three respondents emphasized the importance of causal interactions in NC^3 mechanisms. Three other respondents provided reasons that do not match the New Mechanists' framework.

In contrast to the indicative responses from a total of twenty-three of the questionnaire respondents, nine respondents did not provide any reasons for characterizing niche choice, conformance, and construction as mechanisms (six nonresponses, three answers that did not provide any reasons), and five respondents explicitly denied that NC^3 are mechanisms. Four other respondents expressed uncertainty about whether they are mechanisms (in addition to identifying reasons why they might be mechanisms). One explanation for the uncertainty and lack of consensus concerning the status of NC^3 mechanisms is that these concepts were only recently developed within the CRC at the time of the questionnaire. A greater consensus developed during the course of the funding period of the research consortium, as use of the term "NC^3 mechanism" became more commonplace. For instance, in the interviews a year later, nobody questioned the status of the NC^3 mechanisms as mechanisms, and interviewees in nine of the ten interviews talked fluidly about NC^3 mechanisms and what their outcomes are. Another reason for the initial uncertainty and lack of consensus is the difference between underlying molecular mechanisms and NC^3 mechanisms (see section 3.1). Many biologists think of mechanisms in terms of molecular interactions, which was reflected in other parts of the questionnaire (data not reported).

Initial uncertainty notwithstanding, biologists do use the term "mechanism" to describe niche choice, conformance, and construction, and they can generally justify this choice. Most importantly, they refer to NC^3 as mechanisms to emphasize that they lead to *specific outcomes or phenomena* and that describing them explains *how* these phenomena are brought about. This corresponds well with the claims of the New Mechanists that mechanisms bring about specific phenomena (Glennan 1996, 52; Craver 2007, 122), that mechanisms specify how things work (Craver and Darden 2013, 15), and that describing mechanisms thus explains how a specific phenomenon is brought about (Machamer, Darden, and Craver 2000, 2; Bechtel 2006, 27). The references to *causal interactions, processes, and complex organization* are also in line with how mechanisms are often conceived (Machamer, Darden, and Craver 2000; Woodward 2012; Craver and Darden 2013; Glennan 2017).

To conclude, the biologists in the CRC do not use the term "mechanism" arbitrarily, nor is it just a way to lend scientific work an air of credibility. They have plausible reasons to call niche choice, conformance, and construction mechanisms, and these reasons are in line with how philosophers think about mechanisms.

4. EXPLAINING HOW PHENOTYPE–ENVIRONMENT MATCH AND FITNESS CHANGE

4.1 Diverse Explanatory Practices

Standard understandings of mechanisms have it that they bring about specific phenomena; they are mechanisms *of* these phenomena (Glennan 1996, 52; Craver 2007, 122), and describing a mechanism explains the phenomenon that it brings about. Generally, the phenomenon is crucial for the identity of a mechanism, and it determines what is a component of a mechanism and what is not (e.g., Craver and Darden 2013, 52; Kaiser 2018a, 124–26).

What is the phenomenon that NC^3 mechanisms bring about and that the biologists in the CRC seek to explain? When analyzing the explanatory practices in the CRC, we are confronted with a *broad variety of different explanatory strategies and targets,* some of which are very closely related or even overlap. The biologists working on the NC^3 mechanisms investigate how individualized phenotypes and individualized niches arise and change, how a match is produced between an organism's environment and its phenotype, how and why individuals change their environments and phenotypes, how individual differences arise and persist in a population, and how organism–environment interactions affect ecological and evolutionary processes. They do so in concrete study systems that have their own quirks and specificities that demand particular experimental and statistical approaches. Our aim in the next two sections is to show how these various explanatory goals and methods are related and in particular to draw out what it is that the NC^3 mechanisms are supposed to be explaining.

We can first delineate a set of different phenomena that the research projects in the CRC aim to explain. Based on our participatory and empirical work in the CRC, we identified roughly two sets of explanatory targets: changes in phenotype–environment match and fitness on the one hand and individualized phenotypes and individualized niches on the other. This collection of phenomena is evident in the practices of the biologists, as we demonstrate in the following sections. In addition, the existence of various explanatory targets was supported by our empirical work.

In the questionnaire, we asked participants not only what makes niche choice, conformance, and construction mechanisms (the question we looked at in section 3.2) but also what they have in common. The most prominent phenomena cited as the outcome of the NC^3 mechanisms were adaptation or a match between organism and environment (six in each of the two questions about NC^3 mechanisms), an increase in or maximization of fitness (eight for the first question, four for the second question), and individualized niches (five, four). The picture was similar, though slightly different, in the interviews. The most prominent outcome of the NC^3 mechanisms mentioned was individual differences (six of the ten interviews) as well as individualized phenotypes (three) and individualized niches (three). This dominance is likely due to the fact that all interviewees were explicitly asked if NC^3 mechanisms lead to individual differences, individualized niches, and phenotypes. In addition, five of the ten interviews included the idea that NC^3 mechanisms lead to adaptation or a match between an organism's phenotype and its environment, and one interviewee explicitly mentioned an increase in fitness.

In the remaining part of this section, we analyze in more detail the first type of phenomenon, changes in phenotype–environment match and fitness. In section 5, we look at the explanatory targets related to individual differences and identify individualized niches as a second phenomenon explained by NC^3 mechanisms.

4.2 Explaining Changes in Match and Fitness

NC^3 mechanisms reveal how focal individuals interact with their abiotic and biotic environment by engaging in one of three focal activities (recall section 3.1). Individuals either make changes to the environment (niche construction), select an environment (niche choice), or adjust their phenotype (niche conformance). What unifies NC^3 mechanisms is that all these activities result in the same phenomena. Here we focus on how NC^3 mechanisms bring about a change in both the match between an individual's phenotype and environment and the individual's fitness.

