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CONCEPTS, REVIEWS AND SYNTHESES

Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level

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Abstract Behavioral traits and diet were traditionally thought to be highly plastic within individuals. This view was espoused in the widespread use of optimality models, which broadly predict that individuals can modify behavioral traits and diet across ecological contexts to maximize fitness. Yet, research conducted over the past 15 years supports an alternative view; fundamental behavioral traits (e.g., activity level, exploration, sociability, boldness and aggressiveness) and diet often vary among individuals and this variation persists over time and across contexts. This phenomenon has been termed animal personality with regard to behavioral traits and individual specialization with regard to diet. While these aspects of individual-level phenotypic variation have been thus far studied in isolation, emerging evidence suggests that personality and individual specialization may covary, or even be causally related. Building on this work, we present the overarching hypothesis that animal personality can drive specialization through individual differences in various aspects of consumer foraging behavior. Specifically, we suggest pathways by which consumer personality traits influence foraging activity, risk-dependent foraging, roles in social foraging groups, spatial aspects of foraging and physiological drivers of foraging, which in turn can lead to consistent individual differences in food resource use. These pathways provide a basis for generating testable hypotheses directly linking animal personality to ecological dynamics, a major goal in contemporary behavioral ecology.

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Introduction

Individual-based approaches in ecology seek a mechanistic understanding of how variation among individual organisms generates or contributes to patterns at population, community and ecosystem levels. This differs from traditional population-based approaches that treat individuals as ecologically equivalent, as well as phenomenological community approaches that lack lower-level derivations altogether (Schoener 1986). Individual-based approaches in ecology have recently gained traction (e.g., Dall et al. 2012; Sih et al. 2012; Careau and Garland 2012) for several reasons. First, because natural selection occurs at the individual level, studying individual variation clarifies links between ecological and evolutionary processes (Bolnick et al. 2011; Schreiber et al. 2011; Careau and Garland 2012); this is increasingly relevant in light of recognition that evolution can occur over ecological time scales (i.e., eco-evolutionary dynamics: Pelletier et al. 2009; Post and Palkovacs 2009). Second, recent work has shown that intraspecific levels of variation can have ecological effects

greater than among-species variation (e.g., Rall et al. 2011; Rudolf and Rasmussen 2013). In these cases, incorporating intraspecific levels of variation, including individual variation, is essential for understanding population and community dynamics. Lastly, incorporation of individual variation undoubtedly provides a more complete description of an ecological system. While this comes at a cost of increased complexity, new statistical methods allow for explicit consideration of individual effects in empirical studies (Dingemanse and Dochtermann 2013), and advances in computing tools and power permit modeling of higher-level dynamics derived from individual-level processes (Grimm and Railsback 2005; de Roos and Persson 2013).

Over the past 15 years, consistent individual differences in behavior (animal personality) and food resource use (individual specialization) have come to the forefront of behavioral and food web ecology, respectively. Behavioral ecologists have long recognized that conspecific individuals differ in behavioral traits when measured at a single time point. However, relatively recent work has shown that individual behavioral differences are often consistent over time and even across ecological contexts (Gosling 2001; Sih et al. 2004). This phenomenon, termed animal personality, has now been documented across diverse invertebrate and vertebrate taxa (Gosling 2001; Bell et al. 2009). Current research examines the evolution of animal personality (Wolf et al. 2007; Stamps and Groothuis 2010; Careau and Garland 2012; Wolf and Weissing 2010) and its effects on population and community dynamics (Sih et al. 2012; Dall and Griffith 2014). Similarly, food web ecology has seen a renewed interest in individual specialization, defined as individual variation in food resource use within a population that is consistent over time (Bolnick et al. 2003). Individuals function as specialists in such a scenario, utilizing a subset of the resources used by the population as a whole (Van Valen 1965; Bolnick et al. 2003). Individual specialization is also taxonomically widespread (Bolnick et al. 2003) and has major implications for resource competition (Svanback and Bolnick 2007), top-down control (Estes et al. 2003) and patterns of food web connectance and dynamics (Araújo et al. 2011; Layman et al. 2015).

The research areas of animal personality and individual specialization have developed at astonishing rates, but have done so mostly in isolation from one another (Dall et al. 2012). This has prompted the suggestion by Dall et al. (2012) that rapid application of individual-based approaches has divided research, somewhat artificially and prematurely, into separate domains. Here, we argue that this trend is especially problematic with regard to animal personality and individual specialization, because a growing body of evidence suggests that these aspects of phenotypic variation may be causally related within certain ecological scenarios. Araújo et al. (2011) recently identified four major ecological drivers of individual specialization: intraspecific competition, interspecific competition, predation and ecological opportunity. Here, we suggest animal personality as an additional factor contributing to the existence and persistence of individual specialization.

Specifically, we hypothesize that animal personality promotes individual specialization by driving individual differences in consumer foraging behavior. To explore this hypothesis, we first review research on animal personality and individual specialization as relatively recent applications of the individual-based approach in behavioral and food web ecology, respectively, focusing on several shared features and intersections between these phenomena. We then explore how behavioral traits typically measured in animal personality research (activity level, exploration, sociability, boldness and aggressiveness: Réale et al. 2007) can influence multiple aspects of consumer foraging behavior (see also Table 1), which in turn could lead to individual specialization. Specifically, to help guide future research, we suggest five mechanistic links between animal personality and individual specialization (Fig. 1, middle column), which are explored in detail in later sections:

