

Clues to the functionality of vocal signals are available in other studies, indicating that chimpanzees tend to use them selectively, when the experimenter is looking away (Hostetter et al. 2001; Leavens et al. 2004). It is also of some interest that in chimpanzees, unlike the other primates, there are significantly more pre-adult, and fewer adult, cases of innovation than would be expected by chance (Reader & Laland 2001), though it is evidently not known, at present, whether juveniles are also more likely to innovate vocally.

Because new forms emerge in development (West-Eberhard 2003), our attention is drawn to the role of infancy in vocal innovation. An important problem that is solved by infants is the negotiation of their own care during a time when care is likely to be interrupted (Trivers 1974). I have claimed elsewhere that at one or more points in evolutionary history, increased competition for care stimulated novel and more flexible use of vocal behaviors (Locke 2006; Locke & Bogin 2006).

But signaling involves more than signals. For repertoire change, infants would also need to observe the effect of any new vocalizations on others. Ramsey et al. say little about cases where one individual uses other individuals as a tool. The exclusion of such cases would seem to ignore the social nature of many primate groups, wall off our own exceptionally social species from other primates, and complicate the process of evolutionary theorizing.

Human mothers are disposed to repeat their infants' speech-like vocalizations (Pawlby 1977), a practice that appears to reinforce their use (Veneziano 1988). In fact, some frequently babbled patterns are taken up by family members and may diffuse through the community (Ferguson 1964; Locke 2004; 2006). One is curious to know, in this connection, if Ramsey et al., who exclude cases where individuals witnessed a behavior *and* its effect on a conspecific, also wish to exclude cases in which an individual's own behavior elicited reactions by others.

Vocal innovation by infants may provide parents with a free evaluation of their offspring's fitness (Locke 2006). In primates and other animals, there are associations between innovativeness, brain development, and learning potential (Lefebvre et al. 2004). It is interesting, in this regard, that human infants who produce a high rate of syllables per utterance appear more pleasant, friendly, and likeable than infants who vocalize less complexly or rhythmically (Bloom & Lo 1990; Bloom et al. 1993).

It is paradoxical, given the robustness of vocal innovation in humans, that developmental evidence has been reported only sporadically. Observers have noted infants' use of a distinctive intonation pattern when making "requests" (Dore 1974; Ninio et al. 1994), and there is evidence that human infants – like adult chimpanzees – make grunts and labial trills before they begin to speak (Kim et al. 1996; McCune et al. 1996). For some reason, these sounds may be particularly characteristic of retarded infants and children (O'Neill & Happé 2000; Smith & Oller 1981). It has also been reported that typically developing infants use a specific class of (nasally emitted) sounds as "requests" (Goldman 2001).

In babbling, human infants effect a variety of closures within the vocal tract while phonating, thereby producing audible activity that, in its most canonical form, resembles consonant-vowel syllables and, therefore, speech (Oller 2000). A more advanced form, variegated babbling, involves different points of articulation within a single sequence of syllables. This activity demonstrates, and may facilitate, what Oller (2004) calls "contextual freedom," seemingly a phonetic form of Ramsey et al.'s "behavioral flexibility." Later in development, there is evidence for invented words by young children (Becker 1994; Leopold 1949), who are also responsible for the phonological, lexical, and grammatical inventions that occur in the creation of creoles from pidgins (Bickerton 1984). It is clear, additionally, that adolescents play a major role in linguistic change, particularly at the phonological level of language (Eckert 1999; Labov 2001).

Ramsey et al. have provided us with a framework for the evaluation of innovation across primate species. It would be interesting to see what modifications are required for vocal innovation. Working within a properly designed system – one that values synergies between evolution and development – it may be possible to identify candidate processes in the evolution of speech and language (Locke, in press).

Social learning is central to innovation, in primates and beyond

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Abstract: Much of the importance of innovation stems from its capacity to spread via social learning, affecting multiple individuals, thus generating evolutionary and ecological consequences. We advocate a broader taxonomic focus in the field of behavioral innovation, as well as the use of comparative field research, and discuss the unique conservation implications of animal innovations and traditions.