On a general level the outcome of NC^3 mechanisms and thus the phenomenon that NC^3 mechanisms explain can be characterized as the *change in phenotype–environment match and in the individual's fitness.* This phenomenon is brought about by different individual–environment interactions, which can be categorized into the three focal activities introduced in section 3.1. For instance, choosing a different environment (niche choice) will change how well (or badly) an individual's phenotype matches the environment and will change the individual's fitness. Similarly, an individual making changes to its environment (niche construction) or adjusting some of its phenotypic traits (niche conformance) will lead to a change in the phenotype–environment match and in the fitness of the individual.

The fitness concept in the CRC is understood as referring to the number of surviving offspring during an individual's lifetime. Fitness is either measured directly through counting surviving offspring or measured by fitness proxies, such as growth rate, size, time to maturity, or body condition. We are aware of the vast philosophical and biological literature that discusses different fitness concepts and their adequate definitions (for an overview see, for example, Rosenberg and Bouchard 2021). For the purposes of this chapter, however, we do not discuss the fitness concept in any substantial way, but rather adopt the fitness concept of the biologists in the CRC.

The term "match" refers to some kind of intuitive suitability or fitting between an individual (and its phenotype) to the environment that the individual experiences. On an abstract level, we say that a square peg fits into a square hole. Similarly, the skin color of a wild boar matches the vegetation color in German forests (for the aim of camouflage), and the shape of the beak of an avocet matches the conditions in the littoral of the tideland (for the aim of finding food). Phenotype–environment match is thus similar to what is called "ecological fitness" (Rosenberg and Bouchard 2021, sec. 2).

Fitness understood in terms of number of offspring is distinct from phenotype–environment match. However, fitness may be a way of operationalizing match since the increase or decrease of fitness provides the researcher with a way to empirically distinguish matches from mismatches (and better matches from worse). In line with this, fitness is considered by some biologists we work with to be the "ultimate currency" of match. Alternatively, match can also be measured via, for instance, measures of stress levels or well-being, as is common in animal welfare research (Richter and Hintze 2019).

We subsume changes in phenotype–environment match and changes in fitness under one phenomenon because they are closely related in the biologists' practices. In particular, many of the researchers develop hypotheses about how a certain NC^3 mechanism will change both match and fitness. They also design experiments to test these hypotheses, usually measuring phenotypic or environmental outcomes as well as fitness outcomes. For example, biologists study the mechanism of how male zebra finches (*T. guttata*) change their behavior and ejaculate traits in response to the presence of competitors in order to secure more in-pair and extra-pair copulations and fertilization events and thereby increase their chances of having higher reproductive success. The biologists test whether this niche conformance mechanism takes place by looking at whether and how the phenotypic traits change in response to the different environment (with or without competition) and also at how the fitness of the birds (measured as numbers of fertilized eggs and offspring survival) changes as a result. Another example is the niche construction mechanism in which red flour beetles release quinones into their flour and thereby change the microbiota to which they are exposed. The biologists hypothesize that the quinones limit the growth of harmful bacteria and fungi and that more quinones are released when an individual in the group is immunocompromised (for instance, because it has been exposed to a pathogen). Hence, the quinone release is seen as part of a mechanism that might enhance the match between the beetles' phenotypes (for example, whether they are immunocompromised) and their environment (the kinds of flour microbiota). This enhanced match should improve the beetles' fitness by increasing their survival and reproduction. So studying this niche conformance mechanism involves looking at changes in the phenotype–environment match and in fitness.

It is important to note that we characterize the primary phenomenon of the NC^3 mechanisms as a *change,* not an improvement, in match and fitness. Many of the biologists in the CRC hypothesize that NC^3 mechanisms are adaptive, meaning they generate an improvement in match and fitness. Although this is a prominent expectation, it is still posited as a hypothesis to be investigated in concrete cases of each mechanism. In addition, it is assumed that NC^3 mechanisms can consist also of nonadaptive evolutionary processes and that some NC^3 mechanisms might lead to a decrease in match and fitness (Trappes et al. 2022). We therefore take the primary phenomenon that is explained by NC^3 mechanisms to be a change in match and fitness, with the option that it might turn out empirically that these changes are often or generally positive.

The phenomena of NC^3 mechanisms can be depicted as in other standard mechanistic diagrams (Craver 2007, 7) as produced by a combination of entities and activities. In Figure 5.1, we develop an abstract depiction of all three NC^3 mechanisms, showing how they lead to changes in phenotype–environment match and fitness. In later sections, we will explore and add to

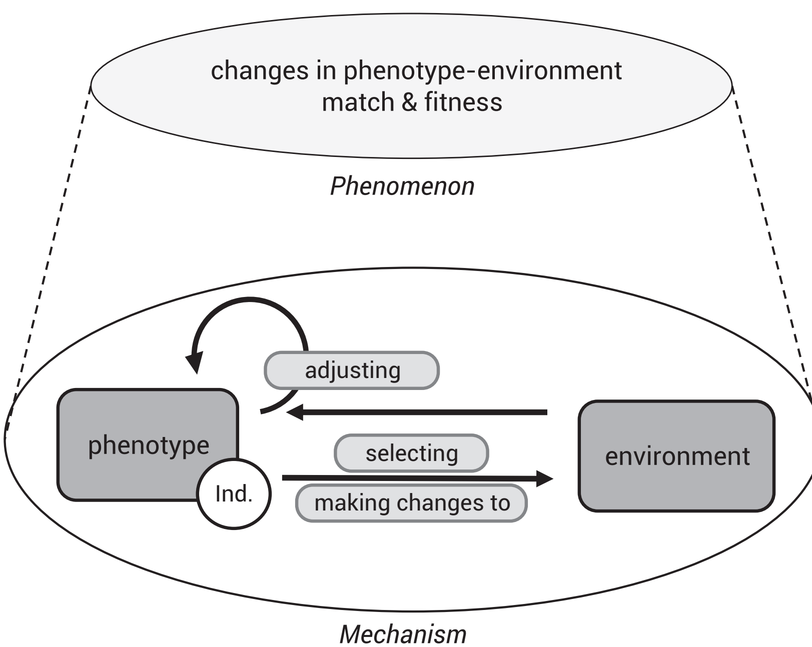

Figure 5.1. Abstract representation of NC^3 mechanisms. An individual (Ind.) interacts with its environment, either making changes to or selecting its environment on the basis of its phenotype or adjusting its phenotype in response to the environment. These interactions among the components generate the primary phenomenon of a change in phenotype–environment match and fitness.

this diagram (section 5) as well as introducing diagrams depicting more specific types of NC^3 mechanisms (section 6).

