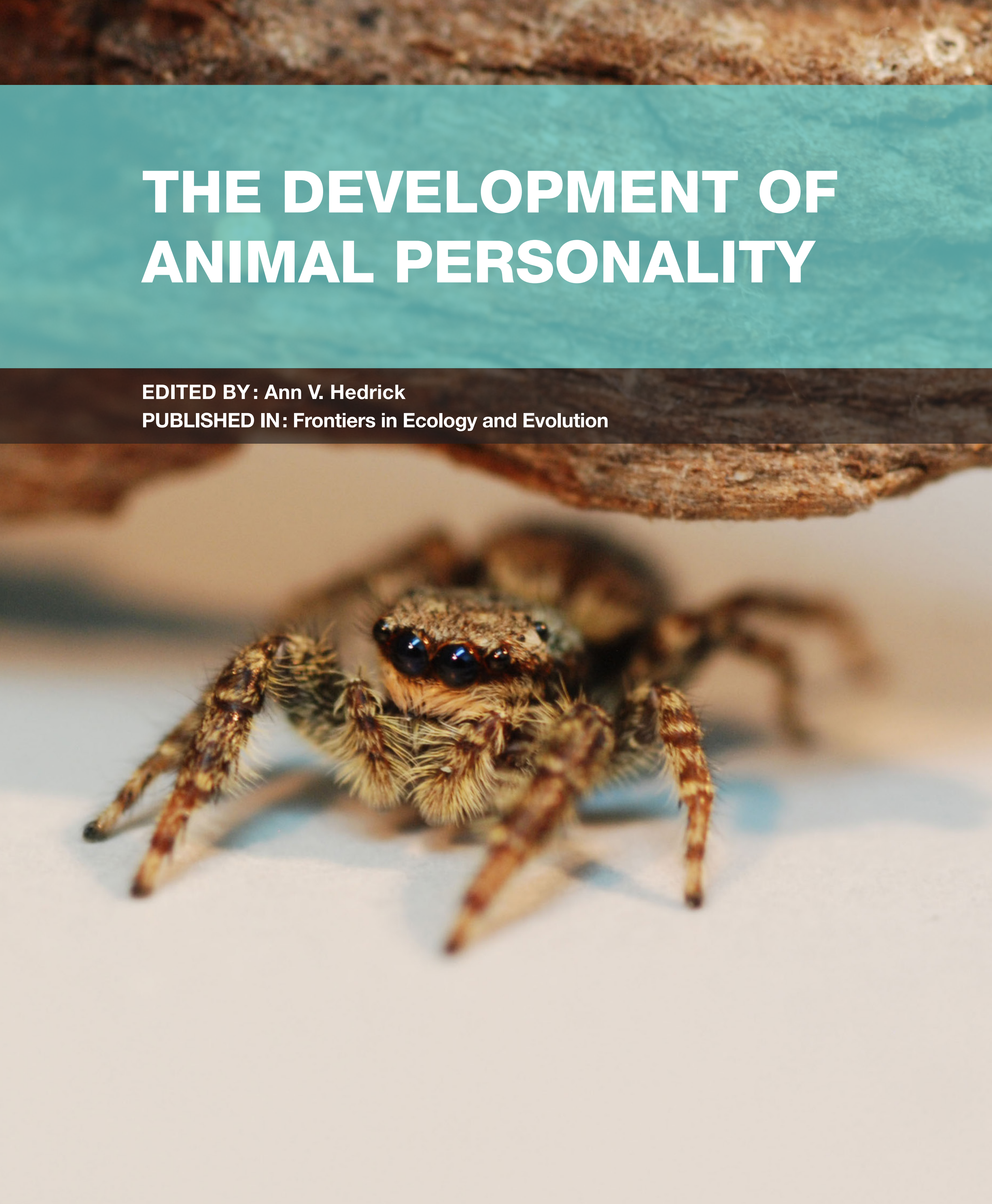

THE DEVELOPMENT OF ANIMAL PERSONALITY

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THE DEVELOPMENT OF ANIMAL PERSONALITY

Topic Editor:
Ann V. Hedrick, University of California, Davis, USA

The jumping spider, *Marpissa muscosa*.
Image by Jannis Liedtke

Although the topic of animal personality has recently generated much interest, the role of development is little understood. This collection of papers deals with the development of animal personality. Topics include the roles of genetic effects, maternal effects, social partners, predation and parasitism risk, and environmental complexity in the development of personality, the effects of personality on survival, and the development of collective personality and movement as a driver of personality development. The organisms covered include insects, spiders, fishes, and birds. This volume illustrates the diversity of approaches that have shed light on the development of animal personality in the past several years.

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EDITORIAL
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Editorial: The Development of Animal Personality

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Keywords: development, animal personality, boldness, exploratory behavior

Editorial on the Research Topic

The Development of Animal Personality

Over the past 20-odd years, researchers in behavioral ecology have increasingly focused on consistent individual differences in behavior, also known as animal personality, and their causes and consequences. In 2010, Stamps and Groothuis published a highly influential paper drawing attention to the importance of development in the study of animal personality and lamenting the lack of research on this topic (Stamps and Groothuis, 2010). Since then, researchers have increasingly focused on this gap in our knowledge. The current volume draws together nine papers with a variety of approaches on the development of personality, and provides a glimpse into the current state of the art.

Four of the papers are non-empirical (data-free). Davis et al. directly address the issue of data-free papers on animal personality. They find that data-free papers comprise 20% of the papers on animal personality in the last decade, and argue that these papers are vitally important because they can synthesize current knowledge, integrate diverse fields in novel ways, and/or identify important future directions for the field.

Stamps and Krishnan discuss a Bayesian model they have constructed, using it to explain why we would expect individual differences in the developmental trajectories of personality traits, even if all animals are raised under the same conditions. They also examine commonly used experimental protocols (within-individual and replicate individual) and explain why replicate individual designs are better suited to provide estimates of the developmental plasticity of behavioral traits. Finally, they advocate using a Bayesian approach that assumes differences between individuals in the information provided by immediate and distant ancestors to offer insights into the effects of genes, epigenetic factors, maternal effects and personal experiences on the development of personality.

To date, research on animal personality has seldom considered social partners as important determinants of personality. Niemela and Santostefano address how social partners might affect behavioral variation and impose selection on animal personality, a process they refer to as "social carry-over effects." They point out that such effects can create variation among individuals in non-social behaviors, such as boldness, if the proximate mechanisms for these effects are irreversible. They also suggest approaches for studying the attributes and evolutionary outcomes of social carry-over effects on non-social behaviors.

Personality at the level of the group has also been a neglected topic. Bengston and Jandt focus on group-level, or "collective" personality, which they define as an emergent behavioral phenotype displayed at the group level. They emphasize that just as individual behavior changes as the individual matures, so too can group-level behavior change as the group matures. They examine a variety of factors that can generate collective personalities, including the genetic composition of the group and the internal social environment of the group, and discuss ways to evaluate the development of collective personality.

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The remainder of the papers in this volume are empirical, and cover a range of taxa including arachnids, insects, fish and birds. Liedtke et al. examine the effects of environmental complexity on the development of personality in jumping spiders. Using a split-brood design with a non-enriched, socially enriched and physically enriched environment, they find that exploratory behavior is lowest in non-enriched spiders and highest in physically enriched spiders. Moreover, significant family by environment interactions suggest that families differ in their developmental plasticity.

Snell-Rood and Steck use cabbage white butterflies to test the hypothesis that slow versus fast exploration of the environment can affect the development of cognitive abilities, resulting in movement-cognition syndromes in adults. They find that genotypes with smaller thoraxes are slower fliers, better at learning and develop larger brains, and conclude that genetic variation in behaviors such as exploration or movement can affect the development of other behavioral traits resulting in suites of correlated behaviors.

DiRienzo et al. employ a different perspective, and ask whether exposure to pathogens during development creates or diminishes individual differences in behavior in a field cricket. Specifically, they examine whether exposure to a bacterial pathogen as a juvenile affects mean adult boldness, variation in individual boldness, and/or immune response. Surprisingly, they find that a single early exposure to a bacterial pathogen is sufficient to alter the expression of boldness in adults, in that it extinguishes repeatability in boldness for those crickets injected with the pathogen. However, the pathogen exposure has no influence on immune function itself or the boldness-immune function relationship.

In a related paper, Kortet et al. examine the effects of a trematode parasite on personality in Eurasian minnows in the field. The authors assess boldness and activity, and their repeatabilities, in fish from two rivers, one with predatory fish and parasites and the other with neither. They predict that fish in the high-predation, high-parasite river should be bolder (in order to grow more quickly) and more consistent. Their results show that these fish are indeed bolder, but are less active (perhaps because of the parasite), whereas fish in both populations are consistent in boldness and activity. As the authors observe, this is one of the first papers linking predation and parasitism risk to the development of animal personalities.

The final paper in the volume deals with another vertebrate, the Superb Fairy Wren. Hall et al. ask whether variation in life-history strategies is associated with consistent differences in behavior. They assess the relationship between survival and a number of risk-related behaviors. Their results indicate that "proactive" birds are more exploratory in novel artificial environments, move into rooms faster, are more active, are more likely to approach a mirror image, are less docile during handling, and have lower survival rates, conforming to the "pace of life" syndrome. Interestingly, wrens become more exploratory and active when in poorer condition or when environmental conditions are harsher.

In conclusion, this volume provides a road map for estimating the developmental plasticity of behavioral traits, gives approaches for studying social carry-over effects and ways to evaluate the development of collective personality, and offers examples of ways to measure the effects of physical and social enrichment on personality, the emergence of correlations between movement or exploration and cognition, the effects of immune challenges and predation/parasitism on the development of personality, and the relationship between risk-related personality traits and life-long survival. Above all, the papers in this volume illustrate the diversity of approaches that have shed light on the development of animal personality since Stamps and Groothuis' landmark review in 2010, and raise important questions for future study.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

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GENERAL COMMENTARY
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Commentary: Four ways in which data-free papers on animal personality fail to be impactful

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Keywords: animal personality, behavioral variation, ecology, behavior, evolution, citations, data free papers

A commentary on

Four ways in which data-free papers on animal personality fail to be impactful
by DiRienzo, N., and Montiglio, P.-O. (2015). Front. Ecol. Evol. 3:23. doi: 10.3389/fevo.2015.00023

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In a recent Frontiers in Ecology and Evolution paper, DiRienzo and Montiglio (2015) suggest that "the literature on animal personality is dominated by papers lacking any data" and that additional data-free papers do little to move the field forward. Here, we present our quantitative analysis of data-free papers in the animal personality and behavioral ecology literature, as well as discuss the value of such articles. We found that data-free papers composed 20% of all publications on animal personalities in the last decade. We further determined the prevalence of data-free papers within the top-ten most cited papers in other behavioral ecology fields, showing that animal personality did not have an unusual excess of highly cited data-free papers when compared to other subfields of animal behavior. Regarding the impact of data-free papers, we argue that impactful data-free papers provide coherent syntheses and reviews of current knowledge, integrate different fields of thought in novel ways, or identify important future directions within a framework beyond the scope typical of empirical papers. Ultimately, we suggest that a combination of robust empirical studies and effectual data-free papers is vital to advance a field.

To quantify the frequency of data-free papers in the animal personality literature, we conducted a web search using Web of Science (BIOSIS Previews). Specifically, we used the search terms "behavio* syndrome*" OR "animal personalit*" for the period 2005–2014, which follows Sih et al.'s influential papers in 2004 (Sih et al., 2004a,b). Our search differed from DiRienzo and Montiglio's ("individual behavioral variation") because we felt that ours more accurately assessed the overall animal personality literature; however, searches using any combination of these terms yielded the same conclusions. By reading the title and abstract for each paper, we determined whether it contained data. We classified data-free papers into sub-categories: literature reviews, hypothetical ideas/concepts, and general methods. Maintaining consistency with DiRienzo and Montiglio's definition of data-free, all statistical methods, meta-analyses, simulations, or mathematical modeling papers were not considered data-free as they generate quantitative analyses. We excluded papers not explicitly related to behavioral ecology and animal personality (e.g., human studies).

We obtained 473 papers, of which 20% were data-free. Of these data-free papers, 70% were literature reviews, and 19% were hypothetical ideas/conceptual papers. Many of these reviews and idea papers sought to: combine animal personality with other fields, update the state of the field, or survey the animal personality literature within a specific taxon (Jandt et al., 2014). There were also a small number of data-free papers describing general methodologies, approximately 11% of data-free papers. We therefore determined that data-free papers represent the minority of publications in the animal personality field to date, and most of these data-free papers synthesize research to develop conceptual frameworks or reviews.

In addition to overall number of papers, DiRienzo and Montiglio argue that data-free papers receive disproportionately more citations than data papers. However, data-free papers that synthesize information and provide new avenues of research are likely the most highly cited publications in many fields. To test this view, we assessed the number of data-free papers among the top 10 most cited papers in: animal social networks, kin selection, parental care, optimal diet, sexual selection, alternative mating tactics, and anti-predator behavior. We searched citations from 1993–2014, consistent with the years in DiRienzo and Montiglio's analysis. On average, 49% of the top 10 most cited papers in these fields were data-free, with variation from 10% in alternative mating tactics to 80% in kin selection. While this inter-field comparison illuminates the variability of data-free papers among top-cited articles across topics, the fields we evaluated are at different stages and of different scopes. Thus, analyzing the impact and contributions of data-free papers may require a more qualitative approach.

We suggest that data-free papers can be impactful in several ways. Conceptual papers can provide frameworks that bridge multiple fields of thought. Literature reviews can synthesize the state of a field, providing organization and focus to generate predictions. More specific reviews can outline the progression of subfields. Data-free papers can also highlight gaps in a field and suggest future research directions. Notably, as animal personality integrates multiple disciplines, combining concepts from life history (Réale et al., 2010), physiology (Biro and Stamps, 2010), genetics (Van Oers and Sinn, 2013), development (Stamps and Groothuis, 2010a,b), ecology (Sih et al., 2012), and evolution (Wolf and Weissing, 2012), data-free papers can be particularly useful, connecting these diverse topics into cohesive frameworks.

DiRienzo and Montiglio (2015) argue, in particular, that although some earlier data-free publications have substantially inspired the field (Dall et al., 2004; Sih et al., 2004a,b; Wolf et al., 2007; Réale et al., 2010; Stamps and Groothuis, 2010a,b), the continued publication of data-free papers fails to push animal personality forward. We believe that while some excess data-free papers may provide little additional insight, many data-free articles continue to be impactful for the same reasons discussed above. As DiRienzo and Montiglio (2015) mention, time will tell if the data-free papers being published currently ultimately prove valuable. While impact is often evaluated primarily based upon number of citations, we think that the most impactful papers are ones that stimulate future research and provide new avenues to confront complex problems.

Data-free papers that accomplish this goal often necessarily cover an extensive topical scope. DiRienzo and Montiglio suggest that such data-free papers could usually be replaced by empirical studies testing the hypotheses of interest. While papers that simultaneously propose and test a new idea are admirable, we contend that the purview of high impact data-free papers almost always exceeds any one empirical study. Articles with data usually address only a small part of the overall frameworks championed by good data-free papers, partly because journals do not provide the page space to describe both empirical results and a novel, larger framework in one paper.

We close by emphasizing that the advancement of a field requires both empirical and data-free articles. For example, fields inundated with mostly data-free papers (though we doubt that this ever happens) would gain little from further data-free articles, while fields dominated by empirical papers would benefit from data-free papers that organize results within a cohesive, conceptual framework, and provide predictions. This scenario illustrates the notion that measuring impact requires a more nuanced analysis than citation counts, and that arguing that one type of paper could completely replace the other ignores their interrelatedness. Data-free and empirical papers complement each another, and impact has no single, simple definition.

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Individual differences in the potential and realized developmental plasticity of personality traits

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Changes in personality over ontogeny can occur even when every agent (individual or genotype) is exposed to the same set of cues, experiences or environmental conditions. A recent Bayesian model (Stamps and Krishnan, in press) shows how individual differences in the means and variances of prior distributions of estimates of variables such as danger can generate predictable individual differences in behavioral developmental trajectories, and predictable changes in the differential consistency (broad-sense repeatability) of behavior over ontogeny, even if every subject is reared and maintained under the same conditions. We use this model to highlight the distinction between potential plasticity (the ability of an agent to change its phenotype in response to different types of experience) and realized plasticity (the extent to which an agent's phenotype actually changes in response to a specific experience), and to demonstrate why the realized behavioral developmental plasticity of a given agent might vary as a function of the type of cues to which that agent was exposed over ontogeny. We describe two commonly used experimental protocols for studying individual differences in developmental plasticity (within-individual vs. replicate individual designs), discuss the advantages and disadvantages of each for investigating individual differences in the developmental plasticity of personality traits, and explain why replicate individual designs provide better estimates than within-individual designs of the potential developmental plasticity of behavioral traits. More generally, we suggest that a Bayesian approach to development, especially one which assumes that individuals differ with respect to the information provided by their immediate and distant ancestors, can provide valuable insights into how genes, epigenetic factors, maternal effects, and personal experiences might combine across the lifetime to affect the development of personality and other behavioral traits.

Keywords: developmental plasticity, phenotypic plasticity, behavioral reaction norms, boldness, replicate individuals, common garden, ontogeny, behavioral syndromes

INTRODUCTION

One of the defining criteria for personality in humans and animals is that individual differences in behavior are maintained across time (Caspi et al., 2005; Reale et al., 2007; Stamps and Groothuis, 2010a). The temporal consistency of individual differences in behavior is described by differential consistency (also called broad-sense repeatability, Stamps and Groothuis, 2010a). Differential consistency indicates the extent to which individual differences in trait values at one time are comparable to individual differences in the same trait values at one or more later times. Hence, it can be described by measuring the relationship between behavior scores and time for different individuals in the same sample. If the relationship between behavior and age or time is similar for all of the individuals in a sample, differential consistency will be high (**Figure 1A**); conversely, pronounced differences between individuals in the slopes or shapes of this relationship generate lower levels of differential consistency (**Figure 1B**). If behavior is measured at two different ages, differential consistency can be estimated by correlations, across individuals, between their scores at the two ages (e.g., see Hayes and Jenkins, 1997). When behavior is measured at multiple ages, specific versions of the statistic called repeatability (R) may provide reasonable estimates of differential consistency, as long as certain conditions are satisfied (McGraw and Wong, 1996; Nakagawa and Schielzeth, 2010; Biro and Stamps, under review).

Although the differential consistency of personality traits may be high when behavior is measured over short periods of time, it is often lower when measured over longer periods (Roberts and Delvecchio, 2000; Caspi et al., 2005; Stamps and Groothuis, 2010a; Boulton et al., 2014; Riemer et al., 2014). Also, when differential consistency is measured at different periods over the lifetime, it often varies as a function of age. In some species, the differential consistency of personality traits increases with age, i.e., personality is more stable later in life than it is early in life (squid, Sinn et al., 2008; humans, Roberts and Delvecchio, 2000; Caspi et al., 2005; dogs, Fratkin et al., 2013; fish, Edenbrow and Croft, 2011). These observations raise the question of why

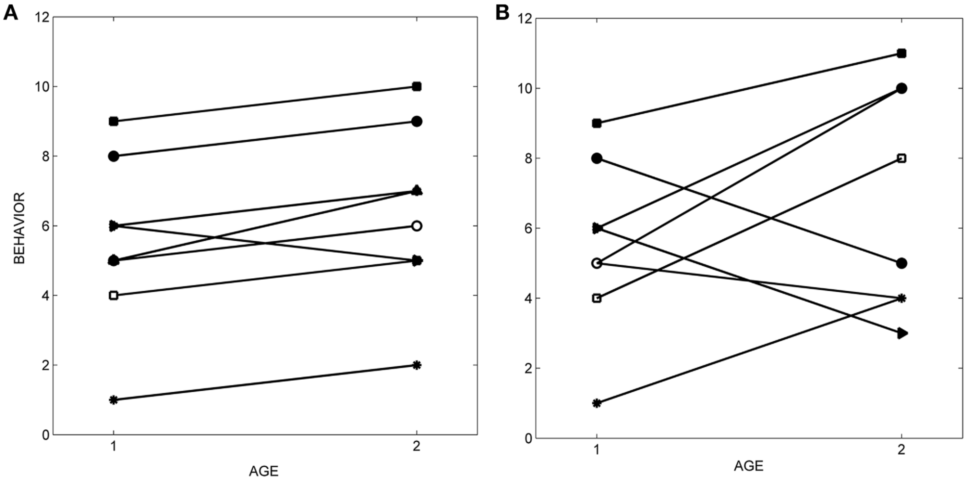

FIGURE 1 | Differential consistency. (A) When differences among individuals in behavior are maintained over age or time, differential consistency (broad-sense repeatability) is high ($r = 0.94$). **(B)** When differences among individuals in behavior change over age or time, differential consistency is lower ($r = 0.37$).

personality traits that are temporally stable over short periods might be less so over ontogeny.

In free-living animals, one obvious reason why the temporal stability of personality might change over ontogeny is that individuals had different experiences during the period in question. It is clear that personality traits can change within individuals as a result of past experience (Stamps and Groothuis, 2010a,b) For instance, Madagascar hissing cockroaches (*Gromphadorhina portentosa*) repeatedly exposed to predators over a 5 week period eventually became shyer, on average, than comparable individuals with no such experience (McDermott et al., 2014). Hence, in free-living animals, individual differences in behavior at a given age could easily occur as a result of differences among them in past experiences. However, this cannot be the whole story, because changes in the differential consistency of personality traits over time are observed even if all the subjects in a study are maintained from birth or hatching in captivity under highly standardized conditions (fish, Bell and Stamps, 2004; Edenbrow and Croft, 2011; squid, Sinn et al., 2008; insects, Gyuris et al., 2012; and primates, Sussman and Ha, 2011). Situations in which the differential consistency of personality changes over ontogeny, even when every subject has been exposed to the same (or at least very similar) experiential factors, imply that individuals differ with respect to the effects of the same experience on their behavioral development. In other words, changes in personality over time could be due to individual differences in developmental plasticity. More formally, in order to understand why personality might change over time, we need to understand individual differences in the developmental plasticity of personality traits. This is the topic explored in the current article.

We use a recent Bayesian model of behavioral development (Stamps and Krishnan, in press) to illustrate a number of basic principles relevant to individual differences in the developmental plasticity of personality traits. We begin with definitions of key concepts (i.e., behavioral developmental plasticity, potential, and realized plasticity) and then describe experimental protocols that empiricists have used to study individual differences in the developmental plasticity of behavior. A brief outline of the assumptions of the model is followed by a description of how it can be used to predict individual differences in developmental trajectories and the changes in the differential consistency of personality over ontogeny that result from those differences. We then show how the model can be used to illustrate the distinction between the potential and realized developmental plasticity of behavioral traits, and to show why relationships between initial scores for personality traits and the developmental plasticity of those traits would be expected to vary as a function of the cues to which individuals were exposed during ontogeny. Finally, we discuss the advantages and disadvantages of using different experimental protocols to estimate differences across individuals in the developmental plasticity of behavioral and other traits. We illustrate our main points by considering the development of boldness, a personality trait that has been studied in a wide range of animals, including humans (Fox et al., 2005; Reale et al., 2007; Conrad et al., 2011).

DEFINITIONS

When applied to behavior, the terms "plasticity" and "developmental plasticity" can be ambiguous because there are many different ways in which behavior can vary within individuals or genotypes as a result of variation in external stimuli (review in Stamps, under review). Here, we follow a longstanding tradition in ethology and psychology of discriminating between situations in which behavior varies as an immediate response to changes in external stimuli (contextual plasticity or activational plasticity) and situations in which behavior varies as a function of changes in external stimuli, experiences or environmental conditions that occurred in the past (developmental plasticity) (Stamps and Groothuis, 2010a; Snell-Rood, 2013). When applied to behavior, the term developmental plasticity encompasses a very wide range of phenomena, including learning, acclimation, and life-cycle staging (sensu Piersma and Drent, 2003), as well as situations in which experiences early in life affect the behavior expressed later in life. Since the current article is primarily concerned with gradual changes in personality that occur over ontogeny, it focuses on situations in which repeated or continuous exposure to specific types of experiential factors over extended periods of time affect the development and expression of personality traits.

When discussing the developmental plasticity of behavioral traits, it is also important to distinguish between potential and realized plasticity. Potential plasticity refers to the ability of an individual or a genotype to change its phenotype in response to changes in external stimuli, experiences, or environmental conditions, while realized plasticity refers to the change in phenotype that is actually observed when a given individual or genotype has been exposed to a specific set of external stimuli, experiences or environmental conditions (Stamps, under review). Potential plasticity is a construct that is central to theories on the evolution and ecological significance of individual differences in plasticity. This is because theoreticians often assume that individuals with high potential plasticity pay costs of maintaining the "machinery" that allows them to detect, monitor and respond to different stimuli, and that these maintenance costs of plasticity are paid even if the individual never expresses that plasticity (DeWitt et al., 1998; Auld et al., 2010). In contrast, realized plasticity is what empiricists actually measure in a given experiment. Concepts similar to potential and realized plasticity have been mentioned in passing by other authors. For instance, Ydenberg and Prins (2012) defined "flexibility" as the ability to adjust foraging behavior as circumstances change, but then noted that flexible individuals might not actually change their behavior if their original behavior performed well under the new set of conditions. Similarly, a recent theoretical model of the effects of phenotypic plasticity on population dynamics distinguished between the range of phenotypes that an individual is able to generate (plasticity-range), and the extent to which an individual's phenotype actually changes in a given situation (plasticity-used) (Gomez-Mestre and Jovani, 2013).

Understandably, empiricists often assume that their estimates of the realized plasticity of different individuals map directly onto the potential plasticity of those individuals. For instance, Thomson et al. (2012) found that initially shy rainbow trout (*Oncorhynchus mykiss*) did not significantly alter their level of boldness in response to a week's exposure to cues from a predator, and interpreted their results as indicating that shy fish were unable to respond to external cues. However, as we show below, the extent to which estimates of realized developmental plasticity reflect potential developmental plasticity can vary, depending on the experimental design that is used to measure differences among individuals or agents in developmental plasticity.

EXPERIMENTAL DESIGNS FOR STUDYING THE DEVELOPMENTAL PLASTICITY OF PERSONALITY TRAITS

Two experimental designs have traditionally been used to study the developmental plasticity of behavior: within-individual (or longitudinal) designs, and "common garden" designs. In within-individual designs, the behavior of the same agents is repeatedly measured at different ages. If subjects are repeatedly measured in the field, the resulting data simply describe how behavior of individual animals and the differential consistency of the individuals within the group changes as a function of age (e.g., Lucas and Donnellan, 2011; Petelle et al., 2013). However, if subjects are studied under carefully controlled conditions in the laboratory, within-individual designs can be used to describe how specific types of external stimuli, experiential factors, or environmental conditions affect the behavioral developmental trajectories of each of the subjects.

Within-individual designs are routinely used to describe individual differences in learning rates (Bell and Peeke, 2012; Thornton and Lukas, 2012), but they can also be used to study individual differences in other types of developmental plasticity, including the developmental plasticity of personality. For instance, by assessing the boldness of the same individuals before and after a period of exposure to cues from predators, researchers can use the difference between the two scores to estimate how each subject's boldness changed as a result of this experience (Bell and Sih, 2007; Thomson et al., 2012; Frost et al., 2013). Similarly, by repeatedly measuring the boldness of individuals reared in a "safe" environment (i.e., raised without any cues from predators, dangerous conspecifics, or other sources of danger), researchers can describe how the boldness of individuals or genotypes changes over the juvenile period as a function of this type of experience (Edenbrow and Croft, 2011; Sussman and Ha, 2011).

In the simplest type of within-individual design, subjects are consistently or repeatedly exposed to one set of cues or experiential factors over the entire study period. A slightly more complicated design involves first exposing subjects for an extended period to one set of cues or experiences, and then exposing them for a second extended period to a different set of cues or experiences. We will consider how both of these within-individual protocols can be used to study individual differences in the developmental plasticity of personality traits.

The second important way to investigate individual differences in developmental plasticity is to use a specific type of common garden experimental design, referred to here as a "replicate individual design." In this version of a common garden experiment, replicate individuals are used as surrogates for individual animals. Replicate individuals are individuals with the same genotype (e.g., clones, isolines, or more approximately, siblings), raised under the same conditions prior to the beginning of an experiment (Stamps and Groothuis, 2010a). Replicate individuals not only share genes, but also important experiential factors (e.g., maternal or sibling effects) that typically vary more among than within genotypes. If such genotypes are derived from individuals randomly sampled from the same population, and have not been subsequently exposed to artificial selection, they can provide a powerful tool for studies of individual differences in various types of behavioral plasticities (Stamps, under review).

When replicate individuals are used to study behavioral development, they allow researchers to estimate how the behavior of each individual would have differed if that individual had been exposed to different experiences earlier in life. To this end, individuals with the same age and genotype are randomly assigned to different treatments. Then the individuals in each treatment are exposed to a different set of stimuli, experiential factors or environmental conditions for a specified period of time. Finally, the behavior of all of the subjects is measured using standard assays at the same age later in life.

Replicate individual designs have, of course, been widely used to study genotypic differences in the developmental plasticity of morphological and life history traits (e.g., Auld et al., 2010). However, they can also be used to describe differences among genotypes in the developmental plasticity of behavior. For instance, researchers have used replicate individual designs to document differences among isolines of *Drosophila melanogaster* in the effects of the larval rearing medium on adult responses to olfactory stimuli (Sambandan et al., 2008), differences among isolines of *D. simulans* in the effects of rearing temperature on female choosiness and mate preferences (Ingleby et al., 2013), and differences among paternal half-sibs of waxmoths (*Achroia grisella*) in the effects of density, temperature, and food levels during the larval period on adult male calling song (Zhou et al., 2008).

MODEL DESCRIPTION

We only briefly summarize the main assumptions of the model here, since details of the model are available elsewhere (Stamps and Krishnan, in press). We assume that at the time of birth or hatching, individuals already possess information about conditions in the external world, information provided to them by their distant ancestors (e.g., via genes, Leimar et al., 2006; Shea, 2007) and by their immediate ancestors (e.g., via inherited epigenetic factors and maternal effects, Uller, 2008; Shea et al., 2011; Keiser and Mondor, 2013; Burton and Metcalfe, 2014). We assume that at birth or hatching, different individuals in the same population begin life with different information from their ancestors, but that after birth or hatching, all individuals have the same personal experiences, which also provide them with information about conditions in the external world. The key assumption of our model is that, within each individual, information from its ancestors and information from a series of personal experiences is combined over ontogeny through Bayesian-like processes to affect behavior. The model focuses on personal experiences (cues) that provide information about the external world but do not directly affect the resources available for growth and development. For instance, it would apply to experiments in which animals were repeatedly exposed to stimuli from predators or conspecifics, but not to experiments in which the "experience" consisted of restricted food rations or infection by pathogens.

As is the case for any Bayesian model of behavior, our model includes four basic components: prior distributions, posterior distributions, likelihood functions and response functions. Informally, a prior distribution specifies an individual's beliefs about a biologically relevant variable (e.g., the state of danger) before it has a given experience (e.g., exposure to cues from a predator), and a posterior distribution specifies that individual's beliefs about that same variable after it has had that experience. The likelihood function for a particular type of experience specifies the probability that that experience would occur, given each possible state of the variable; the response function links belief to action, by specifying the relationship between an individual's current belief (based on its prior or its posterior distribution) and the behavior it expresses based on that belief. Importantly, the posterior distribution after one experience becomes the prior distribution for the next experience. This is why Bayesian approaches are useful for modeling development, where it is typical for a given individual to have a series of experiences over ontogeny, each of which may provide additional information about the state of the world (Frankenhuis and Panchanathan, 2011a,b; Fischer et al., 2014).

The current model assumes that at birth or hatching, individuals have different prior distributions, and that both the variable that individuals are attempting to estimate in the external environment (e.g., the state of danger) and the individuals' behavioral response to that estimate (e.g., their level of boldness) are continuously distributed. When combined, these two assumptions allow us to model personality traits, which may be expressed soon after birth or hatching, and which usually vary continuously across individuals within populations. These assumptions set our model apart from other recent Bayesian models of development, which assume that (1) all of the individuals in a population are born with the same prior distribution, (2) the variable in the external world that animals are attempting to estimate can take on one of only two different states, and (3) there are only two phenotypes, each of which is favored in one of the two states (e.g., Frankenhuis and Panchanathan, 2011a; Fischer et al., 2014). In addition, our assumption that prior and posterior distributions are continuously distributed allows the means and the variances of these distributions to vary independently of one another (see below, Appendix and Discussion); this is not an option in two-state models, since in binomial distributions, the variance is a fixed function of the mean.

In our model, we assume that the variable in the external environment (here, the state of danger) varies continuously from 0 to 1 (we divide the interval from 0 to 1 into 100 equally spaced states for ease of numerical computation), and use beta distributions to describe both prior distributions and likelihood functions. Beta distributions use two parameters (α and β) to generate a wide variety of monotonically increasing, monotonically decreasing, unimodal (hump-shaped), and uniform distributions. We do not, however, consider U-shaped prior distributions or likelihood functions ($\alpha < 1$ and $\beta < 1$), in which extremely high and extremely low values of the variable are both more likely to occur than any intermediate values of the variable. This is because situations in which both extreme values of a variable are more likely to occur than any intermediate value are more easily and appropriately modeled using two-state rather than multiple-state Bayesian models.

We focus on likelihood functions with intermediate reliability, where the term reliability indicates the extent to which a given cue is associated with different states of the variable. With respect to the current model, a cue with the lowest reliability would be one that was equally likely to occur at any of the 100 states of danger, while a cue with the highest reliability would be one that was only likely to occur at only one of the 100 states of danger. Cues with moderately reliable likelihood functions are most relevant for studying the development of personality because cues with very low reliability have little effect on the behavior of any individual, while cues with very high reliability encourage every individual to rapidly develop the same phenotype (Frankenhuis and Panchanathan, 2011a; Fischer et al., 2014), even if those individuals began with different prior distributions (Stamps and Krishnan, in press).

For simplicity, in this article we focus on linear response functions (for discussion of other response functions, see Stamps and Krishnan, in press). That is, we assume that there is a linear relationship between the mean of the prior or posterior distribution at a given age and the mean level of behavior expressed by an individual at that age. Depending on the variable and the behavior, this relationship can be positive or negative. We assume that the level of boldness exhibited by an individual is negatively related to its current estimate of the state of danger (see also Appendix).

In order to investigate how individuals with a range of prior distributions would respond to experiences with different likelihood functions, we use Matlab to model the developmental trajectories of 15 hypothetical individuals, each of which has a different prior distribution for the state of danger. Each individual's prior distribution is described by its mean (0.1, 0.3, 0.5, 0.7, and 0.9) and its variance (0.001, 0.02, and the maximum variance possible for the mean value, given the constraints on the beta distributions noted above). The maximum possible variance for each prior distribution depends on its mean value. For instance, for prior distributions with a mean of 0.1 or 0.9, the maximum variance = 0.0426; whereas for prior distributions with a mean of 0.3 or 0.7, the maximum variance = 0.0864. For a prior distribution with a mean of 0.5, the maximum variance = 0.0833; this is the special case of a uniform distribution ($\alpha = 1$, $\beta = 1$), in which each of the 100 possible states is equally likely to occur. Together, these 15 distributions span the range of prior distributions that are possible under the assumptions of our model.

We assume that each of the 15 individuals begins with a different prior distribution at birth or hatching (at age 0), and that the behavior expressed by each individual at age 0 is directly related to the mean of its prior distribution. Then all of the individuals are exposed to the same cues (same likelihood function) from age 0 to age 1. Each individual's posterior distribution at age 1 is computed by combining its prior distribution with the likelihood function using Bayes' equation, and its behavior at age 1 is assumed to be directly related to the mean of its posterior distribution at age 1. Each individual's posterior distribution at age 1 then becomes its prior distribution for the next experience (from age 1 to age 2). The procedure outlined above is then repeated to generate the posterior distributions and the expected behavior of each individual for each age from 2 to 4, as a function of their prior distributions at birth or hatching, and the likelihood functions for the cues to which they were exposed over the course of ontogeny.

Previous analyses have shown that when prior distributions are continuously distributed, the effects of a given cue (i.e., a given likelihood function) on the development of behavior depend on the mean and the variance of the prior distribution (Stamps and Krishnan, in press). If a prior distribution has low variance, behavior is not expected to change much, if at all, after any cue, regardless of the mean of the prior distribution or the shape of the likelihood function. In contrast, if a prior distribution has high variance, the extent to which a given cue affects behavior depends on the discrepancy between the mean of the prior distribution and the information about the state provided by the likelihood function. An intuitive explanation for these patterns is provided in the Appendix; see also Results.

RESULTS

WITHIN-INDIVIDUAL DESIGNS FOR DESCRIBING THE DEVELOPMENTAL PLASTICITY OF PERSONALITY TRAITS AS A FUNCTION OF EXPERIENCE

Repeated exposure to cues with the same likelihood function

In this section, we assume that individuals with 15 different prior distributions for the state of danger are continuously or repeatedly exposed to the same cues (same likelihood function) from birth or hatching until the end of the juvenile period (see also Stamps and Krishnan, in press). The boldness of each individual is assessed soon after birth, and then again at a series of different ages. The developmental plasticity of boldness of each individual can then be estimated by the slope or shape of its developmental trajectory, either for a portion of ontogeny (e.g., from age 0 to age 1) or across the entire study period (e.g., from age 0 to age 4).

In the current study, we compare the results from three simulated experiments, in which a set of individuals with the same initial prior distributions are either repeatedly exposed to cues indicating that level of danger in the current environment is relatively low (**Figure 2**), to cues indicating that the level of danger is relatively high (**Figure 3**), or to cues indicating that the level of danger is intermediate (**Figure 4**).

In all three situations, scores for boldness tend to converge on the level of boldness that is encouraged by the likelihood function. That is, if cues indicate that the state of danger is low (**Figure 2**), most individuals gradually become bolder, if cues indicate that the state of danger is high, most individuals gradually become shyer (**Figure 3**), and if cues indicate that the state of danger is intermediate (**Figure 4**), most shy individuals gradually become bolder and most bold individuals gradually become shyer.

The variance and mean of each individual's prior distribution together determine how it will respond to a given cue. Individuals whose prior distributions had low variance (indicated by circles) maintain their initial level of boldness across ontogeny, regardless of the cues to which they are exposed. For instance, initially shy individuals whose prior distributions had low variance (red circles) remain shy, even if repeatedly exposed to cues indicating that the world is safe (**Figure 2**). In contrast, if individuals' prior distributions had high variance (indicated by triangles), their developmental trajectories depend on the relationship between the mean of their prior distribution and the likelihood function for the cue. An individual who was very shy at birth but whose prior distribution had a high variance (red triangles) becomes much bolder over ontogeny if raised with cues indicating that the world is relatively safe (**Figure 2**), remains shy over ontogeny if raised with cues indicating that the world is relatively dangerous (**Figure 3**), and becomes somewhat bolder if raised with cues indicating that the world is moderately safe (**Figure 4**). Of course, individuals can have prior distributions with variance anywhere between these two extremes: predicted developmental trajectories for individuals whose prior distributions had an

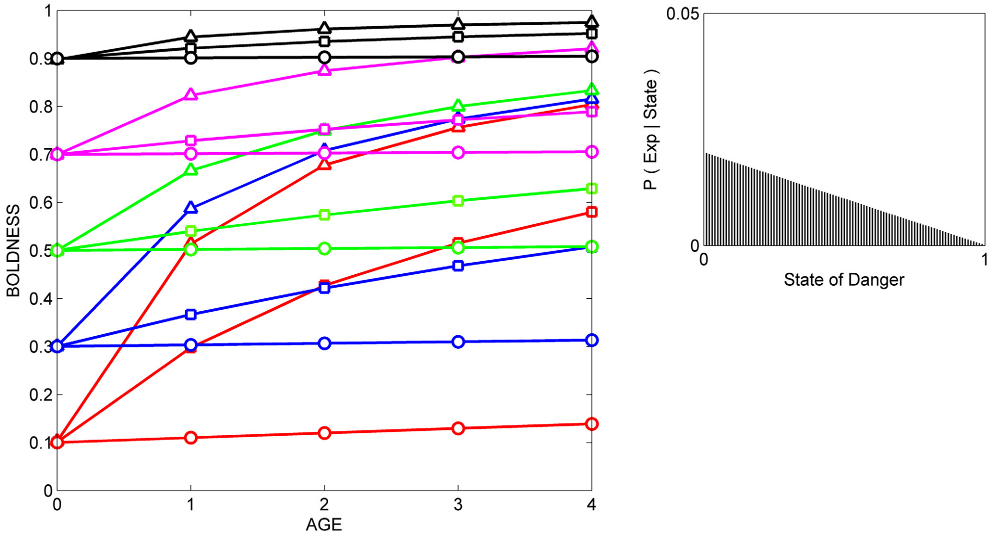

FIGURE 2 | Developmental trajectories for boldness resulting from repeated exposure to cues indicative of safety. Fifteen hypothetical individuals with different prior distributions at birth are repeatedly exposed to the same cue, and their boldness is recorded at 5 ages across ontogeny. The mean of each prior distribution (and the resulting mean level of behavior at age 0) is indicated by color (red: 0.1, blue: 0.3, green: 0.5, magenta: 0.7, black: 0.9); the variance of each prior distribution is indicated by symbols (circles: variance = 0.001, squares, variance = 0.02; triangles, variance = maximal variance for each mean). The likelihood function (right box) indicates the probability of experience given the state (P (Exp|State) for each of the 100 possible states, ranging from 0 to 1. This likelihood function is moderately reliable and left-biased (i.e., the cue is more likely to occur when danger is low than when danger is moderate to high); it was generated by a beta distribution in which α = 2 and β = 1.

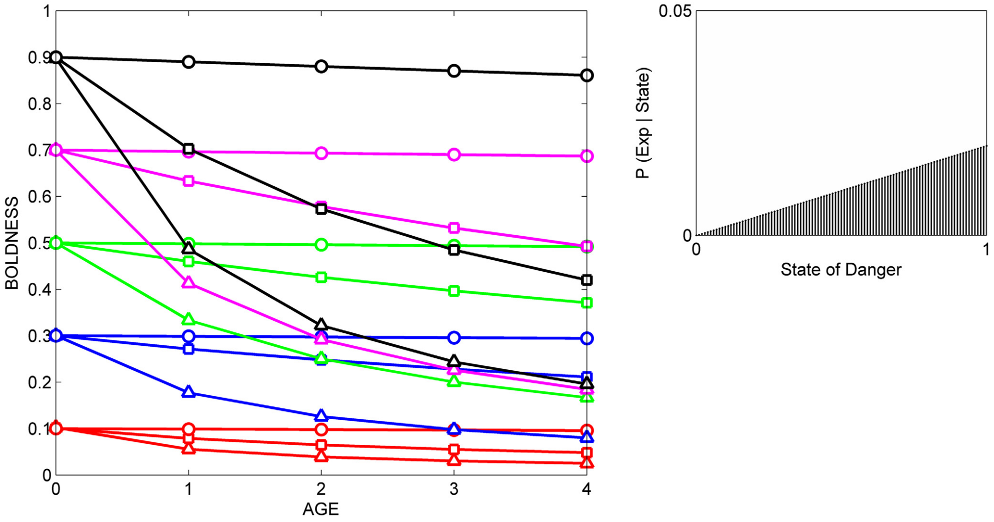

FIGURE 3 | Developmental trajectories for boldness resulting from repeated exposure to a moderately reliable cue indicative of danger. Symbols for prior distributions as in **Figure 2**. The likelihood function (right box) was generated by a beta distribution with α = 1 and β = 2.

intermediate variance of 0.02 are indicated by the lines with squares in **Figures 2–4**.

These predicted differences among individuals in their developmental trajectories for boldness follow directly from basic principles of Bayesian updating (see Appendix). Low variance for its prior distribution implies that, at birth, an individual is quite certain that the estimate of the state of danger provided by its ancestors is correct. Hence, the individual would continue to express the level of boldness encouraged by its prior distribution, even if repeatedly exposed to moderately reliable cues that imply that its initial level of boldness might not be appropriate in the current environment. In contrast, high variance for a prior distribution indicates that, at birth, an individual is very uncertain that the estimate of the state provided by its ancestors is correct. In that case, repeated exposure to moderately reliable cues can lead to a change in the level of boldness

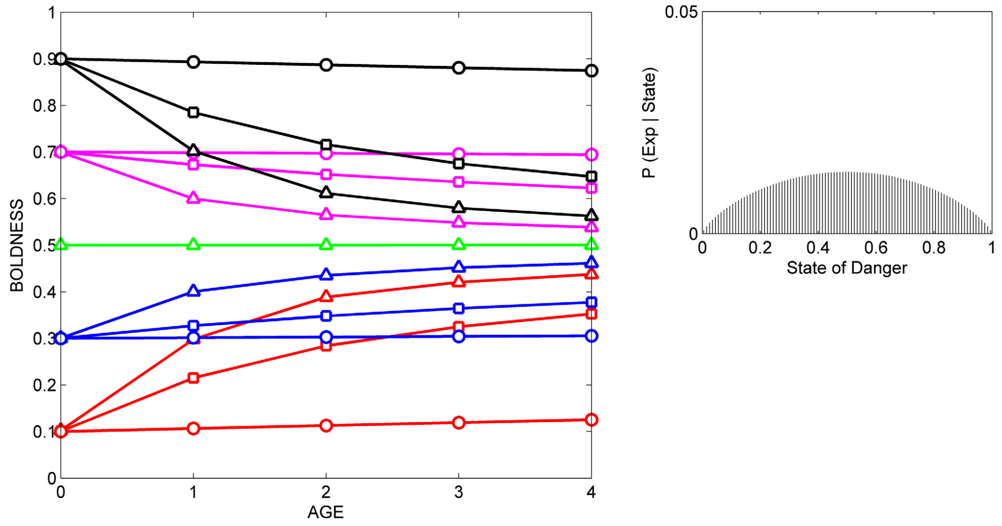

FIGURE 4 | Developmental trajectories for boldness resulting from repeated exposure to a moderately reliable cue indicative of intermediate levels of danger. Symbols for prior distributions as in **Figure 2**. The likelihood function (right box) was generated by a beta distribution with α = 1.75 and β = 1.75.

over ontogeny, but the extent to which behavior changes over time depends on the discrepancy between the estimate of the state of danger provided by the cue and the estimate of the state of danger provided by information from the individual's ancestors.

These patterns also provide a possible explanation for changes in the differential consistency of personality over ontogeny. The differential consistency of boldness for a given period (e.g., from age 0 to age 1) can be estimated by measuring the slope of each individual's developmental trajectory, and then quantifying the extent to which those slopes differ across the 15 individuals in the group. It can be easily seen that in **Figures 2–4**, the slopes of the developmental trajectories differ more across individuals earlier in life (from age 0 to age 1) than they do later in life (from age 3 to age 4). In other words, in the examples illustrated here, the model predicts that the differential consistency of personality will increase with age. Previous analyses indicate that differential consistency would increase with age for many other, though not all, likelihood functions and response functions (Stamps and Krishnan, in press; unpublished data).

In addition, the model predicts that relationships among individuals between personality traits and the developmental plasticity of those traits will vary, depending on the cues to which those individuals were exposed over ontogeny. More formally, across individuals, the relationship between initial scores for behavior (i.e., the intercepts of the development trajectories) and the absolute value (magnitude) of the slopes of the developmental trajectories depends on the likelihood function. For instance, in **Figure 2**, individuals with high initial scores are less plastic than individuals with low initial scores, as is indicated by the negative relationship across individuals between intercepts and the magnitude of the slopes across the entire study period (from age 0 to age 4). In contrast, in **Figure 3**, individuals with high initial scores are more plastic than those with low initial scores (a positive relationship, across individuals, between intercepts and the magnitude of the slopes), while in **Figure 4**, the relationship between intercept and the magnitude of the slopes is U-shaped: bold individuals become shyer, shy individuals become bolder, and intermediately bold individuals maintain their initial levels of behavior.

Finally, these results provide an easy way to grasp the distinction between potential plasticity and realized plasticity. The model indicates that the variance of an individual's prior distribution is directly related to its potential plasticity. Individuals whose prior distributions had low variance have low potential developmental plasticity, in the sense that they would not be expected to change their behavior much, if at all, in response to exposure to any cue over the course of development. In contrast, individuals whose prior distributions had high variance have high potential plasticity, because they are capable of major changes in behavior as a function of exposure to cues during development. Individuals whose prior distributions had intermediate variance have intermediate potential plasticity: they are able to change their behavior as a result of exposure to cues, but to a lesser extent for any given cue than individuals whose prior distributions had high variance.

