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1. Introduction

Faced with a world that changes in space and time, organisms with multiple alternative behaviors available can profit by using experience to determine which alternative to employ. For example, many animals routinely learn which foods to eat, who to mate with, which locations to avoid, where to live, and how to process new foodstuffs (Shettleworth, 2010). If the world changes over time and space with a degree of predictability, experience will be informative; for example, past success with a foraging location or technique will predict future success. However, experience is of no benefit in the face of completely unpredictable change, while genetically encoded conditional strategies can evolve in the face of highly predictable change such as seasonal variation in profitable foraging locations (Boyd & Richerson, 1985; Stephens, 1991). Experience can inform not only which alternative to employ but also the methods used to search for and evaluate alternatives, so-called search strategies. For example, a simple search strategy would be to search where profitable alternatives were previously found. Numerous search strategies are possible, begging the question of how best to choose between search strategies and to maximize the benefits of a chosen strategy, particularly when decisions must be based on incomplete information and when competing with other individuals for the same resources.[1] Considerable work across a range of species has addressed how search strategies are optimized given prevailing circumstances, including the important influence of the social environment (see, e.g., Franks, Pratt, Mallon, Britton, & Sumpter, 2002; Giraldeau & Caraco, 2000; Giraldeau & Dubois, 2008; Stephens & Krebs, 1986; Todd, Hills, & Robbins, 2012). Here, I review causes of individual variation in search strategies, focusing on consistent differences between individuals that cannot be ascribed to local, current environmental conditions.

2. Search and exploration

Search refers to seeking resources or goals under conditions of uncertainty (Todd et al., 2012). These resources or goals could be in the outside environment (external search) or within memory (internal search), and search could be based on reinforcement

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[1] The term “decision” refers to a choice between options, and it should not be taken to imply conscious information processing.

and trial and error (experiential search) or based on mental assessment (cognitive search) (Gavetti & Levinthal, 2000; Hills & Dukas, 2012). “Search” thus refers to a broad range of phenomena in humans, non-human animals, plants, and other organisms (Hills & Dukas, 2012). For example, search includes phenomena such as a mammal focusing foraging efforts on locations of past reward (Hills, 2006), a bird focusing on affordances that have previously led to a solution of a foraging problem (Overington, Cauchard, Cote, & Lefebvre, 2011; Reader, 2003), or a fish locating a mating site by following others (Warner, 1990). Certain behavior patterns may facilitate later search, such as a food storing corvid positioning food caches close together (Balda & Kamil, 1989). In humans and human-designed systems, we could consider as search examples such as a person evaluating different moves in a chess game on the basis of predicted gains, a person trying to recall the location of a lost item by mentally backtracking through the day’s activities, a team of engineers finalizing a new design by building prototypes, a business developing a superior accounting system by conducting pilot studies, and a computer program evaluating solutions to a mathematical problem using a set of predefined rules (Newell, Shaw, & Simon, 1958). In each of these examples, a rule, bias, or strategy is employed to improve the likelihood of success. Following McNamara and Fawcett (2012), these rules and biases are termed “search strategies.” Search strategies can be the product of both experience and evolution.

Search strategies can be defined as those with (a) a goal, (b) uncertainty about the nature, location, or acquisition method of the items to be searched for, and (c) a method for sampling through the search environment (Todd et al., 2012). “Controlled” search strategies add a fourth definitional element: (d) information acquired from the environment is used to guide the search process. Newell et al. (1958) and Newell and Simon (1976) discuss heuristic search, the search for a problem solution, noting that powerful search is characterized by strategies that limit search to a subset of the most likely possibilities, or orders search so that early discovery of a solution becomes more likely. That is, powerful search strategies are not those that unselectively examine many alternatives, but those that selectively examine the alternatives most likely to achieve the current goal. Clearly, concepts of search are tightly allied to those of exploration (Archer & Birke, 1983). Exploration broadly refers to any information-gathering activity. Extrinsic exploration describes activity directed toward an overt goal such as feeding, while intrinsic exploration describes activity not motivated by an immediate overt goal (Archer & Birke, 1983; Berlyne, 1960). Search is thus synonymous with extrinsic exploration, while several authors reserve the term “exploration” for intrinsic exploration alone (Barnett, 1970; Birke & Archer, 1983; Renner, 1988). Many animals demonstrate intrinsic exploration, for example, manipulating objects, exploring locations, or inspecting unfamiliar individuals or even predators in the absence of explicit reward, and the knowledge gained from such exploration can be utilized later (Reader & Laland, 2003). However, the distinction between search and exploration has been questioned and may frequently be difficult to operationalize (Birke & Archer, 1983; Russell, 1983). The precise commonalities between exploratory strategies and strategies of search for a specific item remain to be established, and these commonalities may differ with species characteristics such as energy demands (Birke & Archer, 1983). Here, I treat search as a subset of exploratory behavior. Given the difficulty in separating search and exploration, and the substantial animal literature on exploration, I focus my discussion on the broader category of exploratory behavior. That is, I assume that the causes and consequences of individual variation in exploration are also relevant to search.

3. Variation between individuals in exploration

Individual variation in exploratory behavior across conspecifics has been documented in a large number of species. Moreover, it has been empirically linked to individual success and fitness: It is not trivial variation (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). I discuss two examples that illustrate individual variation in exploratory strategies and possible causes of this variation.