One might doubt that NC^3 mechanisms are examples of constitutive mechanisms, as the dashed lines in Figure 5.1 suggest. Changes in the fitness of an individual seem to be located on the same level of organization as individual–environment interactions, suggesting that NC^3 mechanisms are etiological rather than constitutive mechanisms (on the difference, see Kaiser and Krickel 2017, 751–52). Nevertheless, the change in the match between an individual's phenotype and its environment can be characterized as a process in which the system composed of individual and environment is involved. Consequently, the individual and its environment will be parts of the system involved in the phenomenon and NC^3 mechanisms will be constitutive mechanisms.

5. INDIVIDUAL DIFFERENCES AND NC^3 MECHANISMS

In section 4.1, we mentioned other phenomena that the CRC seeks to explain. A central goal of the CRC is to understand how individuals differ from one another in their phenotypes and ecological interactions. How does the phenomenon of changes in match and fitness relate to these other phenomena? Our main claim in this section is that explaining changes in match and fitness by describing NC^3 mechanisms is interwoven with explaining individual differences in various ways.

The CRC investigates two sorts of individual differences: individualized phenotypes and individualized niches. *Individualized phenotypes* are those phenotypes that differ within a population (and cannot be attributed to obvious population subgroups such as sexes, age classes, and morphs) and are usually stable over time. Paradigmatic examples of individualized phenotypes are color patterns and animal personality (Kaiser and Müller 2021).

Individualized niches, in turn, are ecological niches of individuals that are not shared by all members of a population (nor again by members of sexes, age classes, and morph groups). Individualized niches are modeled on Hutchinsonian ecological niches, multidimensional spaces representing the abiotic and biotic conditions under which a species or population can or does persist indefinitely (Hutchinson 1957; Holt 2009). Since individuals do not persist indefinitely, individualized niches are defined as the conditions under which an individual can survive and reproduce (Takola and Schielzeth 2022; Trappes et al. 2022). Areas within the individualized niche are further distinguished based on a fitness gradient across the various niche dimensions, indicating conditions under which an individual does better or worse. Fitness is thus crucial to defining individualized niches. Individualized niches highlight the multitude of ecological factors and conditions to which individuals relate. However, empirical studies usually focus on particular dimensions of individualized niches, such as prey size, parasite load, or social group size.

Although they are both explanatory targets of the CRC, these two types of individual differences figure in the NC^3 mechanisms in distinct ways. Based on theoretical work with the CRC members as well as an analysis of the CRC's research questions, hypotheses, and experimental designs, we identify the difference as one between components and phenomena. Whereas individualized phenotypes are components of NC^3 mechanisms, individualized niches are a phenomenon brought about by NC^3 mechanisms. We argue for these claims in the next two subsections.

5.1 The Role of Individualized Phenotypes in NC^3 Mechanisms

Recall that the CRC aims to understand how individuals conform to, choose, or construct their environment and why individuals do so in different ways. Individualized phenotypes enter this picture in two ways, depending on which of the three NC^3 mechanisms are at stake.

On the one hand, niche choice and niche construction mechanisms often start with individualized phenotypes. They can thus reveal how individual differences in phenotypic traits, such as behavioral traits, affect how the focal individual brings about changes in the environment (including the social environment). The focal individual's individualized phenotype informs how the individual either makes changes to the environment (niche construction) or selects an environment (niche choice). Hence, one of the central questions addressed by describing niche construction and niche choice mechanisms is: How does the environment change (differently) due to different individualized phenotypes?

Project C04, for example, investigates how individual differences in aggressive behavior determine whether harvester ant queens found a colony alone or cooperatively with other queens. Figure 5.2 represents the main types of components of mechanisms of niche choice and construction and highlights that the causal relation in these mechanisms runs from the phenotype to the environment.[3] An extensive list of examples of projects studying niche construction and choice is included in Table 1 in the Appendix.

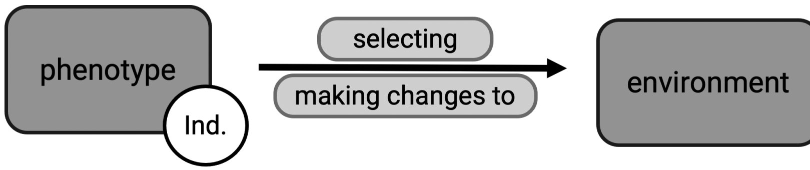

Figure 5.2. Components of niche choice and niche construction mechanisms. An individual (Ind.) selects or makes changes to its environment based on its (individualized) phenotype.

By contrast, mechanisms of niche conformance often start with different environmental conditions or with a change in the environment (including the social environment). They reveal how individuals adjust their phenotypes in response to different or changed environmental conditions.[4] Descriptions of niche conformance mechanisms therefore answer the central question: How do individualized phenotypes change (differently) due to different environmental conditions? In mechanisms of niche conformance, the causal relation thus runs in the opposite direction, from the environment to the phenotype (see Figure 5.3).[5]

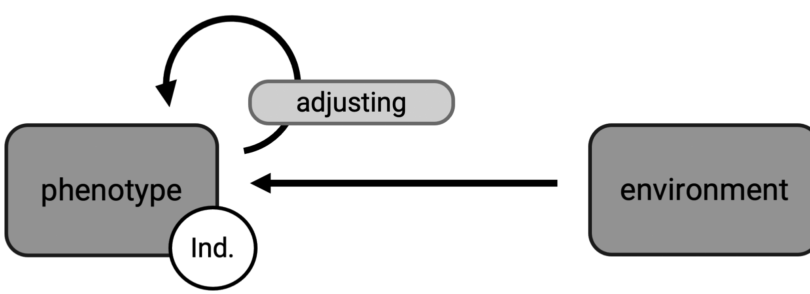

Figure 5.3. Components of the niche conformance mechanism. An individual (Ind.) adjusts its individualized phenotype in response to the environment it experiences.