However, it is also clear from comparison of **Figures 2–4** that individuals with high potential plasticity do not necessarily always exhibit high realized plasticity. Instead, individuals whose prior distributions had high variance may express low realized plasticity, intermediate realized plasticity, or high realized plasticity, depending on the extent to which the estimate of the state provided by their prior distribution contradicts the estimate of the state provided by the cues to which they are exposed. For instance, a potentially plastic individual who initially estimated that the state of danger is intermediate (green triangles) would not be expected to change its level of boldness over ontogeny if exposed to cues that confirmed this initial estimate (**Figure 4**), but would be expected to either increase or decrease its level of boldness if exposed over ontogeny to cues that contradicted this initial estimate (**Figures 2**, **3**).

Sequential exposure to cues with opposing likelihood functions

In this section we consider a slightly more complicated situation, in which individuals are first exposed to one cue (with one likelihood function) for an extended period over ontogeny and then are exposed to a different cue (with a different likelihood function) for a second extended period. We focus on situations in which the likelihood functions are biased in different directions, because if different cues or experiences have similar likelihood functions, they are predicted to have comparable effects on developmental trajectories.

In the first example (**Figure 5A**), individuals born with a range of prior distributions are first exposed from age 0 to age 2 to a cue with a moderately reliable left-biased likelihood function (i.e., a cue that indicates that the state of danger is relatively low) and are then exposed from age 2 to age 4 to a different moderately reliable cue with a right-biased likelihood function (i.e., a cue indicating that the state of danger is relatively high). As one would expect, across all of the subjects, average boldness first gradually increases when individuals are exposed to cues indicative of safety, and then average boldness gradually declines when individuals are exposed to cues indicative of danger. Also, as one would expect from the discussion in the previous section, individuals with low potential plasticity (prior distributions with low variance) do not change their behavior in response to either type of experience.

However, some of the other patterns illustrated in **Figure 5A** are less intuitive. For instance, even though both likelihood functions are equally informative (same shape, albeit biased in opposite directions, see boxes in **Figures 2**, **3**), following exposure to both cues, individuals with moderate to high potential plasticity do not end up with the same level of boldness that they had at birth or hatching (at age 0). Instead, scores for boldness tend to converge on the intermediate values that are appropriate for both likelihood functions. And, despite the change in cues and likelihood functions midway through ontogeny, differential consistency tends to increase as a function of age: the variance across individuals in the slopes of their developmental trajectories is higher from age 0 to age 1 than it is from age 3 to age 4. Thus, several of the patterns expected when individuals are exposed to a single cue through ontogeny are also observed if cues reverse midway through ontogeny.

With respect to providing reasonable estimates of potential developmental plasticity, the sequential within-individual design does a better job than a simpler experimental protocol in which individuals are exposed to just one cue over ontogeny. This is because individuals with high potential plasticity whose behavior is unaffected by initial exposure to a cue with a likelihood function biased in one direction would be expected to change their behavior when exposed to a different cue with a likelihood function biased in the opposite direction. For instance, the potentially plastic "bold" individual indicated by the black triangles in **Figure 5A** maintains its initial level of high boldness (low realized plasticity) as long as it is exposed to cues indicative of safety, but subsequently reduces its level of boldness (high realized plasticity) when it is repeatedly exposed to cues indicative of danger.

However, one problem with using sequential within-individual designs to estimate potential plasticity is that the order in which individuals are exposed to each of a series of cues affects their responses to those cues. This can be seen easily by using the range of scores each individual expresses over ontogeny to estimate its realized plasticity. For instance, in **Figure 5A**, the individual indicated by the red triangles has scores which range from a minimum of 0.1 to a maximum of 0.68 over the period from age 0 to age 4, so it has higher realized plasticity than the individual indicated by the blue squares, whose scores range from 0.3 to 0.4 over the same period. By extension, we can use this method to compare the realized plasticity of individuals

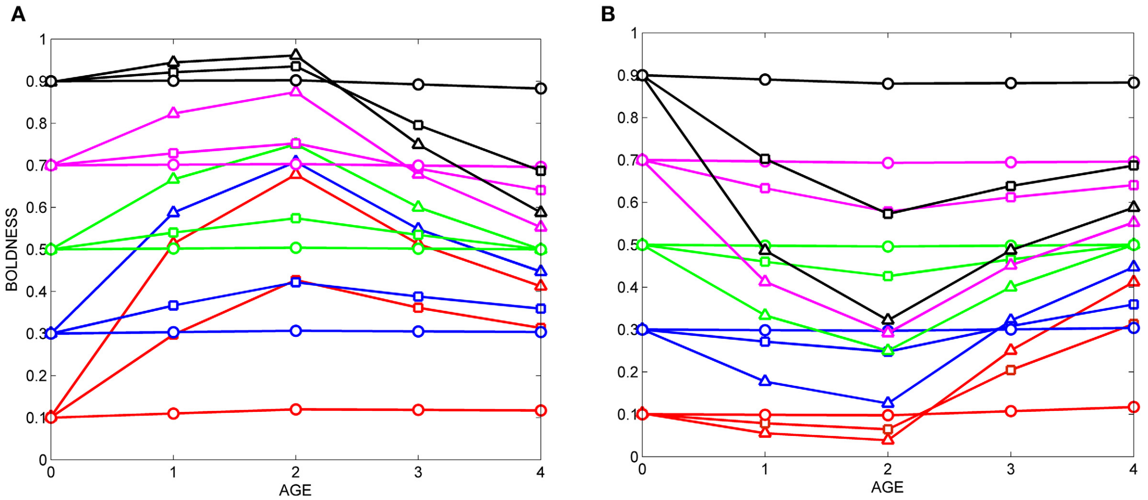

FIGURE 5 | Sequential exposure to cues with different likelihood functions. (A) Fifteen hypothetical individuals are first exposed from age 0 to age 2 to cues indicating that the world is relatively safe (see box in **Figure 2**), then are exposed from age 2 to age 4 to cues indicating that the world is relatively dangerous (see box in **Figure 3**). **(B)** Individuals with the same prior distributions are first exposed from age 0 to age 2 to cues indicating that the world is relatively dangerous (box, **Figure 3**), then to cues indicating that the world is relatively safe (box, **Figure 2**). Symbols for prior distributions as in **Figure 2**.

with the same prior distribution who were sequentially exposed to the same two cues, but in a different order (**Figure 5A** vs. **Figure 5B**). This process shows that the realized plasticity of equivalent individuals depends on the order in which they were exposed to the same cues. For instance, the initially shy individual indicated by the red triangles is more plastic in **Figure 5A** (range of boldness scores: 0.1–0.68) than is the equivalent individual in **Figure 5B** (range of scores: 0.05–0.42). As a result of these differences, the rank-order of realized plasticity for the individuals in the two groups varies as a function of cue order. For example, the individual with the highest realized plasticity in **Figure 5A** is the initially shy individual indicated by the red triangles, but the individual with the highest realized plasticity in **Figure 5B** is the initially bold individual indicated by the black triangles.

The order in which individuals are sequentially exposed to cues over ontogeny affects their realized plasticity because, by its very nature, Bayesian updating incorporates information from the past when estimating the current state of the world (see Appendix, and references on Bayesian updating in Stamps and Krishnan, in press). The notion that order matters when subjects are sequentially exposed to different cues or experiences is quite familiar to empiricists studying another type of developmental plasticity, learning. For instance, in reversal learning experiments, acquisition rates for the first response in the sequence are often different from the acquisition rates for the second response, following the change in the task contingency (e.g., Colwill et al., 2005; Moy et al., 2007; Shettleworth, 2010; Lloyd and Leslie, 2013).

The fact that order matters when individuals are exposed to different cues over ontogeny implies that although sequential within-individual designs provide better estimates of potential developmental plasticity than within-individual designs that only utilize one cue, there may still be substantial discrepancies between the estimates of realized developmental plasticity provided by this method and the potential plasticity of the subjects.

REPLICATE INDIVIDUAL DESIGNS

Common garden experiments using replicate individuals as subjects (i.e., replicate individual designs) measure developmental plasticity differently than is the case for within-individual (longitudinal) experimental designs. Instead of describing how the behavior of each individual changes over time as a function of exposure to a given experience (or sequence of experiences), the scores of matched individuals who have been exposed to different experiences over the same period of time are compared to one another.

A little thought reveals that replicate individual designs are equivalent to simultaneously conducting two or more of the experiments outlined above, except that in this case, the subjects are genotypes (replicate individuals) rather than individual animals. For instance, imagine that one set of representatives of 15 genotypes were raised in the presence of cues indicative of safety (**Figure 2**), and a second matched set of the same genotypes were raised in the presence of cues indicative of danger (**Figure 3**). Then, at age 4, boldness is assessed for each of the subjects in each treatment. The resulting data could then be used to estimate each genotype's developmental response to each set of cues, as indicated in **Figure 6**. Note that instead of plotting the behavior of each agent as a function of age or time, we now plot the mean behavior of each genotype at age 4, as a function of the cues to which they were exposed earlier in life: treatment 1 (reared with cues indicative of safety), vs. treatment 2 (reared with cues indicative of danger).

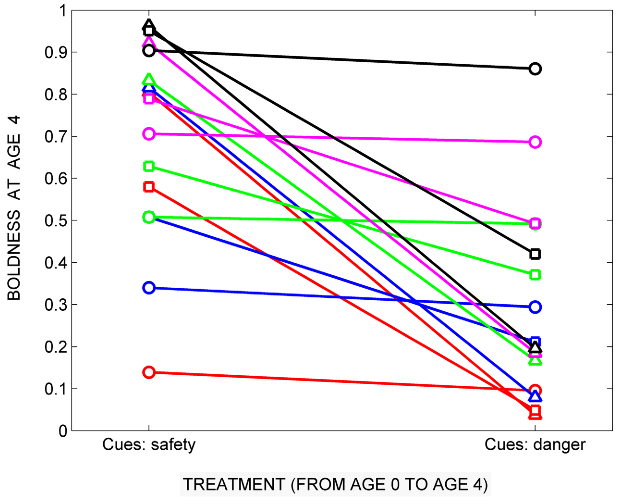

FIGURE 6 | A hypothetical common garden experiment showing how exposure to cues in two different rearing treatments might affect the boldness of 15 genotypes (replicate individuals). Genotypes with the prior distributions specified by the symbols in **Figure 2** are either raised with cues indicative of safety (see **Figure 2**) or with cues indicative of danger (see **Figure 3**). The mean boldness scores at age 4 are compared for the two treatment groups. Realized developmental plasticity is lowest for genotypes whose prior distributions had low variance (circles), intermediate for genotypes whose prior distributions had intermediate variance (squares) and highest for genotypes whose prior distributions had high variance (triangles).

In the simplest replicate individual design, in which matched genotypes are raised in two different treatments and their trait values are compared at the end of the study, the plasticity of each genotype is indicated by the difference between its scores in the two treatments (see Auld et al., 2010). It can be seen that this procedure provides reasonable estimates of the potential plasticity of the 15 genotypes in this study (**Figure 6**). Genotypes whose prior distributions had low variance (circles) have low plasticity: there is little or no difference in their scores at age 4 after being reared in the two treatments. Genotypes whose prior distributions had intermediate variance (squares) have moderately lower boldness scores after treatment 2 than after treatment 1, while genotypes whose prior distributions had high variance (triangles) have much lower boldness scores after treatment 2 than after treatment 1.

Generally speaking, replicate individual designs have several advantages over within-individual designs with respect to estimating the potential developmental plasticity of different agents. Because individuals with the same genotype can be exposed over ontogeny to two (or more) different treatments, individuals with high potential plasticity are expected to change their behavior in response to at least one of them. This is in contrast to the situation when subjects are exposed to just one cue throughout the experiment, since in the latter situation individuals with high potential plasticity may have low realized plasticity if raised with cues that indicate that their initial phenotype was appropriate for the current environment. And, because each set of replicate individuals is reared under a single set of conditions, the order effects that can complicate sequential, within-individual designs are not a concern in replicate individual designs.

On the other hand, information about temporal change in behavior is lost in traditional replicate individual designs. This is because in such designs, the behavior of the different replicate individuals is typically not measured soon after birth or hatching, so there is no way to estimate the extent to which the behavior of each agent changed over ontogeny. Of course, there are also a number of practical issues with replicate individual designs, e.g., replicate individuals are more readily available in some species than others, and because behavior can vary among individuals with the same genotype, large numbers of individuals per genotype may be required to obtain reliable estimates of the behavior of each genotype. These issues are discussed in more detail in Stamps, under review.

DISCUSSION AND CONCLUSIONS

The current article shows that a simple Bayesian model can be very useful for illustrating concepts relevant to the development of personality. It explains why one would expect to see individual differences in the developmental trajectories of personality traits and changes in the differential consistency of personality over ontogeny, even if every subject was raised under the same set of conditions. It shows why we would expect relationships between initial personality scores and the developmental plasticity of personality to vary among empirical studies, as a function of the cues to which those subjects were exposed during those studies. More broadly, it highlights the distinction between realized and potential plasticity, and indicates why certain experimental protocols for studying the developmental plasticity of behavioral traits might provide better estimates than others of the potential plasticity of different individuals or genotypes. In addition, the model may have practical value, in terms of predicting the developmental trajectories of personality traits of individuals or genotypes. This topic is explored in greater detail in Stamps and Krishnan (in press), which discusses ways to estimate the mean and variance of an agent's prior distribution, based on the mean level of behavior, and the short-term spontaneous variability of behavior (intra-individual variability (IIV), or intra-genotypic variability) that it expresses soon after birth or hatching.

Another insight from the model is that different experimental designs provide different information about individual differences in the developmental plasticity of behavioral traits. Within-individual (longitudinal) designs provide the data required to describe individual developmental trajectories and changes in the differential consistency of behavioral traits over ontogeny, but they provide less reliable estimates of the potential plasticity of different individuals or genotypes than do replicate individual designs. Conversely, although traditional replicate individual designs can provide reasonable estimates of the potential plasticity of different replicate individuals (genotypes), they don't provide information about how personality changes as a function of age. In species and situations in which replicate experimental designs are impractical, our analyses suggest that sequential within-individual designs (in which cues switch midway through ontogeny) are more likely to provide reasonable estimates of potential plasticity than are within-individual designs in which the subjects are reared with the same cues throughout ontogeny. In species and situations in which replicate individual designs are feasible, we suggest using hybrid experimental designs, i.e., common garden experiments in which the behavior of the subjects is measured before they are placed in the different treatment groups, and then measured again at regular intervals over the study (e.g., Edenbrow and Croft, 2013). With sufficient statistical power, this type of hybrid design can not only provide estimates of the potential plasticity of different replicate individuals, but also provide estimates of the shapes or the slopes of their behavioral developmental trajectories.

Although experimental studies of individual differences in the developmental trajectories of personality traits are still quite limited, there is some support for the model's general prediction that relationships between initial scores for personality traits and the subsequent plasticity of those traits might vary as a function of the cues to which individuals were exposed over ontogeny. For instance, when pigtailed macaques, *Macaca nemestrina* and clones (genotypes) of Mangrove killifish, *Kryptolebias marmoratus* were raised in the absence of cues indicative of danger, the average boldness of juveniles increased with age, but across individuals or genotypes, shy individuals became bolder and bold individuals remained relatively bold (Edenbrow and Croft, 2011; Sussman and Ha, 2011). Thus, the intercepts and the magnitude of the slopes of developmental trajectories for boldness were negatively related to one another, as predicted by the model (see **Figure 2**, also Stamps and Krishnan, in press). In contrast, when juvenile rainbow trout, *Oncorhynchus mykiss*, were repeatedly exposed to predators over a 2 week period, there was no change in their average boldness, but bold individuals became shyer, and shy individuals become bolder (Frost et al., 2013). This is the pattern predicted by our model if individuals with different initial levels of boldness were repeatedly exposed to cues indicative of an intermediate level of danger (e.g., see **Figure 4**). To our knowledge, to date no one has described the developmental trajectories for boldness for individuals or genotypes who initially expressed different levels of boldness, and who were then repeatedly or continuously exposed to cues indicative of high levels of danger. In this situation, our model predicts a decline in average boldness over ontogeny, and a positive relationship, across agents, between the intercepts and the magnitude of the slopes of developmental trajectories for boldness (e.g., see **Figure 3**).

Although boldness was used to illustrate the main points of this study, the same approach could be used to model the development of other personality traits (e.g., activity, exploratory behavior, aggressiveness). Similarly, although we have focused on cues that might affect individuals' estimates of the state of danger, cues associated with other variables in the external world (e.g., local population density, food availability, etc.) might also affect the development of personality traits. In principle, the general approach outlined in the current study could apply to any continuously variable labile behavioral or physiological trait. In practice, the major challenge for empiricists will be to begin their experiments already armed with reasonable assumptions about the likelihood functions for specific cues, and about the response functions that link prior distributions or posterior distributions with behavior.

In the current article we were able to build upon an extensive literature that indicates that cues from predators (or the lack thereof) convey information about the state of danger, and that levels of boldness should decline as estimates of the state of danger increase. However, it is not always obvious how behavior should change over ontogeny in response to continuous or repeated exposure to a given cue. For instance, there is empirical evidence that juvenile crickets use repeated exposure to acoustic signals from adult males to estimate the type of social environment they will later encounter as adults (see Bailey and Zuk, 2008; Kasumovic et al., 2011; DiRienzo et al., 2012). However, it is currently unclear how exposure to those cues should affect the development of aggressive behavior. Some authors have suggested that exposure to cues indicative of high densities of local competitors should favor the development of elevated levels of aggressiveness in male crickets (e.g., see DiRienzo et al., 2012). But cues indicating that the local neighborhood already contains many older, vigorously calling, territory owners might just as easily favor the development of reduced aggressiveness and enhanced subordinate behavior in callow, young males. This alternate hypothesis is suggested by empirical studies indicating that newly mature male crickets have difficulty competing aggressively with older, established territorial residents (e.g., Dixon and Cade, 1986; Buena and Walker, 2008; Rillich et al., 2011). In fact, preliminary results support the second hypothesis: male *Gryllus integer* reared with conspecific calls exhibited lower levels of aggressiveness as adults in standardized staged encounters than did males reared without them (DiRienzo et al., 2012). Hence, until more is known about the levels of aggressiveness favored when young male crickets emerge in localities with different densities of older, established territory owners, it would be premature to construct theoretical models based on assumptions about the effects of conspecific calls on the development of aggressiveness in this taxon.

Many of the assumptions which underlie the current study are not new, and can be found scattered among different literatures. These include (1) there is standing genetic variation within populations, not only in behavioral trait values but also in the potential plasticity of those traits (Wolf et al., 2008, 2011; Rodriguez, 2013), (2) information provided by parents about the environment can affect the development of personality traits (Reddon, 2012; Schuett et al., 2013), (3) information from ancestors and from personal experiences combines across ontogeny to affect the development of phenotypic traits (Leimar et al., 2006; Frankenhuis and Panchanathan, 2011a; Fischer et al., 2014), and (4) Bayesian-like mechanisms provide the optimal way to combine information from different sources (McLinn and Stephens, 2006; McNamara et al., 2006; Lange and Dukas, 2009). Our main contribution has been to combine these assumptions to generate predictions about individual differences in the developmental trajectories of continuously distributed phenotypic traits. One of the major insights to be gleaned from this approach is that variation among individuals and genotypes in the reliability of information provided by their ancestors may play as important a role as the reliability of information from personal experiences in determining how a given individual or genotype will respond to exposure to a given type of experience over the course of development. That is, our model suggests that an individual who assumes that the information from its ancestors is highly reliable (i.e., a prior distribution with low variance) would have lower potential plasticity than an individual who assumes that the information from its ancestors is less reliable (i.e., a prior distribution with high variance). Thus, our approach complements earlier theoretical studies which indicate that developmental plasticity can be limited by the reliability of the cues to which individuals are exposed over ontogeny (DeWitt et al., 1998; Tufto, 2000; Frankenhuis and Panchanathan, 2011a; Fischer et al., 2014). It expands upon those findings to show that even if every subject is exposed to the same (moderately reliable) cues over ontogeny, individual differences in developmental trajectories would still be expected if neonates start out with different information from their ancestors, a situation which is likely to be common in the natural world (Stamps and Krishnan, in press).

More generally, we suggest that a Bayesian perspective can be helpful for understanding a number of difficult concepts in development. It shows how genes, maternal effects, and personal experiences might iteratively interact with one another across ontogeny to affect the expression of behavior and other phenotypic traits (see also Oyama, 2000; Bateson and Gluckman, 2011). It emphasizes that information about the same state of the world can come from many different sources, at many different times across an individual's lifetime, and that information from genes does not have precedence over information from other sources (see Lickliter, 2008). It demonstrates that information from ancestors can continue to affect an individual's developmental trajectory, even after that individual has had a series of informative personal experiences, and suggests why some individuals might be more sensitive than others to the effects of the same experiential factors on their developmental trajectories. Hence, a Bayesian approach to development may have value that extends well beyond the specific questions addressed in the current study.

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APPENDIX

EFFECTS OF THE MEANS AND VARIANCES OF PRIOR DISTRIBUTIONS ON BAYESIAN UPDATING (REPRINTED, WITH PERMISSION, FROM STAMPS AND KRISHNAN, IN PRESS; ©2014 BY THE UNIVERSITY OF CHICAGO)

Here we show how differences between individuals in the means of their prior distributions affect Bayesian updating. One individual (**Figure A1A**) has a prior distribution with a high mean, indicating that at birth or hatching, this individual estimates that the level of danger is more likely to be high than it is to be low or moderate. This individual is then maintained for a period (e.g., a month) under "safe" conditions, with no exposure to cues from predators, aggressive conspecifics, or any other potential dangers. As is indicated by the shape of the likelihood function, this type of experience is more likely to occur when the level of danger is low than when it is moderate to high. When this individual's prior distribution is combined with this likelihood function, via Bayesian updating, it yields the posterior distribution shown in **Figure A1A**. That is, after the experience, this individual revises downwards its belief about the level of danger. Finally, assuming that "boldness" is negatively related to the mean of the prior or the posterior distribution for danger, we would expect this individual to be bolder after the experience (based on the mean of its posterior distribution) than it was when it was naive (based on the mean of its prior distribution).

A second individual (**Figure A1B**) has a prior distribution with a low mean, indicating that when it is naïve, this individual estimates that the level of danger is more likely to be low than it is to be moderate to high. This individual is then exposed to the same experience (same likelihood function) as was the case for the individual in **Figure A1A**. However, in this case, the estimate of the state of danger provided by this individual's prior distribution is very similar to the estimate of the state of danger provided by the experience. As a result, its posterior distribution is very similar to its prior distribution. By extension, we would expect this individual's boldness score after the experience to be similar to its score when it was naïve.

This example illustrates a very general and very basic feature of Bayesian updating, namely that the effects of a given experience on estimates of the state of the world depend on the discrepancy between the prior distribution and the likelihood function (Courville et al., 2006). One can intuitively see that if a naïve individual believes that the world is a safe place, an extended period of time with no cues indicative of danger simply confirms its initial belief, and hence, has little or no effect on its belief that the world is safe. On the other hand, if a naïve individual believes that the world is dangerous, an extended period of time with no cues indicative of danger is a "surprise," so this experience is more likely to change its estimate of danger.

A second important point is that the effect of a potentially informative experience on an individual's estimate of the state of the world also depends on the variance of its prior distribution (**Figure A2**). Consider a situation in which two individuals both have prior distributions with the same mean value (mean = 0.8). That is, when naïve, both of them estimate that the state of danger is relatively high. However, the variance of the first individual's prior distribution (**Figure A2A**) is much higher than the vari-

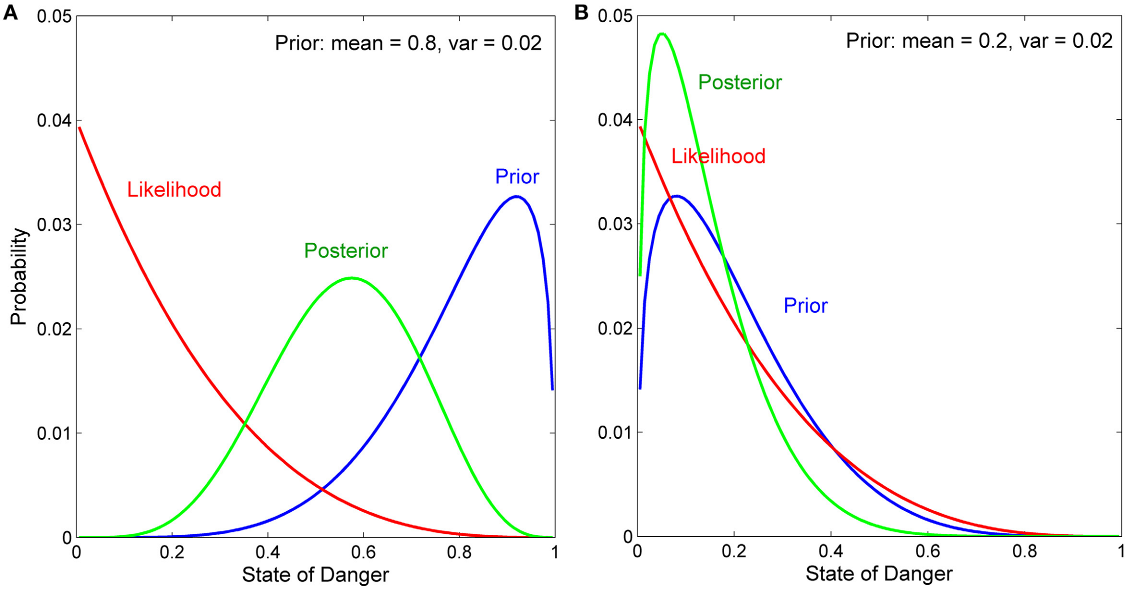

FIGURE A1 | Effect of the mean of the prior distribution on Bayesian updating. Two individuals **(A,B)** are both exposed to the same experience, with the likelihood function indicated in red. The first individual **(A)** has a prior distribution with a high mean; the second individual **(B)** has a prior distribution with a low mean. When the likelihood function and the prior distribution contradict each other **(A)**, the posterior distribution is displaced from the prior distribution. In contrast, when the likelihood function and the prior distribution are concordant **(B)**, the posterior distribution is very similar to the prior distribution.

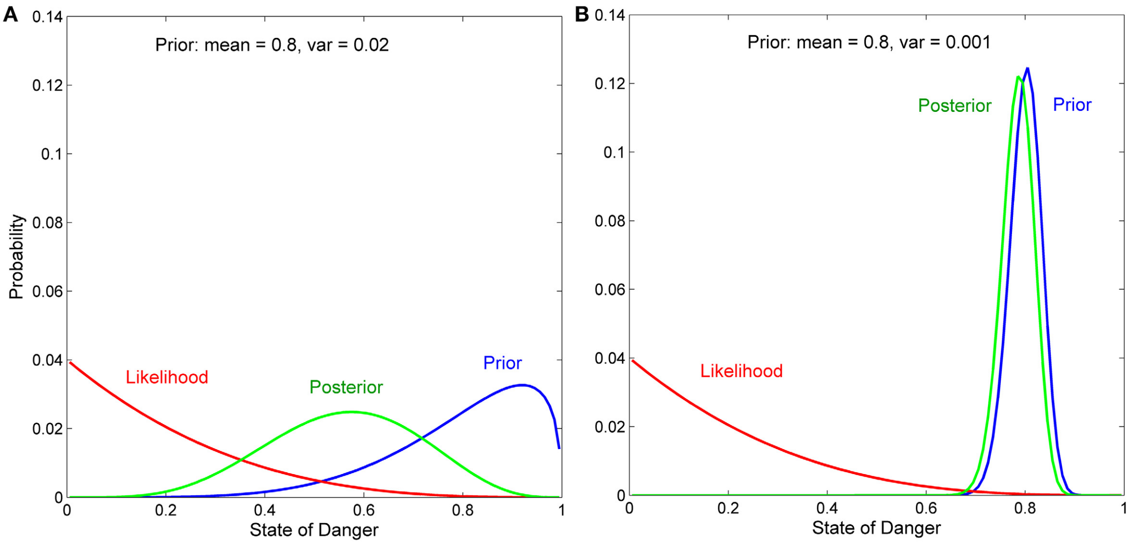

FIGURE A2 | Effect of the variance of the prior distribution on Bayesian updating. Two individuals **(A,B)** are both exposed to the same experience, with the likelihood function indicated in red. Both individuals have prior distributions with the same mean, but the individual in **(A)** has a prior distribution with a high variance, whereas the individual in **(B)** has a prior distribution with a low variance. When variance of the prior is high **(A)**, the posterior distribution is displaced from the prior distribution. However, when the variance of the prior is low **(B)**, the posterior distribution is virtually the same as the prior distribution.

ance of the second individual's prior distribution (**Figure A2B**). Both individuals are then exposed to experience indicating that the level of danger is moderately low. In the case of the first individual, this experience leads to a reduction in its estimate of the level of danger, i.e., a posterior distribution shifted to the left of its prior distribution (**Figure A2A**). However, in the case of the second individual, the same experience has little effect on its estimate of danger; its posterior distribution is very similar to its prior distribution (**Figure A2B**). Thus, although both individuals would be expected to express the same high level of boldness when naïve, after the same experience, the first individual's level of boldness would increase, but the second individual's level of boldness would not change.

In this case, the intuitive explanation is that the variance of an individual's prior distribution indicates the confidence an individual has in its initial belief about the state of the world. If a naïve individual vaguely suspects that the world might be dangerous, experience indicating it is actually safe should alter its estimate of the state of the danger, and hence, its behavior. However, if a naïve individual firmly believes that the world is dangerous, that same experience should have little or no effect on either this belief or its behavior.

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Social carry-over effects on non-social behavioral variation: mechanisms and consequences

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The field of animal personality is interested in decomposing behaviors into different levels of variation, with its present focus on the ecological and evolutionary causes and consequences of expressed variation. Recently the role of the social environment, i.e., social partners, has been suggested to affect behavioral variation and induce selection on animal personality. Social partner effects exist because characters of social partners (e.g., size, behavior), affect the behavioral expression of a focal individual. Here, we (1) first review the proximate mechanisms underlying the social partner effects on behavioral *expression* and the timescales at which such effects might take place. We then (2) discuss how within- and among-individual *variation* in single behaviors and *covariation* between multiple behaviors, caused by social partners, can carry-over to non-social behaviors expressed outside the social context. Finally, we (3) highlight evolutionary consequences of social carry-over effects to non-social behaviors and (4) suggest study designs and statistical approaches which can be applied to study the nature and evolutionary consequences of social carry-over effects on non-social behaviors. Acknowledging the proximate mechanisms underpinning the social partner effects is important since it opens a door to understand in depth how social environments can affect behavioral variation and covariation at multiple levels, and the evolution of non-social behaviors (i.e., exploration, activity, boldness) that are affected by social interactions.

Keywords: behavioral plasticity, behavioral variation, animal personality, behavioral syndrome, social evolution, social environment, social carry-over

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Introduction

Phenotypes vary at multiple levels and research in the field of animal personality has highlighted the importance of distinguishing between behavioral variation that occurs among individuals ("personality") vs. within individuals ("plasticity") (Dingemanse et al., 2010; Dingemanse and Dochtermann, 2013). Targeting within-individual level variation has been the more traditional approach in behavioral ecology (for social contexts: Maynard-Smith, 1982) and its evolutionary significance lies in the ability of plastic individuals to adapt to changing environments in order to maximize fitness in any given environment (Piersma and Drent, 2003; Ghalambor et al., 2007). Even though within-individual variation in phenotypic traits can be present in several different timescales across an individual's lifespan (Piersma and Drent, 2003), the costs and limits of phenotypic plasticity may restrict the optimal response to any single confronted environment

(DeWitt et al., 1998; Auld et al., 2010). Among-individual level variation has more recently come to the foreground in behavioral ecology and, whilst not necessarily predicted by traditional adaptive theory (Dall et al., 2004), it is widespread across the animal kingdom (Sih et al., 2004; Dingemanse and Wolf, 2010; Wolf and Weissing, 2010; Dall et al., 2012), and has major ecological and evolutionary consequences (Wolf and Weissing, 2012). Internal features of the individual (states: metabolic rate, body size, assets) have been widely used to explain the existence of among-individual variation in behaviors (Wolf et al., 2007; Biro and Stamps, 2008; Careau et al., 2008; Luttbeg and Sih, 2010), while they also contribute to variation at the within-individual level due to the fluctuating nature of these features (Wolf and Weissing, 2010). Recently, external features like the social environment, i.e., other individuals, have been suggested as possible factors modifying behavioral variation at both within- and among-individual levels (Bergmüller and Taborsky, 2010; Montiglio et al., 2013; Dingemanse and Araya-Ajoy, 2015). However, almost without exception these levels of variation are neglected in studies of social partner effects (however for within-individual level variation within social context see Wilson et al., 2011a, 2013) and studies of carry-over effects to non-social behaviors expressed outside the social interaction are absent (however see Laskowski and Pruitt, 2014 for group level effects). The proximate mechanisms through which partner effects act can define the temporal patterns of social carry-over effects to non-social behaviors expressed after social interactions. Therefore, understanding the proximate mechanisms gives information about when social carry-over effects affect within- vs. among-individual level of variation and about the strength and temporal patterns of the potential evolutionary effects of carry-overs to non-social behaviors.

Individuals might express behaviors differently in the presence vs. absence of conspecifics (reviewed in Webster and Ward, 2011). A classic example of social interaction is direct contest behavior, usually measured between competing males (Hsu et al., 2006). However, behaviors such as mating, mate attraction, communication and different forms of co-operation are also well studied examples of social behaviors (Bradbury and Vehrencamp, 1998; Griffin and West, 2003; Wright et al., 2010; Lyon and Montgomerie, 2012). Social partners can affect the up- or down regulation of different state variables of a focal individual, like hormonal profiles, the level of energy, or body size, and thus affect the expressed behaviors of a focal individual through these proximate mechanisms (Hsu et al., 2006; Sachser et al., 2013; Wilson et al., 2013). The temporal consistency of the social partner effect on a state variable may define the temporal consistency of the focal individuals' behaviors driven by the given state (Hsu et al., 2006; cf. Wolf and Weissing, 2010). Short term social partner effects are likely based on fast-changing states, like hormonal profiles, while long term social partner effects on behaviors might be mediated through slow-changing states like body mass, neurobiological features or other physiological mechanisms.

Traditionally, social partner effects are explored mainly *within* the social contexts, and only at the phenotypic mean level, so that carry-over effects have been studied from one social interaction to another, i.e., how long winning vs. losing in one social interaction affects the outcome of the next social interaction (Hsu et al., 2006). However, since behaviors can covary through shared proximate mechanisms across contexts (Ketterson and Nolan, 1999; Sih et al., 2004; Sih and Bell, 2008; Garamszegi et al., 2012), social partner effects have the potential to carry over indirectly to behaviors expressed *after* social interactions in non-social contexts, if the underpinning proximate mechanisms persist long enough. Such non-social behaviors can be, for example, exploration, activity, and boldness, expressed after the social interaction. Statistically, social partner effects are present when the identity of the social partner explains a significant amount of variance in the behavior of a focal individual (the individual on which the phenotype is measured), either at the within- or among-individual level of variation (Wilson et al., 2011a, 2013; Dingemanse and Araya-Ajoy, 2015). However, this kind of variance partitioning models have not been applied (nor studied) to the carry-over effects on non-social behaviors expressed outside social interactions (see however Laskowski and Pruitt, 2014 for group level effects). Including a variance partitioning approach in studies of social carry-over effects, together with the knowledge of the underpinning proximate mechanisms, helps to understand the temporal patterns of social carry-over effects, and whether the repeatable or plastic part (or both) of non-social behaviors in focal individuals is affected by the social interactions. Furthermore, studying social carry-over effects in depth is not only mechanistically, but also evolutionary important. Social partners can induce indirect genetic effects (i.e., IGEs), which are present when trait expression is not only affected directly by the genes of a focal individual (i.e., DGEs), but also by the genes of its social partner (Moore et al., 1997; Wolf et al., 1999). IGEs can slow down or speed up the rate of evolution of traits associated directly (or indirectly) with social interactions (Moore et al., 1997; Wolf et al., 1999). Since the temporal patterns of the carry-over effects may depend on the nature of the underpinning proximate mechanism, the underpinning mechanism might also define the strength of the carry-over effect on the evolution of non-social behavioral traits.

Here, we introduce a framework to clarify how the proximate mechanisms might define the temporal patterns of social carry-over effects on behavioral variation at different levels in non-social behaviors like exploration, activity or boldness, expressed *after* social interactions. We (1) review types of proximate mechanisms causing social partner effects over short and long time periods and explain how temporal patterns of social carry-over effects might depend on these mechanisms. We then discuss (2) how within- and among-individual behavioral variance in non-social behaviors and covariance between non-social and social behaviors are affected by social partners depending on the nature of the proximate mechanisms underpinning the social carry-over effects. We also (3) highlight the evolutionary implications and fitness consequences of the carry-over effects and (4) give suggestions on how to empirically study and statistically analyze the existence, temporal persistency (using variance partitioning tools), and evolutionary consequences of the carry-over effects on non-social behaviors. Our framework highlights the importance of carry-over effects on non-social behaviors and helps to (i) predict how far temporally the social carry-over effects have the potential to affect the different variance components (i.e., plasticity and personality) in these behaviors and (ii) learn about consequent evolutionary effects of these carry-overs on non-social behaviors.

Proximate Mechanisms for Short- and Long-Term Social Partner Effects

Behavior is often assumed to be "state-dependent" (McNamara and Houston, 1996; Houston and McNamara, 1999), with "state" being anything that affects the costs and benefits of expressed behaviors: environmental, physiological, neurobiological, or morphological features (McNamara and Houston, 1996; Houston and McNamara, 1999; Wolf et al., 2011). Below, we review fast- and slow-changing state variables underpinning the social partner effects on behavioral *expression* in general and discuss how they can cause carry-over effects outside the social interaction at various temporal scales.

Social Carry-Over Effects on Behavioral Expression through Fast-Changing State Variables

Generally, social carry-over effects which decay quickly might have a basis in hormone- or neurotransmitter levels, short term memory, level of energy, blood pressure or other fast-changing states which affect the behavioral expression of the focal individual accordingly (Hsu et al., 2006; Briffa and Sneddon, 2007; Coppens et al., 2010; Earley et al., 2013). Since fast-changing states are relatively easily affected by external factors (Wolf and Weissing, 2010), they are also sensitive to social partner effects. Because carry-over effects through fast-changing states are measurable only shortly after social interactions, they can carry-over to non-social behaviors, but only over short temporal scales (red line in **Figure 1**). In extreme cases, hormonal profiles return back to the baseline level almost immediately after the social interaction giving no room for social carry-overs. In the Field cricket, *Gryllus bimaculatus*, the level of octopamine in haemolymph after aggressive male-male interactions or female-male courtship interactions dropped back to baseline within a few minutes after the interaction (Adamo et al., 1995), suggesting absence of carry-over effects due to hormonal mechanisms. In the pumpkinseed sunfish, *Lepomis gibbosus*, winner effects are only detectable between 15 and 60 minutes after winning (Chase et al., 1994). This means that, in this species, behaviors measured in non-social contexts shortly after winning a contest might be affected by social partners. Since social interactions are also energetically costly (Hsu et al., 2006; Briffa and Sneddon, 2007), other fast-changing states like amount of energy reserves may play a role in carry-over effects. In the salamander, *Desmognathus ochrophaeus*, oxygen consumption and lactic acid formation significantly increased during both male-male aggressive encounters and male-female courtship (Bennett and Houck, 1983). Energy consumption during social interactions may cause short term physical exhaustion or depletion of resources (Briffa and Sneddon, 2007), and affect non-social behaviors measured shortly after the social interaction accordingly. The temporal consistency of social carry-over effects based on fast-changing states might depend on the length of the social interaction. For example, in the Sierra dome spider, *Neriene litigiosa,* energetic costs of male-male fights increase with the temporal consistency of the fights from 3.5 to 11.5 times compared to that of resting metabolic rate (DeCarvalho et al., 2004). Moreover, in house crickets, *Acheta domesticus*, the energy expenditure increases with the escalation level of a fight, with the oxygen consumed in high escalation stages being up to 40 times more than the baseline level (Hack, 1997). Thus, the magnitude of the social carry-over effects on non-social behaviors of the focal individuals might correlate positively with the length of the social interaction.

Social Carry-Over Effects on Behavioral Expression through Slow-Changing State Variables

If social partner effects are underpinned by slow-changing state variables they can also effectively explain long term carry-over effects in non-social behaviors (blue line in **Figure 1**). However, slow-changing states, like body mass, organ size, or neurobiological features take a long time to change (Wolf and Weissing, 2010), and might not be very sensitive to social partner effects. Nevertheless, slow-changing states may be affected by social interactions if the interaction is prolonged (Jacobs et al., 2011 and refs. therein) or repeated (Wilson et al., 2013). Relatively long term male-female social interactions during the

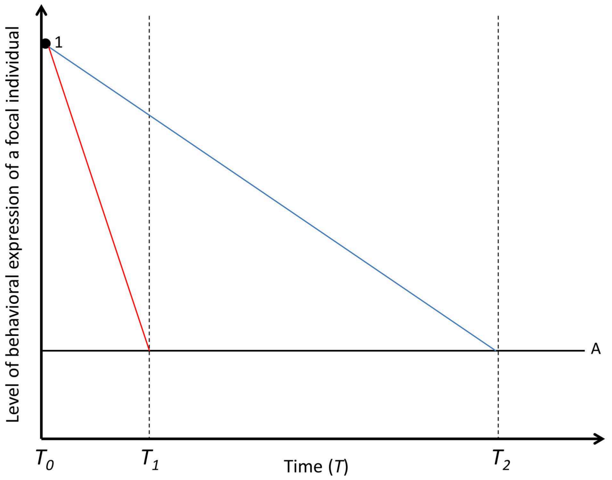

FIGURE 1 | Decay of the social carry-over effect on behavioral expression of a focal individual in time. The solid black line represents the focal individual's (A) baseline level of behavioral expression, while red, and blue lines represent the behavioral expression of a focal individual under social carry-over effects by social partner (round black dot; 1). Carry-over effects are underpinned by either fast-changing (red line) or slow-changing (blue line) state variables. The social partner effect is decayed in T_1 if underpinned by fast-changing mechanisms and in T_2 if underpinned by slow-changing mechanisms. The social interaction is terminated in T_0. For simplicity, the partner effects, driven by fast- and slow-changing states are assumed to be the same magnitude in T_0.

breeding season can modify several slow-changing physiological and morphological features like organ size or amount of lipid storage (Jacobs et al., 2011 and refs. therein) and affect non-social behaviors during the entire time period of the breeding season accordingly. Social interactions can define the amount of resources to which individuals have access to (reviewed in Hsu et al., 2006; Wilson et al., 2013) and lead to changes in body size (Wilson et al., 2013) or any other resource based states. Individuals with high resource inputs may become larger in size or differ otherwise in morphology or physiology compared to individuals with low resource inputs (Stearns, 1992). In the sheepshead swordtail, *Xiphophorus birchmanni*, individuals that are consistently more aggressive and dominant in repeated pairwise social interactions have access to larger amounts of resources and have higher growth rates, irrespective of the initial body size, compared to individuals expressing lower aggression and dominance in these social interactions (Wilson et al., 2013). Slow-changing states of a focal individual, like body size and morphology, can affect several different behaviors across different ecological contexts (Dall et al., 2004; McElreath and Strimling, 2006; Luttbeg and Sih, 2010). For example, large body size can be positively related to boldness if large body size protects individuals from predation and enables individuals to act boldly in a feeding context (McElreath and Strimling, 2006; Luttbeg and Sih, 2010).

In reality, there are multiple fast- and slow-changing state variables affecting behaviors simultaneously and these mechanisms may also act in concert. For example, repeated winner-loser effects, based on fast-changing hormonal profiles, may enable individuals to gain or prevent access to resources, respectively, for a period of time that eventually enables modification of the slow-changing features, like morphology, physiology or neurobiology. Different state variables might also work sequentially: after a fast social interaction, fast-changing hormonal profiles are responsible for carry-over effects, while after a longer interaction, depleted energy resources might define the nature of this carry-over. Therefore, the temporal consistency of the partner effect might generally increase with the length of the social interaction.

Social Carry-Over Effects on *Variation* and *Covariation* in Non-Social Behaviors

Carry Over Effects on Variation in Non-Social Behaviors

Just as focal individuals are repeatable in their behaviors, social partners can consistently differ in the behavioral responses they elicit in others (Wilson et al., 2011a, 2013; Dingemanse and Araya-Ajoy, 2015). This means, for example, that some partners always elicit higher (or lower) aggressiveness in focal individuals compared to other partners, i.e., they make the focal individuals consistently deviate from their average phenotype. Such "social partner repeatability" represents the proportion of phenotypic variance in the focal individual's behavior explained by the social partner identity. Social partners will affect the within-individual variance in the focal individual phenotype (Wilson et al., 2011a, 2013; Dingemanse and Araya-Ajoy, 2015) as a result of adaptive behavioral plasticity of the focal individual to differences in the social environment (social responsiveness) (Webster and Ward, 2011; Taborsky and Oliveira, 2012; Wolf and McNamara, 2013; Wolf and Krause, 2014). Importantly, social interactions can also generate true among-individual variation or covariation between behaviors if social carry-over effects induce permanent environmental effects on focal individuals and if those effects vary among focal individuals. If social partners are not repeatable in the behavioral responses they elicit in focal individuals, they do not modify behavioral variation of focal individuals in a predictable manner. Therefore, we assume here that social partner repeatability exists, which has been the case in empirical research studying this variation *within* social contexts (Wilson et al., 2011a, 2013).

Within-Individual Variance: Plasticity

When carry-over effects are underpinned by fast-changing states, like hormonal profiles or energy levels (Hsu et al., 2006; Coppens et al., 2010), and when focal individuals do not differ in the confronted social environment, social partners will affect the within-individual component of behavioral variance in non-social behaviors, expressed after social interactions (**Figure 2**). For example, in male green swordtails (*Xiphophorus helleri*), the focal individuals' within-individual variance in aggressiveness against conspecifics (social behavior) is partly explained by the social partner identity (Wilson et al., 2011a). Because fast-changing states are easily reversed to the normal level (Wolf and Weissing, 2010), the temporary effect of social partners on non-social behaviors of focal individuals, like exploration, activity or boldness, does not have the potential to carry-over to long temporal scales, but decays steeply after the social interaction (red lines in **Figure 3**). Therefore, the sensitivity of a state to social partner effects is negatively correlated with the temporal consistency of the carry-over effect on non-social behaviors. This means that in short social encounters, like rapid contest situations, the social partner effect might be driven by fast-changing states and therefore be detected only within, or temporally very close to the social interaction (red lines in **Figure 3**). However, the carry-over effect might increase with the length of the social interaction even if the states are fast-changing. For example, increased energy expenditure with increased escalation in aggressive encounters in Sierra dome spiders and House crickets (Hack, 1997; DeCarvalho et al., 2004) indicates that the recovery time after a fight, and thus time for the decay of social partner effect, might increase with the increased time spent in the social interaction.

