neophobia distinguished expanding and established house sparrow populations (Martin & Fitzgerald 2005).

Investigating the relationship between novelty reactions and innovations contributes to our understanding of the underlying mechanisms of innovations and allows us to predict the context in which innovations are most likely to occur. To accurately compare innovativeness across species, as suggested by Ramsey et al., we not only have to take into consideration differences in social transmission, but also the fact that biases may exist towards detecting innovations more frequently in certain contexts. Awareness of the context-specifity of innovations further helps to make comparisons more reliable. Consequently, interspecific comparisons should control for the context in which innovations occur by restricting comparisons to object-related or food-related innovations until other forms of contextdependent innovation have been systematically measured.

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Environmentally invoked innovation and cognition

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Abstract: Behavioral innovations induced by the social or physical environment are likely to be of great functional and evolutionary importance, and thus warrant serious attention. Innovation provides a process by which animals can adjust to changed environments. Despite this apparent adaptive advantage, it is not known whether innovative propensities are adaptive specializations. Furthermore, the varied psychological processes underlying innovation remain poorly understood.

Ramsey et al. argue that behavioral innovation should play an important role in studies of animal social learning, evolution, ecology, and cognition. I agree entirely, and admire their work in establishing and moving the field forward. As there remains much to do, it is important, particularly at these early stages, to reach consensus on clear definitions and delimitation of phenomena. Ramsey et al. argue for revision of Reader and Laland's (2003a) definition of animal innovation, principally excluding environmentally induced novel behavior and defining innovation at the individual rather than population level. Both revisions are debatable. Although a group member can innovate even if another has made the same discovery, such innovations are difficult to discriminate from socially learned innovations, whereas first occurrences may be particularly relevant to identification of the individual and/or environmental variables that favor innovation. Ramsey et al.'s individual-level definition also raises problems regarding the distinction between innovation and individual learning (see Reader & Laland 2003a).

Ramsey et al. exclude environmentally induced innovations from consideration, but change in the physical or social environment may precede much innovation (Hauser 1988; Lee 1991; Reader & Laland 2001), and innovative bird species are more likely to survive than less innovative species when introduced to novel environments (Sol 2003). Moreover, many (but by no means all) reported innovations are responses to humaninduced environmental changes (Lefebvre et al. 1997; 2001; Reader & Laland 2002). Innovation may also be prompted by social demands, where it may be key in outwitting rivals (e.g., innovative tactical deception; Byrne 2003), be frequency dependent, or be prompted or facilitated by existing innovations that create a need or opportunity for further innovation. All these would be considered environmentally induced innovations, but they are innovations nonetheless, and surely of both theoretical and applied interest (e.g., to conservation biology; McDougall et al. 2006). The exclusion of environmentally induced innovations, as Ramsey et al. advocate, will likely eliminate false positives, but may also exclude many interesting and functionally important "true" innovations. Innovation presumably carries maximal advantage as a response to novel circumstances where natural selection cannot have shaped appropriate responses.

Ramsey et al.'s new definition and classification scheme may carry other disadvantages for empirical studies of innovation (Kendal et al. raise complementary points in their commentary). Ramsey et al. propose several characters of potential utility for discriminating innovations from non-innovations, and present a useful exposition of how these characters can be considered together. However, the rate of acquisition, rate of spread, rarity, apparent cognitive complexity, and distribution within or across populations may provide misleading clues for identifying innovations. Such characters are not irrelevant to the study of proposed innovations, but should be interpreted cautiously: many genetic, social, environmental, and experiential influences can impact on the performance of a given behavior. Proper consideration of ecological explanations for behavioral differences between populations, for example, requires consideration of the availability, utility, and risks of alternative behavior patterns. The relative utility and performance of a given foraging behavior could be influenced by, for instance, the availability of other foods, the ease of identifying alternate foods, differences in need (e.g., disease promoting peculiar nutritional requirements), local predation risk, the activities of others (e.g., resource competition), or constraints on performance of alternative behaviors (Dewar 2004; Reader 2004). Exclusion of such "ecological" causes for population differences may be extremely challenging with observational study alone (Laland & Janik 2006). Moreover, as argued earlier, ecological causes would not eliminate the possibility that the behavior was an innovation.

Ramsey et al. suggest using geographic and local prevalence to identify innovations, but how informative are these variables? Innovation prompted by the peculiarities of local sub-habitats would result in a patchy distribution that would correlate with ecological differences. Conversely, with limited solutions to the same problem, an innovative species may repeatedly and independently invent the same behavior in many populations, resulting in high geographic prevalence. Nocturnal feeding by street lights in kingbirds, for example, has been repeatedly reported on several Caribbean islands, suggesting environmental induction in each population (Reader et al. 2002a). Innovative species may also show high local prevalence of novel behaviors. As Ramsey et al. note, reported novel behavior is amenable to experimental investigation in the laboratory, in the field, and with wild-caught captives (e.g., Morand-Ferron et al. 2004; Pfeffer et al. 2002; Reader et al. 2002b), and such experiments provide a vital follow-up to observational data. Experimental investigations of celebrated cases of animal innovation - sweet-potato washing by macaques and milk-bottle opening by titmice - demonstrate that individual rates of discovery may be far higher than was generally thought (Kothbauer-Hellman 1990; Sherry & Galef 1984; 1990; Visalberghi & Fragaszy 1990). Where geographically or locally prevalent innovation suggests that a novel behavior is readily discovered, species comparisons may be informative: Why do some species apparently make these discoveries readily, while sympatric species do not? High local and geographic prevalence in particular species could result from several processes, including general behavioral flexibility, context-specific flexibility, or Ramsey et al.'s "Baldwinized innovations." However, although Baldwin effects have significant theoretical impact for the evolutionary consequences of behavioral flexibility (Sol 2003; Wyles et al. 1983), they lack clear empirical support (de Jong & Crozier 2003).