Many projects in the CRC study niche conformance to explain how individualized phenotypes arise. For example, Project A02 studies how an enriched developmental environment combined with different genotypes influences the level of optimism and pessimism exhibited by adult mice (Krakenberg et al. 2020). Another example is Project B05, which studies the effect of fruit fly (*Drosophila melanogaster*) larval density on adult reproductive and metabolic phenotype. In both cases, the mechanism of niche conformance is proposed to explain how the different environmental factors experienced by individuals lead to different individualized phenotypes.

For an extensive list of examples of projects studying niche conformance, see Table 2 in the Appendix.

Already by looking at individualized phenotypes we can see that the CRC is interested in how different individuals vary with respect to how they choose, conform to, or construct their environments rather than only how individuals generally undertake these activities. Describing NC^3 mechanisms can help explain individualized phenotypes by showing how they are produced in response to the environment (niche conformance) or how they are crucial to the individuals' success in a new environment (niche choice and construction). In addition, regardless of whether we look at niche conformance, choice, or construction, individualized phenotypes are among the components of the NC^3 mechanisms. Recalling that individualized phenotypes require variation between individuals, we can conclude that there can be *components* of the NC^3 mechanisms that vary between different individual instantiations of the mechanism. Indeed, some NC^3 mechanisms require individual differences in the components. For instance, animal personality may in some cases play an essential role in determining which environment an animal selects. We return to this point about variation in section 6.

5.2 The Role of Individualized Niches in NC^3 Mechanisms

Individualized niches are also a central explanatory target of the CRC's investigation of NC^3 mechanisms. Yet they are connected to these mechanisms in a very different way than individualized phenotypes. In this section, we show that changes in individualized niches are an *outcome* of the working of NC^3 mechanisms, albeit in a different way for each of the mechanisms. Specifically, niche choice, niche construction, and niche conformance all change the focal individual's phenotype–environment match and fitness. Together, these imply a change in the individualized niche. Individualized niches are thus located on the phenomenon level, in close relation with the changes in phenotype–environment match and fitness we discussed in section 4.

Take niche choice and construction, which alter the environment side of the phenotype–environment match. On the one hand, choice and construction can introduce new sorts of environmental factors that weren't present before the individual selected or made changes to its environment. In this case, there may be new dimensions added to the individualized niche. For instance, shifting to a new territory may open up new resources for exploitation, thereby adding entirely new dimensions to the individualized niche.

Alternatively, niche choice and construction may shift the range of values taken by an environmental factor in the individual's environment. This would mean that the individualized niche now includes a different range along a preexisting niche dimension. For instance, the red flour beetles studied in Project C01 perform niche construction by releasing quinones, which alter the microbes in the flour. The beetles thereby shift from a higher to a lower range along niche dimensions to do with infection risk by harmful fungal and bacterial species.

Although niche conformance does not involve making changes to the environment, it too affects phenotype–environment match and fitness. By changing its phenotype, the individual will perform better or worse when exposed to certain ecological factors. In other words, niche conformance can change the fitness gradient for a given niche dimension. For instance, the fur seal pups studied in Project A01 conform to the social density they experience, with the hypothesis being that conformance to high density helps pups survive better at a high social density. This means conformance changes the way social density affects fitness, altering the fitness gradient over niche dimensions related to social density. Niche conformance thus alters the individualized niche, not because there are new environmental conditions for the individual to interact with but rather because the individual interacts with the same environmental conditions in a different way.

NC^3 mechanisms therefore bring about changes in individualized niches by altering which dimensions make up the individualized niche, which ranges along those dimensions are included in the niche, or the fitness gradient along different dimensions.[6] They do so because they alter the phenotype–environment match and the individual's fitness. There is therefore an intimate connection between the two phenomena of the NC^3 mechanisms: changes in phenotype–environment match and fitness imply changes in individualized niches. We depict this relation between the phenomena and the NC^3 mechanisms in Figure 5.4.

The phenomena that mechanisms bring about are standardly understood to be important for individuating the mechanisms and their components and boundaries (Craver 2007, 123, 153; Kaiser 2018a, 124–26). Yet it is not entirely clear whether changes in individualized niches are also important for individuating NC^3 mechanisms like the change in phenotype–environment match and fitness. Determining whether a change in the individualized niche has taken place generally involves also looking for changes in phenotype–environment match and fitness. This suggests that the changes in match

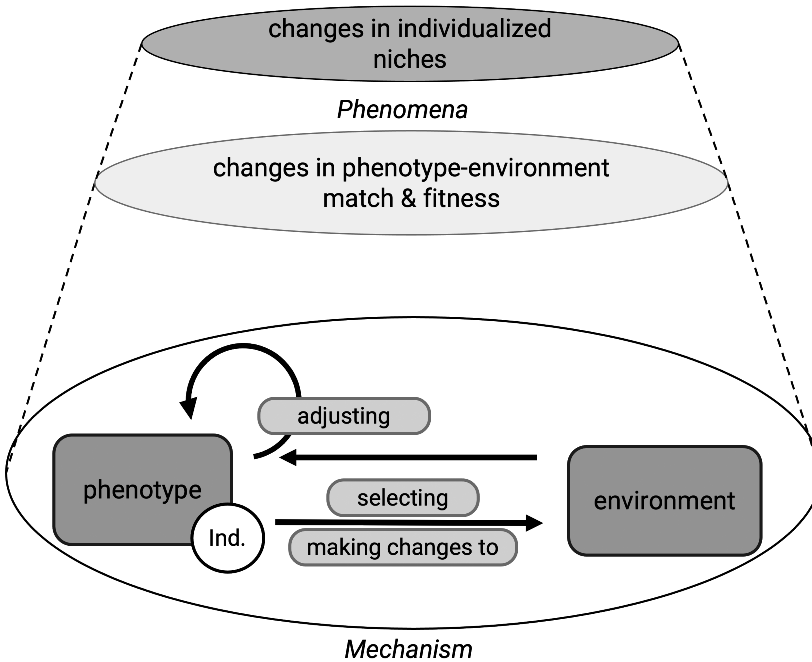

Figure 5.4. Schematic representation of NC^3 mechanisms with two phenomena. Interactions between an individual and its environment bring about changes in phenotype–environment match and fitness and thereby alter the individual's individualized niche.

and fitness are used to individuate NC^3 mechanisms, with the effect on individualized niches being a derived phenomenon.