A major body of research has investigated individual differences in exploration in the great tit Parus major. Over 20 years ago, Verbeek, Drent, and Wiepkema (1994) documented variance in the exploratory behavior of great tits raised under controlled laboratory conditions. Individuals ranged along a continuum from fast, “superficial” explorers, who rapidly explored a novel environment and rapidly approached novel objects in a familiar environment, to slow “thorough” explorers that were slower in both types of test. Thus, tit exploration is an example of a temperament trait, consistent across time and situations, with state-dependent factors such as physical condition not accounting for this variation between individuals. Fast and slow explorers also differed in how they tracked a variable foraging environment. Birds were trained to one food location and this food location was then changed. Fast explorers tended to continue to return to the formerly rewarded location, while slow explorers changed their foraging locations (Verbeek et al., 1994). Extensive follow-up work has established that the individual differences in exploratory behavior are heritable and form part of a correlated suite of behavioral traits (a behavioral syndrome; Sih, Bell, Johnson, & Ziemba, 2004), including aggressiveness, the propensity to use social cues, and learning performance (Guillette, Reddon, Hoeschele, & Sturdy, 2011; Marchetti & Drent, 2000). Moreover, tit exploratory styles are linked to multiple fitness determinants, such as dispersal, reproductive performance, dominance, and territory quality (reviewed in Réale et al., 2007). Fluctuations in environmental conditions are suggested to maintain this diversity of exploration styles, with different temperaments doing better in different years (Dingemanse, Both, Drent, & Tinbergen, 2004). The growing field of animal temperament and personality (reviewed in depth elsewhere, e.g., Mathot, Wright, Kempenaers, & Dingemanse, 2012; Réale et al., 2007; Sih et al., 2004; Stamps & Groothuis, 2010; Wilson, Clark, Coleman, & Dearstyne, 1994) has demonstrated consistent individual differences in exploratory behavior in many populations and species. The theory and data developed by this field on the causes of individual consistency in general are thus also clearly applicable to exploratory behavior in particular.

The second example of individual variation in exploration emphasizes the point that multiple factors shape individual variation. In birds such as ground-feeding nutmeg mannikins Lonchura punctulata, as well as many other species, individuals can locate food and other resources by searching for themselves ("producing") or by attending to and joining the discoveries of others ("scrounging") (Giraldeau & Dubois, 2008). Thus, individuals can search using two alternative information sources: personal information (when producing) and social information (when scrounging). When mannikins forage for food hidden in wells, the two search tactics are incompatible: Producing requires foraging with the head down, while scrounging requires the head up. Incompatibility between search tactics will vary with species and context, but experimental tests where the two tactics are incompatible provide much insight into the costs and benefits of different exploratory tactics (Giraldeau & Dubois, 2008). In mannikins, payoffs to producing and scrounging are negatively frequency dependent, with each tactic having superior payoffs when rare. Scroungers outperform producers when scroungers are rare, but as scroungers become common it becomes more advantageous to be a producer. The prediction can thus be made that a mixture of search tactics will be observed within a group of foragers, with a stable equilibrium frequency of scroungers and producers at the point where the payoffs of producing and scrounging are equal. This equilibrium is predicted to shift according to the payoffs of producing and scrounging. Indeed, experimental manipulation of payoffs demonstrates that groups of mannikins converge on these equilibrium values over repeated days of testing (Giraldeau & Dubois, 2008). Thus, choice of search tactic is sensitive to prevailing conditions, and it can be flexibly adjusted according to local circumstances. However, flexibility is not unlimited. Past experience in conditions either favoring or disfavoring scrounging had carryover effects when mannikins were transferred to standardized foraging conditions, showing that responses to local conditions were learned and took time to learn (Morand-Ferron & Giraldeau, 2010).

Individual phenotype and energetic state also shape the search tactic employed. For example, zebra finches Taeniopygia guttata in poorer body condition, at greater predation risk, or with higher basal metabolic rates were found more likely to scrounge compared to other individuals (Mathot & Giraldeau, 2008, 2010; Mathot, Godde, Careau, Thomas, & Giraldeau, 2009). Similarly, house sparrows Passer domesticus with experimentally decreased energy reserves were more likely to scrounge than control individuals, probably because scrounging provided less variable feeding rates than producing (Lendvai, Barta, Liker, & Bókony, 2004; Mathot et al., 2012). Individual learning performance predicted sparrows' tendency to be a producer, with superior learners more likely to employ producer tactics, suggesting that learning abilities may be linked to the kind of search tactic employed (Katsnelson, Motro, Feldman, & Lotem, 2011). Such data indicate that the choice of search tactic may be phenotype-limited: Despite the capacity to flexibly adjust to changing socio-ecological conditions, some individuals are predisposed to one tactic by their individual characteristics (see also Dubois, Giraldeau, & Réale, 2012). These individual predispositions may be stable over long periods. For example, mannikins' tendencies to scrounge rather than produce were consistent across two experiments 6 months apart (Morand-Ferron, Varennes, & Giraldeau, 2011). The same mannikins were consistent in their plasticity of response to changing environmental conditions and in their tendencies to switch between search tactics. Thus, individuals may not only show consistent tendencies to employ a particular search tactic but also consistency in their propensity to adjust the search tactic to current conditions. Variation in information-gathering strategies also occurs at the population level. For example, doves from a territorial population readily learn from heterospecifics, while group-foraging doves more readily learn from conspecifics (Dolman, Templeton, & Lefebvre, 1996). In summary, intraspecific variation in exploratory strategies is pervasive and occurs even in individuals dwelling in identical physical conditions.

4. The trade-off between exploration and exploitation

Individual variation in exploratory behavior can thus arise as a result of current state, individual predispositions, individual ability, and the current or past socio-ecological environment. Consideration of the steps leading to exploration, and of the costs, benefits and constraints of exploration, and its alternatives, allows us to build a framework to assess causes of individual variation in exploratory strategies.

Acquiring information through exploration carries costs. These costs include time, energy, risk and, importantly, opportunity costs: By exploring, a known option cannot be utilized, while exploiting a known option may mean that an even more profitable option is not discovered. Individuals can thus explore, potentially obtaining valuable information, or they can exploit their existing behavioral repertoire, potentially obtaining resources. This exploration–exploitation trade-off has been studied in diverse fields, in diverse systems, and with a diversity of approaches, including work on neural and genetic mechanisms (Cohen, McClure, & Yu, 2007; Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006; Frank, Doll, Oas-Terpstra, & Moreno, 2009; Fu & Gray, 2006; March, 1991; Rendell et al., 2010; Stephens, Brown, & Ydenberg, 2007; Todd et al., 2012; Toelch, Bruce, Meeus, & Reader, 2011). Thus, a fundamental decision is whether an individual should engage in exploration and change its behavior in order to obtain an updated or otherwise enhanced estimate of the true state of the environment (Ydenberg, Brown, & Stephens, 2007).