Slow-changing states within a focal individual might have the potential to explain longer term carry-over effects on within-individual variation in non-social behaviors of focal individuals (**Figure 2**, blue lines in **Figure 3**). However, since slow-changing states are not very sensitive to partner effects they may need long (or repeated) interactions in order to respond to social environments. For example, repeated contests might enable long term carry-over effects on a focal individual's slow-changing states, like body mass in Sheepshead swordtails (*Xiphophorus*

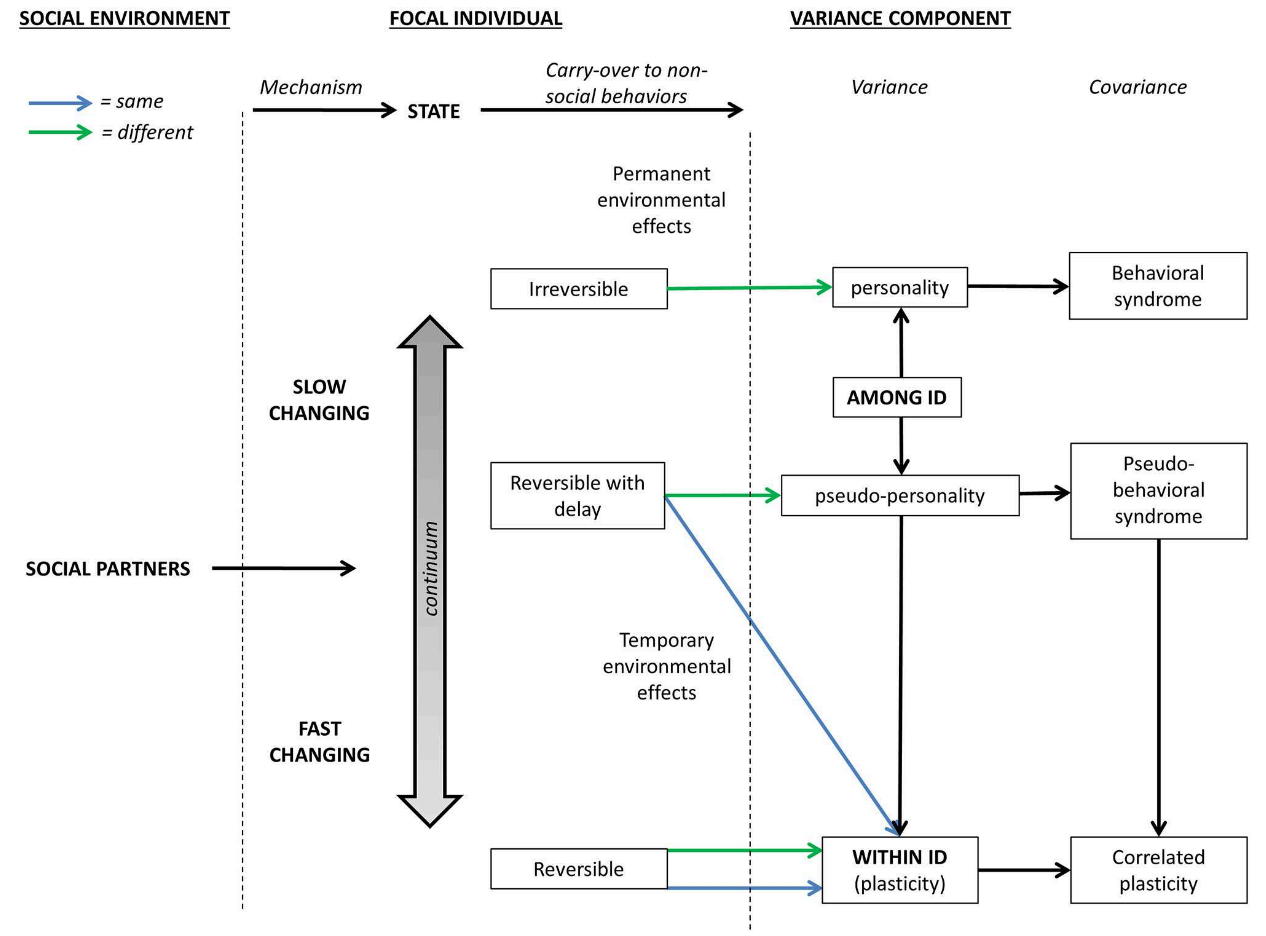

FIGURE 2 | Schematic presentation of how the social-carry-over effects affect within- and among-individual variance components in behaviors expressed in non-social contexts through state variables. Green and blue lines represent social environments/carry-over effects that differ and do not differ among-individuals, respectively.

birchmanni) (Wilson et al., 2013), to emerge. Since slow-changing state variables are not very sensitive to social carry-over effects, i.e., repeatedly confronted social partners do not induce large changes in slow-changing states, they should explain only low amounts of within-individual variance in non-social behaviors of focal individuals compared to fast-changing states.

Among-Individual Variance: Pseudo-Personality vs. True Personality

Social partners can also explain among-individual variance in non-social behaviors of focal individuals, i.e., animal personality, if social partners are confronted non-randomly among focal individuals. However, even though carry-over effects caused by reversible fast- and slow-changing states can explain such variation over different timescales (see above), the measured variance does not represent real animal personality, but rather "pseudo-personality" (**Figures 2**, **4**) (Westneat et al., 2011; Dingemanse and Dochtermann, 2013). Pseudo-personality exists when among-individual variation in a trait is created by among-individual variation in experienced environments and the effect is not permanent, but focal individuals change their behaviors if they are moved to another environment, i.e., focal individuals express plasticity (e.g., Westneat et al., 2011; Dingemanse and Dochtermann, 2013; Dingemanse and Araya-Ajoy, 2015; Niemelä et al., 2015). For example, pairing for the whole reproductive season might cause long term carry-over effects on focal individuals' slow-changing states (Jacobs et al., 2011 and refs. therein) and potentially create among-individual variation for all behaviors expressed *during* the mating season, since focal individuals differ within (but not necessarily between) the reproductive season with whom they mate with. However, if in the next season the individual would pair with another individual (or if it would be experimentally swapped with another individual), the among- individual variance would disappear and the behaviors expressed under social carry-over effect would be expression of within-individual level variation.

Social carry-over effects have the potential to create true among-individual variation in non-social behaviors if the proximate mechanisms are irreversible and thus act as permanent environmental effects (**Figures 2**, **4**). In the wild, this kind

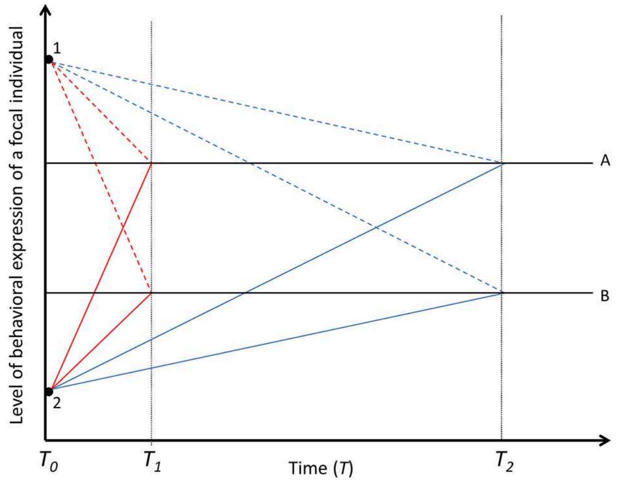

FIGURE 3 | Decay of within-individual variation in time. Solid black lines (A and B) represent two focal individuals with different mean baseline levels of behavioral expression. Colored lines represent the behavioral expression of the two focal individuals (A and B) under the influence of two different social partners (not at the same time) [Black dots; dashed lines for the effect of partner 1 and solid lines for the effect of partner 2, underpinned by fast-changing (red lines, decayed in T_1) or slow-changing (blue lines, decayed in T_2) state in focal individuals]. If social carry-over effects are underpinned by fast-changing states, the social partner (1 and 2) explains within-individual variation in the behavior of the focal individuals only over short temporal scales. If social carry-over effects are underpinned by slow-changing states, the social partners explain within-individual variation in the behaviors of the focal individuals over long temporal scales. The social interaction is terminated in T_0. While we acknowledge that among-individual variation for phenotypic plasticity exist (Nussey et al., 2007), for simplicity, the partner effects are assumed to be the same magnitude in T_0 for both focal individuals and for the fast- and slow-changing states.

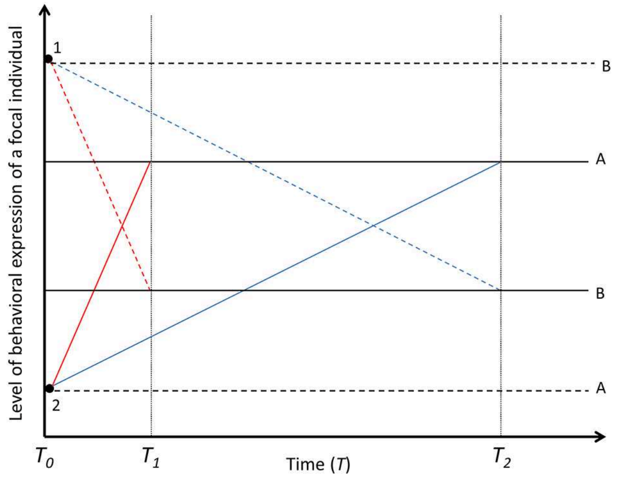

FIGURE 4 | Decay of the among-individual variation in time. Solid black lines (A and B) represent two focal individuals with different mean baseline levels of behavioral expression. Colored lines represent the behavioral expression of two focal individuals (A and B) under the influence of social carry-over effects [Black dots; dashed lines for the effect of partner 1 and solid lines for the effect of partner 2, underpinned by fast-changing (red lines, decayed in T_1) or slow-changing (blue lines, decayed in T_2) states in focal individuals]. If social carry-over effects are underpinned by fast-changing states, the social environment (1 and 2) explains among-individual variation in the behavior of the focal individuals only over short temporal scales. If social carry-over effects are underpinned by slow-changing states, the social partners explain among-individual variation in the behaviors of the focal individuals over long temporal scales. Black dashed lines for focal individuals A and B represent the permanent social carry-over effects, i.e., true animal personality created by social environment. The social interaction is terminated in T_0. For simplicity, the partner effects are assumed to be the same magnitude in T_0 for the fast- and slow-changing states.

of environmentally induced permanent among-individual level variation might be quite common due to long term assortative selection of social partners (Crespi, 1989; Wilson and Dugatkin, 1997; Croft et al., 2005), due to early social interactions like maternal effects (reviewed in Sachser et al., 2013), that both differ among focal individuals and affect state variables permanently, or by feedback loops induced by dominance interactions (Wilson et al., 2013). If there is long term among-individual variation in the confronted social environment or experienced carry-over effects between focal individuals in general, it might cause permanent environment effects on states. Such states might be, for example, any morphological, physiological or neurophysiological feature (McNamara and Houston, 1996; Houston and McNamara, 1999; Wolf and Weissing, 2010) that takes a lot of time or energy to change, or becomes genuinely irreversible. It is important to distinguish between temporary and permanent environmental carry-over effects on among-individual variation in behaviors, since true personality or behavioral syndromes exist only in the latter case (given that social interactions affect among-individual level variation: see above). One of the potential problems in separating temporary and permanent environmental effects from each other is that if temporary environmental effects are underpinned by slow-changing reversible states rather than irreversible permanent states, they may change with delay in a new environment and might be undetected. However, if the change eventually happens after individuals are translocated across environments, it means that the among-individual variation caused by the environment is instead undetected within-individual variance, i.e., plasticity, and the expressed personality or behavioral syndrome (see below) reflects environmental repeatability.

Early life-history stages might be more sensitive to environmental effects compared to adult stages (Stamps and Groothuis, 2010; Sachser et al., 2013), meaning that the same partner effect might cause carry-over of higher magnitude for the same focal individual at the juvenile stage compared to the adult stage. Therefore, permanent social environmental effects on focal individuals' states and behaviors might be triggered by early social interactions like maternal effects or other social interactions during ontogeny (Stamps and Groothuis, 2010; Runcie et al., 2013; Sachser et al., 2013). For example, in a Field cricket (*Gryllus integer*), the social rearing environment during ontogeny affects a suite of state variables like cellular immune defense efficiency and body mass measured later in adult stage (Niemelä et al., 2012). In principle, social partner effects are present at any life-history stage (Montiglio et al., 2013; Runcie et al., 2013; Sachser et al., 2013), but some life-history stages might be more sensitive to these environmental effects than others (Stamps and Groothuis, 2010; Sachser et al., 2013). For example, social interactions during ontogeny may have larger effects on slow-changing state variables, like body size, compared to social interactions after maturation, while effects on fast-changing states, like hormonal concentrations or energy levels, are present over an individual's lifetime.

Carry-Over Effects on *Covariation* between Behaviors

Behavioral syndromes, i.e., among-individual correlations between two or more repeatable behaviors, are of great interest to behavioral ecologists (Dingemanse et al., 2012; Garamszegi et al., 2012). Syndrome structure is important since the existence of a behavioral syndrome in a population suggests that behaviors might not be independent from each other, but their independent evolution can instead be constrained (Dochtermann and Dingemanse, 2013). Generally, it is important to partition the phenotypic correlation in among- and within-individual correlations in order to avoid false interpretations on the existence of behavioral syndromes (Dingemanse and Dochtermann, 2013; Brommer et al., 2014; Niemelä et al., 2015). In the field of animal personality, the common assumption is that social and non-social behaviors like aggression, boldness, exploration and activity can be correlated with each other at the among-individual level forming behavioral syndromes (e.g., Garamszegi et al., 2012). However, social carry-over effects are not taken into account when behavioral syndromes are quantified across social and non-social contexts even though the social partners might partly affect the syndrome structure via carry-over effects on within- and between-individual covariance components.

Within-Individual Covariance: Correlated Plasticity

In the same way that social partners can affect within-individual variance in one behavior, they can affect within-individual level covariance between behaviors of focal individuals, when they affect a state(s) underpinning more than one behavior and if there is no variation between focal individuals in experienced social environments (**Figures 2**, **5**). This within-individual level correlation between focal individual's behaviors is present due to cross-context correlations of partner effects, and integrated plasticity within focal individuals, i.e., correlation of residuals (**Figures 2**, **5**), either between social and non-social behaviors, or between non-social behaviors expressed outside the social context. Like for the within-individual variance in one behavior (see above), the within-individual level correlation between two or more behaviors of focal individuals, caused by social carry-over effects, might be absent if the time lag between the expression of social and non-social behaviors of focal individuals is longer than the decay of the underlying fast-changing state. If social carry-over effects are underpinned by slow-changing states, social partners can explain long term within-individual level covariation in focal individuals' social and non-social behaviors under specific circumstances. Generally, slow-changing states are not sensitive to the environment (Wolf and Weissing, 2010), like social partner effects. Thus, the within-individual level covariation caused by social carry-over effects and underpinned by slow-changing states is generally lower compared to those underpinned by fast-changing states, unless the social interactions are long lasting.

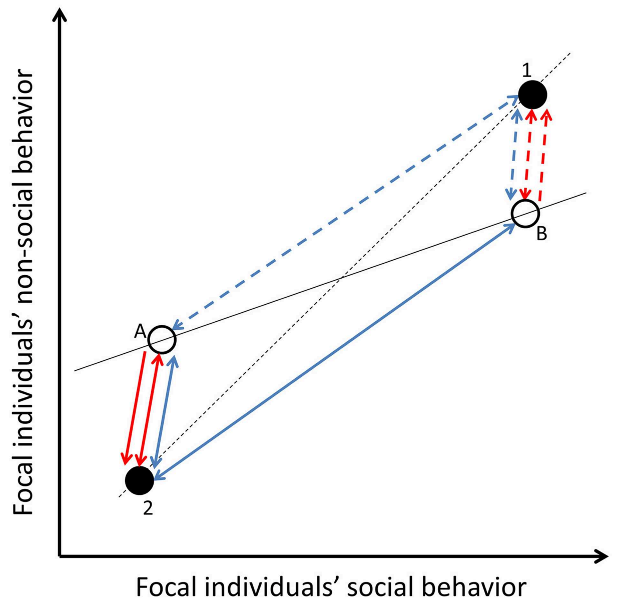

FIGURE 5 | Covariation between focal individuals' social- and non-social behaviors. Open circles (A and B) represent two different focal individuals, while filled circles represent two different social environments or carry-over effects (1 and 2). If there is no among-individual variation in confronted social environments or carry-over effects (i.e., both focal individuals confront both partners), they explain within-individual level correlation between the behaviors of the focal individuals (two-directional blue arrows: dashed lines for carry-over effects from social environment 1 and solid arrows for carry-over effects from environment 2). The temporal consistency of the carry-over effects depends on the temporal consistency of the state underpinning the carry-over effect. If focal individuals differ in the confronted social environment or carry-over effects (i.e., focal individual A confronts environment 2 and focal individual B environment 1), social carry-overs create among-individual level correlation between the behaviors of the focal individuals (red arrows). If this among-individual correlation is underpinned by temporal environmental effects, it is reversible and thus represents plasticity (two-directional red arrows). However, social carry-over effects can also create true behavioral syndromes via permanent environmental effects (one-directional red arrows: dashed lines for carry-over effects from social environment 1 and solid arrows for carry-over effects from environment 2). Two directional arrows refer to temporary environmental effects (i.e., the reversible nature of the carry-over effect) while one directional arrows refer to permanent environmental effects. For simplicity, the social partner effects for different focal individuals (blue arrows) are assumed to be the same magnitude.

Among-Individual Covariance: Pseudo-Behavioral Syndrome vs. True Behavioral Syndrome

If focal-individuals vary consistently in the confronted social environments, social carry-over effects can also explain among-individual level covariance in behaviors, i.e., behavioral syndromes. Among-individual level covariance caused by social carry-over effects can be present at different timescales depending on the nature of the state that underpins the covariance (see above). For example, among-individual level correlations caused by social carry-over effects can be present if some social partners elicit higher hormonal concentrations or greater depletion of resources or growth rates compared to other partners and the focal individuals confront different (sets of) partners repeatedly. However, in this case the among-individual level covariation does not necessarily represent a true behavioral syndrome, but rather "pseudo-syndrome" triggered by non-permanent environmental correlations (**Figures 2**, **5**). "Pseudo-syndromes" caused by social carry-overs occur when the effect of the social environment on the mean level of both behaviors in focal individuals changes when the social environment changes, i.e., the behavioral syndrome is actually caused by integration of plasticity which remains undetected if different focal individuals are always measured in their respective social environments.

Social carry-over effects can also create true behavioral syndromes, i.e., permanent environmental correlations (e.g., Dingemanse and Dochtermann, 2013). Permanent environmental correlations can be created by social carry-over effects when the among-individual variation in confronted social environments is present and when the social partners elicit permanent changes in focal individuals' states that carry-over time and across different contexts also to behaviors expressed in non-social situations (**Figures 2**, **5**) (see discussion in the Section: Among-Individual Variance: Pseudo-Personality vs. True Personality).

Evolutionary Consequences of Social Carry-Over Effects

Studying the social partner effects and social carry-overs is important to fully understand the evolution of associated non-social behavioral traits. Crucially, phenotypes of social partners are expressions of their genotypes, and thus, social environments can evolve (Moore et al., 1997; Wolf et al., 1999). When social partner effects are repeatable, and these effects are heritable (i.e., due to additive genetic variance), they are known as indirect genetic effects, IGEs. For example, in a fruit fly (*Drosophila melanogaster*), IGEs are present on body size of focal individuals (Wolf, 2003). In other words, the genes of the social partners partly define the body size of focal individuals (Wolf, 2003). The first important evolutionary consequence of IGEs is that social partners can speed up or slow down the rate of evolution in traits expressed in, or tightly related to, social interactions if these traits are associated with fitness (Moore et al., 1997; Wolf et al., 1999). This happens when the additive genetic variance in the trait of social partner correlates positively or negatively with the additive genetic variance in the trait of a focal individual, respectively increasing or decreasing the rate of evolution (Moore et al., 1997; Brommer and Rattiste, 2008; Wilson et al., 2009) or if there is a functional integration between traits (Westneat, 2012). For example, in the fruit fly study mentioned above, the IGEs on the body size of focal individuals were negatively correlated with the direct genetic effects (DGEs), constraining the response to selection on body size of the focal individuals (Wolf, 2003). In deer mice (*Peromyscus maniculatus*), the covariance between IGEs and DGEs on agonistic behavior (social behavior) was positive, indicating a more rapid evolution of these behaviors compared to the case if only DGEs would have been taken into account (Wilson et al., 2009). The second evolutionary consequence of IGEs is that the additive genetic variation in social traits of focal individuals might not constrain the phenotypic evolution of those traits since they are also affected by selection through IGEs due to social interactions, i.e., genes of the social partners (Moore et al., 1997; Wolf et al., 1999). Thus, if social partner effects can carry-over to non-social behaviors like exploration, activity or boldness, they may have evolutionary consequences also on these behaviors: the evolutionary speed (rate of evolution) and evolutionary potential (additive genetic variation not restricting the trait evolution) of these non-social behaviors does not only depend on the genes of focal individuals but also on the genes of confronted social partners (Moore et al., 1997; Wilson, 2014). Such effects can be overlooked when the social environment is ignored as a source of variation acting on state variables underlying behaviors expressed outside an immediate social context. IGEs might affect the evolutionary potential of the non-social traits more through slow-changing mechanisms than through fast-changing mechanisms. This is because carry-over effects, and thus the potential IGEs, fade away quickly when they are underpinned by fast changing states. Selection has higher potential to act on non-social behaviors underpinned by slow-changing states since in such cases the carry-over effects persist over longer time periods. Interestingly, if social environments generate true personality, i.e., permanent environmental effects, the IGEs have the highest potential to affect the evolution of non-social behaviors of a focal since the effect of the social environment, causing IGEs, is permanent.

Carry-over effects might also have fitness consequences. According to the social niche hypothesis, individuals adapt their behavior to their own specific social niches in order to achieve maximal fitness (Bergmüller and Taborsky, 2010). Deviations from the optimal strategy should lead to suboptimal behavior for the social niche that the particular focal individual is occupying and potentially lowered fitness. Moreover, learning a specific behavioral strategy may increase its efficiency and increase the costs of switching to an alternative strategy (Rosenzweig and Bennett, 1996; Wolf et al., 2008; Morand-Ferron and Giraldeau, 2010). Therefore, the higher the deviation from the optimal behavioral strategy, due to the effect of social carry-overs, the higher the negative fitness effects should be. In this case, carry-overs caused by fast- and slow-changing proximate mechanisms most likely also differ in the magnitude of their fitness effects. Fast-changing state variables return quickly to the normal (and this case supposedly optimal) level of behavioral expression of a focal individual, while carry-overs caused by slow-changing state variables might take a long time to return to the normal level. Carry-overs caused by slow-changing mechanisms might thus have higher impacts on a focal individual's fitness if the non-social behaviors of a focal deviates from its "optimum" for its social niche for longer time periods.

Experimental Designs and Corresponding Statistical Analyses to Study the Social Carry-Over Effects

In this section, we focus on the key questions to be answered in order to better understand the mechanisms and consequences of social carry over effects on variation of behaviors expressed outside social interactions. Understanding the mechanisms helps us to target, using a variance partitioning approach (i.e., through mixed models), the different levels of behavioral variation on which the social carry-over effects are acting. Social partner effects on behavioral variation have been briefly studied in behaviors expressed *within* a social context, mainly in aggression and reproductive behaviors (e.g., Brommer and Rattiste, 2008; Wilson et al., 2011a, 2013) and the statistical tools for estimating social partner effects on different levels of variation are currently being introduced to the field of animal personality (Wilson et al., 2011a, 2013; Montiglio et al., 2013; Dingemanse and Araya-Ajoy, 2015).

If one is interested in the social partner effects on behavioral variation of focal individuals non-social behaviors at multiple levels, the general experimental setup requires the collection of repeated measurements of behaviors expressed in the non-social context after social interactions. Focal individuals should be tested against multiple social partners, with social partners interacting with multiple focal individuals. The mixed model should include, in addition to the focal individual's identity, also the social partner's identity as a random effect. This enables the decomposition of total phenotypic variance into variance attributable to the focal individual, the social partner, and residual variance. Adding the social partner identity captures previously unexplained within-individual variation (repeatability of the partner effect: the proportion of total phenotypic variance in the focal individuals' behavior explained by the social partner identity) (Wilson et al., 2011a, 2013; Montiglio et al., 2013; Dingemanse and Araya-Ajoy, 2015) or among-individual variation in the focal individuals' social and non-social behaviors. While the experimental setups (below) can test firm hypotheses about which level of variation the social partners affect in focal individuals' non-social behaviors, one can also compare the models with and without social partner identity as random factor. Comparing models would enable one to test exactly how among- or within-focal individual variance components, or both, are affected by the social partners, i.e., if the removal of partner identity increases one of these components. The same statistical approaches can be extended to multivariate models when studying carry-over effects on covariation between social and non-social behaviors of the focal individuals.

Exciting topics to be explored are, (1) do the temporal patterns of expressed *within-individual* variance (in non-social behaviors) due to carry-over effects depend on the length of the social interaction? and (2) whether social carry-over effects can create *among-individual* variation in non-social behaviors and whether this variation persists in time, i.e., temporary vs. permanent environmental effects. A more evolution-oriented study problem is (3) whether IGEs affect the rate of evolution of non-social traits, i.e., whether IGEs on non-social behaviors are present and if they correlate positively or negatively with DGEs (genes of a focal individual).

Temporal patterns of carry-over effects on focal individuals' behaviors might depend on the duration of the social interaction (first study problem). This is especially important if the social partner effects are underpinned by slow-changing states: they are not sensitive to social interaction unless the interaction lasts long enough. One straightforward way to study this is to construct two social treatments, where focal individuals spend short or long amounts of time with several different social partners repeatedly (the identities of the confronted social partners do not differ among focal individuals) and where non-social behaviors, like exploration or activity, are measured after a fixed amount of time (i.e., hours) after each social interaction in both treatments. If longer social interactions allow the social partner to affect slow-changing states in focal individuals, the within-focal individual variation in measured non-social behaviors explained by the social partner should be higher in the prolonged social interactions treatment. If the proximate mechanisms like hormonal level or body mass are measured simultaneously with the behaviors, one could connect the decay in behavioral variation firmly to the decay of the underlying mechanism. Statistically, this can be analyzed by applying a bivariate mixed effect model with the non-social behaviors of focal individuals measured after social interactions as two dependent variables (short and long interaction treatment) and with focal individual and social partner identity as random effects. To test if variance components differ between treatments, the within-individual variances for the two traits are restricted to be the same and the fit of the restricted model is compared to the fit of unconstrained model. Statistical significance of the model can be assessed by, for example, comparing the Log likelihood-values between the constrained and unconstrained model using Chi^2-statistics (Meyer, 1992; Wilson et al., 2010).

The second study question, i.e., the social partner effects on among-individual variation, can be addressed by staging repeated social interactions so that focal individuals differ in their social environments. Among-focal individual variation in confronted social environments can be created by building groups of social partners that are all similar to each other within a group, but differ among groups in a trait value that is hypothesized to cause carry-over effects. These traits can be, for example, body size or aggression of social partners. Each focal individual would thus be tested in repeated interactions, but always with social partners belonging to the same group (i.e., with individuals that have the same mean trait value). A simple experimental design would be to measure first the non-social behaviors of interest before any social interactions (i.e., baseline, T_0: T_0, T_1, and T_2 in here are not related to the ones in figures), then soon after each social interaction (T_1) and lastly some days after the social treatments have been decomposed (T_2). This would allow one to quantify (i) whether among-individual variation in non-social behaviors of focal individuals increases after social interactions compared to the baseline variation due to among-individual variation in social environments (comparing

T_0 with T_1) and (ii) if these carry-over effects on among-individual variation are temporary (i.e., pseudo-personality) or permanent (i.e., true personality) (comparing $T_0$with T_2). If social environments create among-individual variation in the focal individuals' behaviors, the among-individual variation should be higher in non-social behaviors measured directly after social interactions (T_1), compared to the baseline among-individual variation (T_0). One can study the temporary vs. permanent nature of carry-over effects on among-individual variation by comparing the baseline among-individual variance (T_0) to the among-individual variance measured few days after the decomposition of social treatments (T_2). If among-individual variance in behaviors is higher when measured a few days after treatment decomposition compared to the baseline, it would *suggest* the existence of permanent environmental effects. Statistically, this can be analyzed by applying multivariate mixed effect models as in the first study question (see above), where behaviors in T_0, T_1, and T_2 are fitted as three dependent variables, and focal individual and social partner identity as random effects. One can then test if the variance components differ significantly from each other between time points (T_0, T_1, and T_2) of interest by constraining the among-focal individual variances to be the same and by comparing the fit of the restricted model to the fit of unconstrained model. Statistical significance of model comparing can be done, for example, by comparing the Log likelihood-values between the constrained and unconstrained model using Chi^2-statistics (Meyer, 1992; Wilson et al., 2010).

For the third study question, one needs to have a pedigreed population or experimental breeding design that allows the estimation of quantitative genetic parameters from the collected data (e.g., Moore et al., 1997; Wolf et al., 1999). This kind of design allows the estimation of DGEs, IGEs and the covariance between these genetic components from the data collected from repeated social interactions (for details: Wolf, 2003; Brommer and Rattiste, 2008; Dochtermann and Roff, 2010; Wilson et al., 2011b). As stated earlier, the positive covariance between DGEs and IGEs suggests a potential increase in the rate of evolution for measured non-social traits (affected by carry-overs) while a negative covariance suggest restriction for the rate of evolution (Wolf, 2003).

Conclusion

Here we introduced a conceptual framework about the potential proximate mechanisms behind social carry-over effects on behavioral variation in non-social behaviors. One of the main goals in the field of animal personality is to study the ecological and evolutionary causes and consequences of expressed behavioral variation at different levels. In our paper, we clarified how social partners have the potential to affect the expressed within- and among-individual level behavioral variation and covariation of focal individuals outside social contexts over various temporal scales. Moreover, our framework gives new insights on the evolutionary potential of carry-over effects, which can also be extended to non-social behaviors. It is important to acknowledge the social carry-over effects on behavioral (co)variation of behaviors expressed outside social interactions since they may allow us to make predictions about the patterns of variation generated by social environments and the evolution of non-social behavioral traits.

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The development of collective personality: the ontogenetic drivers of behavioral variation across groups

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For the past decade, the study of personality has become a topic on the frontier of behavioral ecology. However, most studies have focused on exploring inter-individual behavioral variation in solitary animals, and few account for the role that social interactions may have on the development of an individual's personality. Moreover, a social group may exhibit collective personality: an emergent behavioral phenotype displayed at the group-level, which is not necessarily the sum or average of individual personalities within that group. The social environment, in many cases, can determine group success, which then influences the relative success of all the individuals in that group. In addition, group-level personality may itself evolve, subject to the same selection pressures as individual-level behavioral variation, when the group is a unit under selection. Therefore, we reason that understanding how collective personalities emerge and change over time will be imperative to understanding individual- and group-level behavioral evolution. Personality is considered to be fixed over an individual's lifetime. However, behavior may shift throughout development, particularly during adolescence. Therefore, juvenile behavior should not be compared with adult behavior when assessing personality. Similarly, as conditions within a group and/or the local environment can shift, group behavior may similarly fluctuate as it matures. We discuss potential within-group factors, such as group initiation, group maturation, genetic make-up of the group, and the internal social environment, and external factors, such as how local environment may play a role in generating group-level personalities. There are a variety of studies that explore group development or quantify group personality, but few that integrate both processes. Therefore, we conclude our review by discussing potential ways to evaluate development of collective personality, and propose several focal areas for future research.

Keywords: collective behavior, social groups, social insects, within-group variation, group growth

DEFINING AND EVALUATING COLLECTIVE PERSONALITIES

Non-human personality, e.g., inter-individual differences in behavior that are consistent through time, has become an increasingly popular area of study in the past decade (Koolhaas et al., 1999; Sih et al., 2004; Stamps and Groothuis, 2010; Dall et al., 2012, 2004). This may be in part because of the seemingly ubiquitous nature of animal personalities, which have been found in nearly every taxon in which they have been investigated, as well as their profound effect on behavioral plasticity and long-term fitness consequences (Sih et al., 2004; Smith and Blumstein, 2008; Stamps and Groothuis, 2010; Wray and Seeley, 2011; Jandt et al., 2014a). For example, in great tits (*Parus major*), there are inter-individual differences in exploratory behavior ("fast" vs. "slow"; Verbeek et al., 1994; Dingemanse et al., 2002). This individual variation is both highly repeatable through time, and heritable in both wild caught and lab reared populations (Dingemanse et al., 2004, 2002). Moreover, these differences affect both adult and offspring survival, as fluctuating environmental conditions drive selection for different personality types from year to year (Dingemanse et al., 2004).

Studies measuring the development of personality tend to focus on unitary organisms and the role of early experience (DiRienzo et al., 2012), maternal effects (Groothuis et al., 2008) and persistence across life stages (Bell and Stamps, 2004). It has been shown that the consistency of personality can vary through ontogeny and upon maturation. For example, in the dumpling squid (*Euprymna tasmanica*), individuals are consistent in their boldness as juveniles and as adults, but are inconsistent for a period as they reach sexual maturity (Sinn et al., 2008). In yellow bellied marmots (*Marmota flaviventris*), boldness was only predictable in yearlings, while docility was consistent across all age classes (Petelle et al., 2013). On the other hand, lake frogs (*Rana ridibunda*; Wilson and Krause, 2012) and firebugs (*Pyrrhocoris apterus*; Gyuris et al., 2012) show consistent personality (activity and exploration, boldness and exploration, respectively) across all life stages. The flexibility of some personality traits and the persistence of others may signal that some traits may be adaptively fixed, while others are plastic so as to respond to age-specific situations (Petelle et al., 2013).

Personality differences can also be observed at the level of the group or colony, referred to here as "collective personality." While human social groups have been the primary focus of collective personality studies (e.g., aggression or communication differences among human groups; Duncan, 1999; Hofmann and Jones, 2005; Halfhill et al., 2005), social animal groups are becoming more popular research models. Collective behavior is perhaps best understood in eusocial insects (e.g., ants, bees, wasps, and termites that exhibit cooperative brood care, overlapping adult generations and division of labor between reproductive and non-reproductive castes; Hoölldobler and Wilson, 1990). In these systems, there is selection at the colony-level (Korb and Heinze, 2004). As such, colony development has been studied extensively. However, only recently has colony-level personality been considered, and little work on the development of collective personality exists. In this review, to differentiate between eusocial and social species, we will use "colony personality" or "colony behavior" when referring to social insects, and "group personality/behavior" when referring to non-eusocial species.

Stamps and Groothuis (2010) suggest that studies measuring the development of personality fall into three categories: (1) those that measure how specific, early experiences influence adult personality, (2) those that consider if and how personality changes throughout the lifetime of an organism, and (3) how genes influence personality development. These questions can also be asked at the group-level: (1) How do events during group formation shape later group- and individual-level behavior? (2) How does group-level behavior change across group ontogeny or as the group encounters different environmental and social circumstances? (3) How is group-level behavior affected by the genotypes that comprise it? It is important to consider these questions of development at both group- and individual-levels for a variety of reasons. First, individuals and groups have different lifespans, and individuals within the group may develop at different rates or at different times during the group lifespan. Therefore, the different experiences that individuals encounter as juveniles may influence their adult personality type, and thus affect the distribution of personalities that comprise the group. Second, the relatedness among individuals and heritability of personality traits within a group are likely to further influence collective personality. For example, if there is a high broad-sense heritability of personality, then groups comprised of offspring that remain at the nest will maintain less variation in personalities than groups where heritability is low or unrelated individuals can join the group.

The distribution of individual personalities within a group can impact group performance, and thus fitness. However, the interactive dynamics of those individuals can additionally produce an emergent collective personality that differs from one calculated by only averaging the behavioral types of all individuals (Johnson and Linksvayer, 2010; Bengston and Dornhaus, 2014; LeBoeuf and Grozinger, 2014). Understanding how emergent collective personalities arise from groups of individuals is a key component to understanding how they develop. For example, if there is a centralized force influencing group behavior, such as experienced individuals guiding naïve individuals, then the personality of the individual could be much more important. Furthermore, if experienced individuals have a disproportionate influence over the group's behavior, then the growth rate of the group (and thus, the rate of new, inexperienced individuals joining the group) may be particularly important during group ontogeny, as it would alter the ratio of experienced to inexperienced individuals. Alternatively, if collective behavior is the result of a decentralized process, where individuals respond to changing conditions based upon previously established rules (innate or learned) or fluctuating feedback systems, this may either lead to more stabilized (if individual behaviors are buffered by the group; Dussutour et al., 2009; Sasaki and Pratt, 2011) or destabilized (if positive feedback processes lead to exaggeration of small effects; Sinha, 2006) collective personality.

There are few studies that investigate collective personalities (e.g., Scharf et al., 2012); most of which focus on measuring mature groups (those capable of reproducing or budding into new groups; e.g., Sasaki and Pratt, 2011; Wray and Seeley, 2011; Sasaki et al., 2013). This is likely because measuring the development of a collective unit is more complicated than measuring the development of an individual: to explore developmental factors affecting individual personality, measurements can readily be repeated on juvenile and adult individuals to determine the effects of experience or ontogeny on personality types (Bell and Stamps, 2004; Stamps and Groothuis, 2010). However, groups tend to develop at a much slower pace than individuals, and collecting or monitoring multiple groups over extended periods of time can be difficult.

Here, we discuss potential within-group (group initiation, group maturation, genetic make-up of the group, and internal social environment) and local environmental factors that may play a role in the development of collective personality in animal groups. We also highlight the importance of understanding a group's developmental phase when assessing personality type. Finally, we propose several new avenues of research that will increase our understanding of collective personalities and potentially important consequences for group fitness and adaptability, especially across changing environments.

WITHIN-GROUP FACTORS

A group's behavior emerges from the collective decisions and behaviors of individual members (e.g., the social environment). Furthermore, just like individual behaviors, group behavior can change as it matures (**Figure 1**; e.g., *Pogonomyrmex barbatus*; Gordon, 1991). In this section, we use the suggestions from Stamps and Groothuis (2010) to show how (a) group initiation (i.e., early experiences); (b) group maturation (i.e., how personality changes throughout the lifetime of the group); (c) genetic make-up of the group; and (d) internal social environment influence development of collective personality (**Figure 2**).

GROUP INITIATION

Depending on the species, new groups can be initiated by individual founders or by existing groups splitting into multiple smaller groups (via fission or budding) (Wilson, 1975). In groups initiated by founders, individuals have a high potential to shape future group traits by their own behavior. For example, founding individuals often choose a habitat and nest site, and rear the first generation of group members. On the other hand, groups

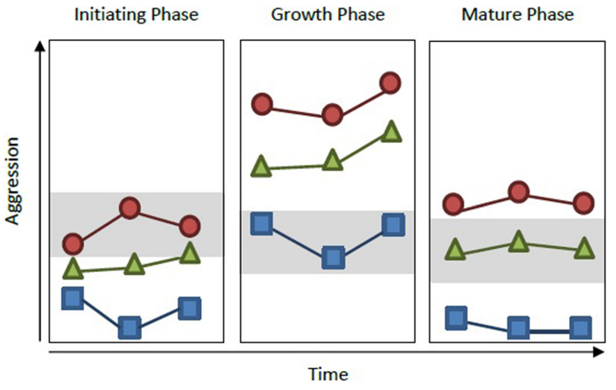


FIGURE 1 | Measuring group personality throughout development. Collective personality is typically measured on groups during one phase of development (typically either the growth or mature phase). However, personality can shift through developmental phases. In *Pogonomyrmex* ants, for instance, colony aggression increases during growth phase, but decreases after reaching maturity (Gordon, 1991, 1995). In the hypothetical example shown here, if measurements were taken on three different colonies (red circle, blue square, and green triangle) within and across each of these developmental phases, colonies would exhibit consistent personality differences. However, if colonies were measured only once, but at different phases of development (e.g., red circle during initiating phase, blue square during growth phase, and green triangle during mature phase), colony aggression levels would overlap significantly (gray boxes) and one would come to the incorrect conclusion that colonies do not vary in personality type.

initiated by splitting from a parent group choose a nest location and rear juveniles based on collective decisions made by the group.

The location that a founder or group chooses to establish a nest can influence colony behavior and survival (Wiernasz and Cole, 1995; Gordon and Kulig, 1996). For example, population density and availability of resources in the local environment can have a significant effect on the colony performance and personality (Gordon and Kulig, 1996; Bengston and Dornhaus, 2014) (see section Local Environment, for more detail).

A founder's personality type may also influence colony-level personality type if (1) that personality type is highly heritable and, therefore, represented among the offspring that remain at the nest, or (2), if its personality attracts joiners with particular personality types. Few studies, however, have investigated the extent to which the personality of the founder or the parent group predicts the personality of the daughter group. Two exceptions are bumble bees (*Bombus terrestris*) and social spiders (*Anelosimus studiosus*). In bumble bees, more cautious queens tend to produce colonies with more cautious workers, although founding queens tend to forage more cautiously and learn more quickly than workers (Evans and Raine, 2014). On the other hand, in social spiders, colonies grow as founders are joined by unrelated individuals. Founders that are more docile tend to attract heterospecific spiders at a faster rate. Compared to aggressive or mixed groups of both docile and aggressive founders, these mixtures of heterospecific individuals initiated by docile founders grow faster and reproduce more often (Pruitt, 2012). In this situation, group performance can be predicted by the personality of the initial founder, and group personality type can remain constant up to 3 years (Pruitt, 2012).

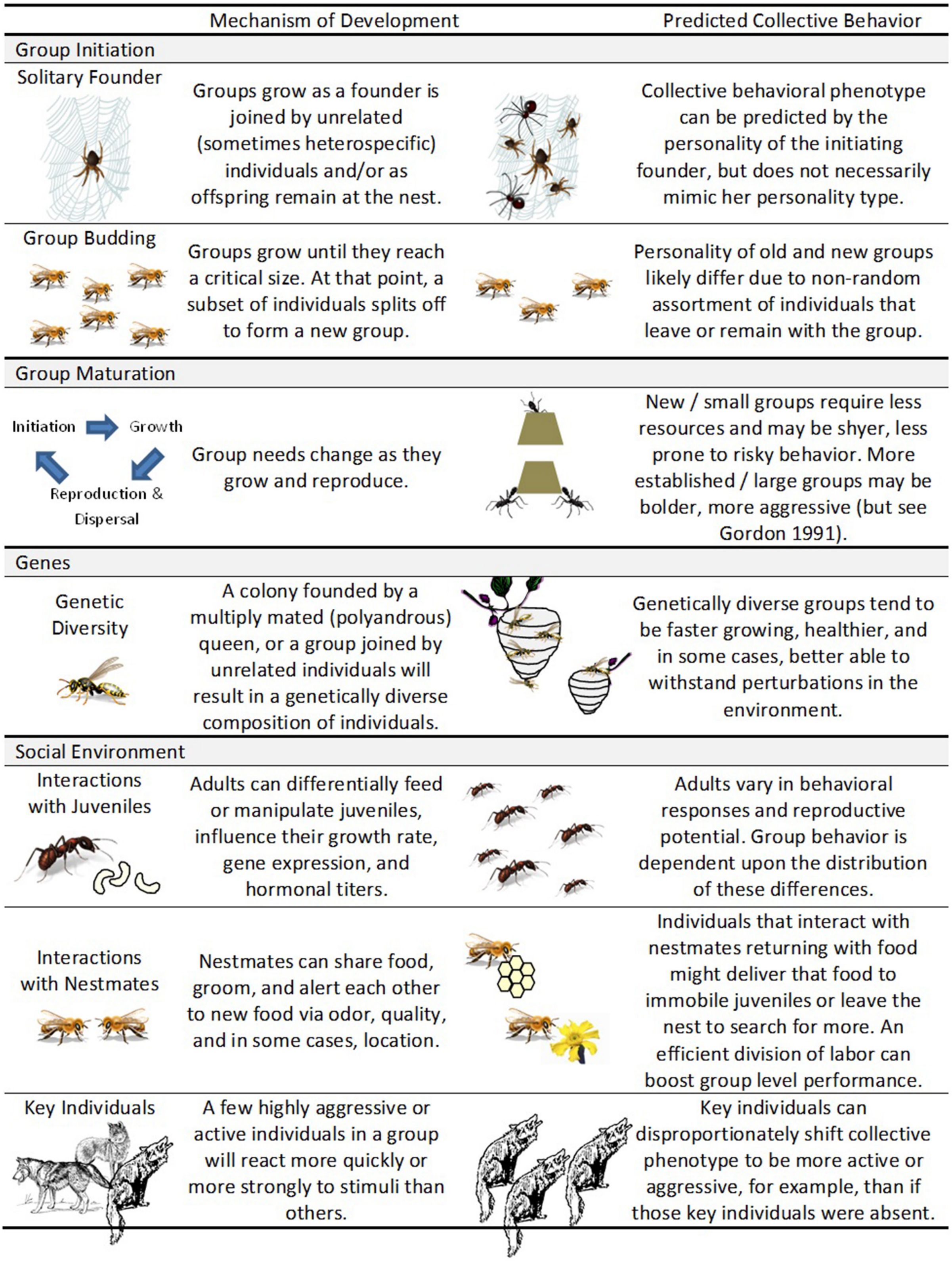
If personality of founders (or key individuals, see section Internal Social Environment) influence group-level personality, then group-level personality should shift when founders are replaced (either naturally or experimentally) with individuals of a different personality-type. A shift in collective behavior may be the result of the key individuals directly influencing the personality of group members already present, or the result of offspring turnover if the founder also acts as the primary reproductive in the group. Unfortunately, locating an adequate sample size of founders before or shortly after colony initiation is difficult. Therefore, research of this type is limited to species with large populations of founding individuals (e.g., foraging bumble bees or ant reproductive swarms) or those that establish their colonies in high densities in open areas (e.g., social spiders or paper wasps).

The initial personality of groups formed by budding may be more heavily influenced by the distribution of individuals that choose to split from the original group. If individuals from the original group are divided randomly, then the personality of the sister groups should mimic each other, particularly if they end up in similar environments (though groups may plastically respond to their new local environment; see section Behaviorally Plastic Responses to Environmental Shifts). However, if the group splits in a non-random fashion, for example one sister group is comprised of older, faster, or more aggressive individuals, then one collective unit may have a very different personality than the other (Modlmeier et al., 2014a). There are indeed significant personality differences observed among house-hunting colonies (i.e., swarms of individuals that recently split from the original group) of honey bees (*Apis mellifera*) (Wray and Seeley, 2011). However, it is unclear whether those differences are the result of non-random assortment of individuals that join the swarm (Grozinger et al., 2014), and whether the composition of those individuals creates a collective personality that differs from a sister colony.

GROUP MATURATION

The analogy between individual and group development is most apparent in eusocial insects, where selection occurs at the level of the colony. Like individuals with germ (reproductive) and somatic (non-reproductive) cells, colonies are comprised of reproductive (queen) and non-reproductive (worker) individuals (Wilson, 1985; Szathmáry and Smith, 1995). Furthermore, colonies grow, mature, reproduce, and disperse; and fitness is achieved not when new individuals are produced, but when a new colony is initiated (Wilson, 1985).

Throughout development, collective behavior may shift with the changing needs of the group (**Figure 1**). For example, group-level behavior can change as group size increases—a trend observed across eusocial taxa (Dornhaus et al., 2012). In honeybees, even though some colonies are consistently more aggressive than others (Pearce et al., 2001; Hunt, 2007), aggression levels increase with colony size (Wray et al., 2011), and/or when resources become scarce (Downs and Ratnieks, 2000). This trend of increased aggression with colony size or state of maturation



	Mechanism of Development	Predicted Collective Behavior
Group Initiation		
Solitary Founder	Groups grow as a founder is joined by unrelated (sometimes heterospecific) individuals and/or as offspring remain at the nest.	Collective behavioral phenotype can be predicted by the personality of the initiating founder, but does not necessarily mimic her personality type.
Group Budding	Groups grow until they reach a critical size. At that point, a subset of individuals splits off to form a new group.	Personality of old and new groups likely differ due to non-random assortment of individuals that leave or remain with the group.
Group Maturation		
Initiation Growth Reproduction & Dispersal	Group needs change as they grow and reproduce.	New / small groups require less resources and may be shyer, less prone to risky behavior. More established / large groups may be bolder, more aggressive (but see Gordon 1991).
Genes		
Genetic Diversity	A colony founded by a multiply mated (polyandrous) queen, or a group joined by unrelated individuals will result in a genetically diverse composition of individuals.	Genetically diverse groups tend to be faster growing, healthier, and in some cases, better able to withstand perturbations in the environment.
Social Environment		
Interactions with Juveniles	Adults can differentially feed or manipulate juveniles, influence their growth rate, gene expression, and hormonal titers.	Adults vary in behavioral responses and reproductive potential. Group behavior is dependent upon the distribution of these differences.
Interactions with Nestmates	Nestmates can share food, groom, and alert each other to new food via odor, quality, and in some cases, location.	Individuals that interact with nestmates returning with food might deliver that food to immobile juveniles or leave the nest to search for more. An efficient division of labor can boost group level performance.
Key Individuals	A few highly aggressive or active individuals in a group will react more quickly or more strongly to stimuli than others.	Key individuals can disproportionately shift collective phenotype to be more active or aggressive, for example, than if those key individuals were absent.

FIGURE 2 | Development of collective personalities. Collective personality development can manifest itself in multiple ways—through group initiation, group maturation, genes, and social environment.

is true for many species, including wasps (yellowjacket wasps: *Vespula* spp., Akre et al., 1976; paper wasps: *Polistes* spp., Hunt, 2007), but cannot be generalized across all social insect taxa. For example, in the red harvester ant (*Pogonomyrmex barbatus*), aggression levels actually *decrease* as colony size increases (**Figure 1**; Gordon, 1991) and in *Temnothorax ruagatulus* ants aggression is completely unrelated to colony size (Bengston and Dornhaus, 2014).