Alternatively, changes in match and fitness might gain their interest from their relation to individualized niches. This would mean that the aim to explain changes in individualized niches would be central for individuating NC^3 mechanisms, and explaining changes in match and fitness is only an intermediary step to this goal. Understanding and explaining niches is indeed often proclaimed as a target of ecological and evolutionary research, and this transfers to research on individualized niches (Bergmüller and Taborsky 2010; Dall et al. 2012; Trappes et al. 2022). The very names of the NC^3 mechanisms highlight the phenomenon of changes to the individualized niche. On the other hand, there is some debate about whether the niche concept is actually the target of explanation, given that researchers usually just investigate a handful of ecological conditions and organism's relations to those conditions (Justus 2019).

It may even be that biologists studying NC^3 mechanisms sometimes focus on one phenomenon and sometimes on the other, in which case the phenomena may deserve equal standing in any general characterization of the NC^3 mechanisms. As with the relation between match and fitness, the role of the two phenomena in the NC^3 mechanisms cannot be decided based on our case study and remains a crucial question for further philosophical research.

6. COMPONENTS OF NC^3 MECHANISMS

We have introduced the focal individual and the three focal activities as the major components of NC^3 mechanisms (section 3.1), specified the two phenomena that NC^3 mechanisms explain (sections 4 and 5), and discussed how NC^3 mechanisms fit into the explanatory practices of the CRC, which focus on individual differences (section 5). Now we can take a closer look at concrete examples of NC^3 mechanisms and analyze how they are studied in the CRC. The goal is to get a more specific understanding of NC^3 mechanisms, in particular what their components are and how these components are organized.

Whereas sections 3, 4, and 5 were concerned with characterizing the general mechanism type "NC^3 mechanism" and its three subtypes "mechanism of niche choice, conformance, and construction," this section analyzes more *concrete examples of NC^3 mechanisms*. These are still types of mechanisms, but much more specific ones (for example, the mechanism of how fire salamanders choose where to deposit their larvae). Even though both parts of our analysis draw on the same research projects and examples, they take place on different levels of abstraction and concern different mechanism types (the more abstract type "NC^3 mechanism" and more concrete types such as "niche choice mechanism in fire salamanders").

Our analysis shows that the general picture presented so far is correct but also *simplistic* in four different ways. First, the focal individual is often not the only individual that is crucial for the working of the mechanism. Second, the focal activity is not as such among the components of NC^3 mechanisms but is rather realized by one or more specific component activities. Third, NC^3 mechanisms involve many more entities and activities than the focal individual, other individuals, and the activities that realize the focal activity. Fourth, individual differences are also not explicit components of concrete NC^3 mechanisms. Together these four claims show that concrete cases of NC^3

mechanisms are much more complex on the component level than suggested by the general picture developed so far and illustrated in Figure 5.4. Looking in more detail at specific cases, we come to better understand the specificities of the components of individual-level ecological mechanisms.

First, recalling section 3.1, NC^3 mechanisms are individual-based mechanisms because they reveal how a certain type of individual, the focal individual, interacts with its environment and thereby changes its fitness and how well its phenotype matches the environment. Despite this focus on one focal individual, in most NC^3 mechanisms, other conspecific individuals also play an important role. We distinguish two different ways in which *additional individuals* can be involved in NC^3 mechanisms.

On the one hand, additional conspecific individuals can constitute the social environment with which the focal individual interacts and that contributes to the change of the focal individual's match and fitness. For example, in the social niche conformance mechanism of zebra finches (Figure 5.5), the focal individual is an adult zebra finch male. The focal male forms a

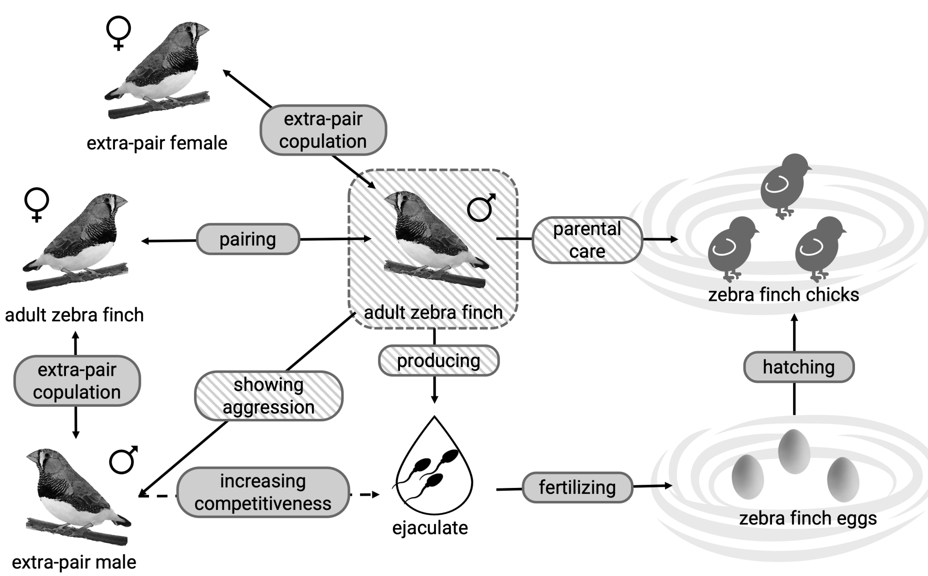

Figure 5.5. Niche conformance mechanism in zebra finches. A focal male (marked with hatching) engages in many different activities in interaction with many other individuals at different times. Three activities—"showing aggression," "producing ejaculate," and "parental care" (marked with hatching)—realize the focal activity of the niche conformance mechanism. The dashed arrow "increasing competitiveness" represents one of the hypothesized effects of an extra-pair male, part of the social environment, on the focal individual's ejaculate traits, an individualized phenotype.

pair with a zebra finch female but also copulates with other females. It also shows aggression toward other males. These other individuals are part of the social environment to which the focal individual conforms, changing its behavior (more or less aggression and parental care) and its ejaculate properties. One of the hypotheses is, for instance, that the presence of an extra-pair male leads the focal individual male to show more aggression and invest less in parental care.