There are numerous stages involved in the exploration–exploitation decision: Fig. 1 presents a simplified view. To understand how and why an animal explores in a particular manner, understanding is also required of the alternatives to exploration open to that animal (Dall & Johnstone, 2002). We can consider an organism as possessing prior knowledge, the combined result of genetic inheritance and environmental influences. It also possesses a behavioral repertoire of options with different expected utilities, such as a set of foraging locations, a set of techniques for opening encased foodstuffs, or a set of techniques for solving mathematical problems. For example, tool-using birds have a genetic predisposition to manipulate and insert twigs into crevices that, combined with learning in an environment where certain types of crevice contain food, results in birds acquiring a repertoire of feeding sites and the tool-using techniques to access them (Kenward, Rutz, Weir, & Kacelnik, 2006; Kenward, Weir, Rutz, & Kacelnik, 2005; Tebbich, Taborsky, Fessl, & Blomqvist, 2001). Where foods are readily available elsewhere, tool-use is not employed (Tebbich, Taborsky, Fessl, & Dvorak, 2002). The individual will also have relevant prior knowledge beyond the repertoire, such as different possible exploratory strategies, the likelihood that different exploratory strategies will be successful, or the likelihood that prior information will be out-of-date. The repertoire and other prior knowledge will allow an individual to assess whether exploration versus exploitation is likely to be profitable.

An individual must also select the strategies used for exploration and exploitation, and, importantly, the time and effort invested (McNamara & Fawcett, 2012). Exploration need not be an all-or-nothing decision, and low-cost sampling may be common. Even risky options can be sampled cautiously. For example, wild birds may show very slow acceptance of novel foods, and it has been suggested that sampling passes through three stages before full acceptance, thus reducing risk: (a) visual inspection, (b) occasional sampling or consumption only when familiar food is absent, (c) regular consumption, but eaten last of the foods available (Marples & Kelly, 1999). The exploration–exploitation decision will depend upon the behavioral possibilities later in the sequence of decisions illustrated in Fig. 1: An animal with knowledge of a low-cost exploration technique, for instance, may be more likely to explore.

Once a choice is made, both exploration and exploitation will provide information (Stephens, 2007). For example, successful exploration may add a new, profitable act to the repertoire, while failed exploration can indicate a new act is of zero profitability. Exploitation will update previous knowledge about the outcome of an act. For example, a previously rich food location may be exhausted of food. The effort exerted will alter the informational value of success or failure: A cursory effort resulting in failure may provide little information of the potential payoffs of an act, while failure of an alternative with high expected payoffs and with considerable effort invested strongly suggests that the world has truly changed. Moreover, both exploration and exploitation will provide information beyond the repertoire level, such as allowing assessment of the exploratory strategy employed or estimating parameters useful in assessing the likely value of exploration versus exploitation, such as the rate of change of the environment.

In reality, the situation will be more complex than this exposition, with delimitations between categories less discrete than suggested. Several processes may occur simultaneously. For example, animals exploiting a food patch could listen for calls from conspecifics that have located food, and thus simultaneously gather social information (Elgar, 1986). Similarly, individuals could scan for feeding conspecifics and predators at the same time (Mathot & Giraldeau, 2008). Acts within the repertoire may also not be discrete; for example, a cluster of nearby locations may have similar foraging characteristics, or similar modifications of foraging techniques may have similar utility, and thus the act of foraging at one location or using one technique may provide information on other acts. Assuming animals act to maximize the net payoffs of exploration, variation between individuals can arise at each step, since the relevant costs, benefits, and constraints will differ from individual to individual. For example, an individual with an extensive repertoire of profitable acts may benefit little from exploration, a high-ranking individual or one with great physical strength may be better able to exploit foods (Reader & Laland, 2001), poor perceptual performance may hamper exploration, while an individual with poor memory may be forced to explore to update forgotten items. Different individuals will have different functions relating exploration effort to its costs and benefits, and these functions will vary across contexts and situations. Fig. 2 illustrates how individual differences in exploration emerge under different assumptions about their payoff functions. Furthermore, Fig. 2 illustrates that an individual with restricted resources to invest in exploration may be unable to achieve a net benefit. Similar payoff functions can be applied to sex and age differences. Fig. 3 presents a hypothetical example. Here, small, young individuals explore at high cost relative to the benefits they can gain, for example, because they are at increased predation risk, and thus exploration is disfavored. As males and females increase in size, exploration has a net benefit, but the payoff functions of exploration diverge, leading to more exploration in females than males. The payoff functions could diverge because, for example, foraging success results in greater fitness benefits in females than males (Sargent & Gross, 1993). Laland and Reader (1999) applied such reasoning to explain the greater exploratory tendencies of female compared to male guppies Poecilia reticulata. While these simple representations address the effort exerted in exploration and whether an individual explores or not, they could also be applied to choices between exploratory strategies, since different strategies will have different payoff and cost functions.

5. Is exploration a unitary phenomenon?

Key to understanding individual variation in exploration and exploratory strategies is knowledge on the mechanisms underlying exploration and the independence of these mechanisms from each other and from other processes. If exploration is closely tied to other traits, as appears to frequently be the case (Réale et al., 2007), then differences in exploratory strategy may appear as a result of evolved or developmental changes in these traits. Thus, some variation in exploratory strategy may be a byproduct of variation in another trait. Variation in behavioral, cognitive, physiological, and morphological traits may all cause variation in exploratory behavior. It has been suggested that exploratory strategies are partly the result of a general process that extends across domains (Hills, 2006; Hills, Todd, & Goldstone, 2008). If this is so, the ability to fine-tune exploration to a given context may be restricted. However, if exploratory mechanisms are highly modular and domain specific, relevant knowledge may not be applied across domains. Thus, a vital empirical issue is establishing the extent to which exploration is a unitary phenomenon.

Much exploration is likely to be the result of multiple underlying processes. For example, it has been suggested that avian exploratory behavior results from the combined influences of neophilia and neophobia, which do not form a simple continuum (Greenberg & Mettke-Hofman, 2001). For instance, ravens Corvus corax are frequently highly attentive to novelty (neophilia) while simultaneously being very avoidant of novel objects (neophobia) (Greenberg, 2003; Heinrich, 1995). I propose that such a combination can result in a tendency to try a variety of different methods to solve a problem, potentially explaining the high rates of innovation in such species. Neophilia ensures that a novel object is attended to and manipulated, but neophobia results in an animal frequently disengaging and re-engaging with a task and so favors the use of different variants. This “skittish innovator” hypothesis results in the novel prediction that neophobia may speed, not slow, problem solving, if combined with neophilia. Other processes that cause disengagement and re-engagement with a task may have similar effects. The hypothesis suggests a cognitively simple process leading to innovation and could thus apply to a range of species and situations. The fact that exploration rests upon multiple processes may provide novel pathways by which evolution and development alter and adjust exploratory strategies.