1. *Foraging activity* Activity level measured in non-food situations often predicts the foraging activity of individual predators and the activity level of the prey they tend to consume (Pruitt et al. 2012; McGhee et al. 2013; Sweeney et al. 2013; Toscano and Griffen 2014).
2. *Foraging across the "landscape of fear"* Boldness as a personality trait has been shown to influence the risk individuals are willing to take while foraging (Griffen et al. 2012), and high-risk versus low-risk habitats often differ in available food resources (Godin 1990; Houtman and Dill 1998; Hernández and Laundré 2005).
3. *Social aspects of foraging* Several animal personality traits have been linked to intraspecific, social aspects of foraging, such as competitive hierarchies (Briffa et al. 2015) or foraging independently versus in groups (Kurvers et al. 2010), thereby influencing the resources an individual has access to.
4. *Spatial aspects of foraging* Animal personality traits often covary with individual dispersal, migration tendency and home range size in natural populations (Fraser et al. 2001; Cote et al. 2010; Chapman et al. 2011; Quinn et al. 2011; Cote et al. 2013), suggesting that personality can lead to individual specialization when resources are distributed heterogeneously across the landscape.
5. *Physiological drivers of foraging* Animal personality is often related to energetic traits, such as baseline metabolic rate (Careau et al. 2008; Biro and Stamps 2010;

Table 1 Studies (see Online Resource 1 for full references) that demonstrate how five major animal personality axes (activity level, exploration, sociability, boldness, aggressiveness) can affect the foraging behavior of consumers

Consumer–resource system	Consumer behaviors measured	Personality axes	Personality methodology	Main result	Citation
Ocher sea star (*Pisaster ochraceus*)–turban snail (*Chlorostoma funebralis*)	Distance traveled within an enclosure	Activity level	Repeatability in a single context	Active starfish consumed snails with low-risk avoidance, less-active starfish consumed snails with high-risk avoidance	Pruitt et al. (2012)
Old field jumping spider (*Phidippus clarus*)–house cricket (*Acheta domesticus*)	Time to climb to top of holding vials	Activity level	Repeatability in a single context	Active spiders consumed sedentary crickets, sedentary spiders consumed active crickets	Sweeney et al. (2013)
Common mud crab (*Panopeus herbstii*)–scorched mussel (*Brachidontes exustus*)	Proportion of time active in the absence and presence of a predator	Activity level, boldness	Repeatability in a single context, cross-context behavioral correlation (referenced)	Crab activity level increased mussel consumption	Toscano and Griffen (2014)
Wolf spider (*Pardosa milvina*)–various insects	Distance traveled within a plastic arena	Activity level	Repeatability in a single context	Activity level composition of spider groups altered insect prey community structure	Royauté and Pruitt (2015)
Threespine (*Gasterosteus aculeatus*) and ninespine (*Pungitius pungitius*) sticklebacks–water fleas (*Daphnia* spp.)	Latency of fish to leave refuge habitat and attack prey	Boldness	Repeatability in a single context	Bolder sticklebacks consumed a greater share of prey in interspecific pairs	Webster et al. (2009)
Namibian rock agama (*Agama planiceps*)–insects and plant material	Flight initiation distance	Boldness	Repeatability in a single context	Bold male agamas fed at a higher rate than shy males	Carter et al. (2010)
Barnacle geese (*Branta leucopsis*)–ryegrass (*Lolium perenne*)	Minimum distance from a novel object, and time elapsed to reach a novel object	Boldness (or exploration)[a]	Cross-context behavioral correlation	Shy geese tend to join feeding groups and spend less time feeding than bold geese	Kurvers et al. (2010)
Common mud crab (*Panopeus herbstii*)–scorched mussel (*Brachidontes exustus*)	Proportion of time spent in refuge in the presence of predation threat	Boldness	Cross-context behavioral correlation	Crab refuge use decreased mussel consumption in the presence of a higher-order predator	Griffen et al. (2012)
Black widow spider (*Latrodectus hesperus*)–field cricket (*Gryllus integer*)	Tendency to settle in safe versus high-risk foraging environments	Boldness	Repeatability in a single context	Bold spiders preferentially consumed bold crickets, while shy spiders preferentially consumed shy crickets	DiRienzo et al. (2013)
Great tits (*Parus major*)–firebugs (*Pyrrhocoris apterus*)	Reaction to novel objects, behavior in a novel environment	Exploration[a]	Cross-context behavioral correlation	Exploratory birds were more likely to attack a novel aposematic prey (firebugs)	Exnerová et al. (2010)
Comb-footed spider (*Anelosimus studiosus*)–termites (species not given)	Distance between spiders after 24 h of pairing in a container	Sociability	Repeatability in a single context	Asocial spiders exhibited a quicker response to prey and consumed more prey	Pruitt et al. (2008)

Table 1 continued

Consumer–resource system	Consumer behaviors measured	Personality axes	Personality methodology	Main result	Citation
Northern pike (*Esox lucius*)–three-spined stickleback (*Gasterosteus aculeatus*)	Latency to orient toward and attack prey	Unknown	Repeatability in a single context	Reciprocal behavioral plasticity during predator–prey interactions	McGhee et al. (2013)

Only studies of wild as opposed to domestic animals are included. Furthermore, to be included, studies must demonstrate the persistence of individual behavior across time or contexts, or reference studies that have demonstrated persistence within the same consumer population. Columns include the consumer–resource system, the consumer behaviors measured, the personality axes these traits fall under (as indicated in the study), the methodology used to demonstrate personality (e.g., repeated behavioral measurements on a single individual) and the main result. Studies were found using online literature searches and by consulting review articles on the ecological consequences of animal personality (e.g., Sih et al. 2012)

[a] Occasionally, our definitions of the five major personality axes (see Fig. 1) differed from those used by the author(s) in the original study, or the original study did not suggest a personality axis; in these cases, we also list the personality axis measured as defined in Fig. 1

Careau and Garland 2012). Thus, individual consumers may specialize or expand diet breadth to satisfy their specific energetic demands.