On the other hand, additional individuals can be part of NC[3] mechanisms in so far as the focus of the mechanism lies not on one focal individual but rather on a pair or group of focal individuals, which are said to jointly engage in the focal activity. For instance, the buzzard niche construction mechanism (Figure 5.6) involves a pair of adult common buzzards (*Buteo*

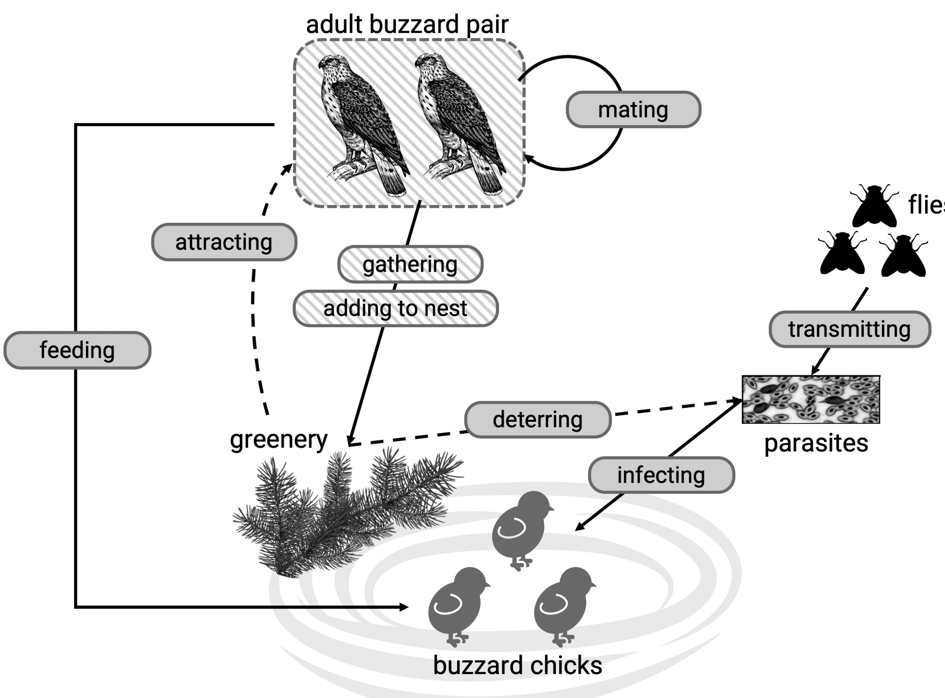

Figure 5.6. Niche construction mechanism in common buzzards. A pair of adult buzzards, both focal individuals (marked with hatching), engage in a number of different activities. The activities that realize the focal activity (marked with hatching) are "gathering" and "adding" greenery to the nest to alter the nest environment. Dashed arrows "attracting" and "deterring" represent hypothesized effects of the greenery on mate quality and parasite levels, respectively.

buteo) jointly engaging in the activities of gathering greenery and adding this greenery to their nest. The biologists hypothesize that the buzzards, by adding greenery to the nest, alter the abiotic and potentially also biotic environment of their offspring. The buzzard pair thereby alters the environmental conditions affecting their own fitness.

Second, when describing concrete cases of NC^3 mechanisms, it seems inadequate to refer to the focal activities as such. Activity descriptions such as "making changes to its environment," "selecting an environment," or "adjusting its phenotype" are too general. They need to be specified in concrete cases. Hence, *focal activities* are not among the components of concrete NC^3 mechanisms, but rather are *realized* by one or more specific component activities. This can be illustrated in the case of the fire salamander larvae depositing niche choice mechanism (Figure 5.7). The focal activity of selecting an environment, in which the focal individual (the adult fire salamander female) is engaged, is specified by the activity of depositing the larvae in a stream or a pond.

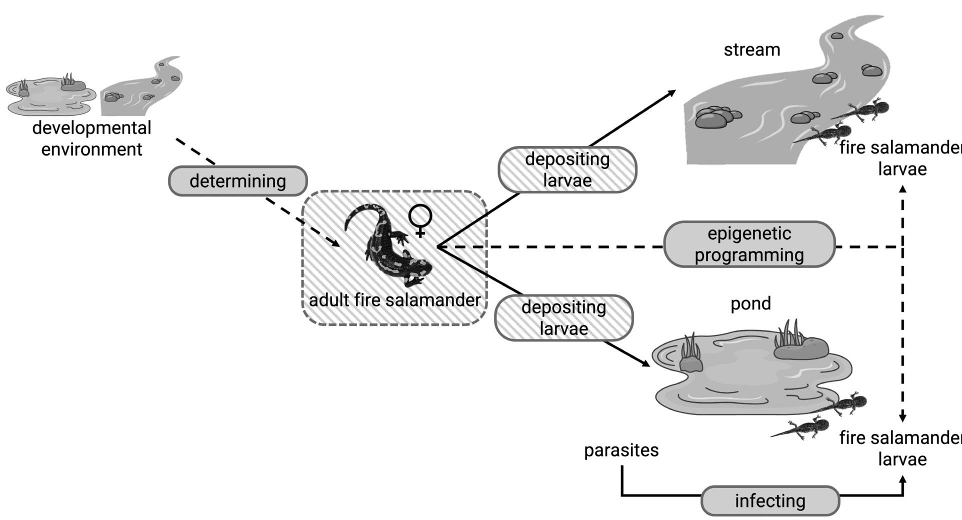

Figure 5.7. Niche choice mechanism in fire salamanders. A focal female (marked with hatching) has a choice between two locations in which to deposit its larvae. The activities that realize the focal activities (marked with hatching) are "depositing larvae" in stream and "depositing larvae" in pond. Dashed arrows "determining" and "epigenetic programming" represent hypothesized ways in which the female's own developmental environment affects its choice and how the female may affect the success of her offspring in the chosen environment.