In addition to genetic and neurobiological studies of the mechanisms underlying exploration, behavioral, evolutionary, and comparative studies can aid in examining the independence of exploratory strategies from one another. For example, training, reinforcement, and manipulation of developmental experience could be used to address the degree to which exploratory strategies are malleable and can be independently influenced within an individual’s lifetime. If reinforcement of one strategy facilitates or impedes the development or expression of another trait, this provides evidence for their non-independence (Hills et al., 2008; Reader, 2006). Similarly, in fast-breeding organisms experimental evolutionary studies can be used to address the degree to which exploratory strategies evolve independently (Reader, 2006).

6. Social influences on exploration

The tendency to group with and attend to other individuals is a notable example of a factor likely to covary strongly with exploratory strategies, perhaps limiting their indepen- dent expression. Clearly, grouping will alter the costs and benefits of exploration, for example, by changing predation risk or the available social information (Krebs & Inman, 1992; Morand-Ferron & Quinn, 2011; Overington, Cauchard, Morand-Ferron, & Lefebvre, 2009; Reader & Lefebvre, 2001). The activities of other individuals provide a major source of information on which behavior patterns are profitable. Thus, we expect that many information-gathering strategies will be focused on how best to gain information from others (Giraldeau & Dubois, 2008; Laland, 2004). Moreover, information-gathering strategies themselves may also be acquired from others, either by directly learning the strategy itself from others, or indirectly, by socially learning some correlate of the strategy, such as risk-taking. For example, rainbow trout Onchorhyncus mykiss observing others interact with novel objects alter their responsiveness to novel objects (Frost, Winrow, Ashley, & Sneddon, 2007). Furthermore, social cues may indicate that exploration is potentially profitable. For example, Toelch et al. (2011) exposed human participants to social cues indicating that others had performed well or poorly, before the participants played a game involving an exploration–exploitation trade-off. Participants that saw highperformance cues were more likely to exploit novel discoveries. Exploration may also leave physical cues that guide the exploration and exploratory strategies of others. For instance, animals may follow or avoid the trails left by others.

Grouping can constrain or facilitate exploration of novel alternatives in other ways. Grouping individuals can specialize in particular resources or search strategies while simultaneously benefiting from the opportunity to take advantage of other specialists within the group (the “skill pool” effect; Giraldeau, 1984). When resources are uniformly distributed, theoretical modeling shows that grouping can lead to differential sampling of the environment, because nearby group members specialize on and exhaust specific resources, forcing group mates to sample novel alternative resources (van der Post & Hogeweg, 2006). However, the same model demonstrates that when resources are patchily distributed, group members will be exposed to identical resources since they visit patches together, leading to similarity within groups and differentiation between groups. Empirical data support the idea that grouping can constrain exploration of alternative options, even leading to suboptimal choices (Laland & Williams, 1998; Lindeyer & Reader, 2010; Reader, Bruce, & Rebers, 2008). In guppies, increased group size facilitated discovery of a hidden food source when animals could remain in visual contact during exploration, but hindered discovery when successful exploration involved breaking visual contact with the group (Day, MacDonald, Brown, Laland, & Reader, 2001). Where individuals must leave the group to explore, much exploration may go unobserved by others.

Theoretical analyses of human decision making show that the structure of the social network between individuals or groups has a complex effect on the benefits of exploration, even when all are attempting to collectively solve a common problem (Kollman, Miller, & Page, 2000; Lazer & Friedman, 2007). Efficiently connected networks outperform other networks when the time available to locate a solution is short or a problem is simple. However, with complex problems and more time available, intermediately connected networks outperform well-connected networks, because more independent exploration occurs and thus a diversity of solutions are investigated (Lazer & Friedman, 2007). These findings have experimental support (e.g., Mason, Jones, & Goldstone, 2008). This cautions against a simplistic view that greater connectivity and access to social information is universally beneficial and illustrates how well-connected networks may increase information diffusion but decrease information diversity.

In summary, differential access, attention, and processing of social information will potentially contribute to increased individual differences in exploratory tendencies. Social information may also reduce differences between individuals. For instance, animals of an inferior phenotype may, through learning from others, be able to gather information on exploratory strategies they would be incapable of gathering alone.

7. Concluding remarks

Consideration of how the costs and benefits of exploration lead to individual differences in exploratory tendencies has tended to focus on the role of current socio-ecological conditions, individual phenotypes, and the degree to which an individual can correctly assess the true state of the environment based on recent experience. Prolonged experience and experience in early life are also likely to be important influences. For example, human cognitive search strategies are themselves shaped by experience (Gavetti & Levinthal, 2000), while experience during interactions with others or the physical environment could be used to assess personal characteristics and capacities (Fawcett & Bleay, 2009; Stamps & Davis, 2006). Relatively small individual differences may become accentuated by positive feedback. Minor differences in predispositions may cause certain individuals to enter particular environments or to learn from particular individuals and thus acquire a specific repertoire, leading to further experience and thus improved performance with a particular exploratory strategy. This can lead to individuals specializing in these strategies and differentiation between individuals. Another possibility is that cues from early life, such as the degree of parental care, are used to "adaptively program" exploratory strategies (Diorio & Meaney, 2007). Such developmental influences could potentially lead to stable exploratory strategies throughout life and provide a low-cost method to adopt locally adaptive exploratory tendencies in a slowly changing environment (Lindeyer, Meaney, & Reader, 2013). Three studies, all in rodents, have demonstrated that differences in maternal care confined to early life shape individual differences in the tendency to learn from others (Levy, Melo, Galef, Madden, & Fleming, 2003; Lindeyer et al., 2013; Melo et al., 2006). The relative influence of early versus recent experience on exploratory strategies remains largely uninvestigated, although in humans related phenomena such as risk-taking have been found to result from interacting effects of early experience and immediate conditions (Griskevicius et al., 2013).