Individuality in behavioral and food web ecology

Here, we briefly review research on animal personality and individual specialization with emphasis on a number of commonalities between these phenomena (see also Dall et al. 2012). These commonalities lay the groundwork for potential covariation or causal relationships between personality and specialization in nature. For more exhaustive review and synthesis, we direct the reader to work by Sih et al. (2004, 2012) on animal personality and to work by Bolnick et al. (2003) and Araújo et al. (2011) on individual specialization.

Animal behavior and diet were traditionally viewed as being plastic within individuals. In contrast, animal personality and individual specialization research suggests that these aspects of phenotype vary among individuals, with surprisingly low within-individual variation (Gosling 2001; Bolnick et al. 2003). Furthermore, among-individual variation in behavioral traits and diet is often consistent over relatively long timescales within an organism's lifespan (Estes et al. 2003; Woo et al. 2008; Bell et al. 2009), and even across ecological contexts (Sih et al. 2004). Specifically, animal personality describes consistent individual differences in fundamental behavioral traits, which can be categorized into five major behavioral axes: activity level, exploration, sociability, boldness and aggressiveness (Réale et al. 2007; see Fig. 1 for definitions). Within animal personality, behavioral types describe among-individual variation in a single behavioral trait that is consistent over time, while behavioral syndromes describe correlations between two or more behavioral traits, or correlations between measures of a single behavioral trait across different ecological contexts (Huntingford 1976; Sih et al. 2004). Similarly, individual specialization describes consistent individual differences in diet within a population, where for example, a seemingly generalist population is actually composed of individual specialists with little dietary overlap (Van Valen 1965; Bolnick et al. 2003). Like animal personality, temporal consistency is a key feature of individual specialization, often measured by long-term indicators of food resource use such as stable isotopes (e.g., Bearhop et al. 2004; Gownaris et al. 2015). Thus, animal personality and individual specialization describe similar concepts of temporally consistent individuality in behavioral and food web ecology.

These patterns of individual-level phenotypic variation, animal personality and individual specialization, provide an important conceptual departure from optimal behavior theory which previously dominated research in behavioral
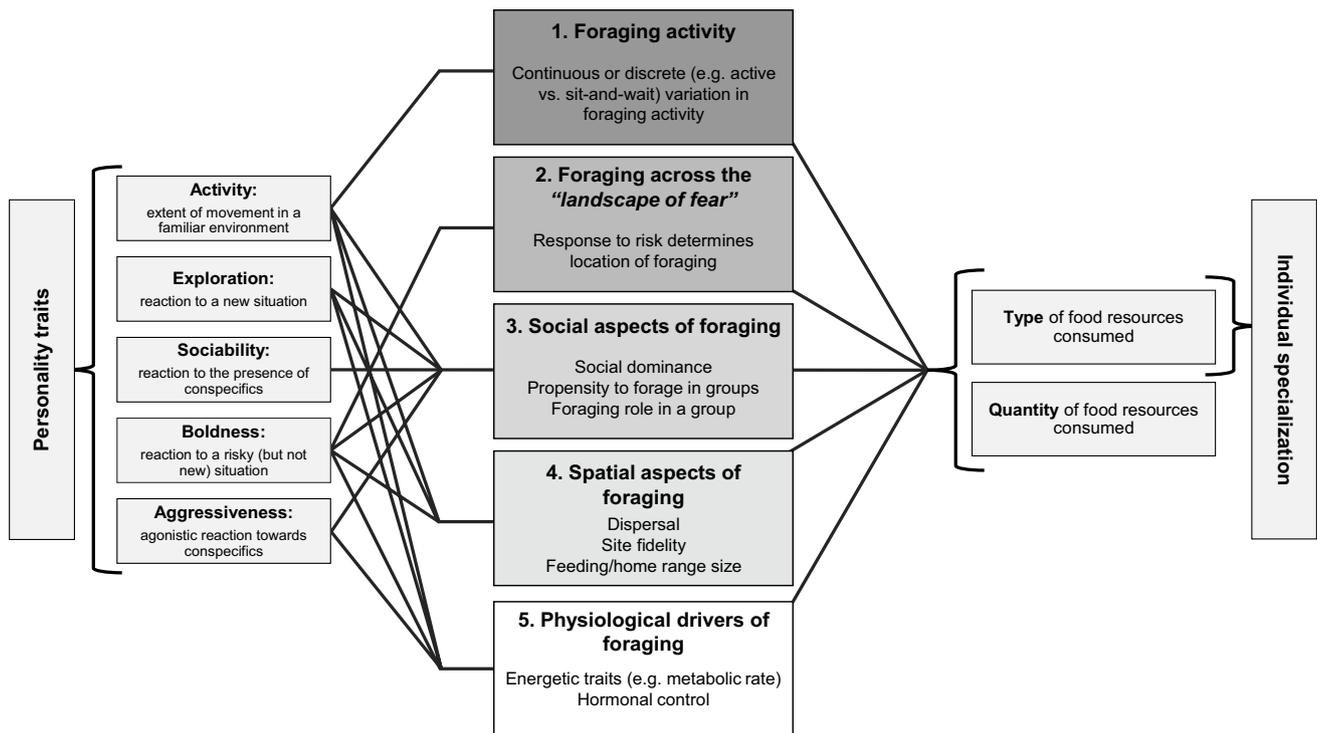
Fig. 1 A conceptual diagram illustrating how animal personality helps to explain the existence and persistence of individual specialization (i.e., individual diet breadth <population diet breadth: Bolnick et al. 2003) by driving differences in individual consumer ecology and food resource use. Links between the five personality traits and specific aspects of foraging behavior are supported by previous studies (Table 1) or hypothesized (see main text). Definitions of personality traits follow Réale et al. (2007)