We agree with Ramsey et al. on the importance of an operational definition of innovation. This will clarify communication and direct our focus to significant examples of innovation for closer analysis. However, we suggest a shift in the emphasis. It is useful, as Ramsey et al. do, to discriminate between novel individual innovation and socially learned behavior. However, they focus on the former to the extent that social learning is primarily considered something to discard in the search for examples of "true" (purely individual) innovation. Ramsey et al. define innovation as a process and product attributable to a single individual. To this end, they exclude social learning from the phenomenon they define and discuss. Individual innovations are certainly interesting and worthy of study. However, the importance of innovation stems mostly from its capacity to spread via social learning.

Although ultimately originating from single individuals, innovations become most important when they transcend their solitary origins and become more prevalent. As the authors point out, innovation is a key component of most definitions of culture, and is important because it can affect a species' ecology and evolution. In both respects, innovations are relatively insignificant when restricted to a single individual. An innovation can become part of a culture only through social learning. Likewise, innovations are important factors in the ecology and evolution of a species only when shared by many individuals. Although it may be possible for multiple individuals to independently produce similar innovations, this is not what we typically see in nature. Instead, when innovations become sufficiently widespread to play an essential role in a species' ecology and evolution, they usually have done so through social learning (Laland & Hoppitt 2003; Laland & Janik 2006; Mann & Sargeant 2003; Yurk et al. 2002).

There are important benefits to a broad taxonomic scope in the study of animal innovation. Primates are of special interest to anthropologists because of their relatedness to humans. However, some of the most important questions surrounding the capacity for innovation concern its evolutionary origins and consequences and its ecological effects. The most powerful tool in biology for addressing such questions is the comparative method (Freeman & Herron 2004; Harvey & Purvis 1991; Perry 2003). The strength of comparative analysis depends on

how many taxa and independent origins are considered for the phenomenon of interest. Primates present many of the best-known examples. However, animal innovation is taxonomically widespread, and other groups are also noteworthy for the frequency and importance of behavioral innovation. We discuss two examples next. Incorporating as many taxonomic groups as possible in our consideration of innovation can greatly increase the strength and generality of our inferences.

Cetaceans (toothed whales and dolphins) have exceptionally large brains, high levels of intelligence, mental flexibility, and a capacity for behavioral innovation (Marino et al. 2007). Field studies on wild cetaceans have revealed a diversity of behavioral traditions apparently derived from individual innovations (Rendell & Whitehead 2001). As is true of primates, many behavioral traditions in bottlenose dolphins (*Tursiops truncatus*) involve specialized foraging techniques (Chilvers & Corkeron 2001), and some also involve tool use (Mann & Sargeant 2003). To date, the best information comes from one long-term field study (Mann & Sargeant 2003). Through comparison across multiple populations, we could better understand which behaviors are instinctive or environmentally induced, and which are valid examples of innovations that have become distinct local traditions. Clearly, there is opportunity for such comparative field study in this species, as several potential examples of behavioral traditions and innovation have not yet been investigated. For example, many unusual foraging specializations have been identified in various populations of bottlenose dolphins in and around the Gulf of California (Leatherwood 1975).

Behavioral innovations are well documented in crows (*Corvus* spp.) and other corvids (Emery & Clayton 2004b). Examples include tool use in wild populations, with evidence for social transmission and cumulative social evolution (Hunt & Gray 2003). It has been proposed that corvids and apes share the same “cognitive toolkit,” including abilities for causal reasoning, prospecting, imagination, and flexibility (Emery & Clayton 2004b). The reason that similar cognitive traits have evolved in both groups may be that both needed to solve similar socioecological problems, including locating and exploiting unpredictable food resources, and understanding relationships among individuals in large social groups (Emery & Clayton 2004b). Similar selective pressures have also been implicated in the evolution of the cognitive abilities of cetaceans (Marino et al. 2007).