This review has presented evidence that individual variation in exploratory strategies is likely to be pervasive, to have multiple causes, and to have important consequences for individual and group success. Understanding the causes and consequences of this individual variation can be helped by analysis of the payoffs of exploratory behavior and its alternatives. Many open questions remain. For example, can we predict exploratory strategies of different species based on species characteristics such as life history and metabolic rate (Careau, Bininda-Emonds, Thomas, Réale, & Humphries, 2009)? To what degree do non-human animals engage in search versus (intrinsic) exploration, and how often do non-human animals adopt behaviors to produce novel information as opposed to taking advantage of happenstance? How unique are the processes underlying human exploration and search? Exploration has been repeatedly linked to creativity, problem solving, and innovation, and as a basis for trial-and-error learning, but can innovation be considered as part of a continuum of exploration, or are advanced and/or derived cognitive capacities involved (Eysenck, 1995; Reader & Laland, 2003; Russell, 1983; Simonton, 2003; Thornton & Samson, 2012)? What are the major factors favoring exploration? Kummer and Goodall (1985) argued that much exploration and innovation occur at elevated rates during “periods of plenty,” such as during a period of food abundance or when receiving parental care (the “spare time hypothesis”), in conflict with the “necessity hypothesis” (Kendal, Coe, & Laland, 2005; Laland & Reader, 1999; Morand-Ferron, Cole, Rawles, & Quinn, 2011), which argues that need is the more significant force. This discussion mirrors debate in the organizational sciences over the conditions under which excess (“slack”) versus limited resources favor innovation (Greve, 2003). Cross-pollination between fields has allowed significant inroads to be made into the understanding of exploratory strategies, and it will continue to aid progress in understanding individual variation in exploratory behavior.

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References

Archer, J., & Birke, L. I. A. (Eds.) (1983). Exploration in animals and humans. Wokingham, UK: Van Nostrand Reinhold.

Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery by three corvid species. Animal Behaviour, 38, 486–495.

Barnett, S. A. (1970). Search and Explorations. In J. R. Young & E. M. Strock (Eds.), Contemporary readings in behaviour (pp. 33–45). New York: McGraw-Hill Inc.

Berlyne, D. E. (1960). Conflict, arousal and curiosity. London: McGraw-Hill.

Birke, L. I. A., & Archer, J. (1983). Some issues and problems in the study of animal exploration. In J. Archer & L. I. A. Birke (Eds.), Exploration in animals and humans (pp. 1–21). Wokingham, UK: Van Nostrand Reinhold.

Boyd, R., & Richerson, P. J. (1985). Culture and the evolutionary process. Chicago: University of Chicago Press.

Careau, V., Bininda-Emonds, O. R. P., Thomas, D. W., Réale, D., & Humphries, M. M. (2009). Exploration strategies map along fast-slow metabolic and life-history continua in muroid rodents. Functional Ecology, 23, 150–156.

Cohen, J. D., McClure, S. M., & Yu, A. J. (2007). Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. Philosophical Transactions of the Royal Society B, 362, 933–942.

Dall, S. R. X., & Johnstone, R. A. (2002). Managing uncertainty: Information and insurance under the risk of starvation. Philosophical Transactions of the Royal Society B, 357, 1519–1526.

Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B., & Dolan, R. J. (2006). Cortical substrates for exploratory decisions in humans. Nature, 441, 876–879.

Day, R. L., MacDonald, T., Brown, C., Laland, K. N., & Reader, S. M. (2001). Interactions between shoal size and conformity in guppy social foraging. Animal Behaviour, 62, 917–925.

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. Proceedings of the Royal Society B, 271, 847–852.

Diorio, J., & Meaney, M. J. (2007). Maternal programming of defensive responses through sustained effects on gene expression. Journal of Psychiatry & Neuroscience, 32, 275–284.

Dolman, C. S., Templeton, J., & Lefebvre, L. (1996). Mode of foraging competition is related to tutor preference in Zenaida aurita. Journal of Comparative Psychology, 110, 45–54.

Dubois, F., Giraldeau, L.-A., & Réale, D. (2012). Frequency-dependent payoffs and sequential decisionmaking favour consistent tactic use. Proceedings of the Royal Society B, 279, 1977–1985.

Elgar, M. A. (1986). House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. Animal Behaviour, 34, 169–174.

Eysenck, H. J. (1995). Genius: The natural history of creativity. Cambridge, England: Cambridge University Press.

Fawcett, T. W., & Bleay, C. (2009). Previous experiences shape adaptive mate preferences. Behavioral Ecology, 20, 68–78.

Frank, M. J., Doll, B. B., Oas-Terpstra, J., & Moreno, F. (2009). Prefrontal and striatal dopaminergic genes predict individual differences in exploration and exploitation. Nature Neuroscience, 12, 1062–1068.

Franks, N. R., Pratt, S. C., Mallon, E. B., Britton, N. F., & Sumpter, D. J. T. (2002). Information flow, opinion polling and collective intelligence in house-hunting social insects. Philosophical Transactions of the Royal Society B, 357, 1567–1583.

Frost, A. J., Winrow, A., Ashley, P. J., & Sneddon, L. U. (2007). Plasticity in animal personality traits: Does prior experience alter the degree of boldness? Proceedings of the Royal Society B, 274, 333–339.

Fu, W.-T., & Gray, W. D. (2006). Suboptimal tradeoffs in information seeking. Cognitive Psychology, 52, 195–242.

Gavetti, G., & Levinthal, D. (2000). Looking forward and looking backward: Cognitive and experiential search. Administrative Science Quarterly, 45, 113–117.

Giraldeau, L.-A. (1984). Group foraging: The skill pool effect and frequency-dependant learning. American Naturalist, 124, 72–79.

Giraldeau, L.-A., & Caraco, T. (2000). Social foraging theory. Princeton, NJ: Princeton University Press.

Giraldeau, L.-A., & Dubois, F. (2008). Social foraging and the study of exploitative behavior. Advances in the Study of Behavior, 38, 59–104.

Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In S. M. Reader, & K. N. Laland (Eds.), Animal innovation (pp. 175–196). Oxford, England: Oxford University Press.

Greenberg, R., & Mettke-Hofman, C. (2001). Ecological aspects of neophobia and exploration in birds. Current Ornithology, 16, 119–178.

Greve, H. R. (2003). Organizational learning from performance feedback. A behavioral perspective on innovation and change. Cambridge, England: Cambridge University Press.