ecology and food resource use (Pyke et al. 1977; Stephens and Krebs 1986; Sih and Christensen 2001). Optimality theory broadly predicts that individuals adaptively modify their behavior or diet depending on ecological conditions to maximize some fitness-related function (MacArthur and Pianka 1966; Stephens and Krebs 1986). In contrast, animal personality and individual specialization suggest constraints that limit individuals from behaving or utilizing food resources optimally across situations. Thus, trade-offs exist, where a relatively active individual, for example, will forage at a higher rate in the absence of a predator but incur a relatively high risk of mortality in the presence of a predator (Smith and Blumstein 2008). Animal personality and diet specialization can therefore help to explain suboptimal (i.e., seemingly maladaptive) behavior and food resource use in natural populations (Quinn and Cresswell 2005; Carter et al. 2010).

Another key shared feature of animal personality and individual specialization is that among-individual variation in behavioral traits and food resource use is often independent of other more easily measured aspects of phenotype (e.g., age, size, sex, trophic polymorphism: Bolnick et al. 2003). For example, variation in exploration behavior among individual great tits (*Parus major*) is unrelated to sex, age or condition (Dingemanse et al. 2002). Similarly,

individuals of a piscivorous cichlid species (*Lepidiolamprologus profundicola*) consistently use a small subset of nine possible hunting techniques that are unrelated to size, sex or color morph (Kohda 1994). Thus, demonstrating animal personality and individual specialization requires satisfying similar criteria with regard to temporal consistency in among-individual variation and independence from more basic phenotypic aspects.

Integration of animal personality and individual specialization

Consideration of animal personality and individual specialization in the literature has increased substantially since the turn of the twenty-first century, coinciding with important reviews by Gosling (2001) and Bolnick et al. (2003) that helped establish the taxonomic ubiquity of animal personality and individual specialization, respectively. Specifically, a literature search within the ecological sciences revealed that since the year 2000, 619 papers have mentioned a term related to animal personality, while 176 papers have mentioned a term related to individual specialization, with the number of papers mentioning these terms per year increasing. Nevertheless, the same literature search detected only

four papers (Grinsted et al. 2013; McGhee et al. 2013; Toscano and Griffen 2014; Royauté and Pruitt 2015) that mention *both* a term related to animal personality and a term related to individual specialization, suggesting a striking lack of integration between these subfields (searches were conducted in April 2016 using Web of Science ™ Core Collection with animal personality search terms: "animal personality", "behavioral/behavioural syndrome", "behavioral/behavioural type", "coping style", "repeatable individual behavior/behaviour", "temperament"; individual specialization search terms: "individual specialization", "individual resource specialization", "intraspecific diet variation", "individual niche width", "type B generalist").

Several explanations exist for this lack of integration. First, animal personality and individual specialization research rely on different methodologies [e.g., laboratory behavioral assays or open field tests in animal personality (Dall and Griffith 2014), stable isotopes in individual specialization (Bearhop et al. 2004)]. Thus, it is possible that a lack of shared skills or techniques among behavioral and food web ecologists has limited integration of animal personality and individual specialization research (see also 'Discussion: Methodological constraints'). Second, insufficient communication and collaboration between behavioral and food web ecologists could explain the lack of integration between animal personality and individual specialization. The majority of animal personality research is published in behavioral journals (e.g., Animal Behavior, Behavioral Ecology, Behavioral Ecology and Sociobiology), and this research has only recently begun to infiltrate more general ecological journals familiar to consumer–resource or food web ecologists.

Foraging behavior as a functional link between animal personality and individual specialization

Consumer–resource interactions are central to ecological community structure and dynamics. Understanding factors that influence consumer foraging behavior is thus an important and perennial goal in ecology (Stephens and Krebs 1986). Here, we suggest that foraging behavior provides a key link between animal personality and individual specialization. While individual specialization is inherently tied to consumer–resource interactions, animal personality has only recently been linked to the process of predation (Kurvers et al. 2010; Griffen et al. 2012; Pruitt et al. 2012; Sweeney et al. 2013; Toscano and Griffen 2014; see Table 1 for examples). We examine this emerging body of research through the lens of the five aforementioned mechanisms to explore how personality might lead to individual specialization via individual foraging behavior (Fig. 1). It is important to note that some of these mechanisms are most likely driven by

a single personality axis (e.g., 'Foraging across the landscape of fear' driven by boldness), while other mechanisms could be driven by one or more of the five major personality axes (Fig. 1). Furthermore, we emphasize that none of these links have been demonstrated empirically to our knowledge and thus represent hypotheses in need of research attention.

Foraging activity

Activity level, one of the most well-studied personality traits (Careau et al. 2008; Bell et al. 2009), has been shown to vary consistently within populations of amphibians (Urszán et al. 2015), fish (Colléter and Brown 2011), reptiles (Mafli et al. 2011), birds (Quinn and Cresswell 2005), mammals (Boon et al. 2007) and invertebrates (Pruitt et al. 2011; Toscano and Griffen 2014). This trait is typically measured as the spatial or temporal amount of individual movement in an environment familiar to the test animal. This definition distinguishes activity level from another commonly measured personality trait, exploration, which in contrast measures the amount of space covered in an environment that is novel to the test animal (Dingemanse et al. 2002; Réale et al. 2007).