Provisioning of juveniles may also fluctuate as the group matures, creating different experiences for developing individuals, a factor that could influence the variation of individual personalities in the group. For example, founding termite queens of *Reticulitermes speratus* lay fewer, but larger, eggs early in the colony cycle when the queen has less time to devote to brood care. Later in the colony cycle when workers are available to forage and tend brood, the queen will switch and begin laying more eggs of a smaller size that take longer to develop than the larger eggs (Matsuura and Kobayashi, 2010). To determine whether changes observed in early vs. late workers are due to egg size or the differential social environment in which eggs are reared (i.e., with or without workers), insect eggs can be collected from nests and grafted onto different regions of the nest or placed back in the nest at different points of the colony cycle. If this difference in early rearing environment (in terms of resources available to the egg) influences worker development (and thus personality), large eggs reared later in the colony cycle should exhibit personalities similar to those reared early. Alternatively, if the stage of the colony cycle, and/or the different interactions with founders and siblings, has a stronger influence on the development of individual personality, then offspring reared early and late in the colony cycle would develop very different personality types, regardless of egg size.

In *Polistes* wasps, there is a clear shift in the way queens interact with developing larvae that develop early vs. late in the colony cycle. Early in the colony cycle, *Polistes fuscatus* queens provision larvae with less food and drum their antennae on the nest while feeding larvae. Those larvae develop into workers that will forage and tend the second cohort of brood (Hunt, 2007; Suryanarayanan et al., 2011a). The second brood cohort receives more food as larvae but no drumming. They develop into the next generation of queens that do not engage in colony tasks but instead conserve their energy to overwinter (Hunt, 2007; Suryanarayanan et al., 2011a). Further, when this drumming is artificially delivered to nests later in the colony cycle, developing larvae react to the vibrational interactions by developing less fat stores, a physiological trait more similar to that of workers (Suryanarayanan et al., 2011b). In both the termite and wasp examples, the differential interactions that adults have with developing juveniles, both behaviorally and nutritionally, can affect a large change in collective behavior, and possibly the collective personality observed at the colony-level. The next step will be to tease apart the relative role that behavior, nutrition, and other environmental factors may play on the development of different personality types in individuals, how those personalities correlate across populations, and how that corresponds to collective personalities observed in different environments.

GENETIC MAKE-UP OF THE GROUP

Personality traits can vary in heritability (e.g., h^2: 0.01–0.014, stickleback aggression; 0.66, chimpanzee dominance, Weiss et al., 2000; reviewed in van Oers et al., 2005). Therefore, the extent that founders predict the personality of a group comprised of offspring that remain at the nest or kin that co-found or join the nest likely varies across taxa. Further, as cooperating founders are often unrelated (e.g., fire ants: *Solenopsis invicta,* Bernasconi and Keller, 1999; paper wasps: *Polistes* spp., Jandt et al., 2014b, social spiders: *Anelosimus studiosus*, Pruitt and Goodnight, 2014) or solitary foundresses can be polyandrous (i.e., multiply mated) (e.g., honeybees: *Apis mellifera*, leaf-cutter ants: *Acromyrmex* spp., red harvester ants: *Pogonomyrmex badius*; reviewed in Oldroyd and Fewell, 2007), relatedness of individuals within a group can vary. Social heterosis (Nonacs and Kapheim, 2007, 2008), a process whereby genetically dissimilar individuals benefit by outperforming groups of genetically similar individuals, has been observed in social organisms from microbes (Vos and Velicer, 2006) to primates (Wooding et al., 2006). Increased genetic variation may result in faster growing, healthier, and perhaps more homeostatic groups better able to withstand perturbations in the environment (reviewed in Oldroyd and Fewell, 2007). In species that co-found with related individuals, such as the facultatively social bee, *Exoneura robusta*, strong reproductive skew can exist, with skew positively correlated to increased relatedness between reproductives (Harradine et al., 2012). This is a pattern seen in many social mammals as well, in which a dominant matriarch produces a disproportionate majority of the offspring (meerkats: *Suricata suricatta*, Clutton-Brock et al., 2001; marmots: *Marmota* spp., Allainé, 2000; naked mole rats: *Heterocephalus glaber*, Clarke and Faulkes, 1997); though the mechanism underlying this reproductive skew may vary. In these systems, increased relatedness is expected to offset the skew and costs of cooperation (Hamilton, 1964).

The genetic composition of individuals within the group may have indirect genetic effects on other group members as well. For example, in a group of *Drosophilia* males, aggressive behavior (influenced by genotype) of one individual can influence the interactions between the others, and impact mating success (Saltz, 2013). Therefore, understanding the genetic make-up of the group, and how that changes over time, may influence the developmental trajectory of the collective personality.

Within the group, behavioral variation in threshold sensitivity, due to heritable and gene expression differences (**Box 1**; **Figure 3**), may influence how a group divides and performs tasks (Beshers and Fewell, 2001), and how it responds as a collective unit (Jandt and Dornhaus, 2014; LeBoeuf and Grozinger, 2014). For example, a honeybee's predisposition to collect nectar or pollen is partially based on a genetic predisposition to recognize sugar (e.g., their sucrose thresholds; Page et al., 2012). Colonies bred to maintain individuals with particularly high or low thresholds to respond to sucrose (pollen vs. sucrose foraging personalities, respectively, see Jandt et al., 2014a) will themselves develop a nectar or pollen foraging collective personality (Page and Fondrk, 1995; Page et al., 2012). In this case, if the queen were to be replaced with one bred to exhibit the opposite sensory threshold, the collective foraging personality of that colony would

Box 1 | From the genome to the sociome and back.

Variation in gene expression is a mechanism that can produce behavioral variation among individuals—even among highly related individuals—within a group (Toth and Robinson, 2007; Zayed and Robinson, 2012). There are a number of studies that show a correlation between gene expression and long-term developmental differences (physiological and behavioral) in individuals (Toth et al., 2009; Page et al., 2012; Dolezal and Toth, 2014). For example, novelty-seeking behavior (i.e., scouting for new nest sites or food resources by the same individuals as colony needs change) in honey bees correlates with a down-regulation of a dopamine receptor gene in the brain (Liang et al., 2012), a pattern similar to that observed in mammals (Viggiano et al., 2002).

Changes in gene expression throughout a lifetime can also be a mechanism that allows individuals to transition between behavioral states (Dolezal and Toth, 2014). Indeed, in honey bees, behavioral transitions across tasks (often referred to as task polyethism) correlate with widespread changes in brain gene expression (Whitfield et al., 2003, 2006; Alaux et al., 2009). At least some of these changes in gene expression appear to precede changes in behavior and some have been demonstrated to have causal influences on individual behavioral tendencies (Page et al., 2012). The social environment, including colony maturation, can also have a profound influence on an individual's gene expression (honey bees *Apis mellifera*, Grozinger et al., 2003; Wang et al., 2008; fire ants *Solenopsis invicta*, Manfredini et al., 2013; paper wasps *Polistes metricus*, Toth et al., 2014), and it is the dynamic interplay between the genome and the social environment (a field referred to as "sociogenomics") that makes the development of colony-level behavior so complex and fascinating (**Figure 3**).

As an individual develops, its gene expression can change, both between and within life stages (e.g., Whitfield et al., 2006; Hoffman and Goodisman, 2007; Toth et al., 2014). In adult social insects for example, changes in the expression of cGMP-dependent protein kinase (PKG) affect the probability that an individual will forage (honey bees *Apis mellifera*, Ben-Shahar et al., 2002); red harvester ant *Pogonomyrmex barbatus* (Ingram et al., 2005); yellowjacket wasp *Vespula vulgaris* (Tobback et al., 2008). These changes can be brought on by abiotic (e.g., light or temperature), developmental (e.g., changes in hormone titers during development), or social factors (e.g., pheromone exposure, interactions with other insects). Furthermore, in honey bees, where colonies can vary quite dramatically in aggressive personalities (Pearce et al., 2001), exposing an individual to an alarm pheromone can result in the up-regulation of several genes involved in biogenic amine signaling (similar to that observed in vertebrates, Nelson and Chiavegatto, 2001), which in turn results in increased aggression or defensive behavior exhibited by the individual (Alaux et al., 2009). In both of these examples, changes among individuals can lead to changes in the social regulation, and thus possibly the personality, of the colony (Page et al., 2012). Therefore, gene expression differences among individuals may have consequences for the extended phenotype of colony personality.

There is evidence that many gene networks or functional pathways associated with social behaviors, such as brood care, aggression, and dominance, are conserved across animal taxa (e.g., overlap in molecular pathways found in wasps, honeybees, flies, and mice; Toth et al., 2014, 2010). Although the degree to which "personality genes" are conserved across all animal taxa is unknown, given the ubiquitous nature in which personality is observed across taxa, it is likely. To date, at least one gene has been directly associated with an individual personality in social insects (dopamine receptor in novelty-seeking honeybees; Liang et al., 2012). Whether such genes affect collective personality, and could therefore be considered "collective personality genes," is a distinct possibility.

gradually shift with the change in the genotype of the colony—offspring of the original genotype would be gradually replaced with offspring of the new genotype.

Division of labor within a colony, in general, has been described as a major contributor to the ecological success of eusocial groups, such as ants (Wilson, 1987; Wilson and Hölldobler, 2005). As colonies develop and the needs of the group change, tasks may be allocated among individuals differently such that the relative proportion of individuals engaging in particular tasks (i.e., foraging vs. guarding) may change (Gordon, 1995; LeBoeuf and Grozinger, 2014). Furthermore, variation in individual personality types within a group can facilitate division of labor (Holbrook et al., 2014). Because division of labor observed at the colony level is partially influenced by the differential gene expression of individuals in the group, changes in gene expression throughout an individual's development will affect their task preference. Therefore, as colonies develop and individuals mature, dynamics of division of labor and colony phenotype will shift, a factor that could have significant impact on the collective personality (**Figure 3**). Therefore, the division of labor, and how that changes throughout development, is likely to impact the collective personality of the group. This prediction can be tested by removing specialists or cohorts of individuals particularly efficient at performing group tasks and quantifying the collective personality of what is left of the group after they have begun working again (e.g., Jandt and Dornhaus, 2014).

INTERNAL SOCIAL ENVIRONMENT

The social environment can influence the production of within-group variation by affecting gene expression or hormone titers in developing individuals, predisposing them to exhibit specific personalities as adults (see **Box 1**). Within groups, these individual differences can influence group performance (Modlmeier and Foitzik, 2011; Pruitt and Riechert, 2011; Pamminger et al., 2012), division of labor (LeBoeuf and Grozinger, 2014), and also likely collective personality (Modlmeier et al., 2014a).

In some social groups, the repeated interactions of individuals may drive the level of behavioral variation within the group via a process known as social niche specialization (Montiglio et al., 2013). For example, in the social spider, *Stegodyphus mimosarum*, longer group tenure leads to higher variation in boldness between individuals, and higher individual consistency in boldness (Laskowski and Pruitt, 2014). A similar pattern was found in *S. dumicola* spiders, despite having an independent evolutionary origin of sociality (Modlmeier et al., 2014c). These studies suggest that as a group matures, the flexibility of individual behaviors may decline, perhaps stabilizing overall group behaviors (though not if large perturbation cause groups to mix and re-form; Modlmeier et al., 2014c). However, social niche

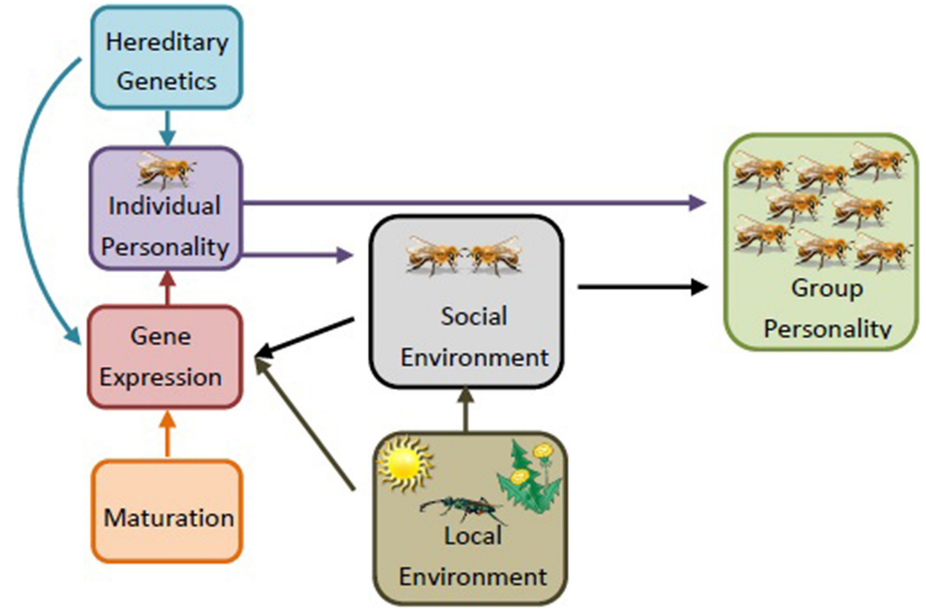


FIGURE 3 | Sociogenomics of personality. An individual's personality develops from a combination of hereditary genetics and differential gene expression. The group-level personality, then, is influenced by a combination of individual personalities and the social interactions among individuals (e.g., social environment). The social environment, age, and local environment (e.g., presence of parasites and predators, food availability/consistency, variation in climate) can influence the gene expression of the individual. These changes can influence an individual's personality, and therefore the social environment, leading to a change in group level personality. Local environment can also influence social environment, though less is known about these mechanisms. The development of the group is an adaptive, dynamic process, constantly shifting as the demographics of the group, such as age structure and group needs, change. For simplicity, regulatory elements and epigenetics are here lumped into the category "gene expression," but with the recognition that these factors play significant roles in shaping the individual's phenotype as well (figure adapted from Dolezal and Toth, 2014).

specialization is not a ubiquitous trait. For example, studies of stickleback fish (*Gasterosteus aculeatus*, Laskowski and Bell, 2014) and meerkats (*Suricata suricatta*, Carter et al., 2014) show no evidence for it. It is currently unknown why some social groups develop social niches while others do not; though social niches are expected in groups with relatively stable social structures (i.e., little fission or fusion). Within a group, it has been shown that specific genotypes may predispose some individuals to occupy specific social niches over others (Saltz, 2013; Saltz and Nuzhdin, 2014). Genetic variation is also one proximate explanation for division of labor in social insects (Page and Robinson, 1991; Robinson, 1992; Beshers and Fewell, 2001; LeBoeuf and Grozinger, 2014). While division of labor and social niche specialization likely are intertwined and feed back upon each other, the specifics of this relationship are thus far unknown and provide a promising area of future research.

Furthermore, in some groups, one or a few "key" individuals (also referred to as "keystone", Modlmeier et al., 2014b; "elites", Pinter-Wollman et al., 2012b; "leaders", Conradt and Roper, 2003) can have disproportionate influence on the behaviors of others in the group (for a full review see Modlmeier et al., 2014b). Over time, as groups grow in size, the influence of key individuals may change, resulting in significant changes in the collective personality. Hormone mediated interactions are largely presumed to be the mechanism by which key individuals influence the group (Modlmeier et al., 2014b). This may be episodic, such as the hormonal changes among individuals following dominance conflicts (Jandt et al., 2014b), or more permanent, such as pheromones exuded by the alpha female that suppress reproductive development in subordinate group members (Richard and Hunt, 2013).

Experimental removal or replacement of key individuals can be used to illustrate the degree to which those individuals influence the personality of a group, and/or personality of individuals within that group. In the zebrafish (*Danio rerio*), removal of key individuals with high social centrality decreases overall performance in learning group-foraging skills (Vital and Martins, 2013). In other groups, key individuals may simply maintain or improve social order and cohesion, such as bottlenose dolphins (*Tursiops truncatus*, Lusseau and Newman, 2004) and pigtailed macaques (*Macaca nemestrina*, Flack et al., 2006). However, not all key individuals provide a benefit to the group. In yellow baboons (*Papio cynocephalus*), the presence of a hyper-aggressive individual can drastically increase the level of stress hormones and decrease lymphocyte production in other individuals within the group (Alberts et al., 1992).

In most cases, key individuals are measured in mature groups. As such, it is not clear when these individuals first appear in group ontogeny. It is possible that the group must be a certain size before key individuals become highly influential. Alternatively, individuals may need to have a specific length of tenure in a group before becoming disproportionately important. As their presence or absence can be highly influential to group behavior, an obvious next step is to understand how key individuals originate (Modlmeier et al., 2014b).

LOCAL ENVIRONMENT

In addition to the factors that drive the development of collective personality within the group, experience from the local environment plays an important role as well (e.g., Pinter-Wollman et al., 2012a). Indeed, in guinea pigs (*Cavia aperea*), the length of the photoperiod juveniles are exposed to predicts their resting metabolic rates, cortisol levels and fearlessness through ontogeny (Guenther et al., 2014). In tarantulas (*Brachypelma smithi*), juveniles reared with environmental enrichment form a correlated suite of four behaviors that reflect a bold personality; whereas those reared under minimal conditions form a correlation between only two traits (Bengston et al., 2014). These examples challenge the assumption that personality is fixed, particularly when environmental conditions vary throughout an organism's (or group's) lifetime (Stamps and Groothuis, 2010). A group's lifetime may be considerably longer than that of a single individual, so different age cohorts of individuals may experience different environmental interactions. Therefore, the group as a collective unit would have been exposed to a wider variety of local conditions than a single individual within the group. Further, even if only a few individuals alter their behavior based on changes in the local environment (e.g., fluctuating temperatures or food availability, predation risk, etc.), this may suffice to alter the dynamics driving overall collective behavior (see section Internal Social Environment).

BEHAVIORALLY PLASTIC RESPONSES TO ENVIRONMENTAL SHIFTS

Ecologically relevant factors in the local environment can significantly impact collective behavior in highly social species. For example, the ant *Temnothorax longispinosus* is susceptible to attacks from the parasitic brood-robbing (slavemaking) ant *Protomognathus americanus*. The presence of *P. americanus* can increase colony-level aggression in *T. longispinosus*, a response not seen when exposed to non-parasitic competitors (Pamminger et al., 2011). Moreover, *P. americanus* founding queens have more successful invasions against less aggressive colonies, suggesting that the presence of this species may act as a selective agent for an aggressive response (Pamminger et al., 2012). The increased aggressive response disappeared after 14 days, suggesting that this personality trait may be temporary or is primarily the result of behavioral plasticity (Pamminger et al., 2011). In the arid social spider *Stegodyphus dumicola*, colonies are able to plastically adjust their collective foraging behavior when introduced to a new environment. However, it is not an immediate response. Rather, the colonies are able to respond more rapidly to prey after being in the new environment longer (Keiser et al., 2014).

Individual variation can still persist, however, even when there is plasticity in group-level response to environmental variability. For example, black harvester ant colonies (*Messor andrei*) maintain significant inter-colony differences in both foraging and response to disturbance, even though they flexibly adjust their movement speed in response to humidity (Pinter-Wollman et al., 2012a). A similar pattern is seen in red harvester ant colonies (*Pogonomyrmex barbatus*), which also show consistent inter-colony differences in foraging behavior, but will decrease their rate of foraging behavior in dry conditions (Gordon et al., 2013). Flexibly adjusting to humidity is a selectively advantageous trait, as desiccation costs are high for these desert foraging ants (Gordon, 2013). This implies that while different colony-level personality types can be maintained within a population, colonies can be flexible in their responses to environmental conditions.

BEHAVIORALLY FIXED RESPONSES TO ENVIRONMENTAL SHIFTS

Plasticity may allow groups to track environmental variation in the short term, but it is relatively unknown if exposure to environmental conditions can create fixed or long-term effects on collective personality. In the ant *Temnothorax rugatulus*, colony-level risk-tolerance, as reflected by foraging effort and defensive response, varies across a longitudinal gradient (Bengston and Dornhaus, 2014). Examination of the local environment revealed risk tolerance level is well predicted by competition for nest sites, and aggression is affected by how closely clustered the nest sites are (SE Bengston, unpublished data). It is unknown if this is the result of local adaptation due to natural selection or if colonies are able to assess colony density and respond accordingly. In the closely related species, *T. longispinosus*, colonies also exhibit higher levels of aggression and productivity as the population becomes more crowded (Modlmeier and Foitzik, 2011). Manipulating colony density does not affect defensive behavior, suggesting this behavior, which may be due to local adaptation, is fixed in these populations (Pamminger et al., 2012). Similarly, in the social spider, *Anelosimus studiosus* (Pruitt and Goodnight, 2014), colonies maintain an ideal group composition of behavioral phenotypes that varies between populations. If perturbed from the ideal, colonies either perish or return to the ideal mixture, though exactly how groups correct their compositions is yet unknown. In this example as well, colonies in different populations may be locally adapted to exhibit a specific collective personality type. These personality types remain fixed and are imperative to the survival of the group in that region. Therefore, while having the ability to plastically respond to changing environments may be beneficial, in more environmentally stable regions, having a fixed behavioral group-level phenotype would have selective advantages as well.

FUTURE DIRECTIONS

The development of collective personality truly presents a new frontier to those interested in both personality and collective behavior. We propose several areas of focus to initiate research that may illuminate understanding of how collective personalities of social organisms develop.

FITNESS EFFECTS

Collective personalities have consequences for both group- and individual-level fitness. Depending on the degree to which individuals within the group are related, the heritability of personality traits, and the social structure of the group, the way in which selection acts at the individual- and group-level may vary. The different mechanisms that can drive collective personality may further compound the fitness effects on individuals and/or the group. For example, if the collective personality of a newly founded colony (with only a few individuals) can be influenced by the personality type of a key individual, the success or failure of that new colony, and all the individuals in it, may be closely tied to the fate of that single individual. This is the case for the social spider *Stegodyphus dimucola*, where the presence of just one key individual leads to an increase in body weight for the rest of the colony by 400%, and an increase in individual colony member survivorship by 30% (Keiser et al., 2014).

Few studies specifically explore the fitness consequences of maintaining collective personality differences in a population, and no study to date has explored the fitness consequences of maintaining consistent personalities throughout group development. If behavior of the group shifts to respond to changing needs during different developmental phases (**Figure 1**), what are the fitness consequences to these behavioral shifts? If group personality becomes less consistent during specific developmental phases, as it does during the adolescent phase in squid (Sinn et al., 2008), what are the fitness consequences of having less consistency for short periods of group development? Are groups more vulnerable at stages of their development when personality is more or less consistent?

Measuring group-level fitness is not a trivial process. In eusocial insects, for example, fitness could be measured as the production of new queens and males, but a more accurate measure of fitness would consider the number of new colonies initiated by those new queens (Wilson, 1985). However, the success rate of new queens founding colonies can be low (Aron et al., 2009; Pull et al., 2013), and dependent upon many variables (e.g., climate conditions, predator/parasite density, availability of nesting sites, etc.,) (Voss and Blum, 1987; Tschinkel, 1993; Bernasconi and Keller, 1999). Still, group-level fitness can be measured in multiple ways. As mentioned above, fitness could be measured as the number of new groups initiated in 1 year or throughout the group's lifetime. However, this may be difficult, as daughter groups may be hard to track and monitor in the field, or establish in the lab (though not impossible; see Gordon, 2013; Pruitt, 2013). Additionally, fitness could be measured by proxies such as group mass, survivorship, or ability to avoid predation or parasitism (Keiser et al., 2014). Moreover, these factors—growth, survivorship, and reproduction—could be affected by personalities on different axes, so it is important to consider multiple-dimensions of personality, both among individuals and colonies.

STABILITY OF COLLECTIVE PERSONALITIES

Collective personalities may be more prone to instability than individual personalities. Migration in or out of the group, individual turnover, or fluctuation in the ratio of experienced to inexperienced individuals, for example, will affect the social environment and may alter the collective behaviors, and thus the personality, of the group (**Figure 3**). If the shift in behavior with individual turnover through group development is a mechanism that allows colonies to adapt to changing environments, then groups with faster rates of turnover should out-compete those with slower rates of turnover. On the other hand, groups with more consistency in collective personality may out-compete groups with higher rates of turnover in fixed environments.

A collective personality may also become more stable as a group matures if an increase in the number of individuals within a group decreases the "noise" from the variation within the group. In studies on collective decision-making, groups of individuals often make better decisions than solitary individuals; a phenomenon described as "wisdom of crowds" (Simons, 2004; Conradt and List, 2009). As group size increases, the efficiency of this decision-making can also change (Sasaki and Pratt, 2011; Kao and Couzin, 2014). When more individuals sample the environment, the group is provided with more information and may be better able to plastically alter their behavior or otherwise maintain adaptive stability (Raine and Chittka, 2007). If this is similarly affected by group size, it may be even more important during ontogeny as the group grows (Dornhaus et al., 2012).

The degree to which a group is fixed or stable under varying environmental conditions, or as the group size increases, may itself be an important characteristic that varies in a population. Therefore, understanding how consistent group-level behavior is across developmental stages is not the only important factor to consider. The degree to which groups plastically respond to disturbance, as well as the degree to which this is adaptive under a given environmental type, will also be an important area for future studies understanding collective personality.

COLLECTIVE REACTION NORMS

Individuals of the same genotype may behave differently in different environments (Gordon, 2013). The interaction between environment and genotype and its effect on phenotypic plasticity, often referred to as a reaction norm, is a common consideration in personality research. Though the mechanisms may be more complex, and thus difficult to quantify, behavioral reaction norms may still affect how collective personality is studied. For example, the level of genotypic variation within a group may influence the plasticity of emergent behaviors. As such, more highly related groups may vary more predictably between environments, while groups formed by unrelated aggregations may vary more erratically. Alternatively, increased within-group genetic variation may result in greater homeostasis. That is, although individuals with different genotypes may vary in response to perturbations in the environment, groups with greater genetic diversity may be more resilient and respond more consistently as environmental conditions fluctuate (Oldroyd and Fewell, 2007).

As groups grow and change in composition (of both personality type and genotype), the genotype by environment interaction may shift. This may allow groups to more plastically react to environmental conditions, or conversely destabilize adaptive responses as emergent behaviors are formed. Furthermore, these group-level reaction norms may vary across species that occupy similar habitats and/or across populations. Future research that accounts for the local environment, genotype, and degree to which groups respond appropriately to perturbations throughout development will provide a comprehensive understanding of collective personality.

CONCLUSIONS

Collective personality is a relatively new area of focus for behavioral ecologists. As such, there is limited evidence for precise mechanisms or selective agents. However, our understanding of how collective behaviors emerge and how group-level differences are maintained has provided a strong platform with which hypotheses can be drawn and tested. Here, we summarized what is known about the within-group and environmental factors that may influence collective personality through ontogeny, and propose potential new avenues of research.

In this review there has been a strong bias toward studies with social insects as the focal species, which reflects the current state of the literature. Arthropods, and in particular those species that live in groups, are ideal to test hypotheses that address the evolution of sociality. Unlike vertebrates, arthropods tend to have shorter generation times, and a variety of tools are available to study the internal developmental mechanisms (e.g., fixed neural pathways or epigenomic factors) that affect the personality type expressed by an individual (Kralj-Fišer and Schuett, 2014). As a result, social invertebrate colonies are particularly useful to study colony personality, and more specifically, the development of colony personality. In many cases, the entire colony cycle can be monitored from initiation throughout maturation (Ingram et al., 2005; Gordon, 2013; Pruitt, 2013), as well as across multiple generations.

However, with growing interest in collective personality, researchers should begin considering how other social groups develop and maintain collective personalities. Though selection may act more strongly on the level of the individual in non-eusocial species, group personality still holds implications for individual-level fitness by affecting overall group performance. It is our hope that the theory presented here will be used generally, and the lessons learned to understand collective personality in social insects can be applied to other social groups.

In conclusion, researchers must be cautious to consider environmental context when assessing behavioral changes over time, as they may be due to long term individual changes in early development or circumstantial changes that are tracking current environmental conditions. Recognizing the role that group age, stage of development, social environment, heritability, and environmental pressures have on group-level phenotype is the first step to understanding and assessing important group-level differences. When groups exhibit differences in personality type, then indeed there may be significant ecological implications for selection of personality types within groups. These implications could stretch across multiple levels of organization, including populations and individuals, making group personalities relevant to all social animals.

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Early Environmental Conditions Shape Personality Types in a Jumping Spider

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Individuals of many species across the animal kingdom are found to be less plastic than expected, even in behavioral traits. The existence of consistent behavioral differences between individuals, termed "personality differences", is puzzling, since plastic behavior is considered ideal to enable animals to adaptively respond to changes in environmental conditions. In order to elucidate which mechanisms are important for the evolution of personality differences, it is crucial to understand which aspects of the environment are important for the development of personality differences. Here, we tested whether physical or social aspects of the environment during development influence individual differentiation (mean level of behavior) using the jumping spider *Marpissa muscosa*. Furthermore, we assessed whether those behaviors were repeatable, i.e. whether personalities existed. We applied a split-brood design and raised spider siblings in three different environments: a deprived environment with no enrichment, a socially and a physically enriched environment. We focused on exploratory behavior and repeatedly assessed individual behavior in a novel environment and a novel object test. Results show that the environment during development influenced spiders' exploratory tendencies: spiders raised in enriched environments tended to be more exploratory. Most investigated behaviors were repeatable (i.e., personalities existed) across all individuals tested, whereas only few behaviors were also repeatable across individuals that had experienced the same environmental condition. Taken together, our results indicate that external stimuli can influence the development of one aspect of personality, the inter-individual variation (mean level of behavior), in a jumping spider. We also found family by environment interactions on behavioral traits potentially suggesting genetic variation in developmental plasticity.

Keywords: animal personality, arachnids, arthropod, behavioral syndromes, exploration, rearing, salticid, temperament

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INTRODUCTION

Consistent behavioral differences among individuals of the same population are widespread across various taxa in the animal kingdom (reviewed in e.g., Gosling, 2001; Bell et al., 2009; Kralj-Fišer and Schuett, 2014). This means individuals differ in their mean level of behavior (inter-individual behavioral variation) while being (more or less) consistent in their behavior over time and/or different contexts (intra-individual consistency). The existence of such personality differences is puzzling, given that it would seem sensible for individuals to be plastic and to adjust their behavior adaptively to changes in the environmental conditions (e.g., Sih et al., 2004).

Hypotheses that explain the adaptive value of animal personalities are linked to information use (McElreath and Strimling, 2006; Wolf et al., 2008), life-history (McElreath et al., 2007; Wolf et al., 2007), sexual selection (Schuett et al., 2010), and social interactions (McNamara et al., 2009) amongst others (Mangel, 1991; Dall et al., 2004; Nettle, 2006; Réale et al., 2007; Dingemanse and Wolf, 2010), yet empirical tests of these hypotheses remain scarce (but see e.g., Schuett et al., 2011b; Kralj-Fišer and Schneider, 2012; Nicolaus et al., 2012; Schuett et al., 2015). In order to understand the evolution of personality differences, it is also crucial to elucidate the development of personality differences. There is a general consensus that across species, on average about 30% of inter-individual variation in behavior (e.g., Stirling et al., 2002; van Oers et al., 2005; Quinn et al., 2009; van Oers and Sinn, 2011) and about 50% of personality variation is genetically inherited (Dochtermann et al., 2015), while the remaining variation originates from environmental sources (Buss and Greiling, 1999). In particular, environmental conditions experienced during early life may contribute to the development of personality differences by directing individuals into different life-history strategies and personalities ("early experiential calibration", Buss and Greiling, 1999; see also Carere et al., 2005). It has been proposed that similar to life-history traits, personality traits can adjust within a genetically predetermined reaction norm (see e.g., Dingemanse et al., 2010; Groothuis and Trillmich, 2011). As for developmental behavioral plasticity in general, the potential for these plastic responses might be restricted to sensitive periods during ontogenesis (e.g., Groothuis and Trillmich, 2011; or "developmental windows": Luttbeg and Sih, 2010; Faulk and Dolinoy, 2011), since changing an once adopted behavioral phenotype is associated with cost (reviewed in Snell-Rood, 2013). These processes can therefore lead to consistently different phenotypes even with similar genotypes (see Sih et al., 2004; Luttbeg and Sih, 2010) and these differences may be under frequency dependent selection (Lichtenstein and Pruitt, 2015).

To truly understand the evolution of personality differences, we need a comprehensive understanding of the specific environmental aspects shaping the development of personality differences (see Duckworth, 2010; Stamps and Groothuis, 2010). Previous studies have already shown developmental effects on mean behavioral levels such as social interactions (Iba et al., 1995; Arnold and Taborsky, 2010; Ballen et al., 2014; Liebgold, 2014), motor activity (Carducci and Jakob, 2000; Buchsbaum and Morse, 2012), or parental care (Margulis et al., 2005; Branchi et al., 2006). More studies are now desirable that investigate whether behavioral differences induced by developmental effects are consistent and stable, i.e., whether environmental conditions experienced influence animal personalities. Indeed, there is an increasing number of studies focusing on the development of animal personality (e.g., Sinn et al., 2008; Brodin, 2009; Schuett et al., 2011a; Gyuris et al., 2012; Hedrick and Kortet, 2012; Niemelä et al., 2012b; Petelle et al., 2013; Sweeney et al., 2013; Tremmel and Müller, 2013; Guenther et al., 2014; Johnson et al., 2015). To clearly identify underlying processes, experimental studies in which environmental conditions are manipulated are needed. The majority of studies that measured personality development in an experimental setting manipulated either food availability (e.g., Carere et al., 2005; Edenbrow and Croft, 2013), or stress by inducing immune challenge (e.g., Butler et al., 2012; DiRienzo et al., 2015), by increasing antipredator pressure (e.g., Bell and Sih, 2007; Niemelä et al., 2012a; Edenbrow and Croft, 2013), or by preventing access to shelter (Bengston et al., 2014).

Another aspect (potentially overlapping with above mentioned environmental aspects), which might influence the development of personality, is the complexity of the environment itself. Studies on animal intelligence have shown that increasing complexity in the social and/or in the physical environment induces behavioral and neural responses across different taxa (see e.g., Renner and Rosenzweig, 1987; Schrijver et al., 2004; Gonda et al., 2009; Brockmark et al., 2010; Kotrschal et al., 2012). This suggests that an increase in complexity directs animals to develop enhanced cognitive abilities allowing them to cope with increased information. Increased cognitive abilities (i.e., the ability to perceive and compute information) may itself lead to changes in individual behavior and life-history strategies (reviewed e.g., in Mettke-Hofmann, 2014; Trompf and Brown, 2014). Therefore, we assume that exploratory behavior, for example, should be generally positively linked to the amount of information (i.e., the complexity) available in the environment because knowledge of the environment allows behaving adaptively (at least up to a certain point; compare e.g., Niemelä et al., 2013). If, however, information gathering is potentially harmful individuals may show less exploratory tendencies. Such potentially harmful situations might be predation risk or risky interactions with conspecifics. To date, only few studies have investigated the effect of environmental complexity on personality either by increasing the social (Carere et al., 2005; DiRienzo et al., 2012) or the physical complexity (Bolhuis et al., 2005; Fox and Millam, 2007). Also, it remains unclear whether both aspects induce similar or different responses as these two aspects have rarely been manipulated in conjunction (but compare Carere et al., 2005; Bengston et al., 2014). A better understanding of these aspects is essential for elucidating which mechanisms are important for generating and maintaining personality.

In this study we investigated the effects of the social and the environmental complexity as well as genetic effects on the development of personality types using the jumping spider *Marpissa muscosa*. Jumping spiders are active hunters, have highly developed eyes and are sensitive to multiple aspects of their environment (Foelix, 2011). Therefore, we expect their personality development to be influenced by external stimuli (see for an example Royauté et al., 2014), including environmental complexity. Furthermore, we expect exploratory behavior to be a highly relevant behavior for jumping spiders because, among others, they need to search for prey, shelter, and mates. Carducci and Jakob (2000) showed indeed that jumping spiders reared in a physically enriched environment were on average more exploratory later in life. Here, we also added a social component to compare potential effects of the physical environment with effects of the social enrichment (see above).

We used a split-brood design and raised jumping spider siblings in three different environments: a deprived environment with no enrichment, a socially, and a physically enriched environment. This design allowed us to test for family effects, environmental effects, and their interaction on personality (mean level of behavior; behavioral repeatability within and among treatment groups) and plasticity. We repeatedly measured individual behavior in a novel environment and towards a novel object, and interpreted these as measures of exploratory behavior (see e.g., Réale et al., 2007). We predicted that enrichment, both physical and social, would lead to the development of more exploratory personalities (mean level of exploratory behavior) because information gathering in complex environments should be more advantageous than in less complex or deprived environments. However, we predicted that on average group living spiders might be less exploratory than physically enriched spiders due to the risk of harmful interactions with conspecifics. Even though *M. muscosa* are not considered social animals, they repeatedly interact with conspecifics in their natural environment (on and beneath the bark of trees). Furthermore, we assessed whether, beside those predicted effects on the mean behavioral level, behavior was also repeatable among and within treatment groups, i.e., whether personalities existed in the investigated traits. Finally, by presenting two different analytical approaches (i.e., analyzing repeatability over the whole data set vs. within each treatment separately) we want to highlight the possibility of obtaining different results when ignoring potential effects of developmental background on behavior. For example, the characteristics of the study area (from which individuals are sampled), such as the area's size, might influence the likelihood to detect personality differences: with increasing area the environmental heterogeneity often increases, too, and with it maybe also the potential of detecting (environmentally-induced) personality differences.

METHODS

Rearing Conditions

A total of 160 individuals of 14 maternal lines participated in the experiment. These were derived from three different cohorts and were assigned to one of three experimental groups (for details see below and **Table 1**).

In June–July 2012 we collected in total 18 adult and 17 subadult females and 18 males in northern Germany. Those females, which did not produce eggsacs in captivity (i.e., had probably not yet successfully mated in the field), were mated in the laboratory (by placing the female with a male in a box over night; males were used only once). Females were held solitary in plastic boxes (145 × 110 × 68 mm) enriched with some dry leaves, bark and white tissue paper. For the experiments we used spiderlings derived from the nine females, which were first to produce offspring. Eggsacs were separated from these females 2 weeks after they had been built to prevent any post-hatching maternal effects. After hatching juvenile siblings were assigned to one of three treatments pseudo-randomly (to ensure a balanced number of siblings in all treatments): a "deprived", a "physically enriched", or a "socially enriched" treatment.

TABLE 1 | Summary of sample sizes.

Treatment	Cohort 1	Cohort 2	Cohort 3	$\sum$
d	11	18	22	51
p	20	16	22	58
g	13	10	28	51
$\sum$	44	44	72	–

Numbers of individuals are given for each treatment group (d = "socially and physically deprived"; g = "socially enriched"; p = "physically enriched") and for each cohort. For more details please see text.

In all three treatments, spiders were held in translucent plastic boxes with holes that were covered with blue gauze to ensure air circulation. We raised spiders in the "deprived" treatment (treatment: "d") alone and without visual contact to conspecifics in boxes of 98 × 58 × 35 mm size. The bottom of the box was covered with white tissue paper and a small ball of the same material was included to give the spiders the opportunity to hide. Spiders in the "physically enriched" treatment (treatment: "p") were raised alone and without visual contact to conspecifics in boxes of 145 × 110 × 68 mm size. These boxes were enriched with both natural and artificial objects [such as bark, Iceland moss (*Cetraria islandica*), dry leaves, orange colored cords, Lego©bricks, bottle caps]. We increased the degree of enrichment over the weeks until an age of 46 weeks (by which time most spiders had reached maturity) and we altered the arrangement of objects every other week. Also a wooden plateau was included to increase the surface and structure of the box. The bottom of the box was covered with white tissue paper. In the "socially enriched", group treatment (treatment: "g") siblings were held together in groups of five to 15 individuals in one box (mean ± SE = 8.1 ± 3.3). The actual number of individuals per group depended on the total clutch size from which the siblings were allocated to the treatments, i.e., only siblings from large clutches reached the maximum size of 15 group members. The size of the box was matched to the actual group size so that on average each spider had a surface area of roughly 222 cm^2, which is similar to the area in the deprived treatment. The bottom of the box was covered with white tissue paper and a few paper balls were included to provide cover. In the socially enriched treatment, we separated spiders from their group when they reached subadulthood (at mean ± SE = 44 ± 8.4 weeks) to prevent uncontrolled matings. The new boxes had the same size and content as in treatment "d" but were put in close proximity to facilitate visual contact among conspecifics.

All animals were kept in the same laboratory room under constant conditions with a 17:7 h light:dark regime and temperatures between 22 and 24°C. Humidity was between 30 and 60% in the room (higher in boxes due to regular spraying into boxes). Depending on its age we fed each spider with 3–15 *Drosophila* spec. per week. Because spiders were held in groups in the social treatment the number of flies consumed by individual spiders might have varied. A total of five cannibalistic acts were observed in four out of twelve social groups. Every other week we monitored the developmental stage of each spider (juvenile, subadult, or mature) by inspecting the reproductive organs. At maturity the pedipalps of males are differentiated and turn dark and the epigyne of females becomes more pronounced and turns dark.

In 2012, we lost 56 of 142 spiderlings through unsuccessful molting or escapes (equally distributed across treatments: unsuccessful molting: GLM, $\chi^2 = 0.745$; $p = 0.689$; escapes: GLM, $\chi^2 = 4.368$; $p = 0.113$). To compensate for the reduction in sample size we also included individuals from family groups in which spiderlings had been raised together in a physically deprived environment for 2 months after hatching within larger groups (11–35 spiderlings per group). We pseudo-randomly assigned these spiders into the three treatments groups as described above. In the following we will refer to the original spiders as "cohort 1", to the spiders that were included later to compensate for the loss of individuals as "cohort 2".

In June 2013, we collected additional 23 adult, and presumably mated, females from the field. The offspring of five of those females were used to create cohort 3. These spiderlings were raised in similar ways to cohort 1 with some minor variations: we constantly provided small plastic tubes filled with wet cotton wool to prevent dehydration problems. Secondly, in the first week hatchlings received a sugar water drop in addition to the three flies. Finally, to prevent hatchlings from escaping their boxes (in the deprived treatment) they were held in plastic cylindrical containers (5.5 cm diameter). After 10 weeks they were transferred to the standard boxes described above for the deprived treatment.

Behavioral Tests

We tested all individuals twice each for their behavior in an open field and towards a novel object. In total, we recorded eight different behaviors during these tests of which seven were analyzed (see below; **Table 2**). Behavioral tests took place in a soundproof room with no windows between 16.07.2013 and 10.08.2013 for cohort 1 and 2 when spiderlings were 51.0 (± 0.85 SD) and 52.2 (± 1.9 SD) weeks of age, respectively. Spiders of cohort 3 were tested between 27.02.2014 and 26.03.2014 aged 35.1 (± 0.97 SD) weeks. All individuals were retested after 7 days to determine behavioral consistency. We tested three individuals simultaneously, if possible one from each (49%) or at least from two (40%) treatments. All spiders were tested in visual isolation from one another.

The open-field test started after a 30 min acclimatization phase to the test room. In a similar approach to Carducci and Jakob (2000) we divided the arena (a plastic box 145 × 110 × 68 mm) into 30 small quadratic fields (2.80 × 2.90 cm) with a central and an edge area to quantify activity (see **Figure 1**). Acclimatization started after the spider was put into a white opaque plastic cap (5.5 cm diameter, 1.2 cm high, **Figure 1**). The cap was half-covered with gray plastic foil to generate cover for the spiders. The rationale was that the cap would function as a safe retreat that the spiders would only leave when motivated to explore the open field. Spiders were given a total of 60 min to climb out of the start cap and to explore the arena. If spiders did not leave the start cap we removed them from analyses for that trial (in the first trial: d: $N = 3$, g: $N = 6$, p: $N = 4$ and in the second trial: d: $N = 3$, g: $N = 2$, p: $N = 2$).

TABLE 2 | Variables recorded from the open field (OF) and novel object (NO) test as measures of exploratory behavior.

Variable name	Description	Test
Latency to emerge OF	Latency to leave the start cap	Open field
Percentage of area visited OF	Percent of fields visited	Open field
Visitation central area OF	Whether (yes/no) the individual entered the central area in the last 7.5 min	Open field
Activity in central area OF	Duration of being active in the central area relative to the total exploration time, i.e., after leaving the start cap	Open field
Resting OF	Total duration of resting once the spider had left the start cap (>3 s without movement)	Open field
Touched NO	Whether (yes/no) the spider touched the NO or not	Novel object
Latency NO	Latency to touch the object (of those who did touch the NO)	Novel object

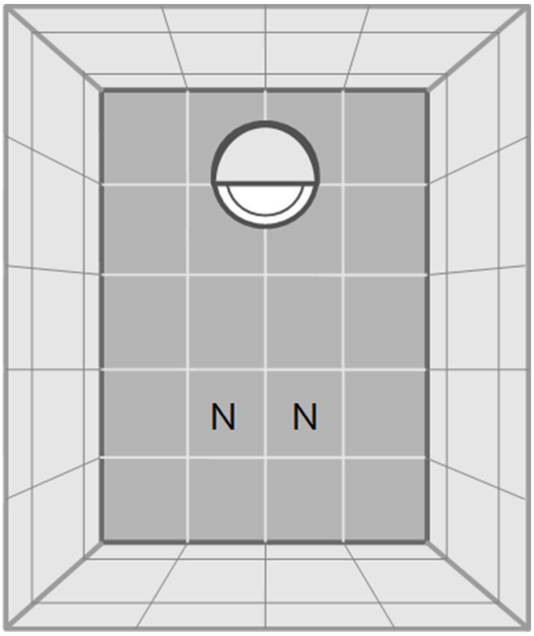

FIGURE 1 | Schematic drawing of the test arena for both, the open field and the novel object test. Dark gray fields indicate ground, light gray fields indicate walls. In one end of the arena a white opaque plastic cap is shown which functioned as start point. The cap was half-covered with gray plastic foil to generate shelter for the spiders. The letters "N" indicate the two possible positions in which the novel object was introduced at the beginning of the novel object test. The drawing is not to scale.

After the open field test we transferred spiders back into the plastic cap, which was covered to prevent spiders from climbing out. A novel object (a greenish wooden barrel: 1.5 cm diameter, 1 cm high) was placed at the opposite end of the arena (**Figure 1**). After removal of the cover of the cap the spiders were allowed to explore the arena and the novel object for 30 min.

We videotaped the behavior and the experimenter (D.R.) left the room for the duration of the tests. After each test the arenas and novel objects were cleaned with water.

Video Analysis

All video clips were anonymized and randomized by a third person before being analyzed (by D.R.). For the open field test we analyzed the first 7.5 min and at minutes 22.5–30 of each trial (15 min total). The remaining minutes were not included in order to reduce time of analyzing. For the novel object test all 30 min were analyzed.

Data Analyses

All analyses were done using R 3.1.0 (R Core Team, 2014) except calculations using the R package "rptR" (Schielzeth and Nakagawa, 2011) for which we used R 2.15.1 (R Core Team, 2012) because this package was not yet implemented for latest R versions.

In order to explore whether different behavioral variables correlated with one another we ran Spearman rank correlations with data obtained from the first trial. To avoid duplication of results we excluded the total number of fields visited during the open field test (visits and revisits) which correlated strongly with the percentage of total area visited in the open field ("percentage of area visited OF"; $r_s = 0.606$; $p < 0.001$). All other variable combinations correlated only moderately or less ($r_s < 0.42$) and thus a total of seven variables were included in further analyses (see **Table 2**). We also ran a principal component analysis to reduce the number of variables. However, sufficient principal components together should account for 90 % of the total variation (Crawley, 2013). In our case this would have meant to use nearly as many components as original variables. We therefore only used the original variables which are easy to interpret and facilitate comparison with other studies.

To assess the influence of our treatments and cohorts on the behavioral level of individuals, we used several GEEs (general estimated equations); GEEs are extensions of GLMs and are a robust way for analyzing correlated data (here: data of individuals from the same family) and especially useful when comparing population averages (Liang and Zeger, 1986; Quinn and Keough, 2002; Zuur et al., 2009; Zhang et al., 2012). We used the R package "geepack" (Halekoh et al., 2006) to estimate the effects of rearing conditions (treatment and cohorts) on the population mean level of the in **Table 2** mentioned seven behavioral variables obtained from the first test series. Thus, each individual contributed only one data point for these analyses. To account for potential family effects, we included the ID of the mother as cluster variable. In all models we included the two-way interactions between treatment and cohort and between treatment and sex as explanatory variables, as well as their main effects. We also included the variables "latency to emerge OF" and "latency to emerge NO", respectively, in the analyses because we wanted to control for differences in the actual duration each individual had spent in the arena outside of the start cap. The "latency to emerge OF" was not included in the analysis of the variable "activity in central area OF" which is a relative estimate. Here, the variation in the time in the arena is already corrected for by different start times. Because many spiders did not touch the novel object (37 of 141) and thus were removed for estimations of the depending variable "latency NO" we excluded the factor "sex" in this analysis as not to overly decrease the sample size (the sex could not be determined for all individuals).