Griskevicius, V., Ackerman, J. M., Cantu, S. M., Delton, A. W., Robertson, T. E., Simpson, J. A.,

Thompson, M. E., & Tybur, J. M. (2013). When the economy falters, do people spend or save? Responses to resource scarcity depend on childhood environments. Psychological Science, 24, 197–205.

Guillette, L. M., Reddon, A. R., Hoeschele, M., & Sturdy, C. B. (2011). Sometimes slower is better: Slowexploring birds are more sensitive to changes in a vocal discrimination task. Proceedings of the Royal Society B, 278, 767–773.

Heinrich, B. (1995). Neophilia and exploration in juvenile common ravens, Corvus corax. Animal Behaviour, 50, 695–704.

Hills, T. T. (2006). Animal foraging and the evolution of goal-directed cognition. Cognitive Science, 30, 3– 41.

Hills, T. T., & Dukas, R. (2012). The evolution of cognitive search. In P. M. Todd, T. T. Hills & T. W. Robbins (Eds.), Cognitive search: Evolution, algorithms, and the brain. Str€ungmann Forum Reports, vol. 9. (pp. 11–24). Cambridge, MA: MIT Press.

Hills, T. T., Todd, P. M., & Goldstone, R. L. (2008). Search in external and internal spaces: Evidence for generalized cognitive search processes. Psychological Science, 19, 802–808.

Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. (2011). Individual-learning ability predicts socialforaging strategy in house sparrows. Proceedings of the Royal Society B, 278, 582–589.

Kendal, R. L., Coe, R. L., & Laland, K. N. (2005). Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. American Journal of Primatology, 66, 167–188.

Kenward, B., Rutz, C., Weir, A. A. S., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. Animal Behaviour, 72, 1329–1343.

Kenward, B., Weir, A. A. S., Rutz, C., & Kacelnik, A. (2005). Tool manufacture by naive juvenile crows. Nature, 433, 121.

Kollman, K., Miller, J. H., & Page, S. E. (2000). Decentralization and the search for policy solutions. Journal of Law, Economics, & Organization, 16, 102–128.

Krebs, J. R., & Inman, A. J. (1992). Learning and foraging: Individuals, groups, and populations. American Naturalist, 140, S63–S84.

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. Philosophical Transactions of the Royal Society B, 308, 203–214.

Laland, K. N. (2004). Social learning strategies. Learning & Behavior, 32, 4–14.

Laland, K. N., & Reader, S. M. (1999). Foraging innovation in the guppy. Animal Behaviour, 57, 331–340.

Laland, K. N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. Behavioral Ecology, 9, 493–499.

Lazer, D., & Friedman, A. (2007). The network structure of exploration and exploitation. Administrative Science Quarterly, 52, 667–694.

Lendvai, A. Z., Barta, Z., Liker, A., & Bókony, V. (2004). The effect of energy reserves on social foraging: Hungry sparrows scrounge more. Proceedings of the Royal Society B, 271, 2467–2472.

Levy, F., Melo, A. I., Galef, B. G., Jr, Madden, M., & Fleming, A. S. (2003). Complete maternal deprivation affects social but not spatial learning in adult rats. Developmental Psychobiology, 43, 177–191.

Lindeyer, C. M., Meaney, M. J., & Reader, S. M. (2013). Early maternal care predicts reliance on social learning about food in adult rats. Developmental Psychobiology, 55, 168–175.

Lindeyer, C. M., & Reader, S. M. (2010). Social learning of escape routes in zebrafish and the stability of behavioural traditions. Animal Behaviour, 79, 827–834.

March, J. G. (1991). Exploration and exploitation in organizational learning. Organization Science, 2, 71–87.

Marchetti, C., & Drent, P. J. (2000). Individual differences in the use of social information in foraging by captive great tits. Animal Behaviour, 60, 131–140.

Marples, N. M., & Kelly, D. J. (1999). Neophobia and dietary conservatism: Two distinct processes? Evolutionary Ecology, 13, 641–653.

Mason, W. A., Jones, A., & Goldstone, R. L. (2008). Propagation of innovations in networked groups. Journal of Experimental Psychology: General, 137, 422–433.

Mathot, K. J., & Giraldeau, L.-A. (2008). Increasing vulnerability to predation increases preference for the scrounger foraging tactic. Behavioral Ecology, 19, 131–138.

Mathot, K. J., & Giraldeau, L.-A. (2010). Family-related differences in social foraging tactic use in the zebra finch (Taeniopygia guttata). Behavioral Ecology and Sociobiology, 64, 1805–1811.

Mathot, K. J., Godde, S., Careau, V., Thomas, D. W., & Giraldeau, L.-A. (2009). Testing dynamic variancesensitive foraging using individual differences in basal metabolic rates of zebra finches. Oikos, 118, 545– 552.

Mathot, K. J., Wright, J., Kempenaers, B., & Dingemanse, N. J. (2012). Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. Oikos, 121, 1009–1020.

McNamara, J. M., & Fawcett, T. W. (2012). Optimal strategies and heuristics for ecological search problems. In P. M. Todd, T. T. Hills, & T. W. Robbins (Eds.), Cognitive search: Evolution, algorithms, and the brain. Str€ungmann Forum Reports, vol. 9 (pp. 301–315). Cambridge, MA: MIT Press.

Melo, A. I., Lovic, V., Gonzalez, A., Madden, M., Sinopoli, K., & Fleming, A. S. (2006). Maternal and littermate deprivation disrupts maternal behavior and social-learning of food preference in adulthood: Tactile stimulation, nest odor, and social rearing prevent these effects. Developmental Psychobiology, 48, 209–219.

Morand-Ferron, J., Cole, E. F., Rawles, J. E. C., & Quinn, J. L. (2011). Who are the innovators? A field experiment with two passerine species. Behavioral Ecology, 22, 1241–1248.

Morand-Ferron, J., & Giraldeau, L.-A. (2010). Learning behaviorally stable solutions to producer-scrounger games. Behavioral Ecology, 21, 343–348.

Morand-Ferron, J., & Quinn, J. L. (2011). Larger groups of passerines are more efficient problem solvers in the wild. Proceedings of the National Academy of Sciences of the United States of America, 108, 15898– 15903.

Morand-Ferron, J., Varennes, E., & Giraldeau, L.-A. (2011). Individual differences in plasticity and sampling when playing behavioural games. Proceedings of the Royal Society B, 278, 1223–1230.