In the study of foraging behavior and consumer–resource interactions, foraging activity, as opposed to activity level per se, underlies a dichotomy in predator foraging or hunting modes. Specifically, active predators search for prey, while sit-and-wait or ambush predators rely on prey movement to initiate predator–prey contact, though in reality, many predators forage along a continuum between these extremes (Huey and Pianka 1981; Perry 1999; Schmitz 2008). As a result of alternative foraging modes, active predators tend to capture prey that are stationary, while sit-and-wait predators tend to capture prey that are more active (locomotor crossover hypothesis: Huey and Pianka 1981; Scharf et al. 2006; Schmitz 2008; Pruitt et al. 2012; Sweeney et al. 2013). For example, actively foraging stoneflies almost exclusively capture and consume sedentary or slow-moving prey as opposed to active prey in feeding preference experiments (Allan et al. 1987; Tikkanen et al. 1997).

Recent studies have successfully linked activity level as a personality trait to foraging activity. Notably, three studies (Pruitt et al. 2012; McGhee et al. 2013; Sweeney et al. 2013) demonstrate that individual predator activity level, measured in independent behavioral assays, predicts the behavioral type of prey consumed in laboratory feeding trials: active predator individuals tend to consume prey individuals that are inactive, while relatively inactive predator individuals tend to consume prey individuals that are active (Pruitt et al. 2012; Sweeney et al. 2013). Thus, these studies

show that the locomotor crossover hypothesis, originally developed at the species level (Huey and Pianka 1981), also applies within populations or species. These studies paired a single predator species with a single prey species with both predator and prey individuals exhibiting consistent variation in their behavioral traits. In a situation with multiple prey species differing in activity, predator activity level as a personality trait could drive individual differences in the species or functional group of prey consumed. Though this link between personality and individual specialization is yet to be demonstrated, the above evidence suggests that this scenario is possible in natural populations.

Foraging across the "landscape of fear"

Boldness, defined as an individual's reaction to a risky (but not novel) situation, represents another of the five major behavioral axes commonly studied in animal personality research (Réale et al. 2007). One example of a ubiquitous risky situation is the presence of predator, where risky behavior increases the chances of being consumed. While animals often modify their behavior to avoid being consumed (Lima and Dill 1990), animal personality research suggests individual constraints that drive differences in responsiveness to predation risk with important fitness consequences (Smith and Blumstein 2008).

Predation risk often varies among habitats and this concept has been dubbed the "landscape of fear" (van der Merwe and Brown 2008). Landscapes (or seascapes) of fear are even visible from space, as indicated by the spatial distribution of grazed algae around the refuge habitat of herbivorous coral reef fish (Madin et al. 2011). Prey animals may respond to landscapes of fear by concentrating foraging activity in habitats with relatively low risk, though these habitats may harbor reduced food resource availability due to intraspecific competition or food resources of lower quality. Work by Hernández and Laundré (2005), for example, shows that elk (*Cervus elaphus*) shifted their use of foraging habitat from risky open meadows to safer forest edges coinciding with the reintroduction of wolves into Yellowstone National Park, USA. This habitat shift resulted in reduced diet quality for elk, as indicated by lower nitrogen content in fecal pellets (Hernández and Laundré 2005; see also Christianson and Creel 2008). Similar examples of diet shifts associated with predation risk have been shown in fish (Werner et al. 1983; Ibrahim and Huntingford 1989), lizards (Cooper 2000) and spiders (Rothley et al. 1997). Thus, the level of predation risk among habitats is a major determinant of diet (Godin 1990; Houtman and Dill 1998).

Considering widespread variation in individual boldness within populations, we contend that risk-dependent selection of foraging habitat can drive individual specialization. Bold individuals are more likely to forage in habitats with high predation risk compared to shy individuals, and these habitats often differ in available food resources. Evidence related to this hypothesis is presented in a study by Griffen et al. (2012), which demonstrates that mud crabs (*Panopeus herbstii*) are distributed spatially according to their level of individual boldness: bold mud crabs, as measured in an independent behavioral assay, tend to inhabit subtidal portions of oyster reefs, while shy crabs tend to inhabit intertidal portions of reefs. Crabs inhabiting subtidal reef habitat are more exposed to predatory fish due in part to greater submersion time, but greater submersion time also allows crabs to potentially spend more time foraging (Griffen et al. 2012). While this study suggests a potential link between boldness and the amount of food resources consumed, the effects of boldness on individual specialization (i.e., diet) remain unexplored.

Social aspects of foraging

Several personality traits, including activity level, boldness, aggressiveness and exploration (Aplin et al. 2014, 2011; David et al. 2011; Favati et al. 2014; González-Bernal et al. 2014), have been shown to influence social aspects of foraging behavior, which in turn may lead to differences in the food resources an individual can access and consume. This can occur through several mechanisms. First, personality often determines position in social dominance hierarchies (e.g., boldness: Rudin and Briffa 2012; exploration: Favati et al. 2014; aggressiveness: Wilson et al. 2013). In turn, an individual's place in a dominance hierarchy can determine the food resources it consumes (e.g., Gende and Quinn 2004; Hansen and Closs 2005). Second, among socially foraging species, individuals may differ in their propensity to forage among conspecifics depending on their behavioral type (Michelena et al. 2009; González-Bernal et al. 2014). Foraging in isolation versus in groups can lead to consistent individual differences in food resource use. Third, an individual's behavioral type may determine its specific role in foraging groups, which may influence the food resources it consumes (best studied in producer–scrounger systems: Kurvers et al. 2010). For example, foraging is more energetically costly for producers (individuals that find resource patches) than for scroungers (individuals that join producers at resource patches) (Vickery et al. 1991; Jolles et al. 2013), and thus the persistence of both foraging modes suggests a trade-off. One explanation for this trade-off is that producers, by entering food patches first, can access the highest-quality resources available before scroungers arrive, thus balancing their greater energetic costs.