Prior to analysis we excluded missing data so that sample sizes vary for different analyses (see **Table 3**). If required, variables were transformed using the "powerTransform" function of the R package "car" (Fox and Weisberg, 2011) or adequate error structures were used to meet model assumptions (i.e., binomial error structure for binary data; see **Table 3**). Maximal models were simplified step-wise by taking each term out in turn, then excluding the least significant term at each step, starting with interactions first, given the removal of a term did not significantly reduce the explanatory power of the model (Crawley, 2002). We tested whether the explanatory power of the simpler model was significantly reduced compared to the more complex model using Wald statistics (Zuur et al., 2009). Model simplification was continued until the minimal model was found, i.e., the model which included only significant explanatory variables (or main effects which were included in significant interactions). *P*-values and associated test statistics given for non-significant terms come from the time a term dropped out of the model (see **Table 3**). When the rearing variables (treatment p, d, and g and cohorts 1, 2, and 3) were not included in significant interactions but had significant effects on the response variable, we checked for differences between the levels by merging factor levels (compare Crawley, 2002) and compared the explanatory power of the simpler and more complex model. *P*-values given come from these comparisons (see **Table 4**). Please note that we did not adjust *p*-values for multiple comparisons.

To assess behavioral consistency we estimated behavioral repeatabilities and their 95% confidence intervals from generalized linear mixed effects models using R package "rptR" (with 1000 bootstraps and permutations; Nakagawa and Schielzeth, 2010). If confidence intervals did not include zero, repeatability was regarded as significant. We analyzed repeatability over the whole data set (**Table 5**) and within each treatment separately (**Table 6**). As above noted we did not adjust *p*-values for multiple comparisons. For further details on the specific models used, please see **Tables 5, 6**.

To test whether the degree of behavioral consistencies differed among treatment groups, we would have needed to test whether repeatability differed significantly among treatments. Yet, sample sizes within each treatment were rather low and many behavioral variables were not repeatable within each treatment group (see **Table 6**). Therefore, we only tested whether the population mean level of behavior differed among treatment groups and whether those behaviors were stable over all individuals (regardless of the environment they had experienced), i.e., whether measured behaviors are personality traits in the species.

In further analyses we investigated genotype by environment interactions. We used the maternal line as a proxy for genotype (but please note that individuals within a family were not genetically identical and that we cannot rule out pre-hatching maternal effects; we therefore use the term "family by environment" interaction). We fitted generalized linear models,

TABLE 3 | Model outputs (GEEs) indicating effects on the mean level behavior shown in an open field test (OF) and a novel object test (NO).

Response variable	Error structure	N	Coefficients (of explanatory variable)	Estimate	Std. error	χ^2	*p*-values
Latency to emerge OF	Gaussian	136	Mean	4.788	0.187		
			Treatment × Cohort			$\chi^2_{(4)} = 1.52$	$p = 0.82$
			TreatG:Cohort2	(−0.363)	(0.602)		
			TreatP:Cohort2	(0.284)	(0.399)		
			TreatG:Cohort3	(−0.157)	(0.468)		
			TreatP:Cohort3	(−0.256)	(0.567)		
			Treatment × Sex			$\chi^2_{(2)} = 2.04$	$p = 0.36$
			TreatG:SexF	(−0.620)	(0.451)		
			TreatP:SexF	(−0.325)	(0.391)		
			Treatment			$\chi^2_{(2)} = 11.5$	$p =$ **0.003**
			TreatG	−0.268	0.557		
			TreatP	−0.339	0.532		
			Cohort			$\chi^2_{(2)} = 25.0$	$p <$ **0.001**
			Cohort2	0.077	0.207		
			Cohort3	−0.858	0.192		
			SexF	(0.231)	(0.189)	$\chi^2_{(2)} = 1.5$	$p = 0.22$
Percentage of area visited OF	Gaussian	135	Mean	12.391	0.437		
			Treatment × Cohort			$\chi^2_{(4)} = 1.67$	$p = 0.8$
			TreatG:Cohort2	(−0.816)	(2.252)		
			TreatP:Cohort2	(−0.635)	(1.097)		
			TreatG:Cohort3	(−1.406)	(1.594)		
			TreatP:Cohort3	(−1.129)	(1.099)		
			Treatment × Sex			$\chi^2_{(2)} = 1.26$	$p = 0.53$
			TreatG:SexF	(−1.524)	(1.439)		
			TreatP:SexF	(−0.281)	(1.055)		
			Treatment			$\chi^2_{(2)} = 15.7$	$p <$ **0.001**
			TreatG	−0.116	0.616		
			TreatP	1.266	0.400		
			Cohort			$\chi^2_{(2)} = 2.22$	$p = 0.33$
			Cohort2	(0.328)	(0.563)		
			Cohort3	(1.012)	(0.752)		
			SexF	(0.180)	(0.240)	$\chi^2_{(1)} = 0.56$	$p = 0.45$
			Latency to emerge OF	−0.005	0.001	$\chi^2_{(1)} = 40.8$	$p <$ **0.001**
Visitation central area OF	Binomial	135	Mean	0.009	0.796		
			Treatment × Cohort			$\chi^2_{(4)} = 25.6$	$p <$ **0.001**
			TreatG:Cohort2	0.335	0.914		
			TreatP:Cohort2	0.842	1.092		
			TreatG:Cohort3	−1.914	0.347		
			TreatP:Cohort3	1.108	1.159		
			Treatment × Sex			$\chi^2_{(2)} = 2.08$	$p = 0.35$
			TreatG:SexF	1.513	1.066		
			TreatP:SexF	0.293	0.818		
			Treatment				
			TreatG	1.225	0.288		
			TreatP	0.111	0.760		
			Cohort				
			Cohort2	−0.666	1.080		
			Cohort3	−0.460	0.904		
			SexF	−0.643	0.374	$\chi^2_{(1)} = 2.95$	$p = 0.086$
			Latency to emerge OF	0.001	0.001	$\chi^2_{(1)} = 1.0$	$p = 0.32$

(Continued)

TABLE 3 | Continued

Response variable	Error structure	N	Coefficients (of explanatory variable)	Estimate	Std. error	χ^2	*p*-values
Activity in central area OF	Gaussian	114	Mean	0.508	0.050		
			Treatment × Cohort			$\chi^2_{(4)} = 13.8$	$p =$ **0.008**
			TreatG:Cohort2	0.045	0.054		
			TreatP:Cohort2	−0.098	0.051		
			TreatG:Cohort3	−0.006	0.045		
			TreatP:Cohort3	−0.095	0.053		
			Treatment x Sex			$\chi^2_{(2)} = 4.22$	$p = 0.12$
			TreatG:SexF	(−0.031)	(0.036)		
			TreatP:SexF	(−0.071)	(0.035)		
			Treatment				
			TreatG	−0.016	0.039		
			TreatP	0.074	0.048		
			Cohort				
			Cohort2	0.015	0.053		
			Cohort3	−0.025	0.059		
			SexF	(−0.008)	(0.015)	$\chi^2_{(1)} = 0.30$	$p = 0.59$
Resting OF	Gaussian	132	Mean	0.787	0.041		
			Tratment × Cohort			$\chi^2_{(4)} = 5.89$	$p = 0.21$
			TreatG:Cohort2	(−0.071)	(0.059)		
			TreatP:Cohort2	(−0.030)	(0.031)		
			TreatG:Cohort3	(−0.088)	(0.039)		
			TreatP:Cohort3	(−0.029)	(0.037)		
			Treatment × Sex			$\chi^2_{(2)} = 6.5$	$p =$ **0.039**
			TreatG:SexF	−0.041	0.025		
			TreatP:SexF	0.015	0.022		
			Treatment				
			TreatG	0.018	0.015		
			TreatP	−0.055	0.016		
			Cohort			$\chi^2_{(2)} = 22.4$	$p <$ **0.001**
			Cohort2	−0.020	0.025		
			Cohort3	−0.010	0.024		
			SexF	0.010	0.021		
			Latency to emerge OF	(−0.00003)	(0.00002)	$\chi^2_{(1)} = 1.5$	$p = 0.22$
Touched NO	Binomial	141	Mean	1.035	0.261		
			Treatment × Cohort			$\chi^2_{(4)} = 6.62$	$p = 0.16$
			TreatG:Cohort2	(4.50e + 15)	(1.45e + 06)		
			TreatP:Cohort2	(0.397)	(0.481)		
			TreatG:Cohort3	(−0.986)	(1.13)		
			TreatP:Cohort3	(0.357)	(1.14)		
			Treatment × Sex			$\chi^2_{(2)} = 0.68$	$p = 0.71$
			TreatG:SexF	(1.590)	(0.644)		
			TreatP:SexF	(−0.346)	(0.834)		
			Treatment			$\chi^2_{(2)} = 1.28$	$p = 0.53$
			TreatG	(0.345)	(0.537)		
			TreatP	(0.246)	(0.341)		
			Cohort			$\chi^2_{(2)} = 0.52$	$p = 0.77$
			Cohort2	(−0.123)	(0.601)		
			Cohort3	(0.279)	(0.439)		
			SexF	(−0.217)	(0.364)	$\chi^2_{(1)} = 0.36$	$p = 0.55$
			Latency to emerge NO	(−0.001)	(0.001)	$\chi^2_{(1)} = 0.65$	$p = 0.42$
			Resting time OF	(0.287)	(1.213)	$\chi^2_{(1)} = 0.06$	$p = 0.81$

(Continued)

TABLE 3 | Continued

Response variable	Error structure	N	Coefficients (of explanatory variable)	Estimate	Std. error	χ^2	*p*-values
Latency NO	Gaussian	115	Mean	8.940	0.962		
			Treatment × Cohort			$\chi^2_{(4)} = 10.0$	$p =$ **0.04**
			TreatG:Cohort2	−3.405	1.451		
			TreatP:Cohort2	−0.551	1.279		
			TreatG:Cohort3	−0.710	1.614		
			TreatP:Cohort3	−0.232	1.647		
			Treatment				
			TreatG	1.473	1.240		
			TreatP	−0.245	0.847		
			Cohort				
			Cohort2	2.054	1.125		
			Cohort3	0.374	1.345		
			Latency to emerge NO	0.005	0.001	$\chi^2_{(1)} = 0.65$	$p <$ **0.001**
			Resting time OF	(1.929)	(3.159)	$\chi^2_{(1)} = 0.373$	$p = 0.54$

*P-values derived from Wald tests comparing models with and without the explanatory variable (Zuur et al., 2009). P-values for significant terms (indicated in **bold**) derive from minimal adequate models. P-values for non-significant terms derive from models just before the terms were dropped. Coefficients for significant terms derive from minimal adequate models. Coefficients for non-significant terms (in brackets) derive from models just before the terms were dropped (please note that estimates of coefficients alter during the model simplification and that they are based on models with transformed response variables). Reference levels ("Mean") are always treatment = "d", i.e., deprivedly reared spiders; cohort = "1"; and sex = "male". "TreatG" refers to treatment "g", i.e., socially enriched reared spiders; "TreatP" refers to treatment "p", i.e., physically enriched reared spiders. "SexF" refers to female spiders. N = sample size, i.e., number of spiders tested.*

TABLE 4 | Model outputs (GEEs) testing for behavioral differences among treatments or cohorts in an open field test (first trial).

Response variable	N	Explanatory variables					
		Treatment: d;g	**Treatment: d;p**	**Treatment: g;p**	**Cohort: 1;2**	**Cohort: 1;3**	**Cohort: 2;3**
Latency to emerge OF	136	**$p < 0.001$** $[\chi^2_{(1)} = 11.5]$	**$p = 0.037$** $[\chi^2_{(1)} = 4.35]$	$p = 0.47$ $[\chi^2_{(1)} = 0.52]$	$p = 0.71$ $[\chi^2_{(1)} = 0.14]$	**$p < 0.001$** $[\chi^2_{(1)} = 20.1]$	**$p < 0.001$** $[\chi^2_{(1)} = 17.6]$
Percentage of area visited OF	135	$p = 0.85$ $[\chi^2_{(1)} = 0.04]$	**$p = 0.002$** $[\chi^2_{(1)} = 10.0]$	**$p = 0.007$** $[\chi^2_{(1)} = 7.3]$	–	–	–
Resting OF	136	–	–	–	$p = 0.4187$ $[\chi^2_{(1)} = 0.65]$	**$p < 0.001$** $[\chi^2_{(1)} = 15.55]$	**$p < 0.001$** $[\chi^2_{(1)} = 14.8]$

*The letters in the columns for explanatory variables indicate the treatments (d = deprived; g = group living; p = physically enriched) and the cohorts (1, 2, and 3) that were compared. P-values derived from Wald tests comparing models (Zuur et al., 2009) with and without the indicated levels merged together. N = sample size, i.e., number of spiders tested. Significance is indicated in **bold**.*

TABLE 5 | Repeatabilities of behavior shown in the open field test (OF) and the novel object test (NO) over all individuals.

Response variable	Error structure	N Ind.	N Tr.	*R*	*SE*	CI	rptR method	Link function
Latency to emerge OF	Gaussian	158	300	0.33	0.077	**0.183–0.478**	LMM.REML	–
Percentage of area visited OF	Gaussian	159	310	0.264	0.08	**0.105–0.415**	LMM.REML	–
Visitation central area OF	Binomial	159	311	0.278	0.081	**0.07–0.391**	PQL method	logitlink
Activity in central area OF	Gaussian	146	249	0.341	0.089	**0.165–0.507**	LMM.REML	–
Resting OF	Gaussian	155	285	0.477	0.066	**0.332–0.597**	LMM.REML	–
Touched NO	Binomial	160	320	0.203	0.071	**0.085–0.357**	PQL method	logitlink
Latency NO	Gaussian	140	232	0.045	0.076	0–0.247	LMM.REML	–

*Estimates derive from models with bootstraps and permutations (each 1000). Variables are listed in the left column and repeatabilities (R), their standard errors (SE), and 95% confidence intervals (CI; given in original scale) are given. "rptR methods" refers to the used method in the analysis (see Nakagawa and Schielzeth, 2010). Not each individual participated in both test runs; therefore number of trials are not twice the number of individuals. N Ind., number of individuals; N Tr., number of trials. Significance (i.e., confidence interval not including zero) is indicated in **bold**.*

TABLE 6 | Repeatabilities of behavior shown in the open field test (OF) and the novel object test (NO) tested separately for each treatment.

Variable	Error structure	Treatment d					Treatment g					Treatment p				
		N Ind.	**N Tr.**	***R***	***SE***	**CI**	**N Ind.**	**N Tr.**	***R***	***SE***	**CI**	**N Ind.**	**N Tr.**	***R***	***SE***	**CI**
Latency to emerge OF	Gaussian	51	96	0.208	0.135	0–0.481	50	94	0.306	0.136	**0.038–0.561**	57	110	0.310	0.120	**0.067–0.540**
Percentage of area visited OF	Gaussian	50	95	0.196	0.133	0–0.465	51	101	0.308	0.124	**0.044–0.520**	58	114	0.227	0.121	0–0.462
Visitation central area OF	Binomial	50	96	0.358	0.144	0–0.574	51	101	0.227	0.134	0–0.488	58	114	0.228	0.124	0–0.440
Activity in central area OF	Gaussian	44	69	0.217	0.167	0–0.572	48	82	0	0.101	0–0.339	54	98	0.678	0.081	**0.499–0.809**
Resting OF	Gaussian	48	87	0.450	0.450	**0.161–0.661**	50	96	0.613	0.093	**0.386–0.759**	57	102	0.355	0.123	**0.107–0.566**
Touched NO	Binomial	51	102	0.176	0.128	0–0.434	51	102	0.139	0.122	0–0.400	58	116	0.263	0.118	0–0.483
Latency NO	Gaussian	44	69	0.154	0.159	0–0.518	47	79	0	0.103	0–0.351	49	84	0.165	0.145	0–0.474

Estimates derive from models with bootstraps and permutations (each 1000). Variables are shown in the left column and repeatabilities (R), their standard errors (SE), and 95% confidence intervals (CI; given in original scale) are given. "rptR methods" refers to the used method in the analysis (see Nakagawa and Schielzeth, 2010). Not all individuals participated in both test series, so that the numbers of trials are not twice the number of individuals. N Ind., number of individuals. N Tr., number of trials. Significance (i.e., confidence interval not including zero) is indicated in ***bold***.

GLMs, with our behavioral variables as responses and the interaction between maternal line and treatment as well as their main effects as explanatory variables. We included only families for which we had data from at least two individuals per treatment (total number of individuals per families and test ranged from 10 to 17 across treatments). Only data of the first round of behavioral tests were used in these analyses. In order to meet model assumptions, data were either transformed using the "powerTransform" function of the R package "car" (Fox and Weisberg, 2011) or adequate error structures were used (see above; for details see **Table 7**). Significance of interactions was tested with likelihood ratio tests comparing the model with and without this interaction (see Crawley, 2002).

RESULTS

Early Environmental Effects on Inter-Individual Variation in Behavior (Mean Level Differences)

All behavioral variables were affected by the rearing condition with the exception of whether or not spiders touched the novel object ("touched NO"; **Table 3**). Spiders from the deprived treatment tended to be least exploratory: they needed longer to leave the start cap ("latency to emerge OF") than spiders from the physically and socially enriched treatments in the open field test (**Figure 2A**; **Table 4**). Spiders from the physically enriched treatment visited more percent of the total area ("percentage of area visited OF") than spiders from the other two treatments (**Figure 2B**; **Table 4**). There was a significant effect of treatment on resting duration ("resting OF") depending on the sex of the individual with males resting less in the deprived and physically enriched treatments but more in the social treatment than females (**Table 3**). Furthermore, there were treatment effects on the likelihood for entering the central area ("visitation central

TABLE 7 | Model outputs (GLMs) testing for family × environment interactions fitting an interaction between maternal line and treatment as explanatory variables on behavior shown in the open field test (OF) and the novel object test (NO).

Variable	Error structure	*DF*	Test-statistic	*P*-values
Latency to emerge OF	Gaussian	10,60	$F = 0.54$	0.858
Percentage of area visited OF	Gaussian	10,70	$F = 0.78$	0.648
Visitation central area OF	Binomial	1	$\chi^2 = 18.7$	**0.044**
Activity in central area OF	Gaussian	8,48	$F = 1.69$	0.125
Resting OF	Gaussian	10,66	$F = 1.72$	0.326
Touched NO	Binomial	1	$\chi^2 = 19.38$	**0.036**
Latency NO	Gaussian	10,52	$F = 2.14$	**0.038**

We included only families in which we had data from at least two individuals per treatment (five families for "activity in central area", six families for all other variables). P-values derived from likelihood ratio tests ("F" = F-test; "χ^2" = Chi-square test) of models with and without the interaction. Significance is indicated in ***bold***.

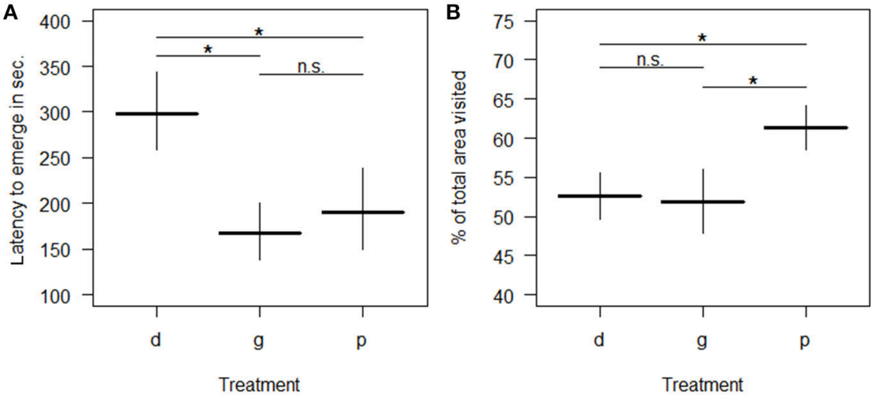

FIGURE 2 | Predicted mean levels (± SE) of behavioral responses in an open field test by spiders raised in one of three different treatment groups (d = "socially and physically deprived"; g = "socially enriched"; p = "physically enriched"). Panel **(A)** shows the latency to emerge; Panel **(B)** shows the percentage of area visited. All predictions derive from general estimated equations models (GEEs) after stepwise reduction to minimal adequate model including only significant terms. "n.s." indicates non-significant ($p > 0.05$) and "*" significant ($p \leq 0.05$) differences between the mean levels of groups.

area OF"), time spent active in the center ("activity in central area OF"), and in the latency to touch the novel object ("latency NO") but different for the cohorts (cohort x treatment, **Table 3**). Finally, cohort 3 needed less time to climb out the start cap in the open field tests and rested less than spiders from the other two cohorts (**Table 4**).

Repeatability

All behavioral measures were repeatable over time, except the latency to touch the novel object ("latency NO"; **Table 5**). The significant repeatabilities were moderate (0.203–0.447). However, when analyzed separately for each treatment, few behavioral variables remained significantly repeatable (**Table 6**): one in the deprived ("resting OF") and three out of seven in the socially ("resting OF"; "latency to emerge OF"; "percentage of area visited OF") and in the physically ("resting OF"; "latency to emerge OF"; "activity in central area OF") enriched treatment. Furthermore, confidence intervals of most repeatability values overlapped greatly among treatment groups.

Family by Environment Interactions

Family by environment interactions were found on those three behavioral variables that were not repeatable in any of the three treatment groups, namely: whether or not spiders entered the central area of the open field, whether they touched the novel object, and the latency to do so (**Table 7**). The effects were not driven by single families (as seen from visual inspection of interaction plots and model estimates, not shown); yet, the exact patterns of these interactions are beyond the scope of the manuscript.

DISCUSSION

The early environment in which spiders were raised significantly affected their exploratory tendencies (i.e., the population mean level of behavior). All but one behaviors measured were repeatable (at least over the whole study population), hence, we found evidence for personality differences. These findings combined indicate that external stimuli can influence the development of personality traits. We also found evidence for family by environmental interactions on behavioral traits. This means that families differed in their response to environmental conditions and suggests that families differed in their plasticity.

We found differences in the mean level of behaviors in our treatment groups, suggesting that the early environment influenced the development of exploratory behavior in the jumping spiders. In particular, individuals raised in the physically enriched treatment group were more exploratory than their siblings in the deprived treatment. This finding corroborates results from earlier studies on spiders (e.g., Carducci and Jakob, 2000; Buchsbaum and Morse, 2012; Bengston et al., 2014), nematodes (Rose et al., 2005), and vertebrates (e.g., Rosenzweig and Bennett, 1996; van Praag et al., 2000). Exploration, as an information-gathering process, might be more beneficial in an enriched (or generally more complex) than in a deprived (or generally very simple) environment with little to explore. Exploration can be costly (e.g., in terms of increased metabolism, or mortality risk) and thus individuals should not explore if not necessary. We found furthermore a sex-dependent treatment effect on the resting duration with group living males resting more than solitarily reared ones. Sexual size dimorphism is associated with a risk of cannibalism by the larger females (Wilder and Rypstra, 2008; Liedtke, J., personal observation), which may suggest that group living males are less active and thereby reduce encounter rates with females (compare sex-reversed pattern found in mice offspring: Heiming et al., 2009; and Hedrick and Kortet, 2012, for sex-dependent consistency over metamorphosis). Accordingly, a plastic response to the (early) environmental condition that an individual experiences seems sensible. Indeed, external influences particularly during development might have long lasting effects (reviewed in e.g., Snell-Rood, 2013).

The different responses of the three cohorts in our experiment may be an indication for sensitive phases (e.g., Groothuis and Trillmich, 2011) or "developmental-windows" (Luttbeg and Sih, 2010; Faulk and Dolinoy, 2011) within the developmental process of personality differences. The cohorts experienced different experimental conditions: in contrast to spiders from cohort 1 and 3, spiders from the cohort 2 were raised in groups for the first 2 months before they were assigned to the three treatments. Therefore, this cohort received an early social enrichment, regardless of later treatment. Results show that individuals from cohort 2 differed from the other two cohorts in several behaviors. Although it is difficult to explain the direction of these effects, these results indicate that, at least for the social enrichment, environmental conditions encountered in the first 2 months seem to have long lasting effects (permanent environmental effects *sensu* Dochtermann et al., 2015) on the development of behavioral tendencies. These patterns deserve further attention by follow-up studies in order to understand the proximate mechanisms of these apparently sensitive periods and if such effects can be induced by manipulation of the physical environment as well.

Group living also had positive effects on exploratory behavior in non-social contexts. This is in contrast to previous studies showing no effects of group living on behavior in non-social tests (reviewed in Taborsky et al., 2012). Yet, other studies found impairments of social isolation in multiple aspects of behavior (reviewed in e.g., Ballen et al., 2014). Hence, at least in some species contact to conspecifics can induce stable behavioral differences in other than the social realm. This suggests that early environment conditions can create behavioral differences in a context-general way.

Noteworthy, we found significant family by environment interactions on three of the investigated behavioral variables. This potentially indicates genetic variation for plasticity and suggests that plasticity itself might be under natural selection (Pigliucci, 2005; Dingemanse et al., 2010). Whether higher or lower plasticity is favored might depend on how stable and predictable environmental conditions are over time, with more stable conditions potentially favoring lower plasticity (see e.g., Dingemanse et al., 2010; Snell-Rood, 2013). But please note that we cannot rule out pre-hatching maternal effects in our study. Further studies are required to provide more insights, especially studies in which the paternity is also known.

Five behaviors that were repeatable over the whole population were not repeatable in all subpopulations (i.e., treatment groups) when estimated separately. Also, most confidence intervals of repeatabilities overlapped among treatment groups, suggesting repeatability was not necessarily significantly different among groups. Therefore, the extent of repeatability was likely not induced by the environmental conditions experienced. The pattern, that behaviors were repeatable across all individuals but not within all treatment groups, could potentially arise if between-individual variation in behavior within treatment groups is rather low (compared to between-individual variation across treatments) and/or if within-individual consistency in behavior is low. In both behavioral tests the average response of the deprived group was lower than that of the two enriched treatment groups, thereby leading to mean-level consistency (i.e., consistent differences between the average responses of each group; *sensu* Stamps and Groothuis, 2010). These consistent differences between treatment groups may explain why we found significant effects when we tested for repeatability over the whole population. The behavioral consistency of individual spiders within each treatment, on the other hand, may have been rather low, so that we found behavioral repeatability in fewer variables when treatments were assessed separately. This may indicate that for these variables, repeatability is mostly an effect of environmental induction by divergently shifting the mean level of each subpopulation (i.e., deprived group toward lower vs. enriched groups toward higher exploratory tendencies). Yet, these interpretations should be viewed with caution, since the absence of repeatable behavior within treatments in the five variables mentioned above could alternatively be an artifact of lower sample sizes within than among treatments. However, sample sizes in each subpopulation were still decent (≥ 44; see **Table 6**) indicating that these patterns might be biologically relevant and deserve attention in further studies. For example, studies using samples derived from larger study areas may be more likely to find repeatability even with relative low individual stability because they might include individuals with different environmental backgrounds.

Nevertheless, we also should bear in mind that environmental induction does not necessarily lead to differential consistency but could even lead to the opposite. If individuals have different genotypes they may have different innate levels in behavioral expressions. However, plasticity, i.e., the ability to respond sensitively to the environment, could lead to an approximation of these initial differences according to local conditions. Furthermore, we expect that, with plasticity being costly (see e.g., Dall et al., 2004; Pigliucci, 2005), individuals having an innate behavioral level closer to the local optimum to have an improved fitness (all other things being equal) because they need less modification in their responses. This implies that mean level should be under selection which may explain the differences between families in this study.

Taken together, results found in this study indicate that exploratory tendencies of *M. muscosa* are influenced by the environmental conditions experienced; families may differ in plasticity and thus provide the raw material for natural selection to act upon; and finally, observed patterns of personality distribution found in the field may be crucially influenced by plastic responses of sensitive systems.

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Experience drives the development of movement-cognition correlations in a butterfly

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Correlations between behavioral traits are widespread, but the developmental genetic architecture of such correlations is poorly characterized. Understanding the developmental mechanisms that lead to correlations between behaviors has implications for predicting how changing environments might alter the strength, direction and persistence of these associations. Here we test the idea that genetic variation in one behavioral trait can drive the development of traits related to a second behavior, resulting in correlations between them. We focus on correlations between movement and aspects of cognition, in particular accuracy of decision making and neural investment. Such syndromes have been seen across a variety of systems, from insects to birds, but the direction of the correlation often varies. We use cabbage white butterflies as a system because they are easy to rear in large numbers and show ample genetic variation in both movement and learning, facilitating a split-sibling design. We test the prediction that variation in established proxies for movement at emergence will be correlated with the development of cognitive traits later in life (in siblings). Our results suggest that genotypes (full-sibling groups) that emerge with more elongate wings explore their environment more rapidly. In addition, genotypes that emerge with relatively smaller thoraxes are more likely to learn to search for atypical host plants and subsequently develop larger brains and brain regions. Taken together, genotypes that invest less in flight are slower, better learners and develop larger brains. These data are consistent with the idea that movement can drive the development of other behavioral traits, resulting in the emergence of correlated behaviors.

Keywords: flight muscle, wing shape, brain size, cognition, personality

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Introduction

Correlations between movement and aspects of cognition are ubiquitous (Marchetti and Drent, 2000; Dugatkin and Alfieri, 2003; Sneddon, 2003; Bolhuis et al., 2004; Mery et al., 2007; Exnerova et al., 2010). In some studies, fast-moving, bold individuals are those with limited flexibility in behavior, poor long-term memory or smaller brains (Verbeek et al., 1994; Mery et al., 2007; Burns and Rodd, 2008; Exnerova et al., 2010). However, in other instances, there are positive correlations between movement and cognitive traits (Dugatkin and Alfieri, 2003; Sneddon, 2003; Guenther et al., 2014a). Understanding these correlations is important to predict patterns of coexistence and survival within species (Dall et al., 2004; Sih et al., 2004a; Bolnick et al., 2011). For instance, certain personality or movement types may be more likely to colonize new environments, influencing metapopulation dynamics (Bishop and Riechert, 1990; Hanski et al., 2004; Cote et al., 2010). Variation in movement and dispersal can also affect how organisms track environmental change (Higgins and Richardson, 1999; Thomas et al., 2001; Kotiaho et al., 2005; Poyry et al., 2009). However, how this variation in movement is correlated with cognitive abilities may affect whether a colonizing genotype survives in a new environment (Sol et al., 2002, 2005a). For instance, negative movement-cognition syndromes suggest that individuals most likely to colonize a novel environment may be the least likely to learn to use new resources in that environment.

While movement-cognition correlations have been documented across a range of systems, the developmental genetic architecture of these syndromes is unclear (**Figure 1**; Duckworth, 2010; Stamps and Groothuis, 2010a,b). Dissecting such proximate questions about behavioral syndromes is key to understanding how these correlations may break down or persist in the face of environmental or genetic change (Sih et al., 2004b). There are several proximate mechanisms by which correlations between behaviors might arise. In a handful of cases, correlated suites of behavior may stem from a set of genetic variants that are linked physically (e.g., in the same chromosomal region) or at the population-level due to mating patterns (e.g., "anxiety" traits in mice, Henderson et al., 2004). More commonly, behavioral syndromes emerge from pleiotropic effects of one or two genes as in the case of the foraging gene and rover-sitter *Drosophila* (Ben-Shahar et al., 2002; Mery et al., 2007). An idea receiving increasing attention in the literature is that of a niche-picking or niche-construction view in behavioral development (Stamps and Groothuis, 2010a; Stotz, 2010; Saltz and Nuzhdin, 2014). Exposure to different environmental conditions, such as enriched environments, high predation conditions or social stress, can influence the development of behavioral syndromes (Dirienzo et al., 2012; Edenbrow and Croft, 2013; Bengston et al., 2014). Thus, any genetic variation in traits that affect how an individual experiences the environment can result in genetic variation in behavioral syndromes. For instance, genetic variation in social preference has the potential to influence the development of personalities through the effects on a constructed social niche (Saltz, 2011; Montiglio et al., 2013).

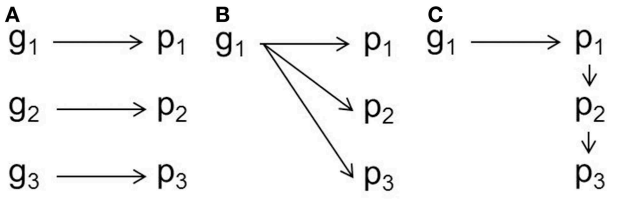

FIGURE 1 | Schematic of developmental genetic mechanisms underlying behavioral syndromes. (A) Linked genes (g) are associated with three correlated phenotypes (p). **(B)** One gene has pleiotropic effects on three phenotypes. **(C)** One gene affects one trait, which affects the development of other phenotypes, resulting in correlated traits. This latter mechanism, the focus of this research, would be considered a special case of "developmental" pleiotropy.

In this work, we focus on the hypothesis that genetic variation in movement-related traits affects the development of movement-cognition syndromes. It is well known that sensory stimulation during development can affect neural and behavioral development: exposure to enriched environments in development, (e.g., more social interactions or a range of resources), can result in neurogenesis, synaptogenesis and increased learning abilities (Van Praag et al., 2000; Arai and Feig, 2011). In more natural settings, an increase in sensory stimulation could stem from movement through different habitats, exposure to a range of resources or a combination of the two. Indeed, both movement and exercise have significant impacts on neural development (Olson et al., 2006). Taken together, these observations suggest that movement-cognition syndromes could emerge out of developmental interactions as organisms move through and interact with their environment.

Here, we test the hypothesis that slow exploration of the environment can affect the development of cognitive abilities, thus resulting in movement-cognition syndromes in adults. The decision-making literature suggests that there are often tradeoffs between the speed and accuracy of a decision (Dickman and Meyer, 1988; Chittka et al., 2009) which likely stems from limited attention and neural processing abilities (Bernays, 2001; Dukas, 2002). Such tradeoffs are thought to explain instances where fast, bold individuals are less flexible in the face of environmental change or invest less in neural machinery (Burns and Rodd, 2008; Sih and Del Giudice, 2012). In particular, it has been suggested that many syndromes may lie on a proactive-reactive axis, where bold individuals are where bold individuals are proactive. Bold individuals quickly explore and learn in a new environment but are less sensitive to new information and less capable of adjusting their behavior to environmental change (Sih....) (Sih and Del Giudice, 2012). We predict that such correlations emerge partly out of developmental interactions: slower exploratory movements earlier in development may drive the development of greater cognitive abilities, resulting in negative movement-cognition syndromes.

Dissecting the developmental basis of behavioral syndromes is challenging because measuring a trait at one time point may prevent or bias the measurement of that trait at a later time point. Family- or sibling-level approaches are one way around this problem which can simultaneously provide data on genetic variation in suites of correlated traits (Stamps and Groothuis, 2010a). In this study, we use a family-level approach to take independent measurements on naïve individuals sacrificed early in adulthood while their siblings, which were exposed to one of several behavioral assays, were tested at a later time point. We use the cabbage white butterfly, *Pieris rapae*, as a study system because they are easy to rear in common garden conditions, facilitating family-level designs (Snell-Rood and Papaj, 2009). In addition, we know learning affects resource use in many butterflies (Papaj, 1986a,b; Papaj and Prokopy, 1989; Weiss and Papaj, 2003), including *P. rapae*, which learn motor patterns for manipulating nectar resources (Lewis, 1986; Kandori and Ohsaki, 1996) and sensory cues associated with locating host plants or rewarding flowers (Traynier, 1984, 1986; Kandori and Ohsaki, 1996; Smallegange et al., 2006). In regards to host-searching behavior, learning is particularly important for locating atypical red hosts (Snell-Rood and Papaj, 2009) and exposure to more difficult learning environments can have positive effects on neural development (Snell-Rood et al., 2009). In contrast, an innate bias to search for green colors minimizes the role of learning when typical, green-colored hosts are present. Overall, cabbage whites are an ideal system for testing how suites of cognitive traits are influenced by developmental experience.

In the present work, we make use of an existing experiment that tested for associations between genetic variation in host plant learning ability and neural investment (Snell-Rood et al., 2009). To the existing dataset, we have added several measurements, including search speed and two morphological proxies for movement. We primarily focus on relative thorax mass, which in butterflies is positively associated with investment in flight, in terms of acceleration and duration (Chai and Srygley, 1990; Dudley, 1990; Marden and Chai, 1991; Dudley and Srygley, 1994; Hill et al., 1999; Kingsolver and Srygley, 2000; Marden, 2000; Berwaerts et al., 2002, 2008; Norberg and Leimar, 2002; Berwaerts and Van Dyck, 2004). We also focus on wing elongation, which is associated with greater acceleration, flight speed and distance (Betts and Wootton, 1988; Dudley, 1990; Berwaerts et al., 2002, 2008; Berwaerts and Van Dyck, 2004; Dockx, 2007). We relate measures of movement to measures of behavioral flexibility at different time points during adulthood. We test the primary prediction that if movement affects the development of cognition syndromes, movement traits at emergence will be related to cognitive traits (brain size and host-finding ability) assayed later in development, but not earlier in development.

Methods

Measures of Flight Capability

We used two morphological proxies for flight ability. First, we focused on thorax mass relative to body size, which has been linked to aspects of flight acceleration, speed and duration in over a dozen species of butterflies, including close relatives of *Pieris rapae* (Chai and Srygley, 1990; Dudley, 1990; Marden and Chai, 1991; Dudley and Srygley, 1994; Hill et al., 1999; Kingsolver and Srygley, 2000; Marden, 2000; Berwaerts et al., 2002, 2008; Norberg and Leimar, 2002; Berwaerts and Van Dyck, 2004). For this measure, we used full siblings that had been sacrificed at emergence given that thorax mass changes over the lifespan of a butterfly (Stjernholm et al., 2005; Stjernholm and Karlsson, 2008; Snell-Rood et al., 2013). Individuals were stored frozen in glassine envelopes until measurement. Wings, head, abdomen and legs were removed from the thorax which was dried at 60°C in a drying oven for at least 24 h. Thoraxes were measured to the nearest 0.1 mg. We calculated the relative thorax mass of a family by running a model with family as a fixed effect and forewing area as a separate measure of body size. Least square means were taken from this model as our measure of size-corrected thoracic investment at emergence. Mean sample size per family was 5.2 individuals (range = 2–14).

Second, we used forewing "circularity" as a measure of forewing elongation. Wing elongation has been linked to acceleration, flight speed and flight distance in at least four butterfly species (Betts and Wootton, 1988; Dudley, 1990; Berwaerts et al., 2002, 2008; Berwaerts and Van Dyck, 2004; Dockx, 2007). To measure circularity, wings of individual butterflies were removed with forceps, photographed and measured in Image J (NIH). Circularity is a function of wing area and perimeter [4π(area/perimeter^2)], thus, larger values indicate a shape closer to a circle, less elongate. For family-level measures of wing elongation, we used individuals sacrificed at both emergence and after host-searching experience because experience did not affect the measurement, for instance through wing damage [$F_{(1,\ 341)} = 1.22$, $P = 0.27$]. Because area is a component of this measurement, we did not correct for size. Mean sample size per family was 10.0 (range = 3–24).

Host-Finding Behavior and Neural Investment

Full description and analysis of the behavioral experiment is presented in Snell-Rood et al. (2009). Briefly, after rearing in a common garden on artificial diet, naïve butterflies were sacrificed at emergence for measures of brain size while their siblings were subjected to one of four host-searching assays (**Figure 2**). Mated female butterflies searched for either a green host (kale) or a red host (photic stressed *Barbarea vulgaris*) in either a simple or complex environment (simple = 50% hosts and 1 non-host type; complex = 20% hosts and 4 non-host types). Female butterflies sample potential host plants through landings where they "taste" chemicals in the plants with their foretarsii (Hern et al., 1996). We recorded all landings made during host searching using Noldus software that included a time stamp for each individual observation. After opportunities to search for hosts over a 2-day period (about 1–2 h of experience per individual), females were sacrificed for subsequent measures of neural investment. This host-searching assay, in a large flight cage (4 × 4 × 2 m tall), was the first opportunity for females to fly for longer distances and extended periods of time – prior to this assay they were housed in smaller 60 × 60 × 60 cm mating cages.

For family-level measures of host-finding performance, we focused on the proportion of host-searching landings on hosts vs. non-hosts (arcsine-square root transformed for normality). We contrasted performance in two of the four search environments—the most "difficult" search environment (red host, complex non-host) and the simplest search environment (green host, simple non-host). "Difficulty" was assessed based on performance (host-finding efficiency) in these host-search environments: both host color and non-host complexity had independent effects on host-finding (see analyses in Snell-Rood and Papaj, 2009; Snell-Rood et al., 2009). For example, initial searching in the red host environment was close to finding hosts at random chance. Additionally, these two environments had the most pronounced differences among full-sibling groups in performance [e.g., red-complex, Family effect = $F_{(9,\ 22)} = 2.35$, $P = 0.04$]. We focused on naïve individuals with at least 20 landings during their first-host-searching test period. We binned landings into a "naïve" category, landings 1–10, and an "experienced" category, landings 11–20. We took the average performance values for siblings from a family, using only families with at least 2 individuals for a given category (range 2–5, mean = 3.4 and 2.7 individuals for red-complex and green-simple environments).

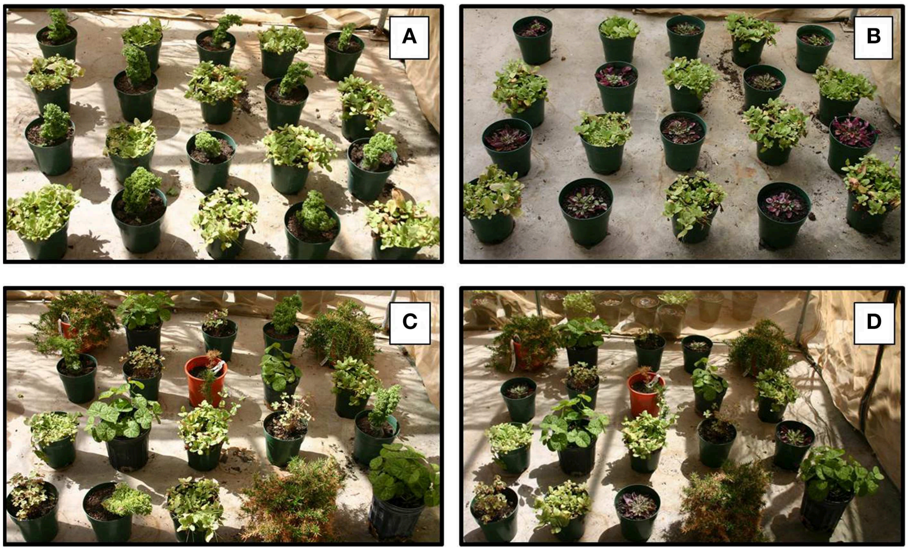

FIGURE 2 | Experimental setup. Individual female butterflies experienced environments that varied in host color (green vs. red color) or non-host complexity, which varied in diversity and density of non-hosts. **(A)** Green host, simple non-host environment. **(B)** Red host, simple non-host environment. **(C)** Green host, complex non-host environment. **(D)** Red host, complex non-host environment.

For measures of search speed, we focused on the median time between host-search landings (in seconds). It is important to note that during this time measurement, female butterflies are visually inspecting plants prior to landing on them and chemically gathering information with foretarsi after landing on them (rev. Hern et al., 1996). Thus, our measure of search time combines two types of exploration into one value. We take time flying between plants and time in contact with plants as one measurement of exploration time. This measure showed significant variation among full-sibling groups for initial landings in a model that controlled for search environment [landings 1–10: Family, $F_{(11,\ 183)} = 2.11$, $P = 0.02$, host color, $P = 0.004$, NH complexity, $P = 0.97$]. For later landings, time variation across families was not significant [landings 11–20: Family, $F_{(11,\ 110)} = 0.55$, $P = 0.86$, host color, $P = 0.02$, NH complexity, $P = 0.16$], but we still analyzed this variable as a contrast between time periods (consistent with our brain and performance measures).

This measure of exploration time focused only on landings butterflies made during active host searching. We focus on active host-searching because these behaviors are presumably the most relevant for fitness. However, we also considered time spent in other activities such as time spent sitting on plants and total search time (which includes time spent trying to escape and time flying around other parts of the flight cage). Time spent sitting on plants and total search time were not related to family variation in thorax mass [sitting time: $F_{(1,\ 9)} = 0.16$, $P = 0.70$; total flight time: $F_{(1,\ 9)} = 0.59$, $P = 0.46$].

A complete description of neural methods and analyses can be found in Snell-Rood et al. (2009). Briefly, butterfly heads were fixed in formalin and stored in cacodylate buffer until dissection. They were stained with osmium, embedded in plastic and sectioned at 15 microns. The volume of each brain region was measured using Image J (NIH). We focused on family-specific estimates of the total brain (from a model that corrected for body size using hindwing area) and the volume of individual brain regions (from a model that corrected for total brain volume). For specific brain regions, we only focused on those that showed family-level variation of experienced individuals (see Table 6, Snell-Rood et al., 2009), the central body, antennal lobes and medulla (part of the optic lobe). Measures of experienced brain size came from models that controlled for specific host-searching experience (host color, non-host complexity and total landings of an individual, $N = 49$ individuals from 7 families).

All statistical tests focused on family-level measures (i.e., each data point is a full-sibling family). Analyses were performed in JMP 9.0 (SAS Institute).

Results

There was significant variation across full-sibling families in both forewing circularity and thorax mass relative to body size [forewing circularity: Family: $F_{(11,\ 114)} = 4.84$, $P < 0.0001$; thorax mass: Family: $F_{(10,\ 41)} = 19.2$, $P < 0.0001$, forewing area: $F_{(1,\ 41)} = 70.9$, $b_{ST} = 0.02$, $P < 0.0001$]. These two proxies for movement were not significantly correlated (Spearman's $\rho = -0.07$, $P = 0.83$).

Butterfly families with more circular wings (less dispersive) were initially slower (i.e., had longer exploration times between host landings) during host search than those with more elongate wings [**Figure 3**; landings 1–10, $F_{(1,\ 10)} = 6.33$, $P = 0.03$]. However, this trend reversed, in a marginally significant manner, later during host search [**Figure 3**; landings 11–20, $F_{(1,\ 10)} = 3.84$, $P = 0.08$]. There were no significant relationships between search speed and thorax mass at emergence [landings 1–10, $F_{(1,\ 9)} = 0.54$, $P = 0.47$; landings 11–20: $F_{(1,\ 9)} = 0$, $P = 0.98$].

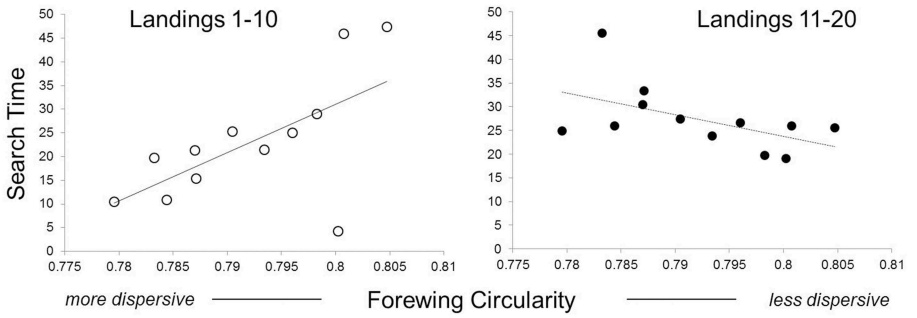

FIGURE 3 | Effects of wing elongation on speed of host-searching. Each data point represents a full-sibling family. Families with more elongate (less circular) wings spent less time initially searching their host environment. Search time is measured as the median time between host-searching landings (in seconds) for a given butterfly family. The left panel shows behavior of naïve individuals (first 10 host-searching landings) while the right panel shows behavior of experienced individuals (second 10 host-searching landings).

TABLE 1 | Associations between thorax mass at emergence and host-finding efficiency.

	Naïve individuals (landings 1–10)	Experienced individuals (landings 11–20)
Difficult search	$F_{(1,\,7)} = 1.75$, $P = 0.23$, $b_{ST} = -\,!\,12.2$	$F_{(1,\,7)} = 19.8$, $P = 0.003$, $b_{ST} = -25.7$
Simple search	$F_{(1,\,8)} = 3.04$, $P = 0.12$, $b_{ST} = -15.9$	$F_{(1,\,8)} = 1.07$, $P = 0.33$, $b_{ST} = -10.1$

Shown are results results of family-level regressions for relationships between thorax mass at emergence (independent variable) and host-finding ability (dependent variable). Host-finding ability (proportion of landings on hosts vs. non-hosts) was considered early in host searching (landings 1–10) and later in host searching (landings 11–20) on the first day of search for naïve females. Females searched in either a difficult or simple search environment, where host color (green vs. red) and non-host diversity and density varied (see ***Figure 2****).*

Butterfly families that emerged with relatively greater thorax mass (more dispersive) had poorer performance in the more difficult host-searching environment, where butterflies searched for red hosts within a diverse and dense non-host environment. However, this relationship was not present for naïve butterflies—it emerged after host-search experience (**Table 1**, **Figure 4**) and remained significant following a Bonferroni correction for four comparisons. There was no relationship between thorax mass and family performance in the simple host-searching environment (**Table 1**). There were no significant relationships between forewing circularity and measures of host-finding performance, although there was a marginally significant positive relationship between forewing circularity and experienced performance (landings 11–20) in the green host, simple non-host environment (**Table 2**).