Newell, A., Shaw, J. C., & Simon, H. A. (1958). Elements of a theory of human problem-solving. Psychological Review, 65, 151–166.

Newell, A., & Simon, H. A. (1976). Computer science as empirical inquiry: Symbols and search. Communications of the ACM, 19, 113–126.

Overington, S. E., Cauchard, L., Cote, K. A., & Lefebvre, L. (2011). Innovative foraging behaviour in birds: What characterizes an innovator? Behavioural Processes, 87, 274–285.

Overington, S. E., Cauchard, L., Morand-Ferron, J., & Lefebvre, L. (2009). Innovation in groups: Does the proximity of others facilitate or inhibit performance? Behaviour, 146, 1543–1564.

van der Post, D. J., & Hogeweg, P. (2006). Resource distributions and diet development by trial-and-error learning. Behavioral Ecology and Sociobiology, 61, 65–80.

Reader, S. M. (2003). Innovation and social learning: Individual variation and brain evolution. Animal Biology, 53, 147–158.

Reader, S. M. (2006). Evo-devo, modularity, and evolvability: Insights for cultural evolution. Behavioral and Brain Sciences, 29, 361–362.

Reader, S. M., Bruce, M. J., & Rebers, S. (2008). Social learning of novel route preferences in adult humans. Biology Letters, 4, 37–40.

Reader, S. M., & Laland, K. N. (2001). Primate innovation: Sex, age and social rank differences. International Journal of Primatology, 22, 787–805.

Reader, S. M., & Laland, K. N. (2003). Animal innovation: An introduction. In S. M. Reader & K. N. Laland (Eds.), Animal innovation (pp. 3–35). Oxford, England: Oxford University Press.

Reader, S. M., & Lefebvre, L. (2001). Social learning and sociality. Behavioral and Brain Sciences, 24, 353– 355.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. Biological Reviews, 82, 291–318.

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T., & Laland, K. N. (2010). Why copy others? Insights from the social learning strategies tournament. Science, 328, 208–213.

Renner, M. J. (1988). Learning during exploration: The role of behavioral topography during exploration in determining subsequent adaptive behavior. International Journal of Comparative Psychology, 2, 43–56.

Russell, P. A. (1983). Psychological studies of exploration in animals: A reappraisal. In J. Archer & L. I. A. Birke (Eds.), Exploration in animals and humans (pp. 22–54). Wokingham, UK: Van Nostrand Reinhold.

Sargent, R. C., & Gross, M. R. (1993). Williams' principle: An explanation of parental care in teleost fishes. In T. J. Pitcher (Ed.), Behaviour of teleost fishes (2nd ed., pp. 333–361). London: Chapman & Hall. Shettleworth, S. J. (2010). Cognition, evolution, and behaviour (2nd ed.). Oxford, England: Oxford University Press.

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. Quarterly Review of Biology, 79, 241–277.

Simonton, D. K. (2003). Human creativity: Two Darwinian analyses. In S. M. Reader & K. N. Laland (Eds.), Animal innovation (pp. 309–325). Oxford, England: Oxford University Press.

Stamps, J. A., & Davis, J. M. (2006). Adaptive effects of natal experience on habitat selection by dispersers. Animal Behaviour, 72, 1279–1289.

Stamps, J. A., & Groothuis, T. G. G. (2010). Developmental perspectives on personality: Implications for ecological and evolutionary studies of individual differencese. Philosophical Transactions of the Royal Society B, 365, 4029–4041.

Stephens, D. W. (1991). Change, regularity, and value in the evolution of animal learning. Behavioral Ecology, 2, 77–89.

Stephens, D. W. (2007). Models of information use. In D. W. Stephens, J. S. Brown, & R. C. Ydenberg (Eds.), Foraging: Behavior and ecology (pp. 31–58). Chicago: University of Chicago Press. Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (Eds.) (2007). Foraging: Behavior and ecology. Chicago: University of Chicago Press.

Stephens, D. W., & Krebs, J. R. (1986). Foraging theory. Princeton: Princeton University Press.

Tebbich, S., Taborsky, M., Fessl, B., & Blomqvist, D. (2001). Do woodpecker finches acquire tool-use by social learning? Proceedings of the Royal Society B, 268, 2189–2196.

Tebbich, S., Taborsky, M., Fessl, B., & Dvorak, M. (2002). The ecology of tool-use in the woodpecker finch Cactospiza pallida. Ecology Letters, 5, 656–664.

Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. Animal Behaviour, 83, 1459–1468.

Todd, P. M., Hills, T. T., & Robbins, T. W. (Eds.) (2012). Cognitive search: Evolution, algorithms, and the brain. Str€ungmann Forum Reports, vol. 9. Cambridge, MA: The MIT Press.

Toelch, U., Bruce, M. J., Meeus, M. T. H., & Reader, S. M. (2011). Social performance cues induce behavioral flexibility in humans. Frontiers in Psychology, 2, 160.

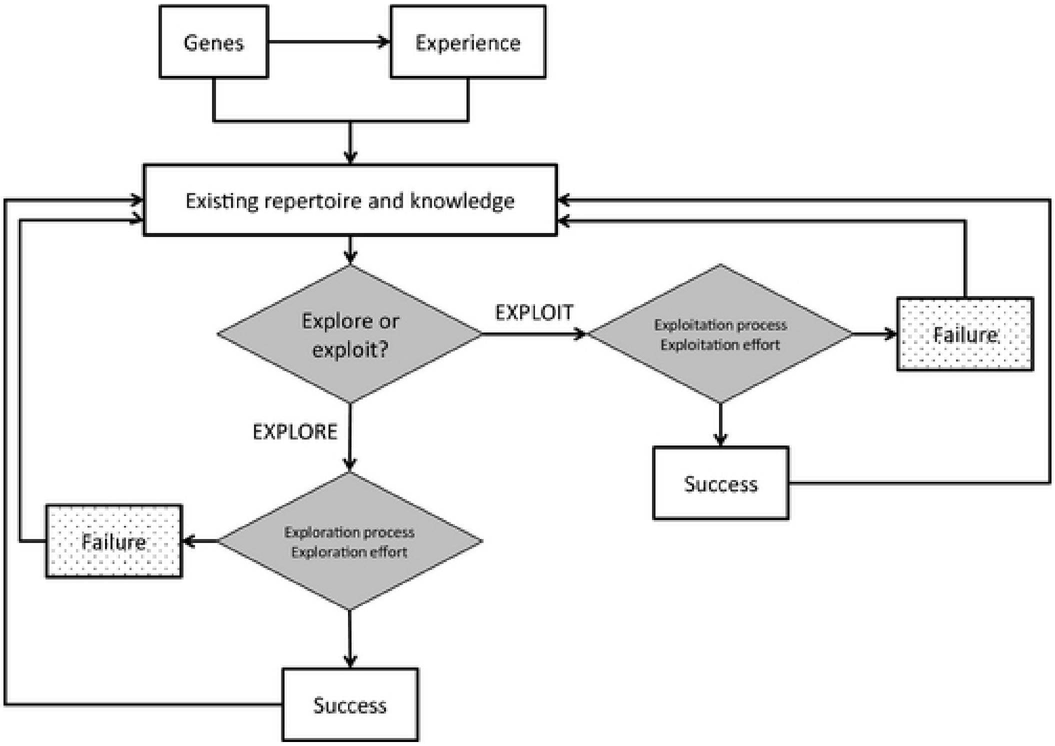
Verbeek, M. E. M., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behavior of male great tits. Animal Behaviour, 48, 1113–1121.