Social dominance in resource use is one of several factors that may promote individual specialization (Van Valen 1965; Holbrook and Schmitt 1992; Estes et al. 2003; Araújo et al. 2011). While body size or physiological traits have often been cited as key predictors of social dominance (Beacham 1988; Metcalfe et al. 1992; Beaugrand et al. 1996; Ward et al. 2006; Cervo et al. 2008), recent research suggests that personality traits such as aggressiveness (i.e., the propensity for agonistic interactions with conspecifics), boldness and exploration may also play important roles (e.g., birds: Fox et al. 2009; David et al. 2011; Favati et al. 2014, but see Funghi et al. 2015; fish: Aplin et al. 2014, 2011; mammals: Gende and Quinn 2004). Furthermore, there is an extensive body of literature regarding the relationship between an individual's position in a dominance hierarchy and diet. Dominant individuals may have access to higher-quality feeding habitats (Holbrook and Schmitt 1992), feed during more beneficial times of day (Alanärä et al. 2001; Hansen and Closs 2005) or forage longer (Daily and Ehrlich 1994) than subordinate individuals. Conversely, subordinate individuals often expend more energy on vigilance while foraging (Waite 1987; Gende and Quinn 2004) or may be forced to generalize their diets to include sub-optimal resources (Holbrook and Schmitt 1992). Differences in diet may even persist in the absence of competition, as subordinate individuals can become "familiar" with lower-quality prey items (Milinski 1982). As might be expected, differences in food resource utilization between dominant and subordinate individuals are particularly prominent in the face of resource scarcity (Alanärä et al. 2001; Gende and Quinn 2004; Hansen and Closs 2005; Clutton-Brock and Huchard 2013; Marshall et al. 2015).

Personality can also determine whether an individual will feed in the absence or presence of conspecifics and, for group foragers, the size and cohesiveness of foraging groups (Michelena et al. 2009; Aplin et al. 2014; González-Bernal et al. 2014). For example, shy cane toads (*Rhinella marina*) are more likely to forage in a novel environment in the presence of a conspecific, whereas bold toads will forage in a novel environment with or without social stimulus (González-Bernal et al. 2014). Similarly, bold sheep (*Ovis aries*) tend to break into sub-groups while feeding, while shy sheep are more likely to stay in large groups even if this means feeding on lower-quality resources (Michelena et al. 2009). The propensity to forage only among conspecifics may therefore limit the resources available to an individual, particularly in novel or risky environments.

Among species that forage in groups, individuals often play different roles to increase group foraging success via the "skill pool effect" (Keynan et al. 2014). This phenomenon can be illustrated by well-studied producer–scrounger

systems, where individuals with socially dominant behavioral types are more likely to be producers and individuals with subordinate behavioral types are more likely to be scroungers (Kurvers et al. 2010; Jolles et al. 2013). While producers are more effective at finding customary food sources, scroungers may be better learners and therefore better at discovering novel food sources (Keynan et al. 2014). These differing abilities may lead to distinct food resource patterns among producers and scroungers. In sum, the effects of personality on various social aspects of foraging represent unexplored pathways by which animal personality can lead to diet differences among individuals.

Spatial aspects of foraging

Animal personality traits often determine individual dispersal tendency within natural populations (Fraser et al. 2001; Cote and Clobert 2007; Cote et al. 2010), while other work demonstrates that personality can influence foraging site fidelity (i.e., the regularity of foraging in a given location) as well as the size of an animal's home range or foraging territory (e.g., Boon et al. 2008; Minderman et al. 2010; van Overveld and Matthysen 2010; Harrison et al. 2015). Personality-driven dispersal and spatial aspects of foraging may therefore determine individual diet when food resources are distributed heterogeneously across the landscape.

Dispersal, defined as the movement of an organism from its natal habitat to its breeding habitat, influences processes such as gene flow, species distributions and invasions, as well as the location of individual foraging behaviors and resource use. Personality traits such as boldness, sociability or aggressiveness have been shown to covary with individual dispersal tendency (i.e., "dispersal syndromes" sensu Clobert et al. 2009). Dispersal distance in Western bluebirds (*Sialia mexicana*), for example, is linked to personality and resource availability: aggressive males, and males with fewer resources in natal territories, disperse farther than conspecifics (Aguillon and Duckworth 2015). While resource availability in this example was defined as the number of available breeding spaces, in many cases food resource availability may be an important factor in the decision to disperse and the ultimate dispersal distance. This is shown in great tits (*Parus major*), where the response to food manipulation varies with personality type. Following the removal of a known food resource, fast-exploring individuals travel farther distances in search of food than slow-exploring individuals (van Overveld and Matthysen 2010). When food resources vary across a landscape, individual differences in dispersal affecting foraging location could promote individual specialization.