Although both have their strengths, comparative field research offers several advantages over captive studies for investigating innovations. Ramsey et al. stressed field studies at the beginning of their article, yet promoted captive studies for confirming innovations. Captive studies can only determine the degree to which a behavior is instinctive, but cannot usually confirm that a particular behavior is an innovation in wild populations. Moreover, the ecological and evolutionary implications of captive studies can be difficult to interpret because of the altered and restricted physical and social environment, especially considering the fact that behavior in large-brained social animals is very sensitive to context (Rendell & Whitehead 2001). Such species are precisely where Ramsey et al. predict finding more innovation. Laboratory experimentation facilitates isolating behavioral variables, whereas field studies examine these variables in their evolutionary context (Bateson 2003; Perry 2003; Smith et al. 2002; Whiten et al. 2005).

The existence of behavioral innovations maintained through social learning, could have a large impact on conservation efforts by giving distinct conservation significance to each unique population. Complementary to the importance of protecting genetic pools, the preservation of behavioral traditions could add a new dimension to conservation priorities and strategies (Whitehead et al. 2004).

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Innovation in sexual display

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Abstract: Much attention has been paid to innovative foraging methods, but little to innovative sexual displays. Innovations may be common in behavioural display, such as song or object use, and could occur in both male display form and female preferences. Similar evidence exists for innovation in display as in foraging methods, but in smaller quantities. Ramsey et al.'s methodology permits rigorous data collection in this field.

The new methodology proposed by Ramsey et al. (2007) has implications for studies in areas beyond the ones they highlight. The majority of their examples, and those in the cited literature, are concerned with foraging methods, or coping with novel or changeable environments. It is striking that one well-studied branch of behaviour is underrepresented. Courtship displays, usually exhibited by males, provide a basis for female choice and offer some of the most elaborate behaviours seen or heard in animals (Anderson 1994). Whilst many displays are morphologically fixed (long tails or bright colours) and likely strongly influenced early in life by genetic factors, others are behaviourally flexible, and candidates for innovation. Innovation may occur in the display form (e.g., song structure, movements, use of objects) and in female preferences (mate choice copying, alternative exploitation of a pre-existing bias). Two examples of sexual display in which innovations are possible are bird song (Marler & Slabbekoorn 2004) and bowerbird's bowers (Frith & Frith 2004).

Why are innovations in sexual display of interest? First, the variety of elaborate sexual displays still demands an explanation. Innovation, coupled with learning (ten Cate & Rowe 2007), provides an additional mechanism to traditional genetic mechanisms of inheritance to explain the rapid appearance and divergence of displays. If this leads to mating isolation of certain populations, then it may also inform the understanding of speciation.

Second, sexual display provides an unusual situation where selection favours innovation per se. Females may prefer innovative males, regardless of the exact form of display exhibited, favouring males that contrast with peers (Burley & Symanski 1998; Elias et al. 2006), perhaps because unusual males are less likely to be relatives, or because innovative males possess a general cognitive ability or can bear a costly brain (Miller 2000). Males exhibiting exaggerated displays, such as large song repertoires, have high mating success (Kroodsma 2004) and one way to extend the repertoire is by generating novel syllables or phrases (Johnson 2006). These become available to other males to copy and incorporate (Slaabekoorn et al. 2003).

Third, the apparent decoupling of reward for innovation (mating or reproductive success) from the display itself provides a useful system to study how individuals decide whether to retain innovations. Sexual displays differ from the exemplar behaviours given by Ramsey et al. (2007). In most cases, such behaviours produce an immediate reward (e.g., food becomes available). A close link between behaviour and reward will likely reinforce the innovative behaviour. Additionally, the reward can be perceived by observers, offering a stimulus for copying (Caldwell & Whiten 2003). Conversely, rewards for producing an innovative display may be long delayed and concealed from observers. Females can continue to sample males and only subsequently return to a preferred novel male (Uy et al. 2001). Males may be unsure of their reward in terms of reproductive success, especially if they provide no parental care. Feedback following innovation demands further investigation.