Warner, R. R. (1990). Male versus female influences on mating-site determination in a coral-reef fish. Animal Behaviour, 39, 540–548.

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. Trends in Ecology and Evolution, 9, 442–446.

Ydenberg, R. C., Brown, J. S., & Stephens, D. W. (2007). Foraging: An overview. In D. W. Stephens, J. S. Brown, & R. C. Ydenberg (Eds.), Foraging: Behavior and ecology (pp. 1–28). Chicago: University of Chicago Press.

FIG. 1



Schematic of steps involved in a decision to explore. A behavioral repertoire and set of prior knowledge are formed by the combined influences of genetic inheritance and experience (including social experience such as learning from others [social learning]). This repertoire and knowledge, combined with individual characteristics and environmental conditions, will influence the decision to engage in exploration versus exploiting known options, as well as the process employed, the effort expended, and the chance of success or failure. Success or failure from both exploration and exploitation will provide additional information on both the environment and on an individual's personal capabilities, and will thus influence the decision of whether to continue exploring or to switch to exploiting. Note that the producer-*scrounger literature (Giraldeau & Dubois, 2008) uses "exploitation" to refer to the exploitation of resources, rather than the sense used here, exploitation of prior knowledge.*

FIG. 2

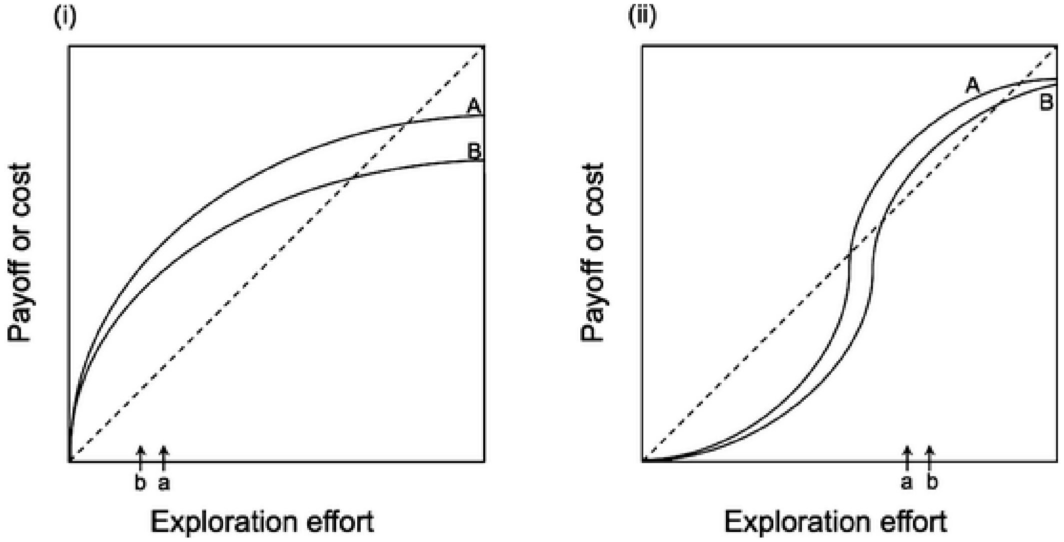
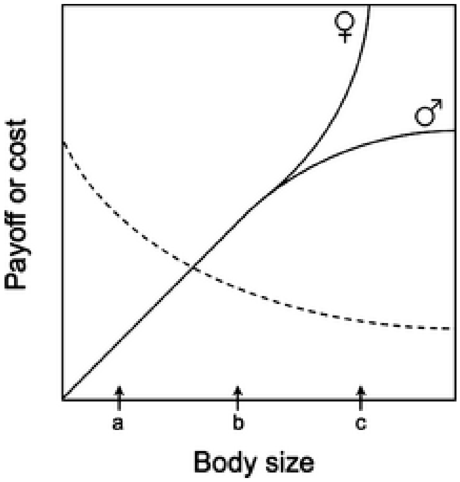


Illustration of the effect of different exploration payoff functions for two individuals, A and B (solid lines), on predicted exploration effort. Cost (dashed line) is assumed to be directly proportional to the exploration effort (e.g., time spent or energy expended). Arrows indicate the point at which maximum net benefits are obtained. (i) Payoffs of exploration are assumed to have decelerating returns with increased effort. Individual A will maximize net benefits (point "a") at a higher exploration effort than individual B (point "b"). When lines A and B cross the dashed line exploration no longer has a net benefit. (ii) Payoffs of exploration are assumed to have accelerating returns followed by decelerating returns. Individual A will maximize net benefits at a lower exploration effort than B. Many other payoff and cost functions are possible. For simplicity, influences of changes in individual state are neglected.

FIG. 3



Hypothetical exploration payoff functions for male and female individuals of different body sizes (solid lines). Cost of exploration (dashed line) decreases with body size, for example, because small individuals are at increased predation risk. At point "a" exploration has a net cost and is disfavored, while at point "b" exploration has a net benefit, and at point "c" male and female payoff functions diverge, leading to greater net benefits for exploration in females than males.