Home range size and site fidelity influence the location and spatial distribution of individual foraging behaviors and are often related to personality. Harrison et al. (2015) found correlations between home range, site fidelity and movement distance among individual burbot (*Lota lota*), defining a continuum from "resident" to "mobile" individuals. Diet variation between resident and mobile individuals was not investigated in this study, but it is possible that individuals with large home ranges and low site fidelity have access to different (or a greater breadth of) food resources than individuals with small home ranges and high site fidelity. In starlings, for example, exploration behavior influences the extent and most frequently used part of the home range (Minderman et al. 2010). For particularly exploratory individuals, large home range size was correlated with lower food quality; these individuals appear to travel greater distances in search of food and utilize different foraging habitats than individuals with small home ranges (Minderman et al. 2010). Similarly, in red squirrels (*Tamiasciurus hudsonicus*), active females travel farther outside of their home ranges than do less active females, potentially in search of food to steal from other squirrels' middens or for the purpose of gathering information about new territories (Boon et al. 2008). Lastly, in sessile giant sea anemones (*Condylactis gigantea*), shy individuals occupy habitats with greater seagrass density and more conspecifics than bold individuals (personality measured as the time between tentacle retraction and relaxation following predator disturbance: Hensley et al. 2012). Although the mechanism driving spatial segregation is unclear (i.e., whether personality influences habitat selection during the mobile larval stage, or whether habitat types favor different behavioral types), the location of individual anemones may influence the food resources available to and utilized by each individual. In aggregate, this work suggests that personality may influence the habitats in which individuals forage, which in turn can generate consistent individual differences in food resource use within populations.

Physiological drivers of foraging

The link between animal personality, foraging behavior and individual specialization may also be driven by physiological processes, notably energetics (Biro and Stamps 2010) and hormonal control (Farwell et al. 2014). Like fundamental behavioral traits (animal personality) and diet (individual specialization), physiological traits have been shown to vary consistently among individuals within populations (Nespolo and Franco 2007; White et al. 2013). Metabolic rate, for example, is repeatable at the individual level within a number of invertebrate and vertebrate species

(Nespolo and Franco 2007), even when corrected for the effect of individual body mass (White et al. 2013). Other physiological traits that influence organisms' energy budget and condition have also been tested for repeatability. In juveniles of the Pacific abalone (*Haliotis discus hannai*), for example, ammonia excretion (as well as baseline metabolic rate) exhibited strong repeatability among individuals over a 4- to 5-month period of measurements (González et al. 2010).

There is growing evidence that animal personality can be related to such proximal physiological components (Careau et al. 2008; Biro and Stamps 2010; Careau and Garland 2012; Bijleveld et al. 2014). For instance, exploration in shore crabs (*Carcinus maenas*) is correlated with physiological condition, as indicated by hemolymph density (a proxy for protein concentration) (Fürtbauer 2015), and activity in a salmonid fish (*Salvelinus fontinalis*) is related to individual levels of cortisol, a stress-related hormone (Farwell et al. 2014). Thus, physiology has emerged as a potential state variable related to animal personality (Bolnick et al. 2003; Careau et al. 2008; Biro and Stamps 2010; Thompson et al. 2011; Careau and Garland 2012). Discussion regarding the causes and consequences of a correlation between personality and individual physiological traits has centered on energy balance models such as the "increased intake model" (Careau et al. 2008). This model holds that energetically expensive behaviors (e.g., activity, boldness, aggression) require higher metabolic rates to support greater energetic demands (Biro and Stamps 2008; Réale et al. 2010). Thus, based on the increased intake model, it can be expected that bolder or more active individuals would exhibit increased foraging activity (Biro and Stamps 2010; Careau and Garland 2012) and this notion has received some empirical support (Careau et al. 2008; McGhee et al. 2013, but see Toscano and Monaco 2015). For instance, in a recent study on pike (*Esox lucius*), metabolic rate was found to be positively related to predatory behavior toward stickleback prey (*Gasterosteus aculeatus*), as measured by attack rate (McGhee et al. 2013). Predictions from the increased intake model may be naturally extended to account for an individual's diet (i.e., individual specialization). Specifically, based on this model, we expect that more active or bolder individuals, whose metabolic rates are higher, should consume more or higher-quality food, or increase their diet breadth to satisfy energy demands.

Discussion

Animal personality and individual specialization are taxonomically widespread with important consequences for population and community ecology (Bolnick et al. 2003;

Sih et al. 2012; Layman et al. 2015). To date, these aspects of individual-level phenotypic variation have been studied almost completely in isolation. We have argued here that animal personality and individual specialization share a number of key features and that these shared features provide the basis for potential causal relationships between personality and individual specialization in nature. In particular, evidence that animal personality traits can exert a strong influence on individual consumer foraging behavior is rapidly emerging (Table 1), and foraging behavior in turn determines the type of food resources that an individual can access and consume. Because personality traits by definition are consistent over time, personality can drive consistent individual differences in food resource use within populations. We have focused on five mechanistic pathways by which personality can influence individual specialization, but this list is not exhaustive. Rather, these pathways are those best supported by empirical and theoretical studies published to date.

Direction of causal relationships between personality and individual specialization

While we propose that animal personality drives individual specialization, we acknowledge that this pathway may operate in the opposite direction (i.e., specialization driving personality). This issue of causality has also been considered in literature linking animal personality to physiological traits (Careau and Garland 2012) as well as other potential state variables (Sih et al. 2015). Interestingly, recent work indicates that personality traits can be stable over ontogenetic development (Groothuis and Trillmich 2011; Wilson and Krause 2012), whereas diet breadth frequently increases over ontogeny due to relaxed mechanical constraints on resource consumption (Werner and Gilliam 1984; Arim et al. 2010; Toscano and Griffen 2012). Therefore, it is possible that personality traits established early in ontogeny can lead to individual specialization later in ontogeny once a broader resource base becomes available. Still, causal effects of individual specialization on animal personality are certainly possible. For example, individual resource use directly influences physiological or energetic traits such as nutrient assimilation and digestive efficiency (Britt et al. 2006), and personality traits are often related to such energetic traits (Careau et al. 2008). Digestive efficiency in particular can increase available energy, leading to increased activity, boldness or other behaviors with high energy requirements (Careau and Garland 2012).