Butterfly families that emerged with relatively greater thorax mass had smaller brains and brain regions, but only for measurements performed on experienced individuals (**Table 3**, **Figure 5**). More specifically, sibling groups with relatively smaller thoraxes had greater total brain volume along with regions of the brain dedicated to the antennal lobes and the central bodies. However, this relationship was specific to brain measurements of experienced individuals, not naïve individuals, although there was a marginally significant relationship between total naïve brain volume and relative thorax volume (**Table 3**). Two of these relationships (antennal lobe and whole brain) remained significant after a Bonferroni correction that accounted for four brain regions, but not when accounting for all eight comparisons. There were no significant associations between forewing shape and neural measures (**Table 4**).

Discussion

Genetic Variation in Movement Drives Emergence of Behavioral Correlations

Our results support the hypothesis that genetic variation in traits related to movement and exploration of the environment can drive the development of behavioral syndromes. Across all described patterns, variation in movement traits at emergence was tied to cognitive traits, but only those behavioral traits measured in experienced individuals, not naïve individuals. We focused on two validated proxies for movement that differed significantly between full-sibling groups of cabbage white butterflies. Previous studies have found that butterflies with a larger relative thorax mass and more elongate wings fly faster and further (Betts and Wootton, 1988; Chai and Srygley, 1990; Dudley, 1990; Marden and Chai, 1991; Dudley and Srygley, 1994; Hill et al., 1999; Kingsolver and Srygley, 2000; Marden, 2000; Berwaerts et al., 2002, 2008; Norberg and Leimar, 2002; Berwaerts and Van Dyck, 2004; Dockx, 2007).

In the present study, we found three general patterns linking movement traits to behavioral traits. The first pattern suggests that individuals with different movement traits have different sampling strategies. Naïve females from families with more elongate (less circular) wings, explored their environment more rapidly when first searching for host plants (**Figure 3**). This suggests that more dispersive families explored visual and chemical plant cues less thoroughly than less dispersive families.

To evaluate whether these differences in movement might lead to the development of different aspects of cognition, we

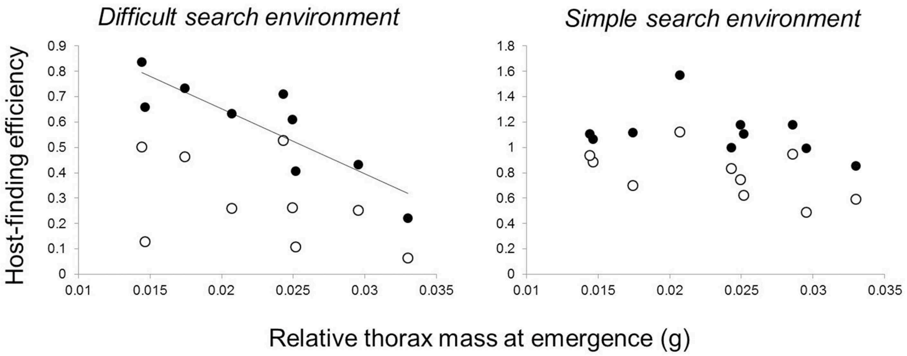

FIGURE 4 | Effects of relative thorax mass on host-finding efficiency. Each data point represents a full-sibling family. Host-finding efficiency (the proportion of searching landings on hosts vs. non-hosts, arcsine-square-root transformed) tended to increase between naïve butterflies (open circles—first 10 landings of a completely naïve host search) and later experience (closed circles—second 10 landings in the same searching sequence). Butterflies searched in either a difficult searching environment, where a red-colored host was interspersed amongst a high density of four non-host types, or a simple search environment where a green-colored host was interspersed in a low density of one non-host type.

TABLE 2 | Associations between forewing circularity and host-finding efficiency.

	Naïve individuals (landings 1–10)	Experienced individuals (landings 11–20)
Difficult search	$F_{(1,\ 7)} = 0.23$, $P = 0.64$, $\mathrm{b_{ST}} = 3.94$	$F_{(1,\ 7)} = 0.60$, $P = 0.47$, $\mathrm{b_{ST}} = 6.74$
Simple search	$F_{(1,\ 9)} = 0.46$, $P = 0.51$, $\mathrm{b_{ST}} = 5.57$	$F_{(1,\ 9)} = 4.23$, $P = 0.07$, $\mathrm{b_{ST}} = 13.7$

Shown are results of family-level regressions testing for relationships between forewing circularity (larger values are less elongate wings) and host-finding ability. Host-finding ability (proportion of landings on hosts vs. non-hosts) was considered early in host searching (landings 1–10) and later in host searching (landings 11–20) on the first day of search for naïve females. Females searched in either a difficult or simple search environment, where host color (green vs. red) and non-host diversity and density varied (see ***Figure 2****).*

TABLE 3 | Associations between neural investment and thorax mass.

	Naïve individuals	Experienced individuals
Antennal lobes	$F_{(1,\ 4)} = 0.01$, $P = 0.93$, $\mathrm{b_{ST}} = 0$	$F_{(1,\ 5)} = 14.7$, $P = 0.01$, $\mathrm{b_{ST}} = -0.11$
Medulla	$F_{(1,\ 4)} = 0.7$, $P = 0.45$, $\mathrm{b_{ST}} = 0.31$	$F_{(1,\ 5)} = 3.2$, $P = 0.13$, $\mathrm{b_{ST}} = 0.66$
Central body	$F_{(1,\ 4)} = 0.2$, $P = 0.68$, $\mathrm{b}_{vST} = 0$	$F_{(1,\ 5)} = 11.7$, $P = 0.02$, $\mathrm{b_{ST}} = -0.01$
Whole brain	$F_{(1,\ 4)} = 6.59$, $P = 0.06$, $\mathrm{b_{ST}} = -3.15$	$F_{(1,\ 5)} = 14.9$, $P = 0.01$, $\mathrm{b_{ST}} = -6.9$

Shown are results of family-level regressions testing for relationships between a family's relative thorax mass at emergence (independent variable) and measures of neural investment for siblings sacrificed at emergence or following host-searching activity. We only analyzed brain regions with significant family-level variation. Measures of individual brain regions account for body size variation.

tested whether movement traits and cognition were correlated in naïve and experienced individuals. In both cases, we found movement-cognition correlations only in experienced individuals. First, females from families with smaller relative thorax mass (less dispersive) were more capable of finding atypical host plants in complex environments (**Figure 4**), but this correlation was only evident in the second 10 host landings, after initial exploration of their environment. This result suggests that families with smaller relative thorax masses can more successfully learn to navigate complex environments than families with larger thoraxes. Second, butterflies from families with smaller thoraxes (less dispersive) were also more likely to develop larger brains (**Figure 5**) with larger regions involved in sensation (antennal lobes) and movement (central body, Strauss, 2002; Neuser et al., 2008). However, there were no correlations between movement traits and neural investment at emergence, consistent with the idea that initial variation in movement may have affected neural development.

Taken together, these data are consistent with the idea that variation between families in movement affects sampling strategy, the ability to find atypical resources, and, over developmental time, learning and neural development. Throughout, we have assumed that the differences between sibling groups reflect genetic variation. However, it is important to note that because we used a full-sibling design as opposed to a split-sibling design, it's possible that the family-level variation stems in part from maternal effects. Either mechanism is consistent with the idea that initial variation in behavior could drive the development of behavioral syndromes, but teasing apart genetic and maternal effects may give insights into how such syndromes might evolve as the environment changes. More specifically, genetic correlations between movement and cognition

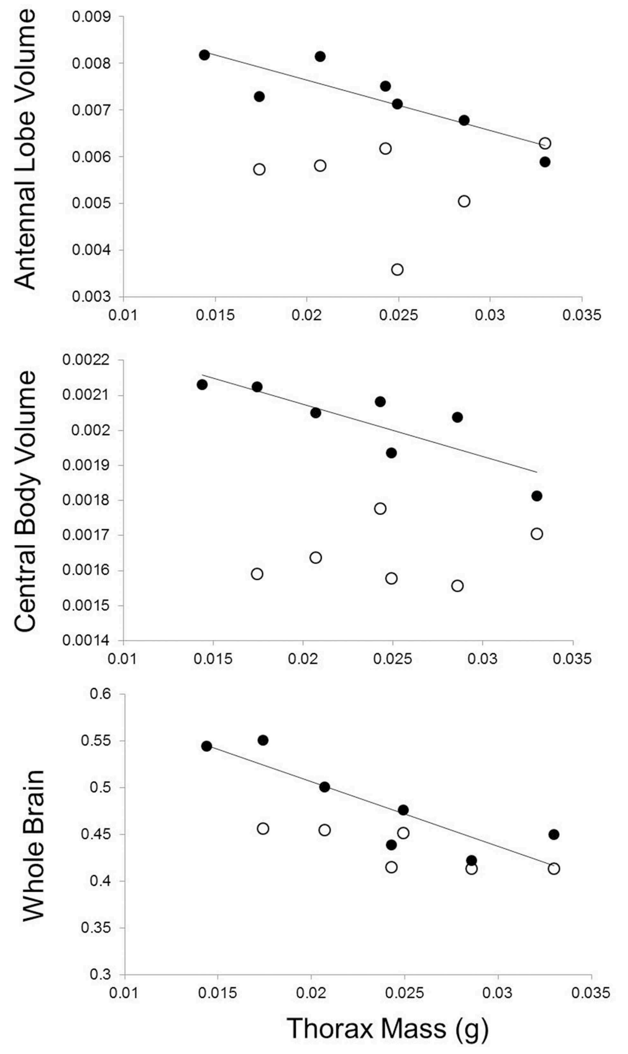

FIGURE 5 | Effects of relative thorax mass on neural investment. Full-sibling families with relatively smaller thorax mass at emergence developed larger brains and brain regions (experienced individuals shown with closed circles). There was no significant relationship between brain measures and thorax mass for brain measures taken on individuals sacrificed at emergence (open circles). Measures of individual brain regions account for body size variation.

that arise through gene-environment correlations have important evolutionary implications (Saltz and Nuzhdin, 2014). Niche-constructing behavior such as habitat preference or modification has the potential for generating complex evolutionary feedbacks because the selective environment potentially has a genetic component (Kerr and Feldman, 2003; Kylafis and Loreau, 2008). For instance, a decline in movement could decrease exposure to a range of environments, potentially weakening selection on learning and plasticity in certain environments (Sultan and Spencer, 2002; Scheiner et al., 2012). In some instances, by increasing the frequency of exposure to certain environments (e.g., atypical hosts), niche constructing behavior can speed up adaptation to those specific environments (Drown and Wade, 2014).

The present dataset is limited to only 12 full-sibling families. A more thorough quantitative genetic dissection of this question would consider a larger number of families. Such a design was not permissible in the present work which originally used behavioral measurements in four separate environments. However, we observed that the emergence of behavioral correlations was more pronounced in the most complex environment, similar to experiments in spiders which manipulated environmental enrichment (Bengston et al., 2014). These experiments suggest that the effects of niche construction and niche picking should be more pronounced in heterogeneous environments where behavioral variation would have more pronounced effects. From an experimental perspective, this suggests that limiting observations to one, complex environment would permit an increase in the number of families sampled, ideally using a split-sibling design to estimate maternal effects. Regardless, the limited family-level sample size for some of our comparisons (e.g., brain measures in **Tables 3, 4**) suggests that some of these comparisons should be treated as preliminary, informing follow-up studies.

We chose our proxies for movement based on existing research on butterfly flight patterns in over a dozen species, including those closely related to cabbage white butterflies (see citations above). Existing flight studies have considered butterflies in flight tunnels, tethered individuals or longer-distance free flight of wild individuals. These test conditions are somewhat different from the flight cage used here. However, the fact that thorax mass and wing shape tend to be important in a variety of experimental assays suggest they are also relevant for our assay. Additionally, while we were focused on short-distance flight patterns here, female cabbage whites move large distances in host-searching, sometimes 500–1000 m or more, spreading hundreds of eggs across many different host plants (Jones, 1977; Suzuki, 1978; Jones et al., 1980; Root and Kareiva, 1984). While it is likely these proxies for movement apply to host-searching in female cabbage whites, it's important that future studies validate the present patterns with measures of flight behavior in the field.

Overall, our results support the idea that variation in movement between families may result in the development of movement-cognition syndromes. For both neural measures and host-finding performance, movement traits (at emergence) were correlated with cognitive traits in experienced, but not naïve, individuals. Given the importance of exercise and enriched environments in neural development (Van Praag et al., 2000; Olson et al., 2006), it is not surprising that variation in movement between families could affect the expression of correlations between movement and cognition. Indeed, the same complex non-host and red host environments used in this experiment were previously shown to have positive effects on neural development in these butterflies (Snell-Rood et al., 2009). These results more broadly suggest that initial variation in a behavioral trait may affect the development of other traits, resulting in correlated behavior.

Insights into Movement-Cognition Syndromes Across Species

Our results linking measures of movement and cognitive behavior recall other systems where bold or dispersive genotypes are

TABLE 4 | Associations between neural investment and forewing circularity.

	Naïve individuals	Experienced individuals
Antennal lobes	$F_{(1,\,4)} = 6.76$, $P = 0.06$, $b_{ST} = -0.09$	$F_{(1,\,5)} = 1.39$, $P = 0.29$, $b_{ST} = 0.05$
Medulla	$F_{(1,\,4)} = 1.21$, $P = 0.33$, $b_{ST} = 0.24$	$F_{(1,\,5)} = 0.34$, $P = 0.58$, $b_{ST} = -0.21$
Central body	$F_{(1,\,4)} = 6.86$, $P = 0.06$, $b_{ST} = -0.007$	$F_{(1,\,5)} = 0.19$, $P = 0.67$, $b_{ST} = 0.002$
Whole brain	$F_{(1,\,4)} = 4.04$, $P = 0.11$, $b_{ST} = 1.82$	$F_{(1,\,5)} = 0.87$, $P = 0.40$, $b_{ST} = 2.44$

Shown are results from family-level regressions testing for relationships between a family's forewing circularity (larger values are less elongate wings) and measures of neural investment for siblings sacrificed at emergence or following host-searching activity. We only analyzed brain regions with significant family-level variation. Measures of individual brain regions account for body size variation.

less behaviorally flexible. Such correlations within species have been seen in both birds and fish (Verbeek et al., 1994; Burns and Rodd, 2008; Exnerova et al., 2010; Guillette et al., 2011). Across species, similar correlations have been noted with respect to migratory birds—migratory species have smaller brains and are less behaviorally flexible than temperate residents that have to cope with drastic changes across seasons (Sol et al., 2005b). Similarly, resident species of parrots (relative to nomadic species) tend to explore their environment more thoroughly and carefully (Mettke-Hofmann et al., 2012). Negative movement-cognition syndromes have also been suggested within humans with respect to attention deficit hyperactivity disorder (Rosenthal and Allen, 1978; Biederman et al., 1991; Blickle, 1996; Furnham et al., 2009).

Across species, however, there are examples of both positive and negative movement-cognition syndromes (Verbeek et al., 1994; Dugatkin and Alfieri, 2003; Sneddon, 2003; Mery et al., 2007; Burns and Rodd, 2008; Exnerova et al., 2010; Guenther et al., 2014a). Taking a developmental niche construction perspective can help to clarify such variation. Increased movement and dispersal may increase the degree of environmental variation an individual experiences, increasing the benefits of behavioral plasticity and learning (Papaj, 1994; Scheiner, 2013). However, if individuals are choosing to interact with only a subset of resources or environments experienced during dispersal, they may actually be experiencing more stable, predictable conditions, which would favor the use of innate behavior. Indeed, our results hinted that more dispersive genotypes (more elongate wings) may do better with more typical, green hosts, for which these butterflies have an innate bias (**Table 2**).

Why might more dispersive individuals invest less in learning and cognition? It is possible that such negative correlations could result from a tradeoff between investment in costly neural tissue and flight muscle (Isler and Van Schaik, 2006; McGuire and Ratcliffe, 2011). However, because negative relationships between neural tissue and thorax mass were less pronounced or entirely absent at emergence suggests there may not be inherent tradeoffs. It is possible that less dispersive individuals are making the "best of a bad situation." Nutritionally stressed larvae, for instance those with poor nitrogen assimilation abilities or access to a poor diet, may emerge as smaller adults, less able to fly around extensively. This idea recalls observations from other systems that early life nutritional environment may affect the development of behavioral syndromes (Andersson and Hoglund, 2012). However, it seems unlikely this explanation can account for the present results. We controlled for body size in our analyses; despite this, there were no significant relationships between family body size (a reflection of larval nutrition) and relative thorax mass or wing circularity. This idea also suggests that thorax mass and wing elongation would be more tightly correlated. A third explanation for such negative relationships between movement and cognition may be coexistence of a continuum of strategies. While more dispersive genotypes are likely to find more typical hosts spread over a broad area, less dispersive genotypes should be more likely to utilize locally common, less typical hosts. Overall, the fitness of these two strategies may well end up being identical. Movement-cognition syndromes may represent an instance where behavioral types coexist as different strategies with different routes to comparable fitness (Wolf et al., 2007, 2008).

Conclusions

This work contributes to a growing literature investigating the development of behavioral syndromes. A large number of studies have considered stability of behavioral correlations across ontogeny (Petelle et al., 2013; Boulton et al., 2014; Guenther et al., 2014b), which can give some insight into developmental mechanisms. A replicate genotype or quantitative genetics approach can give more insight into the developmental genetic architecture underlying a suite of correlated behaviors (Stamps and Groothuis, 2010a). The present study adds empirical weight to the idea that genetic variation in behavior such as movement or exploration can affect the development of behavioral syndromes. Such niche construction can result in gene-environment correlations and complex evolutionary feedbacks (Laland et al., 1999; Saltz and Nuzhdin, 2014). Given that most behavior affects how organisms experience the environment, and thus the subsequent development of traits, it's likely that such developmental feedbacks between traits and the environment (**Figure 1**) are a more general phenomenon in personality development, something that has long been recognized by psychologists studying human personality traits (Scarr and McCartney, 1983; Rutter and Silberg, 2002; Caspi et al., 2005).

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Juvenile pathogen exposure affects the presence of personality in adult field crickets

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Despite the ever increasing interest in animal personalities, i.e., among-individual variation in behavior, there are still several gaps in our understanding of how experiences during ontogeny influence the expression of behavior in adulthood. Immune challenges during ontogeny have been proposed to drive feedback loops between investment in immune function and personality type. In this study we investigate the effects of an early immune challenge, in the form of an introduced bacterial pathogen, on the development of personality in field crickets. Our results indicate that early pathogen exposure does not influence life history characteristics, immune response, or mean level of boldness behavior. Instead, early immune challenge affects the presence of personality later in the adult stage. Specifically, immune challenged individuals lack repeatability in some aspects of boldness behavior, indicating that among-individual variation is not present, while non-immune challenged individuals remain repeatable in their boldness behavior. This study joins a slowly growing body of literature indicating that experiences during ontogeny can have large influences on the among-individual differences in behaviors, thus affecting the presence of personality as adults.

Keywords: animal personality, boldness, *Gryllus*, field cricket, immune function

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Introduction

A wealth of literature shows that animal personalities occur commonly across various taxa (Sih et al., 2004; Dingemanse and Réale, 2005; Bell et al., 2009). These personalities consist of among-individual level behavioral differences that are maintained over time and/or contexts, and result in some individuals being consistently more bold, active, or aggressive, compared to other conspecifics within a population (Bell and Stamps, 2004; Dingemanse et al., 2004; Dochtermann and Jenkins, 2007; Kortet and Hedrick, 2007; Pruitt et al., 2008, 2011). Personalities have been shown to both influence and be influenced by a range of ecological processes (Smith and Blumstein, 2008; Cote et al., 2011; Fogarty et al., 2011; Sih et al., 2012; Wolf and Weissing, 2012). Despite the continuously increasing interest in animal personality, there still exist several major gaps in our understanding of the environmental processes which affect the expressed variation in behavior. One of the suggested ecological forces that may generate and maintain behavioral variation is the experienced pathogenic environment (Kortet et al., 2010). Specifically, exposure to pathogens may drive feedback loops that create or diminish individual differences in behavior (i.e., increased immune function resulting from pathogen exposure facilitates increased boldness/aggression/exploration by reducing risk of parasitism/disease). One major challenge in the field is to understand the role of early life experiences, specifically that of parasitic infections, in explaining the development of personality over ontogeny, especially in relation to the simultaneous development of the immune system. In this study we investigate the effects of juvenile exposure to an opportunistic pathogenic bacteria on expression of mean level of adult boldness behavior, variation in individual boldness scores, and immune response using the cricket, *Gryllus integer*.

The role of early life experience in the development of animal personalities has been given relatively little attention outside of a few model systems (Higley et al., 1991; Caspi et al., 2005; Groothuis et al., 2008). Furthermore, the majority of current research on personality focuses predominantly on adult individuals, and does not consider the role of ontogeny in determining personality. Overlooking the importance of juvenile life stages may lead to misinterpretations as to how stable personality is over time. Several conceptual papers address the importance of early life experience, and discuss the associated implications (Stamps and Groothuis, 2010a,b; Groothuis and Trillmich, 2011). Generally, variation in experiences during ontogeny could cause variation in the expression of developmental plasticity, and in turn alter the consistency of behavior across both time and context, as well as correlations between multiple personality traits (Stamps and Groothuis, 2010b). This could be a byproduct of the costs of plasticity varying over ontogeny, such that the costs of plasticity during development are lower than the costs of plasticity during adulthood (Hoverman and Relyea, 2007). Indeed, several studies have shown that adult personality traits are sensitive to environmental conditions during ontogeny (Butler et al., 2012; DiRienzo et al., 2012; Bengston et al., 2014). For example, crickets reared in the presence of conspecific acoustic signals are less aggressive than those reared in the absence of conspecific acoustic signals (DiRienzo et al., 2012). Given these potentially significant contributions of early life experiences to adult behavioral phenotype, it is important to increase our knowledge about the role of experiential factors during ontogeny in determining adult personality.

We do not currently understand how individuals solve predicted tradeoffs between personality and investment in immune function or parasite tolerance (Kortet et al., 2010). Immune function in itself is costly, both to develop and use, and might force organisms to make tradeoffs with other energetically costly traits, including behaviors (e.g., activity, aggression) (Kortet et al., 2010). The freshwater snail, *Lymnea stagnalis*, exhibits a negative correlation between predator-avoidance behavior and immune function, such that individuals who devote more time to avoidance behaviors suffer from decreased immune function (Rigby and Jokela, 2000; Barber and Dingemanse, 2010). Alternatively, immune function-personality interactions may drive positive feedback loops between the two. Intrinsically efficient immunity or high investment in immune function due to stochastic events early in life may allow for increased expression of costly traits such as boldness, activity, and aggression which attract and/or increase exposure to parasites, but further help the individuals to invest more in immunity through the ability to acquire more resources (Kortet et al., 2010). Additionally, such positive feedback loops may promote consistent among-individual differences in behavior, thus driving the development of personality (Kortet et al., 2010; Luttbeg and Sih, 2010). Understanding how personality is related to immune function is important because behaviors can affect fitness by altering the rate at which an individual encounters pathogens in its environment (Kortet et al., 2010). For example, Wilson et al. (1993) found that in the wild pumpkinseed sunfish, *Lepomis gibbosus*, individuals who were caught in traps, and thus deemed more exploratory, carried higher levels of certain pathogens ("blackspot" infection) relative to the population as a whole. Interestingly, the same exploratory fish also harbored lower levels of other pathogens ("white grub" infection), suggesting that behaviors do not always associate with parasite loads as expected, or alternatively are driven by other state-dependent factors not identified in these experiments.

Early life experience and investment in immune system can undoubtedly interact with one another to affect later adult personality, although how they interact is currently poorly understood (Kortet et al., 2010). The development of the immune system could be directly related to expression of personality later in life. For example, in insects immune challenges at an early age have been shown to produce long-lasting immune system up-regulation or immune priming that can persist for a large proportion of an organism's lifespan (Moret and Siva-Jothy, 2003; Sadd and Schmid-Hempel, 2006). Such an investment could directly affect the level of adult behavioral expression. Indeed, in both rodents and mallard ducks, individuals that experienced an immune challenge as juveniles were found to have more exploratory and active personality types as adults relative to those not given an immune challenge (Rico et al., 2010; Butler et al., 2012). It is hypothesized that such an exposure might be a signal of a pathogen-dense environment, and the associated increases in activity levels might promote the search for a less pathogen-dense environment (Kortet et al., 2010). Still, evidence regarding how exposure to pathogens early in life affects the development of behavioral expression is limited, and it is unknown if juvenile pathogen exposure has a consistent positive effect on later personality type.

The goal of our experiments was to probe the interplay of individuals' early life experiences in the form of a bacterial infection and study how the pathogenic exposure affects investment in immune function and subsequent expression of boldness (i.e., the willingness to expose oneself in a novel, potentially risky environment). We focused on the following three questions: (1) How does exposure to pathogens as juveniles affect among-individual level variation in behavior as adults (i.e., personality)? (2) Does exposure to pathogens as juveniles affect the relationship between immune function and personality as adults? (3) How is adult mean level of behavior affected by pathogen exposure in the juvenile stage? We studied these questions by exposing juvenile field crickets to either a pathogenic bacteria or control solution, and then measured boldness behavior repeatedly as adults. After the behavioral measurements, we assessed two measures of immune function: Phenoloxidase activity, which when activated produces secondary components that aid in pathogen defense

(González-Santoyo and Córdoba-Aguilar, 2012), and encapsulation response, which is an immune response to multicellular foreign bodies (Paskewitz and Riehle, 1994; Gillespie et al., 1997). We predicted that (1) juveniles exposed to pathogens would display greater among-individual variation in behavior relative to those not exposed to pathogens as a result of positive feedback loops between immune function and boldness behavior. We predicted that (2) groups exposed to pathogens would invest more in immune function as a result of the exposure (Moret and Siva-Jothy, 2003; Sadd and Schmid-Hempel, 2006), and thus demonstrate greater immune responses as adults. We also predicted that (3) pathogen-exposed juveniles would demonstrate greater boldness in a novel environment relative to those not exposed to pathogens. Finally, we predicted that (4) exposed juveniles would demonstrate a positive correlation between immune function and boldness as adults.

Materials and Methods

Study Animals

This study was conducted from November, 2011 through March, 2012 at the University of Oulu, Finland. We used field cricket (*Gryllus integer*) individuals from a laboratory population (approximately 8–9th generation) that was founded by individuals from a wild population (Davis, California, USA). The populations periodically received additional wild-caught crickets in order to avoid potential inbreeding and increase genetic diversity. Crickets were maintained at the Experimental Unit of the University of Oulu. At the start of the experiment, we sorted 315 nymphs (∼1 week old) from the laboratory population into individual plastic containers (length 128 × width 98 × height 73 mm). They were held at a 12:12 h light:dark cycle at 27°C ± 1°C, and provided *ad libitum* food (reindeer pellets, Rehuraisio OY, poron herkku) and water. Individuals were provided a unique identification number at the outset. The identification numbers were given in sequential order as the crickets were sorted into their individual containers, and the numbers were written on the individual container the cricket was associated with. Nymphal body mass ranged from 0.0004 to 0.0010 g ($n = 10$). Due to the small size, we did not weigh each nymph beyond the first 10 in order to avoid possible damage from handling.

Treatment Groups

A total of three treatment groups were created: (1) juvenile bacterial injection, (2) juvenile control injection, (3) no injection control. Crickets from treatments 1 and 2 were injected with a Hamilton microsyringe between the 3rd and 4th segment of the abdomen. Injections took place on three separate days (November 28th, 30th, and December 4th, 2012) when individuals were on average at the 3rd instar (range 2nd–4th instar). Group one received a 5 μl injection of a 10^{-4} dilution of a 24-h culture of the opportunistic bacterial pathogen *Serratia marcescens*. Pilot data revealed that injections at stronger concentrations (10^{-3}) were lethal (see also Kortet et al., 2012). Group two received a 5 μl injection of sterile nutrient broth. Group three received no injection. A new bacteria culture was created for each day in which crickets were injected. Bacterial growth was evident each day given the change in color in the growth medium. Individual body mass in all treatment groups was taken at this same time point. All crickets were checked for maturation three times a week on Monday, Wednesday, and Friday. Adult body weight and sex was recorded 5 days after maturation. Of the approximately 315 nymph that were initially sorted (105 per treatment), a total of 224 individuals reached maturity (juvenile bacterial injection $n = 73$, juvenile control injection $n = 73$, control $n = 78$). Sixty four individuals died after the treatment application, but before reaching maturity (juvenile bacterial injection $n = 24$, juvenile control injection $n = 22$, control $n = 18$). The remaining individuals either did not mature, or matured after the 5 month period in which this project was conducted.

Boldness Trials

Individual boldness was quantified using a novel-environment test, which is an established method for assessing boldness in field crickets (Hedrick, 2000; Kortet and Hedrick, 2007; Hedrick and Kortet, 2012; Dirienzo et al., 2013), and has previously been shown to be repeatable (Kendal's $W = 0.337$) (Niemelä et al., 2012). Seven days after adult maturation, individual crickets were placed inside a semi-opaque vial within an unfamiliar arena (19 × 19 × 11 cm). The vial was placed in a vertical position to prevent the cricket from coming out. After a 2 min acclimation period the vial was gently placed in the horizontal position allowing the cricket to exit. We recorded the latency for the cricket to become active after being placed in the horizontal position and the latency for the cricket to fully emerge from the vial. Low values of these measures indicate high levels of boldness (i.e., willingness to expose oneself to risk in a novel environment). All trials were conducted in dark conditions with only dim red light. Cricket vision is poor in red light (Briscoe and Chittka, 2001); thus this minimized external and observer influences while mimicking nocturnal conditions. The boldness trial was repeated on the following day using the same procedures. The vial was cleaned with 70% isopropyl alcohol and the sand in the arena was changed after each trial. All boldness trials were conducted between 9:30 and 15:00. Trials were limited to 20 min for logistical reasons.

Encapsulation Response

Encapsulation response was measured by inserting a small nylon monofilament implant into the abdomen. This method elicits a non-specific immune response that results in the encapsulation of the foreign body (e.g., fungi, nematodes, parasitoids) (Rantala and Kortet, 2003; Koskimäki et al., 2004), and is widely used to estimate the strength of insect immune response (Rantala and Kortet, 2003; Simmons et al., 2005; Kortet et al., 2007, 2012). 24 h after the final boldness trial, we placed a 2 mm-long implant between the 2nd and 3rd segments of the abdomen. The implant was made from 0.16 mm fishing line (Stroft GTM, Reinfeld, Germany), which was knotted at one end and roughened with P400 sand paper to increase encapsulation area. Crickets were immobilized with CO_2 before implantation. The cricket immune system was allowed to encapsulate the implant for 24 h before removal. All implants were cleaned with 70% ethanol before inserting into the cricket. For the removal of the implants, crickets were immobilized again with CO_2. After the removal, the implants were frozen at -20°C for later analysis. Analysis consisted of photographing an individual implant from three angles using a light microscope and attached camera. Using the program Image-J (http://rsbweb.nih.gov/ij/), we measured the gray value of the reflected light from the area of the implant that showed melanization. As the strength of encapsulation we used the average of the three gray values subtracted from the gray value of a clear control implant. Thus, larger values indicate a stronger encapsulation/immune response as less light is reflected from the melanized implant (Rantala and Kortet, 2003).

Phenoloxidase Activity

After the implants were removed, we recovered 5μl of hemolymph by removing one of the hind legs and collecting the hemolymph with a micropipette. After removal of the leg the crickets were quickly sacrificed by decapitation while they were still under the influence of CO_2. The hemolymph was then mixed with 40 μl of a phosphate buffered saline (PBS) solution (pH 7.4, Sigma-Aldrich), and frozen at -20°C until analyzed in May 2013 at the University of Eastern Finland. Total phenoloxidase activity was determined photometrically as the linear rate of increase (compared to the PBS control) in optical density during 30 min at 490 nm, after addition of 180 μl L-Dopa (Sigma-Aldrich, China) in concentration of 2.366 g l^{-1} in 1/15 M KH_2PO_4 (9.073 g l^{-1}): 1/15 M $Na_2HPO_4 \times 2\ H_2O$ (11.87 g l^{-1}) 83:17 buffer (pH 6.2). Samples (20 μl) were analyzed in duplicate. Equal reaction time among samples was ensured by the automated L-Dopa injection in the used plate reader (FLUOstar Omega, BMG Labtech, Germany).

Statistical Analysis

The statistical software package R version 3.1.1 (R Core Team, 2015) was used for all the analyses. The presence of personality (among-individual repeatability) in each of the treatment groups was measured by calculating the repeatability between the first and second measure of the log-transformed latency to become active and binomial measure of if the individual emerged from the vial or not. Repeatability scores of each treatment group were calculated separately using the rptR package, which allows for the calculation of repeatability values (intraclass correlation coefficient) for both Gaussian and binomial data (Nakagawa and Schielzeth, 2010). This package calculates repeatability values for binomial data as the ratio between among-individual variance and among-individual variance plus the residual variance, i.e., total phenotypic variance (fixed to (pi^2)/3 for binomial data). Given that the residual variance in our model is fixed, any changes in repeatability are attributed to differences in among-individual variance (Nakagawa and Schielzeth, 2010).

We assessed the relationship between life history characteristics and covariates using general linear models. The three life history characteristics assessed were adult body weight, the number of days to reach maturity, and growth rate. Growth rate was measured simply as the adult body mass divided by the number of days until maturation given the nymphal mass (0.0004–0.001 g) at the start of the treatment was negligible relative to the range adult mass (0.405–0.858 g). Factors included treatment group and sex. Four models were fitted for each response variable: treatment group as a main effect, sex as a main effect, both treatment and sex as a main effect, and an interaction between treatment and sex. All models, as well as a null model, were fitted using the BBMLE package (Bolker and R Development Core Team, 2014). After fitting they were compared using Akaike information criteria (AIC) (Burnham and Anderson, 2002). If the ΔAICc between two models is greater than two, the model with the lower AIC is considered to fit statistically better (Richards, 2005). Akaike weights, ω_i, were also calculated. These weights estimate the probability of a model being the best fit for the data relative to the other models in the set.

In order to assess if boldness was affected by bacterial treatment as well as by the covariates, we used a combination of generalized linear mixed models. Latency to become active measurements were log transformed to achieve normality (Shapiro-Wilk $W = 0.8026$, $p < 0.001$). We created a series of generalized linear mixed models with normal error distributions. Individual identification number was included as a random effect, and sex, treatment group, development rate, adult weight, and juvenile weight as fixed effects. All models included individual ID as a random effect, and then either one of the factors/covariates alone as a fixed effect. Model with biologically relevant interactions between fixed effects were also created (e.g., juvenile weight $*$ sex), as well as models containing the same pair of fixed effects without the interaction (e.g., juvenile weight + sex). Potentially collinear covariates (e.g., juvenile weight, adult weight, development rate) were never included in the same model. See **Table 1** for a full list of model structures. The cricket latency to emerge values were highly truncated against the 20 min limit of our trial, as a large number of the crickets did not emerge from the vial (percent emerged: juvenile bacterial injection trial one = 60%, trial 2 = 49%, juvenile control injection trial one = 60%, trial 2 = 55%, control trial one = 60%, trial 2 = 56%). Thus, we converted the measure to a binomial measure and used a generalized linear mixed model with binomial error distribution and a logit link function to assess the effect of treatment and other factors on the probability of the cricket exiting the vial (Hammond-Tooke et al., 2012). The model covariate structures were the same as previously used. All models, as well as a null model, were fitted using the lme4 package (Bates et al., 2014). Model R^2 values were calculated following the methods described in Nakagawa and Schielzeth (2013). The methods allows for the calculation of the marginal R^2 value of mixed models, which is the proportion of variance described solely by the fixed effects within the model, as well as the conditional R^2, which is the proportion of variance described by both the fixed and random effects within model (Nakagawa and Schielzeth, 2013).

To understand if immune response is related to personality type we used separate general linear models, because we did not have the measures of immunity for all the individuals (hemolymph samples obtained: juvenile bacterial injection $n = 50$, juvenile control injection $n = 53$, control $n = 50$; implants recovered: juvenile bacterial injection $n = 40$, juvenile control injection $n = 48$, control $n = 44$). The models consisted of phenoloxidase activity or encapsulation response as response variable. Explanatory factors included sex, treatment group, development rate, adult weight, and juvenile weight as fixed effects. Models were created with these covariates as fixed effects only or with interactions between them. Additionally, we created models that included the average of the untransformed boldness scores across the two treatments (average latency to become active and latency to emerge) as variables. We also created models that included the absolute value of the difference in untransformed boldness scores between the two trials as covariates. The averages and absolute value of the boldness scores will allow us to assess how mean level of personality and change in boldness across the two trials are related to immune function, respectively. All models, as well as a null model, were fitted using the lme4 package.

TABLE 1 | List of model structures used to analyze relationship between boldness, treatment, and life history characteristics.

Model Structure
Null
Treatment
Juvenile weight
Adult weight
Growth rate
Sex
Treatment + juvenile weight
Treatment + adult weight
Treatment + growth rate
Treatment + sex
Sex + juvenile weight
Sex + adult weight
Sex + growth rate
Treatment + juvenile weight + treatment*juvenile weight
Treatment + adult weight + treatment*adult weight
Treatment + growth rate + treatment*growth rate
Treatment + sex + treatment*sex
Sex + juvenile weight + sex*juvenile weight
Sex + adult weight + sex*adult weight
Sex + growth rate + sex*growth rate

Response variables consisted of either the latency to become active or the probability of emerging from the vial.

Results

Repeatability of Boldness

Latency to become active within the vial was repeatable in all three treatment groups (**Table 2**). Treatment had a large effect on the repeatability of emergence from the vial (**Table 2**). 45% of juveniles who received a bacterial injection changed their behavior across both trials (e.g., emerge on the first trial, stayed in the second, or vice-versa), compared to 40% of control injections and 29% of non-injected controls. Both control groups were repeatable in terms of their tendency to exit vs. remain in the vial, while juveniles who received a bacterial injection were not repeatable in this behavior. Thus, the among-individual variation decreased as a result of juvenile bacterial injection.

Life History

Bacterial infection did not affect life history characteristics. The best fit models for growth rate, days until maturation, and adult body weight included only the main effect of sex (Δ AIC to next model >3 in all comparisons). Thus, only the top models are presented for the three life history characteristics measured (**Tables 3**). The general trend indicates that males had larger adult body mass than females (female $= 0.579$ g, $SE = 0.007$, male $= 0.624$ g, $SE = 0.008$), faster growth rate (female $= 0.010\ \text{g day}^{-1}$, $SE = 0.000$, male $= 0.012$ g/day, $SE = 0.000$), and took less time to reach maturity (female $= 59.257$ days, $SE = 1.320$, male $= 55.35$ days, $SE = 1.075$). It is important to note the small R^2 values suggest that these best fit models still only account for a small proportion of the variance.

Treatment, Sex- and Size-Dependency of Boldness

The latency to become active within the vial was best explained by two models. The top model contained sex and the weight at the time of injection (**Tables 4**, **6**), and carried a large proportion of the weight ($\omega_i = 0.541$). Parameter estimates indicate that males (1.685 min, $SE = 0.222$) had shorter latencies to become active than females (2.501 min, $SE = 0.338$). The next best fit model had a delta Δ AIC of 1.2 from the top model can carried a moderate proportion of the weight ($\omega_i = 0.296$), indicating it was also a good fit for the data. The model contained an interaction between sex and juvenile weight, but only the parameter estimate for sex was reliably below zero (**Table 6**), again indicating that male crickets had shorter latencies to become active relative to females. The remaining models all had a ΔAIC greater than two

TABLE 2 | Repeatability values for the (log) latency to become active within the vial and the likelihood of fully emerging from the vial.

	Latency to become active			Emergence from vial		
Treatment	***R***	***SE***	***P***	***R***	***SE***	***P***
Control ($n = 78$)	0.247	0.106	0.017	0.477	0.120	0.002
Juvenile bacterial injection ($n = 73$)	0.246	0.111	0.011	0.133	0.108	0.204
Juvenile control injection ($n = 73$)	0.379	0.102	0.001	0.295	0.136	0.022

Values were calculated individually for each treatment group.

TABLE 3 | Top general linear models predicting growth rate, weight at maturation (adult weight), and the number of days until maturation.

	Growth rate				Adult weight				Days to maturation		
Parameter	**ß**	***SE***	***p***	**Parameter**	**ß**	***SE***	***p***	**Parameter**	**ß**	***SE***	***p***
Intercept	−0.234	0.097	0.013	Intercept	0.579	0.008	0.001	Intercept	59.257	1.248	<0.001
Sex	0.442	0.131	0.001	Sex	0.046	0.011	<0.001	Sex	−3.900	1.684	0.0215
$F_{(1,\ 222)} = 11.35, p < 0.001$, $\omega_i = 0.804, R^2 = 0.044$				$F_{(1,\ 222)} = 17.49, p < 0.001$, $\omega_i = 0.700, R^2 = 0.069$				$F_{(1,\ 222)} = 5.361, p = 0.022$, $\omega_i = 0.707, R^2 = 0.019$			

The effect of sex is expressed in terms of males, relative to females.

TABLE 4 | Top five models predicting the latency to become active.

Model structure	**ΔAIC**	***df***	**AIC weight**
Sex + Juvenile weight	0	5	0.541
Sex + juvenile weight + sex*juvenile weight	1.2	6	0.296
Juvenile weight	2.5	4	0.157
Treatment + Juvenile weight	9.3	6	0.157
Treatment + juvenile weight + treatment*juvenile weight	15.8	8	<0.001

Models not listed had an AIC weight <0.001.

TABLE 5 | Top five models predicting the probability of emerging from the vial.

Model structure	**ΔAIC**	**df**	**AIC weight**
Juvenile weight	0	3	0.524
Sex + Juvenile weight	1.7	4	0.220
Treatment + Juvenile weight	3.4	5	0.096
Sex + juvenile weight + sex*juvenile weight	3.6	5	0.086
Treatment + juvenile weight + treatment*juvenile weight	4.0	7	0.073

Models not listed had an AIC weight <0.001.

TABLE 6 | Top generalized linear mixed models predicting the (log) latency to become active within the vial and the likelihood of fully emerging from the vial.

	Latency to become active			Emergence from vial		
Parameter	**ß**	***SE***	***p***	**ß**	***SE***	***p***
Intercept	0.090	0.113	0.263	0.3219	0.129	0.012
Juvenile weight	−0.071	0.076	0.350	−0.349	0.130	0.007
Sex	−0.388	0.153	0.011	–	–	–
	Marginal $R^2 = 0.024$ Conditional $R^2 = 0.285$			Marginal $R^2 = 0.028$ Conditional $R^2 = 0.246$		
Intercept	0.090	0.113	0.263	0.250	0.189	0.186
Juvenile weight	−0.239	0.128	0.062	−0.362	0.133	0.007
Sex	−0.369	0.153	0.016	0.133	0.259	0.608
Juvenile weight * sex	0.259	0.159	0.104	–	–	–
	Marginal $R^2 = 0.032$ Conditional $R^2 = 0.287$			Marginal $R^2 = 0.028$ Conditional $R^2 = 0.246$		

The effect of sex is expressed in terms of males, relative to females. All covariates were centered on their mean value.

and carried a decreasing proportion of the weight, and thus are not presented further.

The probability to emerge from the vial was best explained by two models. The top model contained only a main effect of weight at the time of injection (**Tables 5**, **6**), and carried a large proportion of the weight ($\omega_i = 0.524$). The negative main effect of weight at the time of injection suggests that crickets who were large at the time of injection were less likely to leave the vial during the 20 min trial. To illustrate this effect of body size, one can take the exponent of the parameter estimate multiplied by a juvenile weight to provide the odds an individual will emerge from the vial. In this case, a juvenile who weighed 0.3 g at the time of injection will have approximately 22% chance that they will emerge, while a juvenile who weighed 0.1 g at the time of injection will have approximately a 60% chance of emerging. The next best fit model carried a moderate proportion of the weight ($\omega_i = 0.220$), and contained main effects of sex and juvenile weight. Only the parameter estimate for juvenile weight was reliable below zero, and had nearly the same magnitude as the parameter estimate in the top model. The remaining models all had a Δ AIC greater than two from the top model and carried a decreasing proportion of the weight, and thus are not presented further.

Immune Function-Personality Interactions

Model comparison indicated that adult phenoloxidase activity was not influenced by treatment (linear rate of increase in optical density relative to PBS control: control = 0.122, *SE* = 0.053, juvenile control injection = 0.116, *SE* = 0.044, juvenile bacterial injection = 0.145, *SE* = 0.079), but was influenced by the average latency to become active of the individual (**Table 7**). The top model carried 41% of the weight, and had ΔAIC greater than two from the null model (ΔAIC = 3.1). The parameter estimate indicates a negative relationship between the average level of boldness and phenoloxidase activity such that individuals who become active quickly had higher phenoloxidase activity relative to those who take longer to become active. Encapsulation response did not vary by treatment (difference in gray value from control implant: control = 70.826, *SE* = 3.874, juvenile control injection = 73.670, *SE* = 3.461, juvenile bacterial injection = 70.826, *SE* = 3.021), and instead was best explained by a single

TABLE 7 | Top generalized linear models predicting phenoloxidase activity and encapsulation rate.

	Phenoloxidase activity				Encapsulation rate		
Parameter	**ß**	***SE***	***p***	**Parameter**	**ß**	***SE***	***p***
Intercept	0.129	0.034	0.001	Intercept	76.118	3.135	0.001
Average latency to become active	−0.111	0.049	0.025	Sex	−9.397	4.128	0.0245
–	–	–	–	Juvenile weight	−3.025	3.300	0.361
–	–	–	–	Juvenile weight*sex	2.940	4.316	0.500
$F_{(3,\ 152)} = 5.131$, $p < 0.026$, $\omega_i = 0.402$, $R^2 = 0.026$				$F_{(3,\ 126)} = 2.663$, $p < 0.053$, $\omega_i = 0.673$, $R^2 = 0.059$			

The effect of sex is expressed in terms of males, relative to females. All covariates were centered on their mean value.

model containing an interaction between weight at injection and sex. This model carried 67% of the weight and was greater than 2 AIC points from the nearest model. The model contained a significant sex effect indicating that females had lower encapsulation rates relative to males (**Table 7**).

Discussion

Our results indicate, against our predictions, that early exposure to bacterial pathogens does not directly influence life history characteristics or the mean-level expression of boldness. Instead, exposure to pathogens affected the expression of behavioral variance at the individual level: the repeatability of boldness behavior, in terms of willingness to emerge from the vial as adults, was affected by exposure to pathogen in juvenile stage. Control treatments demonstrated repeatability of boldness as adults, while those who received bacterial injection as juveniles demonstrated a lack of repeatability in their tendency to emerge from the vial. This was counter to our prediction that bacterial infection would increase among-individual level variation in behavior. Together, these results suggest that early life experience may not influence the mean expression of behaviors, as we hypothesized, but instead might decrease the repeatability of behaviors. Finally, and counter to our predictions, treatment had no influence on immune function itself or the boldness-immune function relationship. However, we observed a positive relationship between boldness and phenoloxidase activity in hemolymph that was independent of infection treatment. Yet, we found no such relationship between encapsulation response and boldness.

Experience during development has been shown to influence a range of personality traits in a variety of taxa (DiRienzo et al., 2012; Bengston et al., 2014; Härkönen et al., 2014). Yet, in this study, we found that pathogen exposure during early juvenile stages did not directly influence the level of boldness in the population, but instead impacted the repeatability in one aspect of boldness behavior (emergence from the vial), but not the other aspect of boldness behavior (latency to become active). This result is similar to a recent study in the Eurasian minnows, *Phoxinus phoxinus*, that were experimentally infected with the brain-encysted trematode parasite, *Diplostomum phoxi* (Kekäläinen et al., 2014). Experimentally infected minnows were not repeatable in terms of their exploration behavior, in contrast to the significantly repeatable control groups. Yet, infection had the opposite effect on other behaviors, as infected individuals were repeatable in their activity levels, while control individuals were not repeatable in their activity levels (Kekäläinen et al., 2014). Granted, the brain infecting parasite used in the Kekäläinen et al. (2014) study is dramatically different from the bacterial pathogen used in this study. Yet, the similar trend of a lack of repeatability in response to pathogens is interesting, but the adaptive value, if any, of why individuals will or will not develop consistent variation in behavior in some conditions is unknown. One possible explanation might be that the early pathogen exposure predicts some level of future environmental variability where greater behavioral plasticity is favored. As seen in this study, the decrease in among-individual variance when exposed to pathogens suggest that extreme personality types might be less favored in a pathogen rich environment. Alternatively, increased within-individual variation in behaviors might be a behaviorally mediated risk-spreading strategy against potential future pathogen rich environment instead of increased immunity. Interestingly, the repeatability of the latency to become active was not affected by bacterial treatment. This measure might become uncoupled from the probability of emergence as activity within a safe environment is unlikely to increase encounter rates with pathogens outside the refuge. However, this is highly speculative and a large amount of additional research is needed to understand the fitness consequences associated with highly variable behavior in pathogen rich environments.