In several cases of NC^3 mechanisms, however, the situation is more complex because the focal activity is realized by a set of different activities and it is not obvious which activities these are. For example, when zebra finch males conform to different social environments (Figure 5.5), the focal activity of adjusting their phenotypes is realized by the zebra finch males showing more or less aggression, engaging more or less in parental care, and producing ejaculate with different properties.

Third, concrete cases of NC^3 mechanisms show that the individual–environment interactions can be quite complex and involve *many more entities and activities* than the focal individual, conspecifics, and activities that realize the focal activity. Other entities include parts of the nonsocial environment of the focal individual (for example, the parasites in the ponds infecting the fire salamander larvae, the greenery that the buzzards gather and add to their nests), and other activities include interactions between the focal individual and its social and nonsocial environment that do not realize the focal activity (for example, the extra-pair copulation of the zebra finch males, the adult buzzards feeding their chicks, the developmental environment determining the behavior of the fire salamander females).

What binds together all of these different entities and activities and determines that they are components of a specific NC^3 mechanism is that all of them are relevant to the phenomena that the NC^3 mechanism brings about (Craver 2007, 123; Kaiser 2018a, 124–26). That is, they all contribute to a certain change in the phenotype–environment match and the fitness of the focal individual as well as a change in the individualized niche (recall sections 4 and 5).

Finally, we discussed earlier (section 5.1) how individual differences in the form of *individualized phenotypes* can be components of NC^3 mechanisms. Individualized phenotypes affect how individuals make changes to or select their environments (niche construction and choice), or they result from the adjustment to changed or different environments (niche conformance). As our analysis of three specific cases of NC^3 mechanisms shows, individualized phenotypes are not represented explicitly in the NC^3 mechanisms. Instead, the mechanisms include general phenotypic traits (such as the behavioral traits showing aggression, depositing larvae, and gathering greenery) without also representing the variation between individuals, that is, how individuals instantiate the traits differently.

In addition, not all traits making up focal activities in the NC^3 mechanisms are individualized phenotypes. Some traits may not vary among the individuals in a population, or the variation may not be a focus of the mechanism. For instance, each zebra finch chooses a different mate, and some can be quite picky in making this choice, but mate choice is not a focus of the niche conformance mechanism of how zebra finch males respond to competition.

To conclude, we have seen that the general characterization of NC^3 mechanisms in terms of focal individual and focal activity is an abstraction from the details of the actual mechanisms. Other individuals can be involved in various ways, the focal activity often has to be broken down into a number of concrete activities that the focal individual performs, there are other entities and activities involved, and individual differences aren't directly represented. Nevertheless, the more abstract representation helps understand how the very heterogeneous concrete examples of NC^3 mechanisms are related, highlighting their similar structure and how they contribute to the target phenomena. This interplay between abstract and concrete, simple and complex, is likely to be a pervasive feature of individual-level mechanisms in ecology and evolution, especially given that causal relations are instantiated in many different ways in different ecological systems (Elliott-Graves 2018).

7. CONCLUSION

Our goal was to generate a better understanding of individual-level ecological and evolutionary mechanisms. To do so, we investigated a paradigmatic case, the NC^3 mechanisms. We pointed out how each of the three types of NC^3 mechanisms involves a focal individual and a different focal activity. In niche construction, the individual makes changes to the environment; in niche choice, the individual selects an environment; and in niche conformance, the individual adjusts its phenotype. Although they are not molecular mechanisms, we argued that the biologists call niche choice, conformance, and construction mechanisms for plausible reasons that accord with how New Mechanists understand and characterize mechanisms.

We then went on to analyze which phenomena descriptions of NC^3 mechanisms explain. The CRC pursues a number of explanatory goals by studying

NC^3 mechanisms. An interesting finding of our case study is that describing NC^3 mechanisms explains more than one phenomenon. NC^3 mechanisms lead to changes in phenotype–environment match and fitness and to changes in the individualized niche. Since the CRC focuses on understanding individual differences, we also clarified how studying NC^3 mechanisms is interwoven with studying individual differences. We found that each sort of individual difference, individualized phenotypes and individualized niches, figured in the NC^3 mechanisms in a different way. Whereas individualized niches are phenomena brought about by NC^3 mechanisms, individualized phenotypes are components of the mechanisms, either a starting point or an end point.

Finally, we discussed the complexities of concrete examples of NC^3 mechanisms. Although we can depict the NC^3 mechanisms in a coherent unified form (Figure 5.4), this representation is highly abstract. It simplifies the multiple individuals, different activities, and other sorts of entities involved in the mechanisms. In addition, it fails to depict individual differences. These complexities, which become evident in more concrete examples of NC^3 mechanisms, can be understood as a consequence of the highly heterogeneous nature of ecological systems. In particular, when ecological systems are considered on the individual level, there are many different individual–environment interactions to be investigated mechanistically.

What can we take away from this case study of ecological-evolutionary mechanisms? Although we do not want to overgeneralize, taking these mechanisms as paradigmatic would open up a number of potential avenues to explore. First, there is the existence of multiple explanatory targets involved in the mechanisms in sometimes complex ways. It seems that mechanisms in ecology and evolution can have multiple phenomena and also that researchers sometimes want to explain changes among the components. Second, there is the interplay between the complexity of concrete cases and the simplification necessary to identify common mechanisms and generate representations of these mechanisms. It seems likely that this feature will recur in other ecological mechanisms, and it would be interesting to investigate further how the more abstract representation of NC^3 mechanisms guides the discovery and description of the more specific NC^3 mechanisms. This would contribute to understanding how organismal biologists employ mechanism schema types as a useful strategy for mechanism construction (Craver and Darden 2013, 71–74).

