

Although I have emphasized the weaknesses of existing ethnographic data, I agree with R&W's hypothesis that cetaceans are capable of social learning (and therefore culture). The available experimental evidence suggests that at least some cetaceans possess the requisite cognitive abilities for social learning (e.g., Kuczaj et al. 1998; Xitco & Roitblat 1996). In addition, the available observational data provide valuable cues about possible outcomes of social learning. Such cues are invaluable, but limited. We have used observational data for cues about deception and empathy in cetaceans (Kuczaj et al., in press). These data suggest that cetaceans are capable of deception and empathy, but fall short of demonstrating these capabilities. Similarly, the *suggestion* of social learning is not the same as the *demonstration* of social learning.

In order to understand cetacean culture, we must gather considerably more experimental and observational data. Observations can provide additional insights into the products of culture that are important to cetaceans, as well as into the processes that might be involved. Experiments can help to define the nature and limits of these processes. It is essential that we keep open minds about both products and processes. For example, I would argue that stimulus enhancement is a process, and that limiting the notion of process to imitation and teaching ignores other potentially viable social learning processes. It seems likely that the evolutionary emergence of increasingly sophisticated cognitive abilities and the resulting behavioral plasticity made culture possible. Thus, a theoretical perspective on culture that minimizes or assumes process would be woefully inadequate.

Culture: In the beak of the beholder?

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Abstract: We disagree with two of Rendell and Whitehead's assertions. Culture may be an ancestral characteristic of terrestrial cetacean ancestors; not derived via marine variability, modern cetacean mobility, or any living cetacean social structure. Furthermore, evidence for vocal behavior as culture, social stability, and cognitive ability, is richer in birds than Rendell and Whitehead portray and comparable to that of cetaceans and primates.

Rendell & Whitehead (R&W) present a useful review of cetacean culture. We were stimulated by their analyses of a difficult topic, detailed descriptions of cetacean behavior, intriguing interpretations of cultural activity with respect to these behaviors, and attempted cross-species comparisons. We disagree, however, with R&W on two issues: evolutionary history and avian culture.

First, culture may be an ancestral state predating the cetacean split from their terrestrial ancestors. Based on evidence presented in the target article, cultural traits exist in each of the best-studied species of both cetacean suborders. Not enough is known about their behavioral ecology to estimate when in cetacean evolution culture arose, though parsimony suggests it is not independently derived within the order. Culture is as likely to have been a trait of terrestrial proto-cetacea and among the suite of changes that facilitated cetacea's submergence as to have been the evolutionary product of a marine lifestyle. Cetacean culture may thus be independent of R&W's proffered explanations: marine environmental variability, extensive modern cetacean mobility, or any living cetacean social structure. Possibly terrestrial variability, scaled appropriately to the life span and sociality of ancestral proto-whales, drove evolution of their culture.

Second, avian culture, especially regarding vocal behavior, is richer than R&W portray. Issues involve social stability, sympatric behavior and dialects, imitation, and advanced cognitive abilities. We discuss each in turn.

Social stability should incorporate some notion of scale relative to an organism's lifespan. R&W write "song-bird dialects . . . are apparently not related to stable social groups." Indigo bunting (*Passerina cyanea*) learned vocal elements, however, persist in shared male song long after an individual bird's lifespan (Payne 1996). Also, given many songbirds' short lifespans, interactions with the same individuals over multiple breeding seasons imply stable social groups (Godard 1991).

In comparing mammalian and avian vocal and behavioral cultures, R&W claim that avian cultural groups are not sympatric. Although birds may not exhibit the same population-level sympatry as resident and transient *Orca*, some birds – oscines with group territorial defense such as Australian magpies (*Gymnorhina tibicen*; Brown & Farabaugh 1997), white-browed sparrow-weavers (*Plocepasser mahali*; Wingfield & Lewis 1993) – do have sympatric overlap of social groups possessing within-group shared vocal cultures, which parallels R&W's dolphin and chimpanzee examples.