In addition to potential causal relationships, animal personality and individual specialization may covary without causation (e.g., due to additional underlying state variables unrelated to foraging behavior). The presence of causality, and if so its directionality, represents three hypotheses that can only be distinguished with properly designed experiments. Within an energetics framework, for example, Bijleveld et al. (2014) recently demonstrated a correlation between gizzard mass (a physiologically important organ) and individual exploratory behavior in captive red knots (*Calidris canutus*), but further showed that gizzard mass did not drive behavioral variation. This was accomplished by reciprocally manipulating gizzard mass and measuring the behavioral response of individuals (Bijleveld et al. 2014). Similarly, in the study of personality and individual specialization, personality can be manipulated and diet measured as a response or vice versa to assess the direction of causality or the absence of causality. While diet manipulations are relatively straightforward in captivity, personality can be manipulated with behavioral acclimation (i.e., increasing boldness by exposing individuals to predation risk) or potentially the addition of hormones. These proposed experiments could prove challenging due to the difficulty of manipulating personality or diet without directly affecting other traits. Nevertheless, identifying relationships between phenotypic traits is ultimately necessary to understand how selection affects the total organismal phenotype (Careau and Garland 2012).

Examining links in the field and implications for higher organizational scales

Though animal personality research focuses on behavioral traits that fall within five fundamental behavioral axes (Réale et al. 2007), other work suggests that individual foraging behaviors per se can also persist over time. Alcalay et al. (2015), for example, found that antlions (*Myrmeleon hyalinus*) exhibit consistent individual differences in a number of foraging behaviors (e.g., pit diameter, response time to prey, prey exploitation efficiency), while Woo et al. (2008) showed that individual flight time, diving depth and dive shape in guillemots (*Uria lomvia*) persist over time and are further related to individual diet differences that persist across years (Woo et al. 2008; see also Patrick et al. 2014). Such work is relevant to our present thesis for two reasons. First, the persistence of complex foraging behaviors, in addition to personality and individual specialization, which are persistent by definition, makes the proposed link between personality, foraging behavior and specialization more likely. Second, a major critique of personality research (from an ecologist's perspective) has been the lack of studies demonstrating field relevance and ecological effects (Sih et al. 2012). A key distinction between studies demonstrating personality versus the repeatability of foraging behaviors is that the former studies are most often conducted in the laboratory or under highly controlled field settings, while the latter (e.g., Woo et al. 2008; Patrick et al. 2014; Alcalay et al. 2015; Potier et al. 2015) are conducted

in the field. Thus, examining the relationship between personality and foraging behaviors measured in the field could help address this issue, while simultaneously providing tests of the links between personality and individual specialization proposed here.

Importantly, links between animal personality and individual specialization can potentially propagate to the population-, community- and ecosystem-level, though these effects remain poorly characterized at this point. For example, a number of studies demonstrate that the distribution of behavioral types within a foraging group may scale up to influence the foraging efficiency of that group as a whole (Sih and Watters 2005; Modlmeier et al. 2012; Jolles et al. 2013; Aplin et al. 2014; Keiser and Pruitt 2014; Keynan et al. 2014). Furthermore, a study by Rosenblatt and Heithaus (2011) showed that individual American alligators (*Alligator mississipiensis*) exhibit three unique movement strategies between freshwater marsh and upstream habitats that are related to differences in diet: downstream commuters consumed significantly more marine prey compared to upstream commuters and marsh residents, effectively linking marine and freshwater ecosystems. Though this study (Rosenblatt and Heithaus 2011) did not measure personality, this work suggests that a potential relationship between personality, movement patterns and resource specialization can scale up to alter ecosystem linkages or subsidies.

Methodological constraints

A potential hurdle for future studies examining links between animal personality and individual specialization is methodological constraints. Demonstrating both animal personality and individual specialization requires a substantial number of measurements on a single individual (e.g., demonstrating personality alone requires at least two behavioral measurements per individual), and this could prove prohibitive due to negative effects of handling (see Brommer 2013 for related discussion). Furthermore, these measurements must be sufficiently spaced over time to avoid short-term extrinsic influences on behavior (Bell et al. 2009; Toscano et al. 2014). Similarly, if stomach content analysis is used to demonstrate individual specialization, then at least two diet analyses per individual are required (Seaburg 1957; Bryan and Larkin 1972; Hyslop 1980). Studying links between animal personality and individual specialization will therefore require the combination of techniques that allow for repeated or integrated measurements of these features without altering the study animal's behavior. Stable isotope analysis, for example, effectively bypasses this requirement of multiple longitudinal diet measurements because isotopic signatures represent a long-term integration of food resource use (temporal integration varies based on tissue type; Bearhop et al. 2004). Specifically, carbon isotopes can be used to directly link consumers

to baseline resources (Bearhop et al. 2004). Thus, a simple correlational study between personality traits and individual carbon isotopes could be a useful test for covariation between animal personality and individual specialization.

Conclusions

Examining the link between animal personality and individual fitness is central to understanding the ecology and evolution of personality (Smith and Blumstein 2008). Personality effects on consumer foraging behavior provide an underexplored pathway by which personality can influence fitness. Specifically, foraging behavior determines which resources and how much of these resources an individual consumes, as well as where individuals forage and the predation risk they are exposed to. Ultimately, the energetic costs and benefits of an individual's realized diet determine the energy available for growth and reproduction. We suspect that examining the links between animal personality and consumer foraging behavior, including individual specialization, will further illuminate the ecological and evolutionary consequences of consistent individual variation in behavioral traits, a major goal in contemporary behavioral ecology.

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