Regardless of the adaptive nature, if there is one, this result provides a new insight regarding the sensitivity of personality with respect to environmental conditions during ontogeny. Here, a single event several weeks before adulthood resulted in a difference in the behavioral repeatability, but did not affect the population mean level boldness behavior. This study, as well as other studies investigating the role of experience in personality development, highlight the importance of accounting for experience during ontogeny when investigating personality. For example, if individuals confront repeatable variation in their environmental conditions, which is inevitable in natural conditions, it may generate among-individual variation in behaviors. This in turn would drive environmentally induced personality (Stamps and Groothuis, 2010a). Furthermore, seasonal and yearly variation in environmental conditions will subsequently affect not only the mean personality type in population, but also the level of behavioral consistency. Thus, the impacts of personality on ecological and evolutionary processes will be affected by any associated developmental effects on personality (Wolf and Weissing, 2012).

Contrary to predictions, we did not discover a relationship between personality and immune function within treatments. Yet, we did discover a negative relationship between the latency to become active and phenoloxidase activity independent of treatment. Overall, individuals who became active more quickly also had higher phenoloxidase activity. This result is in line with previous findings indicating that lytic activity, another aspect of invertebrate immune function, demonstrates a negative relationship with freezing time (Kortet et al., 2007). Still this same study did not show a relationship between lytic activity and the latency to become active (as measured in this study). Also, it is important to note that the R^2 of the best fit model ($R^2 = 0.033$) was small, suggesting that boldness itself explains a rather small proportion of the variation in phenoloxidase activity. Current theories suggest that the immune function and personality may become correlated through positive feedback loops where early investment in immune function facilities increases in costly personality traits such as boldness, aggression, and activity (Kortet et al., 2010). While intuitive, empirical studies demonstrating such positive feedback loops between immune function and personality are rare (but see Butler et al., 2012). Alternative theories posit that individuals must make tradeoffs between costly traits, and are backed up by several studies demonstrating a negative relationship between personality traits and immune function (Wilson et al., 1993; Rigby and Jokela, 2000; Barber and Dingemanse, 2010).

The differences in the repeatabilities between the treatment groups suggest that our immune challenge did affect aspects of personality development, likely by increasing adult within-individual variance, but not immune function. The lack of effect of bacterial treatment on immune function could be for several reasons. In this experiment, all individuals were given *ad libitum* food and water. The lack of resource limitation may have prevented individuals from having to make tradeoffs between personality and immune traits (Van Noordwijk and De Jong, 1986; Stearns, 1989). Additionally, the bacterial treatment group received only a single injection. It is possible that it requires more frequent pathogen exposure, or a greater magnitude of exposure, to trigger changes in immune investment compared to changes in behavioral variation. Finally, the pathogen exposure may have affected the mean trait value of other aspects of personality that are more energetically costly, such as aggressive behavior or activity levels which were not measured in this study. Nonetheless, our results provide evidence that immune function and personality are related, yet, the relationship between the two is not affected by the developmental experiences used in this study.

In conclusion, we demonstrate that a single early exposure to a bacterial pathogen is sufficient to alter the expression of boldness personality as adults. Our results underline the sensitivity of early developmental stages for ecological conditions in the context of personality development. Moreover, treatment did not trigger alternative mean level immune investment or an immune-personality tradeoff, potentially due to housing conditions during the experiment (e.g., ad lib. food), or simply because immune function does not covary with this particular aspect of personality. Thus, we suggest additional research is needed to better understand the immune-personality relationship. Future studies will employ more ecologically relevant conditions (e.g., food limitation) and behaviors (e.g., activity) in combination with varied frequencies of pathogen exposure. Nonetheless, our results provide new insight into the important role of early ecological experience in the ontogeny of personality, and highlight both the practical and theoretical necessity of understanding this complex relationship.

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Personality differences in two minnow populations that differ in their parasitism and predation risk

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Animals are often individually consistent in their behavior, not only over time, but also across different functional contexts. Recent research has focused on phenotypic and evolutionary mechanisms explaining such personality differences through selection. Parasitism and predation induce important mortality and fitness costs, and are thus main candidates to create and maintain personality differences in the wild. Here, we present data on the behavioral consistency of the Eurasian minnow (*Phoxinus phoxinus*) from two populations that live in different tributaries of the same river, but whose ecological environment differs fundamentally with regard to predation and parasitism. We experimentally demonstrate that individual minnow in both study populations are consistent in their boldness and activity. However, the two study populations differ notably: in the high predation and parasitism risk population fish show higher mean boldness, but tend to be less active than fish in low predation and parasitism risk population. Parasite (*Diplostomum phoxini*) load was negatively, but not statistically significantly, associated with fish activity level. Our study suggests that parasitism and predation are likely important agents in the ecology and evolution of animal personalities.

Keywords: activity, boldness, exploration, parasitism, predation, personality, *Diplostomum phoxini*

INTRODUCTION

Over the last decade there has been considerable interest in animal personalities (e.g., Bell, 2007; Sih et al., 2012; Carere and Maestripieri, 2013; Kortet et al., 2014). Personalities, also known as "temperaments" or "coping styles", are defined as behaviors that vary predictably among individuals, and are consistent across time and/or contexts within individuals (e.g., Réale et al., 2007; Stamps and Groothuis, 2010). Consistent personalities have been puzzling behavioral ecologists, because they limit behavioral flexibility and occasionally appear to produce seemingly maladaptive behaviors (Dall et al., 2004; Sih et al., 2004). Several mechanisms have been proposed to explain how personality variation is maintained in animal populations over evolutionary time. These mechanisms include, for example, the asset protection principle, i.e., behaviorally mediated trade-offs between current vs. future reproduction (Wolf et al., 2007), related growth-mortality trade-offs (Stamps, 2007; Biro and Stamps, 2008), positive feedback loops and state-dependent behavior (McElreath et al., 2007; Luttbeg and Sih, 2010) and variation in costly cognition (Niemelä et al., 2013). Importantly, these mechanisms are not necessarily mutually exclusive. Rather, they are based on additive and interacting environmental factors such as predation and parasitism that affect the costs and benefits of certain behaviors in various ways.

At the moment, the existence and importance of animal personalities are generally accepted and documented for several taxa, while the relative importance of different ecological factors explaining their evolution and expression are under debate (e.g., Barber and Dingemanse, 2010; Kortet et al., 2010; Niemelä et al., 2012, 2013; Sih et al., 2012). Traditionally, main factors affecting the evolution and ecology of animal personalities have included resource competition (Dingemanse et al., 2004; Cote et al., 2008) and predation pressure (e.g., Bell and Sih, 2007; Dingemanse et al., 2007). Recently, parasitism has also emerged as a potential key driver of the ecology and evolution of animal personalities (Barber and Dingemanse, 2010; Coats et al., 2010; Kortet et al., 2010; Koprivnikar et al., 2012; Poulin, 2013). Parasitism and predation may amplify the effects of each other both additively and in interaction, which emphasizes the importance of understanding their integrative role in inducing selection (Kortet et al., 2010). Unfortunately, most empirical studies so far have ignored the importance of parasitism in the animal personality context.

Within-population and between-population variation in personality traits has been described in a number of taxa including squid (Sinn et al., 2010), spiders (e.g., Hedrick and Riechert, 1989), field crickets (Kortet and Hedrick, 2007; Niemelä et al., 2012), fish (e.g., Bell and Sih, 2007; Dingemanse et al., 2007), crayfish (Vainikka et al., 2011), birds (Atwell et al., 2012) and primates (Weiss and Adams, 2013). In general, it can be predicted that the stronger the environmental selection by parasitism or predation, the more consistently an individual should follow the behavioral trajectory set by its initial and current assets, and the more likely it is that animal personalities will emerge in a population (Kortet et al., 2010). As indirect support for this idea, behavioral syndromes and consistent behavior has been detected especially in high-risk environments. In fishes, both observational and experimental evidence suggests that individuals from high-predation risk environments may behave more predictably than individuals from predator-free populations (Bell and Sih, 2007; Dingemanse et al., 2007; Adriaenssens and Johnsson, 2013). However, according to the best of our knowledge, earlier reports so far have not included risk by parasitism in the interpretation of the between-population differences in personality studies (Barber and Dingemanse, 2010; Kortet et al., 2010). High-parasitism risk environment, often coupled with high-predation risk, may produce interesting patterns in personality traits like boldness and associated phenotypic traits (e.g., Kortet et al., 2007). In general, the theory of parasite-mediated personality evolution suggests that intensified selection by predators and parasites should increase an individual's behavioral consistency over both ecological and evolutionary time scales, by selecting out individuals that do not follow their optimal behavioral trajectories (Kortet et al., 2010).

The aim of the present study was to investigate behavioral consistency in two Eurasian minnow (Cyprinidae: *Phoxinus phoxinus*) populations that differ fundamentally in their predation and parasitism risks, but originate from the same water-course. One of the populations (Kuusoja River) harbors both parasites and predatory fish while in the other population parasites and piscivorous fish are both non-existent (Kolvananuuro Brook). We experimentally assessed boldness- and activity-indicating behaviors and their repeatability in wild-collected minnows by performing three behavioral trials in standardized laboratory conditions: two trials without a predator cue and one trial with predator odor. We predicted that in the high predation and parasitism risk population, fish would show higher boldness and higher behavioral consistency, because they would need to compensate for the energetics costs of parasitism and try to reduce predation risk by growing fast (Kortet et al., 2010). This result would be also in line with the possible parasite-induced behavioral manipulation. We also tested if parasite load would correlate with an individual's personality (see Kekäläinen et al., 2014a).

MATERIAL AND METHODS

NATURAL HISTORY OF THE STUDY SPECIES

The European minnow (or common minnow) is a small cyprinid fish, ubiquitously inhabiting freshwaters in Eurasia, including Britain, Spain, Scandinavia and Siberia. In Finland, the minnow inhabits predominantly cool (summer temperature 12–20°C), brooks streams and well-oxygenated lakes and ponds. It exists also in the brackish water coastal areas of the Baltic Sea. The species adapts well to laboratory conditions and has been used as a model in behavioral studies (e.g., Lai et al., 2013; Kekäläinen et al., 2014a). Many populations of the European minnow harbor harmful trematodean and nematodean parasites that likely impose strong indirect and direct mortality on their hosts. In our previous experimental work, we have demonstrated that minnows infected by the trematodean parasite *Diplostomum phoxini* show higher repeatability in boldness and activity, and reduced repeatability in exploration compared to non-infected fish (Kekäläinen et al., 2014a).

STUDY ANIMALS AND CHARACTERISTICS OF THE SOURCE POPULATIONS

A haphazard minnow sample was collected by dip nets from the two study populations in Eastern Finland in June 28 and June 30 2011. In total of 150 fish were sampled from Kolvananuuro Brook (62° 51N, 29° 59E) and Kuusoja River (62° 48N, 30° 1E). Kolvananuuro Brook is a headwater tributary of Kuusoja River that discharges to Pielisjoki River, in the Vuoksi River watershed. Based on our earlier fish samples and their examination for parasites, Kolvananuuro Brook minnow do not host *D. phoxini*, likely because the lack of a suitable intermediate host in the system. In contrast, in Kuusoja River the prevalence of *D. phoxini* in minnows is close to 100%, which means that virtually all of the fish larger than 30 mm have been infected with this parasite. The nematodean parasite *Philometra ovata* has never been found in Kolvananuuro Brook minnows, while in Kuusoja River the prevalence of body cavity dwelling *P. ovata* in minnows varies from 4.00 to 9.19 percent (Lai et al., 2012). Predation risk by piscivorous fishes in Kolvananuuro Brook is likely non-existent, since we have never encountered any predatory fish in the area (despite numerous fish sampling using traps and landing nets). Potential migration of minnows to areas with predators are not known, but appears unlikely given the abundant physical migration obstacles in the brook. In contrast, based on electrofishing conducted annually during university courses, predatory fish including burbot (*Lota lota*), perch (*Perca fluviatilis*) and pike (*Esox lucius*) are common in Kuusoja River, that also supports small populations of grayling (*Thymallus thymallus*) and resident brown trout (*Salmo trutta*) in addition to the common cyprinids roach (*Rutilus rutilius*) and dace (*Leuciscus leuciscus*).

Study fish were transported to the laboratory at the Department of Biology (Joensuu campus) of the University of Eastern Finland, where they were housed in two 45 l tanks in 15°C water temperature under a simulated natural photoperiod. After 2 days of acclimatization the water temperature was increased to 17°C. Fish were fed daily with commercial fish food (Biomar®; Aqualife, Aarhus, Denmark). After 4 days, a subsample of 50 fish of about the same size from each population was taken. All of the fish were placed individually in one liter plastic containers, in which they were held during the whole experimental period. To ensure adequate oxygen exchange, two walls of the container had been replaced with plastic nets (mesh size: 1 mm). The plastic containers were distributed into two 600 liter tanks (two replicates/group) and were housed in 17°C water temperature under a simulated natural photoperiod. Fish were fed daily *ad libitum* with commercial fish food (Biomar®; Aqualife, Aarhus, Denmark) through a small hole in the cap of the individual container. During the experimental period one fish died, so the definitive sample sizes were 49 fish from Kuusoja River and 50 fish from Kolvananuuro Brook.

BEHAVIORAL EXPERIMENTS

We carried out three sequential behavioral aquarium-scale trials for all individuals: (1) 2 weeks after the fish had been sampled from the field, (2) 4 days after the first behavioral trial and (3) 8 days after the first behavioral trial. The third trial included the predator odor effect. All experiments were always conducted on

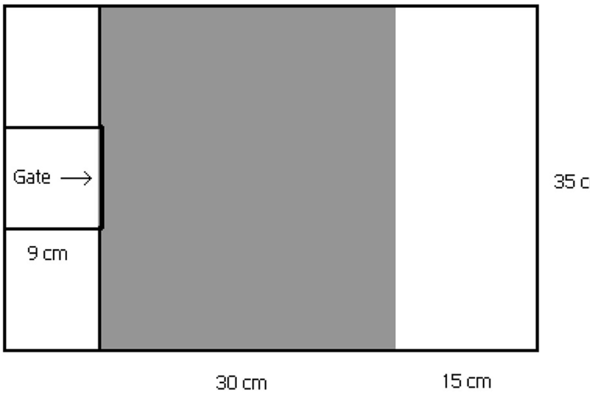

FIGURE 1 | Test arena for the behavioral experiments. Test arena consist three parts: 1. small acclimation area (in the left) with roll-up gate for acclimation period, 2. gray-colored section (in the middle) and 3. white-colored section (in the right). White-colored section is expected to represent more risky environment for the minnows than gray-colored section.

the same day for each group. The predator odor for the third trial came from two live pike (weights 278 and 453 g), that were sampled and brought to the laboratory from the nearby Lake Salmijärvi. The pike were housed in 100 l flow-through tank (water flow 3 l/min), from which the predator odor water was obtained.

In the behavioral trials, individual boldness and activity were studied in a three-part plastic arena (Kekäläinen et al., 2014a) (length 54 × width 35 × height 20 cm, water volume 20 l, **Figure 1**). Each individual was first placed on the small area (i.e., emergence box) at the other end of the arena, where they were allowed to acclimate to experimental conditions for 2 min. After the acclimation period the gate between the acclimation area and the arena was carefully lifted using a thin fishing line so that fish were not able to see the lifter. Then the fish were allowed to swim freely in the arena for 10 min. The actual arena consisted of two parts which differed in floor color (gray and white). Since the gray-colored area more closely resembles the natural camouflage of the minnows, the white area was assumed to represent a more risky environment for the minnows (e.g., Maximino et al., 2010; Kekäläinen et al., 2014a). In the third trial the minnows were exposed to the pike odor by adding one liter of water from the pike rearing tank to the plastic arena. The pike odor water was added to the main part of arena at the end of the acclimation period. Timing of the pike odor addition was chosen to prevent odor from reaching the acclimation box before opening the gate.

In each behavioral trial, we observed fish behavior and recorded nine behavioral variables: total time spent active (1), outside the shelter (2) and in the white-bottomed area (3). In addition we determined the time fish took before showing first activity (4), swimming outside the shelter (5) and visiting the white area (6). Finally, we also counted the number of occasions fish re-activated their swimming behavior after being passive (7), swam from the shelter to the arena (8) and visited in the white-bottomed area (9). Immediately after the experiment, the focal fish were returned to their individual containers. Similar individual aquarium-scale experiments have been demonstrated to predict individual behavior in ecologically relevant contexts in other fish species (Kekäläinen et al., 2014b).

Water temperature in experimental trials was 17°C and water was changed after every trial. To avoid potential disturbance caused by the observer, behavioral observations took place via HD web camera (Logitech, Webcam Pro 9000, Newark, CA, USA), attached above the experimental arena. After the study period all fish were killed with an overdose of tricaine methanesulfonate (MS-222, Sigma®; Sigma Chemical Co., St. Louis, MO, USA) and their length, fresh body mass and sex were determined and the numbers of parasites, including *D. phoxini* brain parasites and *P. ovata* nematodes in the body cavity, were counted. The mean size (± SD) of the fish was similar to that in the populations (50.70 ± 6.45 mm and 1.11 ± 0.40 g: Kolvananuuro Brook 50.43 ± 6.97 mm and 1.06 ± 0.45 g: Kuusoja River). Condition factor K was calculated for each fish as: $K = a\frac{m}{l^b}$, where m is the body mass in grams, l the total body length in cm, the estimated value of b was 2.85601, and the multiplier a was 100 cm^b g^{-1}. Sex was determined by visual inspection. All experiments were performed according to the license of the Finnish Animal Experiment Board (ESLH-2008-03722/Ym-23).

STATISTICAL ANALYSES

To reduce the number of correlated variables, we conducted principal component analysis on the abovementioned nine behavioral variables (**Table 1**). All the variables were Ln-transformed prior to PCA. PCA resulted two principal components (eigenvalue > 1), which explained 72.3% of the variation in fish behavior. When PCA was conducted separately on data from each trial and population, the un-rotated component matrix indicated only marginal differences between the PCAs justifying the use of just one PCA on all data. The first component (PC1) was strongly associated with variables describing fish boldness, whereas the second component (PC2) explained variation in fish activity level. Repeatability of the two principal components was studied using the intraclass correlation coefficient (ICC, Lessells and Boag, 1987). 95% confidence intervals of ICC were used to infer between population differences in repeatability.

Behavioral differences (PC1 and PC2, dependent variables) between populations, sexes and measurement periods were modeled using linear mixed effect models using the parsimony principle in model selection (Johnson and Omland, 2004). The models first included fully factorial terms of population, measurement and sex, and covariates (condition factor and fish length). The models were simplified by removing non-significant terms. AIC (Akaike Information Criteria) was used to choose between the two last model candidates with and without the last (lowest p-value) non-significant term. Paired comparison between sexes (male, female and immature) and measurement periods were conducted using equivalent within factor analyses with Bonferroni *post-hoc* tests.

In the Kuusoja River population, the association between *Diplostomum phoxini* brain parasite number and PC-scores (fish behavior) was tested using a Spearman correlation analysis. A non-parametric test was selected since the distribution of parasite loads could not be completely normalized. A T-test was used

Table 1 | Results of the principal component analysis (with Varimax rotation) on the studied behavioral variables.

Nos	Variable	PC1 (Boldness-Score)	PC2 (Activity-Score)
1	Total time active	0.241	**0.788**
2	Time active outside shelter	**0.862**	0.168
3	Time active in the white area	**0.918**	0.147
4	First time active	0.056	**−0.739**
5	First time outside shelter	**−0.860**	−0.110
6	First time in the white area	**−0.872**	−0.087
7	Number of re-activations	−0.436	−0.463
8	Number of visits outside shelter	**0.898**	0.209
9	Number of visit in the white area	**0.923**	0.139
	Eigenvalue	5.322	1.186
	% of variation	59.1	13.2
	Total variance explained (%)	59.1	72.3

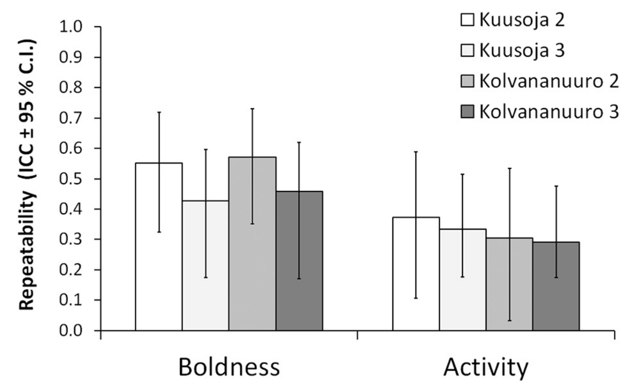

FIGURE 2 | Repeatabilities for boldness and activity in the two study populations (Kuusoja River and Kolvananuuro Brook) over two and all the three trials.

Table 2 | Significance of fixed factors in explaining variance in boldness score according to linear mixed effect model.

Source	*df*:s	*F*	*P*
Intercept	1, 92.58	0.614	0.435
Population	1, 92.49	27.5	<0.001
Sex	2, 92.91	3.67	0.029
Measurement	2, 109.43	25.2	<0.001
Population × measurement	2, 109.43	3.74	0.027

to compare the size and condition of the fish from the two populations. A X^2-test was used to test for population differences in the sex ratio of the study fish. Statistical tests were performed with R (The R Foundation for Statistical Computing, Vienna, Austria): Intraclass Correlation Coefficient (ICC) package (version 2.2.) (ICC analyses), and with SPSS version 21.0 (IBM Corp., New York, USA) (all other statistical analyses).

RESULTS

FISH SIZE AND SEX RATIO IN THE TWO STUDY POPULATIONS

Length and fresh body mass of the individuals did not differ between the studied Kuusoja River and Kolvananuuro Brook populations (t-test, $df = 97$, $P \geq 0.561$), but fish from Kolvananuuro Brook had a 5.1% higher condition factor than Kuusoja River fish (t-test, $df = 97$, $P = 0.001$). The proportion of males, females and juveniles did not differ between the populations ($X = 0.407$, $df = 2$, $P = 0.816$). Samples from both populations included 12 juveniles. 64% of mature individuals were females.

REPEATABILITY OF BEHAVIORAL COMPONENTS AND BEHAVIORAL CORRELATIONS

Both boldness and activity scores were highly repeatable in both populations, both over the first two trials, and across all the three trials, but the repeatability estimates did not differ statistically significantly between the populations (**Figure 2**).

THE EFFECT OF POPULATION, SEX AND MEASUREMENT PERIOD ON FISH BEHAVIOR

Variation in boldness score was not explained by fish length or condition factor. Fish from the Kuusoja River were significantly bolder than fish from Kolvananuuro brook (**Table 2**, **Figure 3**), and males were significantly bolder than females (**Table 2**), but no differences were found between males and juveniles (Bonferroni, $P = 1.00$) or between females and juveniles ($P = 0.233$). The main effect of measurement period (1–3) was highly significant (**Table 2**) and paired comparisons revealed that minnows behaved boldest in the first behavioral test (**Figure 3**; Bonferroni, 1. test vs. 2. test: $P = 0.034$; 1. test vs. 3. test: $P < 0.001$) and were bolder in the second test than in the third test ($P < 0.001$). In other words, on average minnows in each population were less bold in the test where predator odor was present (**Figure 3**). However, we also found a significant interaction between population and measurement period (**Table 2**) that resulted from the abrupt decrease in boldness of Kolvananuuro Brook fish when predator odor was present (**Figure 3**). Such a response was absent in the Kuusoja River population where boldness decreased through all measurements rather linearly (**Figure 3**).

The activity score was higher in Kolvananuuro Brook population than in the Kuusoja River population (scores 0.202 and −0.208 respectively; **Table 3**). Activity stayed unchanged through different measurements within and among populations (**Figure 4**). Source population did not interact with measurement, but the sexes behaved differently at different measurement times (**Figure 4**). The significant interaction was explained by the strong decrease of activity of juvenile fish in the third trial, and the low activity of females in the first trial (**Figure 4**). The negative effect of condition factor on activity was not statistically significant, but the inclusion of condition factor improved the AIC of the model (data not shown).

THE ASSOCIATION BETWEEN *D. PHOXINI* PARASITE INTENSITY AND PERSONALITY

All the minnows in the Kuusoja River population were parasitized by *D. phoxini* with numbers varying from 24 to 922 (mean

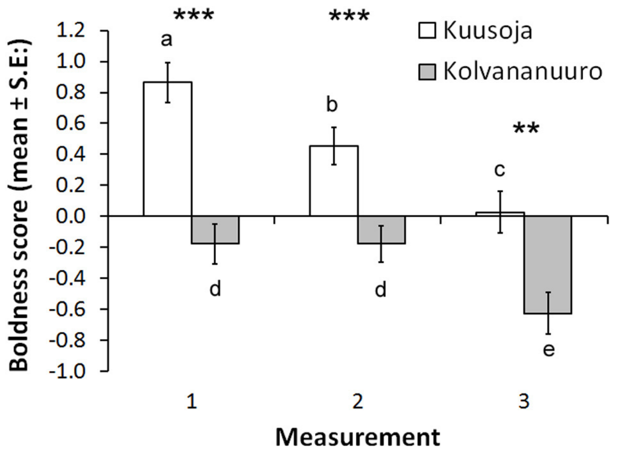

FIGURE 3 | Estimated marginal means for boldness scores in the three behavioral trials in the two study populations (Kuusoja River and Kolvananuuro Brook). Paired differences are indicated with asterisks (*** $P < 0.001$; ** $P < 0.01$), and among measurement differences within populations with different letters (alpha = 0.05).

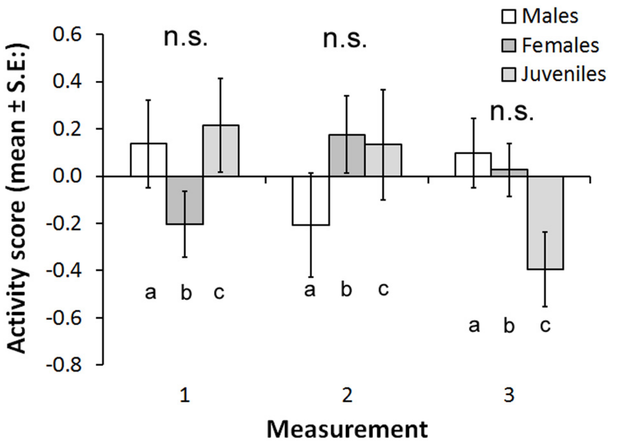

FIGURE 4 | Estimated marginal means for activity scores in the three behavioral trials in the two study populations (Kuusoja River and Kolvananuuro Brook). None of the paired comparisons (both among sexes within measurements and measurements within sexes) were statistically significant.

Table 3 | Significance of fixed factors in explaining variance in activity score according to linear mixed effect model.

Source	*df*:s	*F*	*P*
Intercept	1, 92.14	2.380	0.126
Population	1, 92.00	8.267	0.005
Measurement	2, 132.83	1.125	0.328
Sex	2, 106.76	0.008	0.992
Sex × measurement	4, 132.83	4.216	0.003
Condition factor	1, 92.00	2.391	0.126

171.2 ± 182.7 *SD*) parasites, while none of the minnows from Kolvananuuro Brook hosted *D. phoxini*. Prevalence of body cavity dwelling *P. ovata* was much lower (only 2 fish parasitized with adult worms in Kuusoja River and none in Kolvananuuro Brook), and therefore they were not further analyzed. In the Kuusoja River population the load of *D. phoxini* was found to be weakly (but statistically insignificantly) negatively associated with fish activity (PC2, $r_s = -0.232$, $P = 0.11$, $n = 49$). The correlation was negative in all test-specific analyses (Spearman, 1. test: $r_s = -0.316$, $P = 0.027$; 2. test: $r_s = -0.301$, $P = 0.0363$; 3. test: $r_s = -0.094$, $P = 0.52$, corrected alpha level = 0.025). No association between *D. phoxini* and boldness (PC1) was found (Spearman, $P > 0.8$, in all four tests).

DISCUSSION

We found that minnow were individually consistent in boldness and activity in both of the study populations, while the populations did not differ in the repeatability of behavior. In line with our predictions, we found that in the Kuusoja River population (a high predation and high parasitism risk environment), fish showed higher boldness than fish from Kolvananuuro Brook. However, against our predictions, River Kuusoja minnow appeared less active than Brook Kolvananuuro fish. Parasite (*Diplostomum phoxini*) abundance was negatively, but not statistically significantly, associated with fish activity, which suggests that the infection by these parasites may partly explain the lower activity among parasitized River Kuusoja fish. Since our data come from only two populations, the present results should be interpreted very cautiously.

Recent work in various species has shown that many fishes are fairly consistent in boldness (e.g., Conrad et al., 2011; Kekäläinen et al., 2014b), and that personality components in fish can have heritable components (Kortet et al., 2014). Because fish in both of the study populations were individually consistent in their boldness and activity, the present results are well in line with the previous findings.

We have demonstrated earlier that experimental *D. phoxini* infection increases the repeatability of boldness and activity in the Kolvananuuro Brook population (Kekäläinen et al., 2014a), but the effect did not arise through selective mortality of non-consistent individuals. Furthermore, Coats et al. (2010) and Hammond-Tooke et al. (2012) have also found support for parasite-induced personality variation. In contrast to earlier findings, however, we did not found differences in repeatabilities between our two study populations in the present study. This difference between present and earlier studies may be partly related to the methodological differences between studies. For example, Kekäläinen et al. (2014a) studied the repeatability of behavior within a single population (Kolvananuuro Brook) and after experimental infection, whereas the present study is based on correlative data and a between-population comparison. Furthermore, it has been demonstrated that when behavioral trials are conducted at relatively short intervals (e.g., less than 10 days, such as in the present study), the resulting repeatability estimates are generally higher than those when behaviors are recorded over longer intervals (Bell et al., 2009; Kekäläinen et al., 2014a). Behavioral boldness and activity were decreased in our third trial that included pike odor exposure, but unfortunately the experimental set up did not allow separating possible time effects from the predator odor effects.

D. phoxini was present in all the Kuusoja River individuals whereas it was absent in Kolvananuuro Brook fish. Therefore, the differential parasite load of *D. phoxini* may have an important role in explaining why Kuusoja River fish appeared bolder and less active than Kolvananuuro Brook fish. The negative correlation between activity and parasite load directly supports this conclusion, although the complete lack of this parasite from Kolvananuuro Brook did not allow studying the effect of the parasite on the population means. The lack of correlation between boldness and parasite load does not necessarily mean that the *D. phoxini* does not affect boldness: we have earlier demonstrated (in experimentally infected Kolvananuuro Brook fish) that the effect of *D. phoxini* on boldness and activity may be non-linearly dependent on parasite density (see Kekäläinen et al., 2014a). However, as present results do not support this earlier finding more studies are needed to clarify the impact of *D. phoxini* parasite load on personality traits. We can also argue that the other parasite in the system, i.e., body cavity dwelling *P. ovata*, is unlikely to explain the differences between the populations in the present data, since we have not detected significant effects of *P. ovata* on minnow behavior in our other studies (Lai et al., unpublished observations).

One might suggest that the observed behavioral patterns among parasitized fish may be of an adaptive nature. Possibly, minnows in the Kuusoja River population show bold behaviors because they can thus compensate the direct and indirect costs caused by high parasitism and predation risk in the environment. Parasitized fish show often weakened condition and fitness (Seppälä and Jokela, 2008), and display changes in their behavior (e.g., Santos and Santos, 2013). If bold behaviors of minnow are associated with increased foraging and nutrition intake, they also likely positively affect the development and maintenance of efficient immune defense, and may thus further increase individual's fitness. This kind of process has, indeed, already been proposed to explain individual variation in personality traits (Luttbeg and Sih, 2010). However, fish condition factor did not explain personality variation. It might thus be that the overall selection or habituation to the presence of predator cues in the high risk environment in the Kuusoja River population would explain high boldness.

Finally, the impacts of *D. phoxini* on the host's biology are likely determined by the life history of this parasite. As a trophically transmitted trematode parasite, *D. phoxini* uses the Eurasian minnow in particular as its second intermediate host (Barber and Crompton, 1997a,b). Sexual reproduction of this brain fluke occurs in the intestines of fish-eating birds that act as definitive hosts for the parasite. The infective stages reach the water through bird feces, and enter the first intermediate host, the freshwater snail *Radix peregra*. Snails infected with *D. phoxini* produce freely swimming cercariae larvae, which infect minnows by penetrating through their skin and migrate to the fish brain via the blood circulation system. In the host brain, cercariae will encyst and change into metacercariae, i.e., the maturing and infectious stage of the parasite (Barber and Crompton, 1997a,b). Earlier studies have shown that brain-encysting trematodes have the potential to alter host behavior (e.g., Lafferty and Morris, 1996; Shirakashi and Goater, 2002, 2005; Kekäläinen et al., 2014a). In the brain, *D. phoxini* metacercariae are known to aggregate mainly in the cerebellum, the optic lobes and the medulla oblongata (Barber and Crompton, 1997a), where they cause pathological damage in the brain tissue (e.g., necrosis and disruption in the integrity of brain tissue, Dezfuli et al., 2007). This may cause manipulative effects as a means of increased boldness and thus lead to increased predation by the definitive avian host. However, unlike the parasite-host system of brain trematode *Euhaplorchis californiensis* in killifish *Fundulus parvipinnis* (Lafferty and Morris, 1996; Shaw et al., 2009), the behavioral manipulation of *D. phoxini* metacercariae in minnows in the other populations has never been tested quantitatively but only described briefly (Dönges, 1969; Kekäläinen et al., 2014a). Possible predation susceptibility increasing behaviors of *D. phoxini* -infected host minnows nor possible mechanisms of behavioral manipulation by *D. phoxini* have not been examined in detail. Thus, regarding the lack of necessary knowledge about the interaction between *D. phoxini* and host minnows, the impact of this brain parasite on the biology of host minnows through personality change has remained unclear until recently (Kekäläinen et al., 2014a). In any case, the European minnow provides an interesting model study system with high potential for further work on animal personalities.

To conclude, the present data provide one of the first observations possibly indicating the roles of environmental predation and parasitism risk in the development of animal personalities. The minnows originating from the high predation and parasitism risk population showed higher boldness but lower activity, which is partially in line with the predictions of parasite-mediated personality evolution (Kortet et al., 2010). Since the present data is based on only two populations, the results should be verified by further experimental work by using parasite naïve, experimentally infected, individuals and a common garden set up in low predation and high predation environments. This kind of approach would help us to understand the magnitude of selection on personality caused by predation (with and without parasitism), and the detailed mechanisms for selection to act in the natural environment.

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Animal personality and pace-of-life syndromes: do fast-exploring fairy-wrens die young?

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The pace-of-life syndrome (POLS) hypothesis for animal personality proposes that variation among individuals in life-history strategies is associated with consistent differences in behavior. We tested predictions of this hypothesis in the superb fairy-wren, *Malurus cyaneus*, by investigating long-term individual differences in risk-related behaviors (latency to enter a novel artificial environment, exploration, activity and response to mirror image stimulation) and survival. We found consistent differences between individuals in these behaviors (adjusted repeatability of exploration of artificial novel environment = 0.37). Individual differences were consistent over several years and bi-variate analyses showed a significant among-individual correlation ("behavioral syndrome") between exploration behavior at two life stages (young adult and old adult). Docility at the nestling stage predicted exploration behavior of juveniles. Behavioral traits measured in a risky context were correlated with one another, forming a behavioral syndrome of coping strategies ranging from "proactive" to "reactive." Nestlings that were more active and exploratory in isolation were less docile during handling, while adults that entered the artificial environment fast were more exploratory, active, and aggressive in the artificial environment. Exploration behavior increased within individuals as they aged and when they were in poorer condition, consistent with expectations of more risk-prone behavior with lower residual reproductive value (RRV) (reduced "asset protection"). Risk-related behavior predicted the probability of apparent survival: more exploratory individuals were less likely to be present in the population 12 months later. Our findings suggest that, consistent with the predictions of the POLS hypothesis, individual variation in survival is associated with consistent individual differences in risk-related behavior that are maintained long-term and span developmental boundaries.

Keywords: animal personality, life-history strategy, survival rate, individual variation, risk-taking

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Introduction

Animals differ in their pace of life, from those that are long-lived with slow reproductive rates, to those that "live fast and die young." This "slow-fast" spectrum of life-history strategies has been well studied across species (Roff, 2002), but has only recently begun to attract attention as an explanation for behavioral differences among individuals within populations of the same species (Biro and Stamps, 2008; Smith and Blumstein, 2008; Reale et al., 2010). The trade-off between reproduction and survival that underpins the evolution of diverse life-history strategies among species may also be associated with the evolution of behavioral differences among individuals. Individuals that prioritize survival are expected to behave in ways that are more risk averse, while those that prioritize high reproductive rates are expected to engage in more risky behavior to maximize current reproductive success. The pace-of-life syndrome (POLS) hypothesis for animal personality predicts long term maintenance of consistent behavioral differences among individuals within populations, correlations between risk-related behaviors, and earlier mortality among risk-prone individuals (Reale et al., 2010).

If life-history strategies are associated with behavioral strategies, then individuals pursuing different life-history strategies should show consistent, long-term differences in behavior (Reale et al., 2010). If individuals diverge in their life-history trajectories from very early in life, then these behavioral differences may already be apparent in early life. Although the existence of consistent individual differences in behavior is well established in diverse traits across a large range of animal taxa (Bell et al., 2009), less is known about the extent to which such behavioral differences are maintained over the long term. A recent study on captive zebra finches (*Taeniopygia guttata*) found that nestling activity during begging predicted individual differences in adult activity levels (McCowan and Griffith, 2014). However, repeatability of behavior is often assessed over short time-scales: fewer than 10% of studies reviewed by Bell et al. (2009) spanned more than 1 year, and their meta-analysis showed that repeatability estimates were lower with long than short test intervals. Furthermore, repeatability differed among behavioral traits (Bell et al., 2009). The POLS hypothesis relates specifically to behavioral traits that promote particular life-history strategies (Reale et al., 2010), predicting long-term repeatability of behavioral traits such as boldness, aggression, exploration, and activity, where these are associated with shorter lifespans or increased risk of mortality.

If life-history strategy and risky behavior are linked (Reale et al., 2010), then suites of risk-related behaviors are predicted to be correlated at the between-individual level (a risk-related "behavioral syndrome"). Individuals pursuing a "fast" life-history strategy are predicted to express a variety of risk-related behaviors more than individuals pursuing a "slow" life-history strategy that behave to maximize their likelihood of survival. One context in which such correlations among traits are well established is in research on "coping strategy"—how animals differ in their behavioral responses to stress (Koolhaas et al., 1999; Coppens et al., 2010). Studies on a variety of laboratory, domestic, and more recently wild animals during captivity and handling have shown that individuals vary in a suite of correlated behaviors; "proactive" individuals are risk-taking, bold, aggressive, active, and fast-exploring, while "reactive" individuals are risk-averse, shy, less aggressive, less active, and slow-exploring (Koolhaas et al., 1999; Coppens et al., 2010).

Individuals following different life-history trajectories are expected to show increasing differences in residual reproductive value (RRV) as they age. Differences among individuals in RRV have been suggested as a cause for individual differences in risk-related behavior (Wolf et al., 2007). Specifically, individuals with high RRV are expected to be less likely to engage in risky behaviors to maximize current reproductive success ("asset protection") than individuals with low RRV. Following the same logic, within-individual variation in RRV could explain behavioral plasticity within individuals over time. Since RRV generally declines with age (Roff, 2002), individuals may engage in more risky behavior as they age. Likewise, individuals may be more risk averse when they are in good condition and more risk prone when they are in poor condition.

The POLS hypothesis predicts that short-lived individuals should be more proactive (less risk-averse) than long-lived individuals, linking life-history strategy (fast-slow) with a behavioral syndrome (proactive-reactive) (Reale et al., 2010). In this scenario, the evolution and maintenance of behavioral diversity in a population is maintained by life-history trade-offs, since different life-history strategies can have similar lifetime fitness. In contrast, some behavioral polymorphisms may be maintained by disruptive viability selection on behavior, where individuals at the extremes of the behavioral continuum have higher survival than those expressing the behavior at average levels (Bergeron et al., 2013), or by fluctuating environments, where different behavioral types have higher survival in different years (Dingemanse et al., 2004). Two meta-analyses investigating the fitness consequences of animal personality found mixed evidence for a relationship between individual differences in behavior and survival (Biro and Stamps, 2008; Smith and Blumstein, 2008). This may be because of fluctuating selection (Dingemanse and Reale, 2013), and because different behavioral traits confer different costs and benefits in terms of survival and reproduction in different species. An explicit focus on the relationship between survival and behavioral responses to risk may enable a clearer test of the POLS hypothesis.

We investigated links between risk-related behaviors and survival in the superb fairy-wren (*Malurus cyaneus*), a small passerine native to south-eastern Australia. We measured a suite of behavioral traits in nestlings, and over several years in adults, in contexts likely to be perceived as associated with high mortality risk by wild birds—handling and captivity. We tested the following key predictions of the POLS hypothesis:

1. Individuals show consistent differences in risk-related behavior.
2. Individual differences in risky behavior are maintained long-term, including across the ontogenetic boundary from nest-bound to free-flying.
3. Behavioral traits like exploration, boldness, and aggression expressed in a risky context are correlated.
4. Low RRV is associated with increased risky behavior.
5. Individual differences in risk-related behavior predict survival.

Material and Methods

Study System

We studied a population ranging from 98 to 108 groups of superb fairy-wrens resident in a 28 hectare area (700 × 400 m) around the northern arm of the wetland at Serendip Sanctuary (38.00°S, 144.41°E), near Melbourne in south-eastern Australia. All work was conducted with the approval of the University of Melbourne Animal Ethics Committee (1212537.1), Victorian Department of Sustainability and Environment (10006026), and Australian Bird and Bat Banding Scheme (2073 and 1405). To allow individual recognition in the wild, all birds were banded with a unique combination of colored plastic leg-bands, and a numbered aluminum band supplied by the Australian Bird and Bat Banding Scheme. Banding at the site commenced in July 2009, and intensive monitoring of breeding and individual behavioral traits commenced in July 2011. Adults were captured with Ecotone mist-nets for banding, and we collected body measurements including mass (± 0.1 g), fat (furcular deposit scored from 0 = none visible, to 5 = bulging out from the cavity), and tarsus length (± 0.01 mm), and quantified individual behavioral differences in a novel artificial environment (see below) prior to release. We captured birds to quantify behavior in two sessions each year—pre-breeding (spring) and post-breeding (autumn). During the breeding season (September to January), we banded all nestlings as above, weighed them (± 0.1 g), and measured tarsus and fourth primary pin feather lengths (± 0.01 mm). During the 2011 breeding season, we banded nestlings approximately 7 days after hatching, and conducted a standardized test of nestling behavior on day 9 (see below). To reduce disturbance at the nest, from the 2012 breeding season we removed the nestlings only once from the nest, on day 8, for both the behavioral test and banding. The behavioral test was conducted first, except for adding a single plastic band to one leg of each nestling to distinguish individuals.

We re-sighted color-banded individuals approximately weekly during the breeding season to monitor survival, group membership, and nesting. We recorded group size and individual roles—breeding (dominant) females are identifiable as the only group member that builds nests and incubates eggs, and dominant males are typically the oldest male in the group and molt earliest into seasonal breeding plumage (Mulder and Magrath, 1994). All other group members were considered subordinates. In our population, more than half of dominant pairs had subordinate helpers (50–58% of 98–108 pairs in 2011–2013), and group sizes ranged up to 8 (mean ± s.e. = 2.8 ± 0.1). Among pairs with subordinates, 93–98% had male subordinates (mean ± s.e. = 1.5 ± 0.1, maximum 5 male subordinates) and 2–18% had female subordinates (mean ± s.e. = 1.2 ± 0.1, maximum 2 female subordinates). After finding nests, we checked them approximately every 3 days to record nesting details including the date first eggs were laid, clutch size (modal clutch size = 3 eggs), hatching and fledging, and for banding (see above) and behavioral tests (see below). Nestlings were aged based on hatch date (52 nestlings in nests checked during hatching), or inferred from known lay dates (300 nestlings in nests checked during laying), or estimated based on length of the fourth primary pin feather at banding. The latter was the best predictor of age in day 7–10 nestlings based on analysis of morphometric measurements of the 52 nestlings with known hatch date (β± s.e. for fourth primary = 0.14 ± 0.05, $p = 0.01$, mass = −0.02 ± 0.14, $p = 0.90$, tarsus = 0.02 ± 0.12, $p = 0.88$, exposed feather on fourth primary = 0.01 ± 0.04, $p = 0.88$). We calculated the age of adult birds at the time of their tests as the difference between the test date and their hatch date, divided by 365. For birds first banded as adults, we estimated their minimum age at the time of the test using the mid-point of the breeding season (1 December) prior to the date they were first captured as their "hatch date" to give an estimate of their minimum age. The minimum age of adult birds was thus a continuous measure (in years) that distinguished age differences between tests conducted in the same year.

Nestling Behavior

We quantified behavior at the nestling stage in a standardized test using early separation and handling stress, two stressors routinely used in developmental and physiological studies on birds and mammals (adapted from Fucikova et al., 2009; Brommer and Kluen, 2012). Nestlings were tested at approximately 8 or 9 days old (see above)—as late as possible in the 13-day nestling period to maximize responsiveness to handling while minimizing the risk of premature fledging. We removed nestlings from the nest and placed them in separate compartments (10 × 10 cm) of a shallow box for 60 s. The box was uncovered so that nestlings were exposed to the open, and visually (but not acoustically) isolated from one another. We video-recorded movements of the nest-mates during 60 s of isolation, and then the handling of each nestling in turn for a 30-s test of docility and 10-s assessment of breathing rate. During handling, the docility of each nestling was assessed by placing it on its back on the flat open palm of an observer's hand for 30 s, with the observer's thumb gently on the body to prevent the nestling righting itself ("back-test," Hessing et al., 1994). Breathing rate was measured immediately after the back-test, by recording the movement of the nestling's chest associated with respiration for 10 s with the nestling held enclosed in the observer's hand in a more upright position (to minimize struggling that affected chest movements). Docility and breathing rate were then measured sequentially for the remaining nestlings, noting the order in which they were measured. To limit variation due to handling differences, nestlings were usually tested by one of two experienced observers (278 nestlings by MLH, 155 by TvA, 26 by others). For consistency, one person (Susan Ebeling) scored all nestling videos, with breathing rate scored while playing the video at half-speed to facilitate accurate counting of rapid breathing.

We quantified four behavioral variables over the course of the nestling test: (i) Isolation docility: number of seconds spent still in the compartment while isolated (of 60 s total). (ii) Exploration: the number of "zones" used in the compartment while isolated (of 9 in a 3 × 3 grid). (iii) Back-test docility: the number of seconds spent still during the 30-s back-test. (iv) Breaths: the number of breaths taken in a 10-s period immediately after the back-test. Some individuals ($n = 25$) had missing values due to technical problems with video recording, jumping out of the isolation compartment, or begging disrupting chest movement during the breath-test. We scored all four variables for 459 nestlings in 195 broods in three breeding seasons.

Adult Behavior

We quantified individual differences in behavior of adult birds in an artificial novel environment (similar to the novel environment test of Verbeek et al., 1994). Following processing in the field (above), birds were taken to onsite testing rooms in a cloth bag, and housed in a holding cage containing two perches, a water dispenser, and a tray on the floor with 10 mealworms. We kept birds in holding cages for at least 1 h to acclimatize. The time-course of hormonal stress responses is unknown in fairy-wrens, but a small sample of birds tested for corticosterone levels at the end of the test showed no relationship between corticosterone level and holding time (Jacques-Hamilton et al. in prep.). For animal welfare reasons, we did not keep birds in captivity overnight, as is done in some studies (Dingemanse et al., 2002), to reduce the likelihood of disrupting a complex social system. We minimized disturbance in holding cages with acoustic foam lining on the internal walls and roof of the cage and a cloth curtain drawn across the wire front. Immediately prior to testing, we transferred a bird to a cage (60 × 31 × 37 cm, with two perches and no food or water) connected to one of two test rooms by a 15 cm diameter round opening covered by one-way glass, permitting the bird to see into the lit test room. After 5 min of acclimatization, the glass door was raised by hand to allow the bird to enter the test room. The solid sides, floor and roof of the cage meant that the bird could not see the observer who raised the glass door. Birds would have been aware of the door being raised due to the associated sound and the increase in light-level in the cage (the glass door was slightly tinted).