R&W treat motor and vocal learning independently. Vocal behavior is, however, motoric – muscles produce vocalizations. For whatever ecological and social reasons, vocal learning is evolutionarily rare: only cetacea, parrots, oscine songbirds, hummingbirds, humans, and a bat have vocalizations variable enough that learning can be experimentally established as contributing to the crystallized productions of mature animals. Experimental study of functional production of imitated vocalizations is rarer still, yet critical to the issue of imitative learning. Specifically, R&W appear unaware of the complexities of parrot imitative vocal behavior. Over 20 years of data demonstrate that, at least within the laboratory, Grey parrots' (*Psittacus erithacus*) learned vocalizations represent communicative motor behavior, and that these vocalizations are goal-directed (intentional), not simply stimulus-bound (Pepperberg 1999). Such functional use of vocalizations learned by imitation constitute program-level imitation in a nonmammal (Pepperberg, in press), contrary to R&W.

Given that socially-mediated learning is a cornerstone of culture, we expected R&W to develop more fully cross-species comparisons of the effects of social interaction on learning. Social interaction and/or social demonstrations of functional use are critical for acquiring vocal behavior in humans, dolphins, and birds. For children, certain aspects of social interaction clearly facilitate label acquisition (e.g., Baldwin 1993), and operant-based procedures often fail with developmentally delayed or otherwise dysfunctional children whereas socially-mediated training succeeds (Pepperberg & Sherman 2000). For dolphins, large numbers of trials of food-reinforced operant conditioning produced low-fidelity copies of target sounds (Richards et al. 1984) whereas socially- and functionally-oriented reward conditions yielded, in orders of magnitude fewer exposures, high-fidelity copies of similar computer-generated whistles (Reiss & McCowan 1993). The importance of social interaction for songbird learning was critically delineated in papers by, among others, Baptista & Petrinovich (1984; 1986). In training Grey parrots to produce referential copies of human speech sounds, both a socially-interactive training method (the model/rival technique) and functional use of vocalizations (referent as reward) are necessary (Pepperberg 1999; Pepperberg et al. 1999). Lacking either condition, training is either ineffective or activates simple mimicry but not referential communication (Pepperberg 1998).

Parrots, then, are capable of program-level imitation in vocal behavior and possibly in other motor skills (Moore 1992). Do free-ranging parrots use imitation to pass information culturally? Our work with wild Greys in Africa remains too incomplete to report, but we believe R&W conclude too hastily that only *Orca* and humans share "complex multicultural society" (i.e., socially learned vocal and nonvocal behavior). Amazona parrots maintain vocal dialects that distinguish neighboring roosts (Wright 1996). Thick-billed parrots (*Rhynchopsitta pachyrhyncha*) learn pine nut extraction and predator avoidance from adults (Snyder et al. 1994). Nomadic budgerigars (*Melopsittacus undulatus*) share flock-

specific calls yet maintain individually unique vocalizations; the flock is a permanent structure from which young of both sexes disperse, and budgerigars adjust their contact calls towards those of the flock they enter (Brown & Farabaugh 1997; Farabaugh & Dooling 1996). Social structure within parrot roosts and functions of parrot vocalizations remain poorly understood, but in many social and ecological patterns, these large-brained, social birds may resemble large-brained, social mammals, including primates and cetaceans.

Finally, R&W conclude that cetaceans display greater social stability and cognitive abilities than birds. We disagree with these generalizations. With respect to parrots and corvids, for example, such claims about social stability are false or unknown and about cognitive ability, false or untested. Parrots' and corvids' lifespans are comparable to cetaceans (multiple decades), and research by, for example, Pepperberg (1999) and Balda and Kamil (1998) demonstrate avian cognitive abilities that compare favorably with both cetaceans and nonhuman primates and, on occasion, young children.

R&W bring deserved attention to cetacean culture; their broad view of culture is a fruitful approach. We have attempted to address a shortcoming in their treatment of avian social learning, aiming for a more detailed understanding of independently derived cultures and the roles of sociality and ecology in their evolution.

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Teaching in marine mammals? Anecdotes versus science

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Abstract: The use of anecdotes is not a viable research strategy to study animal culture. Social learning processes can often be documented with careful quantitative analyses of observational data. Unfortunately, suggestions that killer whales engage in teaching are entirely based on subjective interpretations of qualitative observations. Thus, "evidence" of teaching in killer whales cannot be used to argue for the occurrence of culture in marine mammals.