Here are two final definitional points. First, Ramsey et al. introduce "behavioral flexibility" to mean behavior-level flexibility. However, current usage typically considers behavioral flexibility as part of phenotypic plasticity and thus repertoire, not behavior-level, flexibility (Bateson 1983; Schlichting & Pigliucci 1998). Second, the suggested social learning-innovation continuum is unclear and open to several alternative interpretations: (1) Some individuals innovate while others socially learn these innovations; (2) some elements of a behavior are innovated and some are socially learned; (3) social learning involves some innovation, such as when stimulus enhancement attracts a bird to food but the processing methods are individually acquired; or (4) copying errors during social learning result in novel behavior.

An important question not raised by Ramsey et al. is whether innovative propensities are adaptations rather than side-products or indicators of other phenomena, such as general behavioral flexibility. Investigation of the genetic, hormonal, neurocognitive, and developmental mechanisms underlying innovation will help resolve this issue as well as the important questions raised by Ramsey et al. and Reader and Laland (2003a). There is clear potential for integration with research on temperament and behavioral syndromes (Réale et al. 2007; Sih et al. 2004). Although some evidence suggests that innovative propensities may be consistent individual traits (Laland & Reader 1999; Pfeffer et al. 2002, but see Fragaszy & Visalberghi 1990), it is not known whether innovatory propensities are heritable, are impacted by developmental experience, or whether animals can "learn to innovate." A range of psychological processes may be involved in any one innovation, and may differ between different innovations. Progress will require investigation of the causes, consequences, and mechanisms underlying animal innovation; all areas ripe for study.

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Is all learning innovation?

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Abstract: Research on animal innovation is an underdeveloped field, and for this reason we welcome the efforts Ramsey and colleagues have made to stimulate its study in wild populations. However, we feel that in attempting to find an operational definition the authors have overstretched the idea of what we should consider innovation in some areas and over-restricted it in others.

Although we welcome new thought aimed at stimulating research on animal innovation, we find problems with the definitional approach Ramsey et al. have taken, especially with defining innovation at the level of the individual. We are unconvinced by the restriction on cases involving what the authors term "environmental induction" (proposing instead a distinction between "passive" and "active" innovation), and on cases with significant positive fitness impacts. Finally, we don't believe the distinction between behaviour and repertoire flexibility is useful.

First, we do not believe that defining an innovation as something new to the individual, rather than the population, makes sense. No doubt it is individuals that innovate, and it is possible that more than one individual in a population might produce the same innovation independently. However, if innovation is simply another term for asocial (or individual) learning, we have unnecessary redundancy. The concept of innovation at the population level is useful, because it pertains to the process by which new behaviours enter into populations, with potential evolutionary impacts. At the individual level, the concept becomes entangled with processes such as trial-and-error learning that we might describe under the broad term "asocial learning." Furthermore, some forms of learning require both social and asocial processes. For example, individuals may be attracted to a new food source through stimulus enhancement, but then use trialand-error learning to acquire the extraction method. Therefore, perversely, "innovating" as defined by Ramsey et al. would be subsumed within a form of social learning. The commitment to innovation at the individual level is also at odds with our societal sense of what an innovation is - we have a patent system precisely to establish the primacy of whoever *first* came up with something new. Can all individual learning be innovation? We think not.

One possible response to this question is to restrict innovation to those cases not resulting from environmental induction. This separation is unconvincing, not least because most examples of innovation are linked to novel opportunities in the environment. The adaptive value of innovation, indeed behavioural flexibility in general, is surely in dealing with environmental variation. Thus, periods of environmental change are precisely when one might expect higher levels of innovation. Perhaps a landslide caused a pile of stones to appear next to a tree suddenly – does this mean their subsequent use cannot, by definition, be an innovation? Milk-bottle opening by blue tits in the United Kingdom is widely touted as an innovation, but without the environmental induction of soft-topped milk bottles, would never have occurred.

Nonetheless, understanding the role of environmental change in innovation is potentially worthwhile. However, we would draw a rather different distinction to that made by Ramsey et al. Their hypothetical example of chimpanzees switching to stone tools after a forest fire illustrates the point. The switch to stone tools could only occur through a phase of operant learning by the chimpanzees: the use of stones can only be reinforced once an individual has experimented, and succeeded in using one to crack open a nut. Thus, an environmental change may act to provide either the opportunity or necessity for operant learning, which, in the case of the first individual to succeed, we would term "innovation." We feel such cases are fundamentally different to cases in which an environmental event *directly* alters the behaviour of an individual. An individual may learn through being passively exposed to the relationship between two stimuli in its environment. For instance, after being attacked, an individual may learn to associate a particular scent with the arrival of a predator. In future, it may respond to that scent with fear or escape responses. If the individual is the first in the population to form this association, it might be said to be the innovator. We would term that individual a "passive innovator." In contrast, an individual who has learned to use a stone hammer, through operant learning, we would term an "active innovator." We feel this distinction is likely to prove useful as active innovation is more likely to reflect the cognitive abilities of the innovator than passive innovation, which is more likely to rely on chance events.

These issues aside, the target article gives the impression that it would be easy to distinguish non-innovation based on environmental induction, but this is far from the case. For example, the claim that environmentally induced novel behaviours are expected to be adopted rapidly by most of the population following a change in the environment does not hold water if the rapid