The two test rooms (2.8 × 2.8 m, with sloping ceiling 1.95–2.28 m high; see Supplementary Material Figure S1 for schematic illustration of layout) each had two small video cameras (GoPro Hero and GoPro Hero2) attached to the ceiling in opposite corners of the room, with one of the cameras providing a live video feed to monitors in an adjacent "control" room between the two test rooms, to allow scoring of the bird's behavior. An observer used a custom-designed Filemaker Pro layout on an iPhone 4s to record the time and perch used whenever the bird moved among a total of 40 perching areas in the test room. Perching areas included six perches each on two tall (1.69 m) and one medium (1.34 m) wooden stands, four perches on one short (0.75 m) wooden stand, the tops and bases of the four stands, a ledge (11 cm wide × 39 cm long) below the hole via which they entered the room and, since birds also spent time on the floor, nine floor zones (0.9 × 0.9 m) demarcated with a chalked 3 × 3 grid.

We quantified four behavioral variables over the course of the test. (i) Emergence speed: how quickly the bird emerged into the room after the door was raised, fast = <60 s, slow = 60+ s. Birds that did not enter the room naturally were forced to do so by tapping the cage after 3 min (in early tests after 1 or 2 min). (ii) Exploration: the number of unique perching areas the bird used in 5 min after first entering the test room. (iii) Activity: the total number of perching areas the bird used in 2 min after familiarization with the room (starting 6 min after it entered the room). Approximately eight min after the bird entered the room, the one-way glass door was lowered to expose the bird to a 39 × 35 cm mirror. Birds could see their reflections only if perched on the upper four perches of the two stands in front of the mirror, and for this subset of birds, we scored their reaction to their reflection in mirror. (iv) Mirror response: 1 = swooped the mirror, 2 = perched on the ledge in front of the mirror, 3 = pecked at the mirror. We scored movements for 5 min from when the mirror was exposed, or from when the bird first used one of the mirror perches if that was later in the initial 5-min period. At the end of the trial, the observer entered the test room, turned off the light, recaptured the bird by hand, and then released it at its capture location. On average, birds were released 2.65 ± 0.02 h (mean ± s.e.) after capture, and time off-territory did not significantly affect their apparent survival ($\beta \pm$ s.e. $= -0.30 \pm 0.28$, $p = 0.28$). We completed 1093 tests on 678 birds between 24 January 2012 and 12 October 2014. Individuals were tested up to 5 times ($N = 7$ birds, 35 with 4 tests, 59 with 3 tests, 164 with 2 tests, 413 with 1 test) and with tests spanning more than 2 years for 20 birds.

Statistical Analysis

Consistent Individual Differences in Risk-Related Behavior

We tested whether individuals showed consistent differences in their average behavior by estimating adjusted repeatability—the proportion of the total variation in the behavioral trait attributable to among-individual differences, while controlling for other factors to avoid the "pseudo-repeatability" that may arise if behavior is sampled unevenly with respect to environmental variables that influence behavior (Westneat et al., 2011; Dingemanse and Dochtermann, 2013). Alternative analytical approaches are shown in the Supplementary Material ("raw repeatability" and tests of similarity between first and second trials). We used generalized linear mixed models (GLMMs) to quantify adjusted repeatability, including bird, territory, and observer as random effects to assess the variance explained by these factors and a case-level variable to assess the residual variance. We specified territory as the home territory for all birds with known home territories (birds regularly re-sighted in the same area with the same group in our core area), and as the capture territory for birds without a known home territory (birds resident in territories around our core area that were captured in a core territory, or floaters/dispersers). As fixed effects, we included time held (time in holding cage prior to test, mean ± SD: 1.39 ± 0.39 h), time of day (in decimal format, 12.44 ± 2.20 h), test room (538 tests in room 1 and 555 in room 2), test sequence (up to 5 per bird, 1.59 ± 0.88), test interval (days since the bird's previous test (= 0 for the first test, following Dingemanse et al., 2002), 85.5 ± 149.4 days), season (819 tests in autumn/post-breeding and 274 tests in spring/pre-breeding), and year (486 tests in 2012, 377 in 2013, and 230 in 2014). All covariates were centered and standardized by subtracting the mean and dividing by the standard deviation. We included observer (the person who processed the bird through the test) as a random effect rather than a fixed effect because there were 21 observers over the course of the 3 years, and because we were not interested in differences between particular observers per se. To improve model convergence, we pooled observers who had run fewer than ten tests into the single group, "other," so that the random effect had 12 levels.

Long-Term Individual Differences in Risk-Related Behavior

We tested nestling behaviors during isolation and handling as predictors of behavioral differences in juveniles (less than 6 months of age) during artificial environment tests in the autumn following their hatch season using GLMMs, including home territory as a random effect to account for non-independence of birds from the same territory. We modeled error distributions as Poisson with a log link for exploration behavior, and binomial with a logit link for emergence, activity, and mirror response (all as binary responses). As predictors in the models, we included adjusted nestling behavioral scores of three of the four behaviors measured (excluding nestling exploration due to its high correlation with docility in isolation, see Results) and important test-covariates of the adult tests (see Results). Since nestling behaviors varied slightly between handlers, scores were centered and standardized by subtracting the handler-specific mean and dividing by the handler-specific standard deviation. Nestling breathing rate additionally increased with nestling age (1.16 ± 0.28, $p < 0.001$) and with time of day (0.26 ± 0.10, $p = 0.008$). In this case, we therefore used residuals from a model of breathing rate that controlled for handler, nestling age, and time of day. Order of testing did not affect any of the nestling behaviors. The analyses included 175 nestlings from 76 territories whose behavior had been tested in the artificial environment during the catching session after the breeding season in which they hatched, when they were 1.1–5.6 months old (mean = 2.6).

The analyses above identified docility during the back-test as the nestling behavior that best predicted juvenile exploration behavior (see Results). We therefore focused on this subset of behavioral measures to run a multi-variate analysis testing for behavioral correlations in tests across three life-stages, including tests on 186 nestlings, 316 "young" adults (up to 2 years from known hatch season, plus early tests of "old" birds), and 216 "old" adults (2+ years from estimated hatch date). Birds of unknown age that were not tested when they were at least 2 years old were excluded. The 186 nestlings were tested in the young adult stage (5 were also tested as old adults) and a further 53 birds were tested in both young and old adult stages. We quantified between-individual covariances ("behavioral syndromes") between the three response variables (nestling docility and exploration in young adults and old adults) in a multi-variate generalized linear mixed model using Markov chain Monte Carlo methods (implemented with MCMCglmm in R3.0.2, sampling 1 in every 100 iterations after the first 3000 iterations to generate sample sizes of 10 000). We included a random intercept for bird and we set the within-individual covariances to zero (Scenario 4 in Table 2 of Dingemanse and Dochtermann, 2013).

Correlations between Risk-Related Behavioral Traits

We tested for correlations between the four behavioral traits at both between-individual ("behavioral syndromes") and within-individual levels using a similar approach as above, partitioning the phenotypic variance in bivariate MCMCglmms. To quantify correlations, we fitted two variables as response variables into a single bi-variate mixed-effect model with a random intercept for bird. The within-individual variance was fixed to one for the binary variables. The variance-covariance matrix estimated by the model provided estimates of the covariance at both between-bird and within-bird levels. However, since all variables have non-normal error distributions, the estimates of within-individual covariances must be treated with caution (Dingemanse and Dochtermann, 2013). We also tested whether there were behavioral differences between individuals that used a perch with a view of the mirror or not.

Individual Characteristics as Predictors of Behavioral Variation

We tested whether behavioral differences during the test were associated with individual differences in sex, size (tarsus length, in mm), mass, or age (minimum estimated age, in years). We again used GLMMs, testing whether sex, size, mass, or age predicted differences in each of the four behaviors. Since age and mass vary within as well as between birds, we used within-subject centering (van de Pol and Wright, 2009) to determine whether individual differences in behavior were associated with between- or within-individual differences in these traits. As covariates in these models, we included terms indicated as important by the analysis of adjusted repeatability: time of day, test room, year as fixed effects, and bird ID as a random effect. Using model parameters estimated with glmer in R, we ran a simulation with 1000 iterations to estimate effect sizes and 95% CIs (using the function sim in the R package arm). The analyses included only known-sex birds with no missing data for size, mass, and age (875 tests on 506 birds).

Survival and Individual Differences in Risk-Related Behavior

We tested whether behavioral differences among adults predicted their likelihood of surviving 12 months from their first test using a binomial mixed model with a logit link, including home territory as a random effect to control for the non-independence of birds sampled from the same territory. We focused on exploration behavior, since it was the behavioral trait with the highest repeatability (see Results), and considered year and sex as additional explanatory factors in the model. We did not use mark-recapture analysis because the probability of failing to resight an individual that was alive within the study population was extremely low due to intensive observations during the breeding seasons. The assumption that birds that disappeared from the study area had died was justified for males and for breeding females as these are highly philopatric (Mulder, 1995; Cockburn et al., 2008). However, young female superb fairy-wrens have longer natal dispersal distances than males (Mulder, 1995; Cockburn et al., 2008) and young females that disappeared from the study population may have died or emigrated (some emigrants were detected during annual surveys of the area surrounding the study population). We therefore repeated the analysis with a subset of the data excluding females that had not yet completed natal dispersal.

Results

Consistent Individual Differences in Risk-Related Behavior

The behavior of superb fairy-wrens in an artificial novel environment showed considerable variation (Supplementary Material Figure S2 shows frequency distributions of behaviors), with a significant proportion of this variation due to consistent differences between individuals in their average behavior (**Table 1** shows repeatability values adjusted for testing conditions). Between-bird differences explained 37% of the total variance in exploration behavior (adjusted repeatability on both link and original scales) while controlling for other factors. Emergence, activity, and mirror response had lower adjusted repeatability values than exploration behavior, with between-bird differences explaining only around 10% of the total variation in behavior (adjusted repeatability ranged from 6 to 14% on link and original scales, **Table 1**). Raw repeatability was similar to adjusted repeatability for exploration, and slightly higher than adjusted repeatability for the other three behavioral traits (Supplementary Material Table S1), and there were significant similarities between the behavior of individuals in their first and second tests (Supplementary Material Table S2).

Birds from different territories differed little in their exploration behavior (variance associated with territory much lower than that associated with bird; random effects in **Table 1**), but differed more in other behaviors, especially activity (variance associated with territory greater than that associated with bird). None of the variation in the measured behaviors was attributed to the effect of different observers carrying out the tests (observer random effect in **Table 1**).

Average behaviors did not change significantly across the sequence of repeated tests, or with the duration of the interval between repeated tests, the time the bird was held before the test started, or between autumn and spring (**Table 1**). Exploration behavior decreased with time of day, was lower in room 2 than room 1, and was higher in 2013 than in 2012 and higher again in 2014. Activity also decreased over the course of the day, but was unaffected by other test variables. Emergence was faster in test room 2 and in 2014, while birds were less likely to approach the mirror in room 2, with no effects of other variables.

Long-Term Individual Differences in Risk-Related Behavior

Nestlings that were more docile during the back-test were less exploratory as juveniles in the artificial environment in the autumn following their hatch season, when they were less than 6 months old (**Figure 1**, **Table 2**). Other measures of nestling behavior did not predict juvenile exploration behavior, and nestling behaviors did not predict other measures of juvenile behavior (**Table 2**).

Between-individual covariances across life-stages were strong between exploration scores of young and old adults, but not with nestling docility (**Table 3**).

TABLE 1 | Adjusted repeatability of behavior in an artificial environment.

	Emergence (binary)		**Exploration (Poisson)**		**Activity (binary)**		**Mirror response (binary)**	
Fixed effects	**β**	**(95%CI)**	**β**	**(95%CI)**	**β**	**(95%CI)**	**β**	**(95%CI)**
Intercept	**−1.37**	**(−1.69, −1.04)**	**1.54**	**(1.42, 1.65)**	**1.05**	**(0.76, 1.45)**	**−0.57**	**(−1.03, −0.12)**
Time held	−0.10	(−0.26, 0.05)	0.02	(−0.02, 0.07)	−0.02	(−0.18, 0.11)	−0.07	(−0.29, 0.13)
Time of day	−0.04	(−0.20, 0.10)	−0.07	**(−0.11, −0.02)**	−0.19	**(−0.35, −0.05)**	0.03	(−0.18, 0.24)
Test room (2)	**0.56**	**(0.22, 0.80)**	−0.10	**(−0.20, −0.02)**	−0.26	(−0.57, 0.00)	−0.77	**(−1.20, −0.4)**
Sequence	−0.14	(−0.34, 0.07)	0.02	(−0.05, 0.07)	−0.10	(−0.33, 0.07)	0.06	(−0.20, 0.34)
Interval	−0.13	(−0.34, 0.08)	0.02	(−0.05, 0.08)	0.11	(−0.07, 0.35)	−0.15	(−0.45, 0.21)
Season (Spring)	−0.13	(−0.45, 0.28)	0.07	(−0.04, 0.19)	−0.31	(−0.65, 0.06)	−0.16	(−0.73, 0.34)
Year (2013)	0.03	(−0.39, 0.34)	**0.16**	**(0.03, 0.27)**	−0.08	(−0.43, 0.30)	−0.21	(−0.71, 0.32)
Year (2014)	**0.42**	**(0.04, 0.86)**	**0.27**	**(0.13, 0.42)**	0.14	(−0.24, 0.68)	−0.20	(−0.88, 0.27)
Random effects	**σ^2**	**(95%CI)**	**σ^2**	**(95%CI)**	**σ^2**	**(95%CI)**	**σ^2**	**(95%CI)**
Bird	**0.39**	**(0.35, 0.43)**	**0.24**	**(0.21, 0.26)**	**0.61**	**(0.55, 0.68)**	**0.45**	**(0.39, 0.51)**
Territory	**0.13**	**(0.10, 0.17)**	0.01	(0.01, 0.01)	**0.50**	**(0.39, 0.63)**	**0.31**	**(0.24, 0.4)**
Observer	0.00	(0.00, 0.00)	0.00	(0.00, 0.00)	0.00	(0.00, 0.00)	0.00	(0.00, 0.00)
Case	0.00	(0.00, 0.00)	**0.19**	**(0.17, 0.21)**	0.00	(0.00, 0.00)	0.00	(0.00, 0.00)
ADJUSTED REPEATABILITY (BIRD)								
Link−scale	**0.10**	**(0.09, 0.11)**	**0.37**	**(0.35, 0.40)**	**0.14**	**(0.13, 0.15)**	**0.11**	**(0.10, 0.12)**
Original−scale	**0.06**	**(0.04, 0.07)**	**0.37**	**(0.36, 0.38)**	**0.10**	**(0.10, 0.09)**	**0.09**	**(0.07, 0.10)**

Variation in the behavior of 678 birds from 130 territories during 1093 tests was assessed using additive generalized linear mixed models combined with parametric bootstrapping to estimate uncertainty (using functions glmer and sim in R). Mirror response was scoreable in a subset of tests: 601 tests of 427 birds from 125 territories. Effects of continuous predictors are based on variables centered around their mean and standardized by dividing by their standard deviation (Gelman, 2008), and effects of categorical predictors are given relative to a reference level (room 1 for test room, autumn for season, and 2012 for year). Adjusted repeatabilities were calculated from the variances associated with random effects shown, using equations in Nakagawa and Schielzeth (2010) (equations 22–23 for binary models; equations 34–36 for Poisson model). Effects that differ from zero are highlighted in bold.

Correlations between Risk-Related Behavioral Traits

The four traits measured in the novel artificial environment were positively correlated with one another between individuals: birds that were on average more exploratory than others were on average also more likely to emerge fast into the test room, be active, and approach the mirror (**Table 4**). Within-bird correlations between exploration and the three binary traits were very similar to between-bird correlations (except for correlations with emergence, **Table 4**)—in those trials where an individual was more exploratory, it was more likely to be active and to approach the mirror.

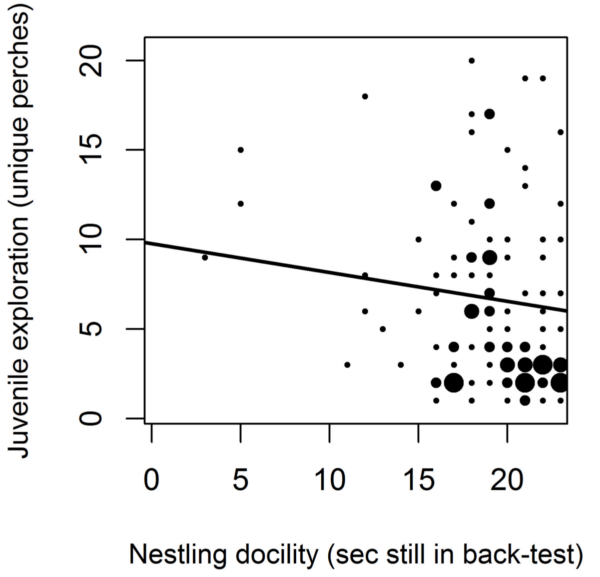

FIGURE 1 | Nestling docility predicts juvenile exploration. Nestlings that were more docile during the back-test (number of seconds not moving) were less exploratory (number of unique perches) during their first 5 min in an artificial novel environment as juveniles (less than 6 months old). Point size is proportional to sample size in each category. Nestling back-test docility remained a significant predictor of juvenile exploration behavior when three nestlings that were docile for less than 10 s were excluded [β (CI) = −0.09 (−0.17, −0.01); compared to **Table 5**].

TABLE 3 | Behavioral covariances between individuals across three life stages.

Life stage 1	Life stage 2	Between-individual covariance (CI)
Nestling docility	Young adult exploration	−0.18 (−0.53, 0.11)
Nestling docility	Old adult exploration	−0.26 (−0.66, 0.25)
Young adult exploration	Old adult exploration	0.68 (0.37, 0.82)

Between-individual covariances between risk-related behavior at different life stages: nestlings around 9 days from hatching, adults in their first 2 years of life, and adults more than 2 years past their (estimated) hatch date.

TABLE 4 | Between- and within-individual covariances between behavioral traits.

Trait 1	Trait 2	Between-individual covariance (CI)	Within-individual covariance (CI)
Exploration	Emergence	0.60 (0.36, 0.79)	−0.23 (−0.53, 0.06)
	Activity	0.88 (0.83, 0.93)	0.83 (0.71, 0.90)
	Mirror response	0.73 (0.54, 0.86)	0.55 (0.22, 0.79)
Emergence	Activity	0.66 (0.36, 0.89)	
	Mirror response	0.92 (0.80, 0.98)	
Activity	Mirror response	0.71 (0.33, 0.92)	

Correlations among behavioral traits (and 95% credible intervals) at the between- and within-individual levels, based on bi-variate mixed models. Estimates of within-individual covariance are not reliable for non-Gaussian distributions (Dingemanse and Dochtermann, 2013)—and not shown for binary variables where the variance was fixed at 1.

TABLE 2 | Nestling behavior as a predictor of juvenile behavior.

	Emergence (binary)		Exploration (Poisson)		Activity (binary)		Mirror response (binary)	
Fixed effects	β	(95%CI)	β	(95%CI)	β	(95%CI)	β	(95%CI)
Intercept	**−1.24**	**(−2.07, −0.25)**	**1.63**	**(1.38, 1.84)**	0.68	(−0.22, 1.53)	0.48	(−0.73, 1.96)
Time of day	−0.24	(−0.59, 0.17)	−0.10	(−0.18, 0.00)	−0.22	(−0.59, 0.11)	0.05	(−0.39, 0.66)
Test room (2)	0.40	(−0.27, 1.11)	−0.01	(−0.16, 0.16)	0.07	(−0.53, 0.88)	−0.72	(−1.83, 0.22)
Year (2012)	0.65	(−0.30, 1.79)	0.18	(−0.03, 0.43)	0.43	(−0.61, 1.45)	−1.05	(−2.68, 0.35)
Year (2013)	0.44	(−0.63, 1.26)	0.10	(−0.12, 0.32)	0.27	(−0.51, 1.40)	**−2.08**	**(−3.53, −0.47)**
Isolation docility	−0.27	(−0.58, 0.08)	−0.04	(−0.10, 0.04)	−0.08	(−0.4, 0.28)	0.27	(−0.29, 0.73)
Back-test docility	0.12	(−0.20, 0.51)	**−0.10**	**(−0.19, −0.04)**	−0.31	(−0.72, 0.05)	0.52	(−0.08, 1.06)
Res. Breaths	−0.06	(−0.17, 0.01)	−0.02	(−0.04, 0.00)	0.08	(−0.02, 0.16)	−0.09	(−0.26, 0.02)
Random effect	σ^2	(95%CI)	σ^2	(95%CI)	σ^2	(95%CI)	σ^2	(95%CI)
Territory	**0.49**	**(0.34, 0.65)**	**0.24**	**(0.19, 0.30)**	0.00	(0.00, 0.00)	**0.62**	**(0.43, 0.90)**

*Results of generalized linear mixed models assessing nestling behavior during handling as predictors of the behavior of 175 juveniles from 76 territories in an artificial novel environment, including important novel environment test variables as covariates (from **Table 1**). Nestling docility in isolation and in the back-test were centered and standardized based on handler-specific means and standard deviations (Gelman, 2008). Since breathing rate varied with nestling age and time of day in addition to handler, we used residuals from a model controlling for these variables. Effects that differ from zero are highlighted in bold.*

The subsample of individuals for which a mirror response could be scored was not biased with respect to exploration behavior: there was no between-individual correlation between whether a bird used a perch with a view of the mirror and exploration (0.01, 95% CI = −0.28, 0.23). The within-bird correlation was negative (−0.43, 95% CI = −0.66, −0.09), indicating that, if anything, the mirror response was less likely to be scoreable during tests when an individual was more exploratory than during those when it was less exploratory.

Nestling behaviors measured during isolation and handling (Supplementary Material Figure S3 shows distributions) were also mostly correlated with one another. Not surprisingly, nestlings that were more docile during the 60-s period of isolation explored fewer zones in their compartment (Spearman $r = -0.68$, $n = 459$, $p < 0.001$). Nestlings that were more docile in isolation were also more docile during the back-test (Spearman $r = 0.19$, $n = 459$, $p < 0.001$). However, the subsequent breathing rate of nestlings was not correlated with their docility in isolation (Spearman $r = 0.06$, $n = 459$, $p = 0.22$) or during the back-test (Spearman $r = 0.03$, $n = 459$, $p = 0.47$).

Individual Characteristics as Predictors of Behavioral Variation

Males and females behaved similarly in the test room, and individual differences in size did not predict differences in any of the measured behaviors (sex and tarsus length effects in **Table 5**). The effect of size on exploration also did not differ between the sexes (interaction $\beta = 0.08$, 95% CI = −0.04, 0.20). Birds with an older mean test age were less likely to emerge into the room fast or approach the mirror, and birds with a higher mean test mass were less likely to emerge into the room fast or be active (bird mean effects, **Table 5**). Within-bird increases in age were associated with increases in exploration behavior, while increases in mass were associated with decreases in both exploration and activity (test-specific deviation from bird mean (dev) effects in **Table 5**). In general, among-bird differences in behavior continued to explain a significant amount of the variation in behavior when these bird characteristics were accounted for (95% CIs for estimates of variance associated with bird random effect did not overlap zero, **Table 5**).

Exploration and activity both decreased with within-individual increases in mass (test-specific deviation from bird mean age and mass (dev) in **Table 5**), suggesting that these correlated behaviors are somewhat condition-dependent. We tested this by assessing effects on exploration of the amount of stored fat birds carried (bird condition) and of recent minimum temperature (environmental conditions: daily minimum averaged over the preceding week). Substituting fat score for mass (including all other terms in the model in **Table 5**, except age) indicated that birds tested with higher fat scores on average, had slightly lower exploration scores than birds with lower average fat scores [effect of Fat (bird mean) = −0.09, 95% CI = −0.17, −0.03]. Within-bird changes in fat score across tests had no effect on exploration behavior [effect of Fat (dev) = −0.01, 95% CI = −0.06, 0.03, but note overlap with 95% CI of between-bird effect]. Birds tested when average minimum temperatures were higher tended to be less exploratory than birds tested when average minimum temperatures were lower [effect of

TABLE 5 | Bird characteristics and between- and within-individual variation in behavior.

	Emergence (Poisson)		Exploration (Poisson)		Activity (binary)		Mirror response (binary)	
Fixed effects	**β**	**(95%CI)**	**β**	**(95%CI)**	**β**	**(95%CI)**	**β**	**(95%CI)**
Intercept	**−1.31**	**(−1.72, −0.94)**	**1.60**	**(1.48, 1.73)**	**0.83**	**(0.36, 1.17)**	−0.51	(−1.01, 0.07)
Time of day	0.01	(−0.15, 0.18)	−0.04	(−0.08, 0.00)	−0.16	(−0.33, 0.00)	−0.04	(−0.27, 0.20)
Test room (2)	**0.48**	**(0.17, 0.78)**	**−0.13**	**(−0.21, −0.07)**	−0.21	(−0.58, 0.04)	**−0.79**	**(−1.18, −0.29)**
Year (2013)	−0.20	(−0.51, 0.29)	0.05	(−0.05, 0.15)	0.01	(−0.35, 0.44)	−0.26	(−0.79, 0.35)
Year (2014)	0.33	(−0.13, 0.83)	0.09	(−0.06, 0.25)	0.39	(−0.12, 0.97)	−0.67	(−1.23, 0.23)
Sex (male)	0.05	(−0.35, 0.36)	0.06	(−0.07, 0.19)	0.38	(−0.06, 0.70)	−0.37	(−0.94, 0.07)
Size	0.06	(−0.13, 0.23)	0.01	(−0.06, 0.07)	0.09	(−0.11, 0.27)	−0.05	(−0.30, 0.23)
Min. Age (bird mean)	**−0.25**	**(−0.41, −0.04)**	0.01	(−0.05, 0.08)	−0.04	(−0.22, 0.15)	**−0.39**	**(−0.73, −0.15)**
Min. Age (dev)	−0.44	(−1.08, 0.08)	**0.29**	**(0.16, 0.41)**	−0.24	(−0.81, 0.36)	−0.13	(−1.1, 0.70)
Mass (bird mean)	**−0.23**	**(−0.44, −0.03)**	−0.06	(−0.13, 0.01)	**−0.36**	**(−0.57, −0.13)**	0.10	(−0.21, 0.40)
Mass (dev)	0.04	(−0.33, 0.37)	**−0.11**	**(−0.17, −0.04)**	**−0.45**	**(− 0.78, −0.07)**	0.17	(−0.43, 0.65)
Random effect	σ^2	**(95%CI)**	σ^2	**(95%CI)**	σ^2	**(95%CI)**		
Bird	**0.30**	**(0.27, 0.34)**	**0.37**	**(0.33, 0.40)**	**0.53**	**(0.46, 0.59)**	**0.24**	**(0.21, 0.28)**
Territory	**0.21**	**(0.17, 0.28)**	**0.03**	**(0.02, 0.03)**	**0.61**	**(0.47, 0.77)**	**0.50**	**(0.40, 0.66)**

*We tested whether individual differences in behavior related to differences in sex, size, age or mass of 570 birds from 130 territories in 971 tests using generalized linear mixed models including important test variables as fixed effects (from **Table 1**, and bird and territory as random effects. Mirror response was scoreable for a subset of tests: 530 tests of 365 birds from 122 territories. Effects of continuous predictors are based on variables centered around their mean and standardized by dividing by the standard deviation (Gelman, 2008), and effects of categorical predictors are given relative to a reference level (room 1 for test room, and 2012 for year). For characteristics that vary within as well as between birds (age and mass), we used within-subject centering to distinguish within- and between-bird effects. We included the bird's mean age or mass averaged across all tests (the "bird mean" term) to assess effects of between-bird differences in age and mass, and the bird's deviation from its mean (the "dev" term) to assess effects of within-bird differences (van de Pol and Wright, 2009). Effects that differ from zero are highlighted in bold.*

minimum temperature (bird mean) = −0.07, 95% CI = −0.14, 0.01], while increases in minimum temperatures across tests within-bird were also associated with decreases in exploration behavior [effect of minimum temperature (dev) = −0.07, 95% CI = −0.11, −0.03].

Within-bird increases in age are statistically confounded with habituation effects and year differences, but the former appeared to better explain increases in exploration behavior. Comparing the effects separately in three different models suggested a better fit (ΔAIC > 2) of the model including within- and between-bird variation in Age (AIC = 5474.7) than models with test sequence and test interval (AIC = 5479.5) or Year (AIC = 5486.5; all models included bird and territory as random effects and start time and room as fixed effects, as in **Table 1**). Furthermore, habituation effects should be strongest when test intervals are short, but exploration behavior instead tended to increase with longer test intervals (β = 0.042, 95% CI = 0.004, 0.085) as well as with test sequence (β = 0.08, 95% CI = 0.04, 0.12). Within-bird increases in age are also statistically confounded with Year [the positive effect of Year in **Table 1** became marginally negative in the model including Age (dev) in **Table 5**]. However, examining changes in exploration scores of cohorts of known-aged birds over the 3 years of testing (**Figure 2**) suggested that within-bird increases in exploration were not driven by higher exploration scores in 2014 tests than in 2013 and 2012 tests (the 2009 and 2012 cohorts showed no increase between test years).

Survival and Individual Differences in Risk-Related Behavior

Mortality (or emigration) was more likely among birds that were more exploratory in the artificial environment test (**Figure 3**, $\beta \pm$ s.e. = −0.58 ± 0.24, $p = 0.02$, in a logistic model controlling for a tendency for higher apparent survival among males 0.50 ± 0.26, $p = 0.06$, $n = 382$ birds from 116 territories). On average, 78.8% of males and 71.4% of females were still present in the population 12 months from their first test date ($n = 383$ birds from 116 territories first tested before 30 September 2013). Apparent survival did not differ between years (−0.30 ± 0.29, $p = 0.30$), and there was no evidence of heterogeneity in selection acting on exploration behavior since the effect of exploration on apparent survival did not differ significantly between years (−0.18 ± 0.52, $p = 0.73$) or between the sexes (0.43 ± 0.50, $p = 0.39$). Excluding females that had not yet completed natal dispersal showed a similar trend for higher apparent survival of birds that were less exploratory in the test (−0.48 ± 0.26, $p = 0.07$, $n = 326$ birds from 115 territories).

Discussion

We found support for several predictions of the pace-of-life hypothesis for personality in superb fairy-wrens. Individuals showed consistent and long term differences in risk-related behavior. Behavioral traits expressed during handling and captivity were correlated to form a behavioral syndrome, consistent with a proactive-reactive continuum of coping strategies. Proactive birds were more exploratory in a novel artificial environment, and more likely to emerge into the room fast, to be active, and to approach their reflection in a mirror. Nestlings that were less docile during handling were subsequently more exploratory in a novel environment as juveniles. More exploratory birds had lower apparent survival rates, consistent with the POLS prediction that individuals with short lifespans are less risk-averse.

Consistent Individual Differences in Risk-Related Behavior

Superb fairy-wrens showed consistent individual differences in the way they behaved when confronted with a novel artificial

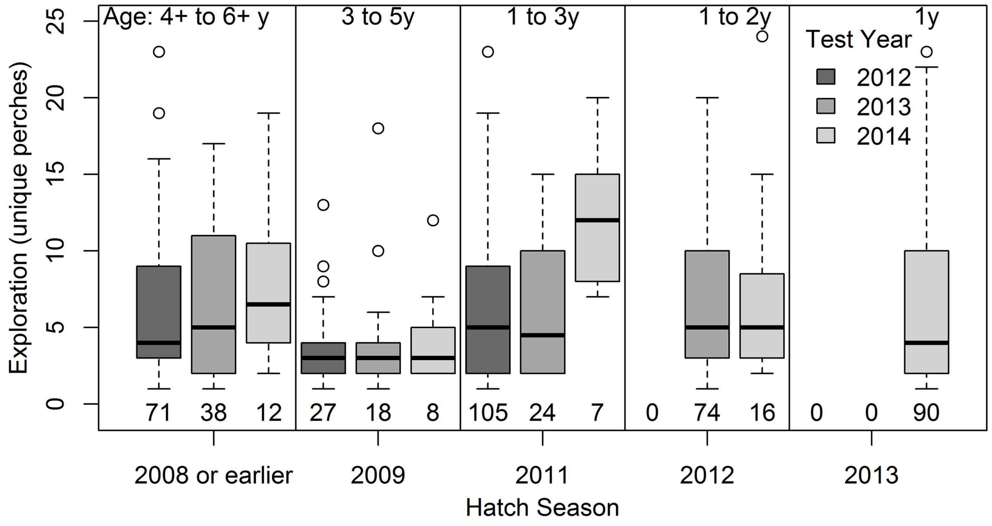

FIGURE 2 | Variation in exploration behavior with age in five cohorts. Exploration scores (number of unique perches) in tests over the three test years for a subset of birds including a cohort of old birds (banded as adults at the start of the study in 2009) and four cohorts of known-aged birds (banded as nestlings in the 2009, 2011, 2012, and 2013 breeding seasons).

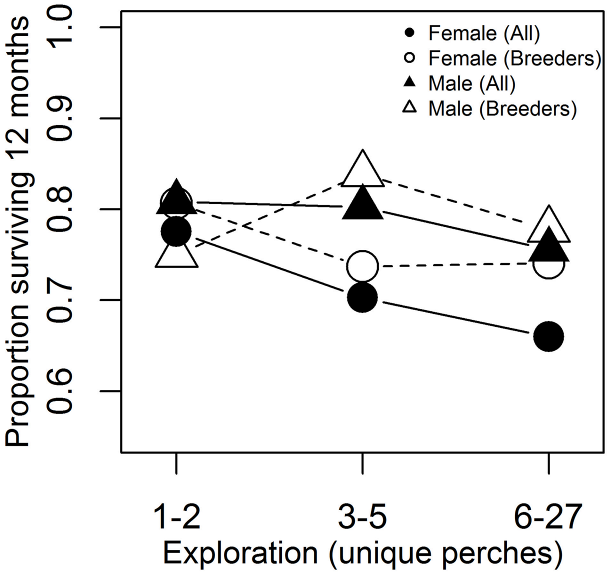

FIGURE 3 | Exploration behavior predicts apparent survival. Individuals that were more exploratory in the artificial environment were less likely to be present in the study population 12 months following the test. See text for results of logistic regression analysis of exploration as a continuous variable (here grouped into thirds for illustration) and controlling for non-independence of birds from the same territory. "Breeders" include only the subset of individuals that have completed natal dispersal, when disappearance from the site is more likely to be due to death alone, rather than a combination of death and long-distance dispersal (most likely for young females).

environment, a context likely to be perceived as dangerous by wild birds. The repeatability of exploration behavior was typical of behavioral traits measured in other studies (Radj = 0.37, the average in the meta-analysis by Bell et al., 2009), while the repeatability of emergence into the test room ("boldness"), activity, and mirror response ("aggression") were lower. These latter traits were all binary—tests and/or scoring methods that do not polarize individuals into two behavioral "types" may allow more powerful estimates of repeatability. Our findings are similar to a large number of studies on a variety of taxa demonstrating consistent individual differences in behavior during an "open field" test (Reale et al., 2007).

We found no overall effect of increasing experience with the test on behavior (sequence and interval effects in **Table 1**), probably because most birds were not tested more than once within the same catching session (spring or autumn). These widely spaced intervals between tests (76% of repeat-tests were conducted more than 3 months after the previous test) thus seemed to minimize effects of prior experience. Other studies have found habituation to the test environment associated with exploration behavior in repeat tests either increasing (when test intervals were short, Dingemanse et al., 2012) or decreasing (Boon et al., 2007) and, within a species, individuals may show substantial variation in short-term habituation patterns (Biro, 2012).

Birds from the same territory were somewhat similar in their activity and mirror response, but not in exploration behavior (territory explained a similar amount of the phenotypic variation to bird in activity and mirror response, but virtually none in exploration; **Tables 1**, **5**). Behavioral similarity among birds from the same territory could be driven by differential settlement patterns (certain behavioral types attracted to certain territories), phenotypic plasticity within individuals to match their behavior with their territory (for example, driven by variation among territories in resources, predation risk, or levels of cover), or genetically-based behavioral similarity among kin (if territory residents are related). In contrast, the social niche hypothesis suggests birds from the same territory would show divergent behaviors associated with role division (Dingemanse and Araya-Ajoy, 2015). The difference in territory effects on behavioral traits of superb fairy-wrens suggests differential effects of these mechanisms. These mechanisms are also likely to affect the sexes differently in superb fairy-wrens. Differential settlement patterns may be relevant to females, since they undertake long-distance natal dispersal to find breeding vacancies, and established female breeders share the territory mostly with relatives (groups form by delayed dispersal of offspring). In contrast, males are highly philopatric with the majority spending their entire life on or close to their natal territory (Mulder, 1995; Cockburn et al., 2008), but male breeders are often unrelated to members of their group due to high rates of extra-pair mating (Mulder et al., 1994; Bain et al., 2014). In this analysis, birds assigned to the same territory included birds resident on the territory and birds not resident in our core area that were captured on the territory (no known territory, so either resident nearby or dispersing through our core area). If these categories of birds differ in their captive exploration scores, this could also contribute to the lack of similarity in this trait between birds from the same territory. Teasing apart the contributions of genetic, environmental, and social effects to individual differences in behavioral traits will help to explain behavioral similarities and differences among birds from the same territory.

The relationship between individual differences in behavior expressed in artificial novel environments and in the wild is a topic of current interest (Niemela and Dingemanse, 2014). In this study, we used the artificial novel environment test to quantify individual differences in response to risk. Some studies have shown positive correlations between exploration of artificial environments and exploration behavior in the wild (for example, Wilson and McLaughlin, 2007; Herborn et al., 2010; Minderman et al., 2010; Bijleveld et al., 2014). Furthermore, research on great tits (*Parus major*) has shown that exploration of an artificial novel environment is related to natal dispersal (Dingemanse et al., 2003), extra-pair mating (Van Oers et al., 2008), nest defense (Hollander et al., 2008; Cole and Quinn, 2014), and territorial defense (Amy et al., 2010). Further work is needed in superb fairy-wrens to determine whether individual differences in behavioral traits assessed in the captive test predict variation in similar traits in the wild, and other aspects of life history.

Long-Term Individual Differences in Risk-Related Behavior

Individual differences in risk-related behavior were fairly consistent over the long-term in superb fairy-wrens, with exploration behavior showing significant repeatability over long test intervals. Nestling docility predicted exploration behavior of juveniles (less than 6 months old), and there was significant between-individual covariation in the exploration behavior of young adults (first 2 years) and old adults (more than 2 years since hatching). However, the between-individual covariation between nestling docility and young adult exploration behavior did not differ from zero (**Table 3**). This may have been because the different test required to assess behavioral responses to risk in the non-mobile nestling stage gave a subtly different assessment of risk-aversion. However, it may also be that early environmental factors influenced juveniles differently, shifting their life-history trajectories and leading to changes in their relative levels of risk-aversion.

Many taxa have ontogenetic boundaries separating life-stages that may differ dramatically, for example, in constraints such as whether individuals are stationary or mobile and in priorities (for example, growth or reproduction). Surprisingly few studies have taken advantage of the opportunity these changed life history contexts provide to improve our understanding of animal personality (Wilson and Krause, 2012a). Although behavior might be expected to shift in association with changes in environments, constraints, or priorities, several studies across a range of taxa have found that consistent individual differences in behavior can be maintained across such ontogenetic boundaries, even if average behaviors change (Niemela et al., 2012; Sprenger et al., 2012; Wilson and Krause, 2012b). The findings of a recent study on captive zebra finches were similar to ours, showing that nestling activity during begging predicted adult activity levels (McCowan and Griffith, 2014).

Correlations between Risk-Related Behavioral Traits

We found correlations between behavioral traits measured in a risky context that were consistent with superb fairy-wrens displaying a proactive-reactive stress coping strategy similar to that identified in a range of other species (Koolhaas et al., 1999). Compared to reactive birds, proactive birds were more likely to enter the test room fast ("bold"), more exploratory, and more likely to be active and to approach their reflection in a mirror ("aggressive"). These between-individual covariances among traits were similar to the covariances among traits varying within individuals across tests (except for emergence; **Table 4**). Nestlings that were less docile in the back-test were also less docile and more exploratory in isolation, and less docile nestlings were more exploratory as juveniles, though the single test meant that we could not distinguish within- and between-individual covariances at the nestling stage.

The proactive-reactive behavioral axis has been described in terms of "fight or flight" vs. "freeze" responses to stress (Coppens et al., 2010). We indeed found that, in the high-threat context of an artificial novel environment, behavioral responses of superb fairy-wrens were rather polarized (often better modeled as binary variables, Supplementary Material Figure S2). Some birds were very active, but most were not, even sometimes freezing for a short while, especially in response to the mirror. While assessing variation in response to risk in less threatening situations might reveal more subtle differences between individuals, the artificial environment test highlighted stark differences in the way individual superb fairy-wrens responded to stress, and a behavioral syndrome of correlated traits.

Individual Characteristics as Predictors of Behavioral Variation

We found no sex- or size-related differences in behavior during the captive test, even though female superb fairy-wrens typically pursue a "faster" life-history strategy than males. Females usually disperse to breed in their first year, whereas males often remain on their natal territory as subordinate helpers for one or more years (female helpers much less common than male helpers in our population, see Study System; also Mulder, 1995) and males must usually survive beyond 3 or 4 years of age to sire offspring (Dunn and Cockburn, 1999). Size is related to life-history strategy in some species, but it is not known whether this is the case in superb fairy-wrens, although male size does not predict within- or extra-pair mating success (Dunn and Cockburn, 1999).

We found mixed support for the proposal that between-individual differences in RRV cause behavioral differences among individuals (asset protection, Wolf et al., 2007). Consistent with the hypothesis, heavier birds (expected to be more risk averse due to higher RRV) were less likely to emerge into the test room fast or be active. However, older birds (expected to be more risk prone due to lower RRV) were instead less likely to emerge into the test room fast or approach the mirror, and between-individual variation in age and mass did not predict exploration behavior. Few other studies have separated between- and within-individual effects of age or mass on risky behavior. Red knots (*Calidris canutus*) showed a negative between-individual correlation between mass and exploratory behavior in captivity (Bijleveld et al., 2014), also consistent with expectations of asset protection.

If variation in RRV underpins variation in risky behavior (Wolf et al., 2007), then within-individual changes in RRV may also explain behavioral variation within individuals. Consistent with this, superb fairy-wrens became more exploratory and active in the artificial environment when they were in poorer condition (weighed less or had less stored fat) or when environmental conditions were harsher (lower recent minimum temperatures), and they also became more exploratory as they aged. Large fat stores can have costs as well as benefits in birds (for example, in terms of flying efficiency and vulnerability to predation, Witter and Cuthill, 1993). However, fairy-wrens do not often fly long distances and tend to maintain low fat levels—in our sample, only 11% of captures had fat scores above 3 (out of 5). The fact that the effect on behavior of reduced fat was similar to that of reduced minimum temperature was consistent with the interpretation that low fat levels indicate poor condition. The effect of age on exploration was inevitably statistically confounded with year and test sequence, but increases in exploration seemed more likely to be attributable to changes with age than to habituation because the effect was larger when test intervals were longer (habituation effects are expected to be greatest with short test intervals, Dingemanse et al., 2012).

While any effects of sex, size, and age on behavior are likely to be directional, effects of mass could involve feedback loops. Positive feedback between individual characteristics that are labile and behavior can promote stable behavioral differences among individuals, whereas negative feedback can erode individual differences (Wolf et al., 2013; Sih et al., 2015). Thus, if risk-averse behavior increased RRV while risk-prone behavior decreased RRV, positive feedback would maintain individual differences in behavior over time. In contrast, if risk-averse behavior decreased RRV, for example if cautious behavior when food was scarce resulted in mass loss, then this negative feedback would erode individual differences in behavior over time. The relatively long-term stability of behavioral differences in superb fairy-wrens suggests that risk-averse behavior had a positive effect on RRV (at least under the environmental conditions characterizing the period of our study). Investigating the effect of risky behavior in the field on subsequent mass, and the effect of mass on subsequent risky behavior would help to determine the nature of any feedback relationships between these labile state and behavior traits in superb fairy-wrens.

Survival and Individual Differences in Risk-Related Behavior

We found that more exploratory birds had lower apparent survival than less exploratory birds (**Figure 3**). We found no evidence of heterogeneity in selection on exploration behavior with respect to sex or year. However, such effects might be more likely when conditions differ between years, and we did not detect overall differences in apparent survival between years. If viability selection on exploration behavior is indeed directional in our population, then the maintenance of behavioral variation would depend on fecundity selection acting in the opposite direction, such that fast explorers have higher annual productivity, or an earlier peak in fecundity, than slow explorers.

Few other studies have investigated the relationship between survival and consistent individual differences in behavior under risk (Smith and Blumstein, 2008). Similar to our finding in superb fairy-wrens, juvenile European rabbits (*Oryctolagus cuniculus*) appeared to experience directional viability selection, since those that were more exploratory were less likely to survive (Rödel et al., 2015). Likewise, female North American red squirrels (*Tamiasciurus hudsonicus*) that were more active in an open field test were less likely to survive until the following spring (Boon et al., 2008). In this species, behavioral variation seemed to be maintained by fitness trade-offs, as females that engaged in more risky behavior in the field were more likely to bequeath their territory to their offspring, a practice that increased offspring fitness (Boon et al., 2008). In contrast, the relationship between novel environment exploration and survival differed between the sexes and between years in great tits in one population (Dingemanse et al., 2004), but not in another (Quinn et al., 2009). In two other studies, less exploratory individuals had shorter lifespans than more exploratory individuals (Banks et al., 2002; Cavigelli and McClintock, 2003).

Death and emigration are not distinguishable in many systems, and many studies reporting links between personality and survival have assessed survival on the basis of local re-sighting or re-trapping (Dingemanse et al., 2004; Boon et al., 2008; Bijleveld et al., 2014; Rödel et al., 2015), thus quantifying "apparent survival," as we did. In the superb fairy-wren system, death is far more likely than emigration to be the cause of disappearance from the site, except in the case of young females at the natal dispersal stage. A 19-year study on superb fairy-wrens found that 72% of males spent their entire life on their natal territory (often inheriting the dominant position there) and, of those that dispersed, 95% settled on a territory immediately neighboring their natal territory (Cockburn et al., 2008). Male disappearance is thus far more likely due to death than undetected dispersal. Natal dispersal distances of females are longer than males and most young females leave the local area, but are thought to suffer high mortality, resulting in the strongly male-biased sex-ratios that characterize superb fairy-wren populations (Mulder, 1995). The weaker effect of exploration behavior on survival when non-breeding females are excluded (clear vs. filled circles in **Figure 3**) suggests that fast-exploring females may be more likely to attempt long distance dispersal. An association between personality traits and dispersal has been found in other studies, including in great tits and bluebirds, *Sialia* spp. (Dingemanse et al., 2003; Duckworth and Badyaev, 2007). For example, there is significant genetic covariance between exploration behavior and local dispersal distances in great tits (Dingemanse et al., 2003; Korsten et al., 2013). Although the precise mechanism is not known, it has been suggested to be mediated by an association between exploration behavior in the novel environment test with exploratory behavior in the field rather than the suite of "proactive" behavioral traits (Korsten et al., 2013).

Alternative mechanisms could explain the relationship between individual differences in exploration behavior and survival (Montiglio et al., 2014). Individuals that engage in more risky behavior may increase their exposure to extrinsic causes of mortality such as predators or pathogens, and suffer higher mortality as a consequence of their risky behavior. Alternatively, intrinsic differences in lifespan among individuals may drive short-lifespan birds to engage in more risky behavior to ensure early reproductive success. Comparative studies have shown that variation in age at first reproduction is linked to metabolic rates and exploration behavior in rodents (Careau et al., 2009), while variation in lifespan across species is linked to rates of telomere shortening in birds and mammals (Haussmann et al., 2003). Resolving the nature of the relationship between individual differences in risky behavior and survival in superb fairy-wrens will require further investigation of the mechanisms involved, such as assessing individual differences in willingness to approach predators, or in intrinsic aging processes.

Author Contributions

MH, ND, MM, and RM conceived and designed the work. MH, TA, and AK conducted the behavioral tests on nestling and adult birds. MH analyzed the data and wrote the article. All authors contributed to interpretation of the data, and revised and commented on drafts of the article.

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Supplementary Material

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2015.00028/abstract

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