Rendell and Whitehead (R&W) wrote an interesting and stimulating target article about behavioral traditions in whales and dolphins. However, they acknowledged only two of many possible approaches to the study of animal culture and they sometimes equated the collection of anecdotal observations of behavior with what they refer to as the "ethnographic" study of behavioral variants in animal populations. This is particularly evident in their discussion of teaching in killer whales, where anecdotal observations are used as evidence for the occurrence of instruction. In this commentary, we argue that there are more research options for the study of animal culture than those discussed in the target article, but that the use of anecdotes is not one of them. After re-examining two of the main studies of "teaching" in killer whales cited by R&W, we conclude that there is no quantitative evidence for the occurrence of instruction in this species, irrespective of whether one emphasizes the intentional or the functional aspects of instruction.

R&W argue that there are two basic approaches for the study of animal culture: controlled laboratory experiments on social learning (where emphasis is on the cognitive processes) and field descriptions of behavioral variation (where emphasis is on their

product: culture). In reality, controlled experiments on social learning can be conducted both in the field and in the laboratory, and behavioral traditions can be studied in both settings as well. Furthermore, processes of social learning and teaching can also be studied with observational data alone and without experimentation, if the observational data are collected and analyzed with careful quantitative procedures and if clear hypotheses are formulated and tested (e.g., Maestripieri 1995; 1996). Although we are sympathetic with the difficulties of conducting experiments with free-ranging marine mammals, we do not believe that such difficulties provide a valid justification for the use of qualitative/anecdotal observations of behavior as evidence for culture.

The limitations of this approach are exemplified by R&W's discussion of the evidence for teaching killer whales. Lopez and Lopez (1985) first reported that while killer whales hunted sea lions in Patagonia, they often pursued their prey near the shore and, as a result, became temporarily stranded on the beach. Regardless of their success at capturing prey, the adult killer whales were always able to arch their bodies, rock sideways, and swim back to sea. In their study encompassing 936 hours of observations and 568 observed incidences of hunting, Lopez and Lopez (1985) observed six hunting-related interactions between adults and juveniles. All the evidence of teaching provided by Lopez and Lopez (1985) is contained in the following statement: "Several times, an adult flung a captured sea lion toward a juvenile which had not caught its own prey, and the juvenile pushed the prey with its head or body, or captured it in its mouth. These observations with adults and juveniles interacting lead us to postulate that the adults may be teaching the young to hunt" (p. 182). Interestingly, Lopez and Lopez (1985) also reported that in some of these adult-juvenile interactions, an adult killer whale flung its prey toward a juvenile who had already caught its own prey. In these situations, "the juvenile did not catch the flung prey, but held on to the sea lion it had caught itself" (p. 182). These observations suggest that the behavior of the adult may have been accidental, and not motivated by intent to teach. According to R&W, the Lopez and Lopez (1985) study showed that adults throw away already captured prey while teaching their young, thus demonstrating that teaching has a cost.

R&W cited the study by Guinet and Bouvier (1995a) as providing the clearest description of teaching in killer whales. According to R&W, the behavior of adult killer whales described in this study fits the definition of teaching given by Caro and Hauser (1992), which involves "modifying the behavior, at some cost or lack of benefit, only in the presence of a naïve observer such as to encourage, punish, provide experience or set an example, such that the observer acquires a skill more rapidly than it might otherwise do otherwise, or may not ever learn." Guinet and Bouvier (1995a) observed four adults and two calves for 446 hours over a 5-year period. In this time period, the two calves performed 88 "intentional strandings," 81 of which took place when no elephant seals were present "and were thus regarded as beaching play events" (p. 30). No evidence was provided to support the notion that strandings were intentional or functionally related to hunting. Guinet and Bouvier (1995a) reported two observations of teaching. On one occasion, a stranded calf had difficulty returning to sea and could only do so with the help of its mother. On another occasion, after a calf began pursuing a seal pup, its mother "accompanied and pushed her offspring with her rostrum towards the seal pup. The calf grabbed the side of the seal while its mother positioned herself between the beach and her calf to prevent it from going too high up the beach" (p. 31).

In both the Lopez and Lopez (1985) and the Guinet and Bouvier (1995a) studies, the evidence of teaching in killer whales consists of the qualitative description of a few behavioral interactions between adults and juveniles and the authors' subjective interpretation of these interactions as teaching. It is not immediately apparent how these observations fit Caro and Hauser's (1992) definition of teaching or any other operational definition of this phenomenon. In our view, the observations reported by Lopez and