In addition to expanding our philosophical understanding of mechanisms in ecology and evolution, our work also promises to help biologists gain clarity about the mechanistic nature of individual–environment interactions. In particular, by highlighting the multiple phenomena of NC^3 mechanisms and how individual differences fit in, we provide material for biologists to better justify their own claims about the NC^3 mechanisms. In addition, delineating the structure of focal individual and focal activity, and seeing how they are instantiated in concrete cases by multiple activities and sometimes several individuals, may aid biologists in bridging from their experimental setups and statistical models to the abstract level of NC^3 mechanisms.

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Table 1. Selected projects studying NC^3 mechanisms to explain individualized niches. Research questions, explananda, and explanatory factors are adapted from the funding application and research publications from the CRC.

Project (PI)	Research Question	Explanandum individualized niche dimensions	Explanatory factors phenotype, other factors	Mechanism
A01 (Hoffman)	Why do mothers choose different breeding sites?	Social density at breeding site	Fitness trade-offs at each site	Niche choice
A02 (Richter and Sachser)	How does optimism/pessimism affect which niche a mouse chooses?	Risk level of niche	Optimism/pessimism	Niche choice
A03 (Schielzeth)	Do predictability and color affect choice of habitat complexity?	Complexity of habitat	Predictability of escape behavior, color	Niche choice
A04 (Caspers)	How do female salamanders choose their mates?	Assortative mating	Microbiome, chemicals, etc.	Niche choice
A04 (Caspers)	Why do female salamanders choose where to deposit their larvae?	Larval deposition in stream or pond	Developmental programming of phenotype, epigenetics	Niche choice

C01 (Kurtz)	How does individual experience affect the production of quinones the flour microbiota?	Amounts and sorts of microbiota in flour	Exposure to immune challenge, immune status	Niche construction
C03 (Krüger)	Why do buzzards use different greenery in their nests?	Differences in nest greenery, parasite abundance	Parent quality, location of nest	Niche construction
C04 (Gadau)	Do individual differences in aggressive behavior affect colony founding type?	Colony type (mono- or polygynous)	Aggressive behavior	Niche construction and niche choice
D03 (Wittman)	How does niche choice affect the maintenance of spatial variation in density?	Spatial variation in density	Various conditions (specified in models)	Niche choice
D05 (Schielzeth and Reinhold)	Do complex habitats allow more scope for niche specialization via NC^3 mechanisms?	Niche specialization (individualized niches generally)	Habitat complexity	Niche choice, conformance and construction

Table 2. Selected projects studying NC^3 mechanisms to explain individualized phenotypes. Research questions, explananda, and explanatory factors are adapted from the funding application and research publications from the CRC.

Project (PI)	**Research Question**	**Explanandum individualized phenotypes**	**Explanatory factors environment, other factors**	**Mechanism**
A01 (Hoffman)	How does social density affect pup phenotype?	Pup behavior, hormones, immunity, transcription, growth, skin microbiome	Social density, maternal programming	Niche conformance
A02 (Richter and Sachser)	How do mice become optimists or pessimists?	Optimism/pessimism	Developmental environment (level of enrichment), genes	Niche conformance
A03 (Schielzeth)	Why do grasshoppers differ in predictability?	Predictability of escape behavior	Habitat complexity, camouflage, individual condition (health)	Niche conformance
A04 (Caspers)	How does larval habitat affect phenotype?	Larval behavior, immunity, skin microbiome, color pattern, etc.	Larval habitat (pond or stream, chosen by mother), maternal programming	Niche conformance
B01 (Kaiser and Sachser)	How do social niche transitions shape biobehavioral profiles?	Endocrinology and behavior	Social group size, social rank	Niche conformance

B02 (Müller)	How does developmental environment affect phenotype?	Larval and adult behavior, physiology, immunity	Developmental environment (access to resources, access to clerodendrins)	Niche conformance
B04 (Korsten and Schmoll)	How is male competitive and parenting behavior affected by sexual competition?	Behavior (competition, mating, parenting), reproductive morphology	Social environment (level of sexual competition)	Niche conformance
B05 (Fricke)	How does population density during development affect adult phenotype?	Adult metabolic & reproductive phenotype	Population density	Niche conformance

NOTES

1. Most empirical studies of NC^3 mechanisms work with groups of individuals that share a particular trait or ecological requirement or relation. Accordingly, most NC^3 mechanisms are represented on the type level, not on the level of token mechanisms with token individuals and activities. For reasons of simplicity, however, we leave out the add-on “type of” in the following.

2. We assume that interactions are activities in which more than one object is involved. A more literal reading of “inter*actions*” would require that the objects that interact have an *active* role. Usually, however, the term “interaction” is used in a wider sense to include activities where only one party is active, a usage we follow.

3. Other factors are also sometimes used to explain the changes in environment, including the environment previously experienced by an individual or the existence of fitness trade-offs for a certain choice. We ignore these for simplicity.

4. Often individuals are confronted with an environment that has changed, meaning researchers study how different individuals conform to the new environment. In other studies, however, individuals face different environments, and the question is how different individuals adjust their phenotypes in response to these different environments. In experiments, these environmental differences are typically restricted to a binary treatment that is intended to represent a continuum. For instance, zebra finches are exposed to two different levels of competition (low or high competition), and drosophila larvae are exposed to different social densities (low or high density). Nevertheless, the researchers acknowledge that in nature the differences are much more gradual (Trappes 2021b).

5. Additional explanatory factors include genotype and maternal epigenetic programming. Again, for simplicity, we leave these out of the representation of the mechanisms.

6. It is also possible to distinguish the effects of the NC^3 mechanisms on *realized* (or actual) individualized niches and *fundamental* (or potential) individualized niches (Trappes et al. 2022). For simplicity, we leave this distinction out.

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