

social behaviors. What is surprising and yet enduring, in so many arenas, is a fascinating reluctance to deal with the dolphin in pragmatic terms: the dolphin *qua* dolphin. Still, the work of so many animal behaviorists from Griffin (1984) to Seyfarth and Cheney (1990), has moved us considerably ahead in our ability to shift paradigms in our thinking about animal culture. Rendell and Whitehead's (R&W's) piece opens that dialogue even further by addressing the full complement of cetacean behavior within a scaffolding of strong ethological and behaviorist theory.

Following on the heels of Vincent Janik's (2000) recent work on whistle matching, which establishes important evidence for the possibility of the transfer of ideas in *Tursiops*, R&W offer a more broadly conceptualized rationale – drawing on definitions of culture – for establishing their own idea of culture.

R&W's approach to the study of animal behavior and culture is as nuanced and sophisticated as any I have read. Their work complements a set of discourses that have allowed us to rethink "science" in ways that have enabled their subtlety and complexity. It is, I think, critical in this context to acknowledge the rise of the women's movement in the last few decades and the advent of feminist theory, such as the work of Haraway (1989; 1990), Keller (1983), and Longino (1990), in our understanding and appreciation of how animals "work." Needless to say, this includes the research of Goodall (2000) and many other women who relied more heavily on synthesis rather than reductive analysis as an enabling way of thinking about animals. The methodological and conceptual changes that have been incorporated into science have, of course, been critical to a general willingness to understand animals differently.

Other work in the cultural studies of science have allowed us to strip away the veneer of reductive empiricism, in an effort to reveal how science is "constructed." This approach, often vilified by scientists, has actually helped open science up by recognizing that the strict limits of objectivity can interfere if we seek to understand the intricate nature of biological processes. Whether we turn to the work of Latour (1987), Lewontin (1993), or Oyama (2000), we are all better practitioners if we understand the cultural constructions of our own modes of inquiry.

The work of cultural studies of science is not only useful in terms of understanding process, but also in evaluating content. It is a mode of thinking that addresses the lacunae of culture, reminding us that culture does not only exist in observable phenomena. As we begin to define cultural patterns in other groups of animals, particularly in cetaceans which are not easily observed for lengths of time, it is critical to resist the impulse toward positivist conclusions. Just as culture may be comprised of behaviors that are learned and transferred from one individual to another, it may also be marked by patterns of behavior that individuals (or groups) resist or avoid. By way of example, it may be instructive at least to look at the practice of breastfeeding – a physiological and a cultural practice – in American culture in recent decades. An intrinsically biological activity (with strong genetic and behavioral components), breastfeeding was *not* common practice among middle class women in the 1950s, 1960s, and even 1970s. But, of course, the withdrawal from the practice was not *outside* of culture. Quite the contrary, it reflected a strong, if localized, group-specific cultural movement in response to shifting community values. Interesting to note, a subsequent cultural shift, relying on cultural transmission of values and practices, has recently increased the frequency of breastfeeding within the very same social context.

In my own work on captive *Tursiops*, many years ago (1983), I noted a behavior I called "bottom sink" where an individual rests at the bottom of a pool for about a minute or more. Was this a "cultural practice" that pelagic animals learned from shallow-water peers? Is it a behavior that responds to the dynamics of an acoustically challenging concrete environment that the animals learn in captivity? The answers are unclear and more important elusive, given the difficulty of observing the *absence* of behaviors in a group or even the gradual acquisition of a behavior. But if we are

interested in understanding the full complexity of culture, our questions must explore ideas of culture that may ask us to invert question of adaptive fitness. Such questions, particularly for animals that we study in captivity, are critical if we are to begin to understand the pragmatics of animal culture. R&W have extended the possibilities of that mode of understanding; their essay will be the springboard for the kind of sophisticated and nuanced treatment that cetacean behavior has deserved for decades.

Social learning and sociality

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Abstract: Sociality may not be a defining feature of social learning. Complex social systems have been predicted to favour the evolution of social learning, but the evidence for this relationship is weak. In birds, only one study supports the hypothesis that social learning is an adaptive specialisation to social living. In nonhuman primates, social group size and social learning frequency are not correlated. Though cetaceans may prove an exception, they provide a useful group with which to test these ideas.

Rendell & Whitehead (R&W) provide a timely review of cetacean culture, with compelling evidence for group-specific suites of socially learned behaviour patterns in sympatric populations. In particular, the association of vocal mimicry and motor imitation in cetaceans fits with a wide-ranging trend that includes parrots (Dawson & Foss 1965; Moore 1992), songbirds (Campbell et al. 1999; Lefebvre et al. 1997), and possibly humans (Iacoboni et al. 1999). In many ways, the evidence for cetacean cultures could be considered more compelling than that for apes (Whiten et al. 1999) because of the sympatric element, voiding geographical variation as an explanation for behavioural variation between groups. We agree that the ethnographic approach will often be the only feasible method of collecting social learning data in cetaceans. Determination of the precise social learning mechanism will be difficult, if not impossible, to ascertain in the field, but, as R&W argue, the exact mechanism of transmission has little relevance to definitions of culture (Heyes 1993b; Reader & Laland 1999a). It is important that ethnographic social learning data are collected, since cetaceans provide a valuable opportunity to study the evolution of cultural transmission, brain size, and cognitive capacities in a group both phylogenetically distant from humans and with a very different brain architecture to that of primates (Marino 1996).

However, we are concerned that a common theme of the target article, that stable social groups favour the evolution of social learning, reinforces an (often implicit) assumption that is becoming increasingly common in the social learning literature. R&W argue that the need to maintain group identity in the highly mobile cetaceans provides a selection pressure for vocal learning, which provides the roots of sophisticated social learning. Further, they argue that stable social groups increase the opportunities for cultural transmission and information exchange which could increase inclusive fitness if other group members are kin. R&W may be correct that, in cetaceans, the maintenance of group identity has favoured the evolution of social learning capacities: we do not have the comparative data to address this issue at present. Nevertheless, there are some relevant data available for other animal groups, and we note below that the evidence for a link between sociality and social learning is equivocal at best.

A number of authors have predicted a correlation between group living and an enhancement of the propensity or capacity to socially learn, with species that live a gregarious lifestyle predicted to rely more on social learning processes than solitary species (Klopfer 1959; Lee 1991; Lefebvre & Giraldeau 1996; Lefebvre

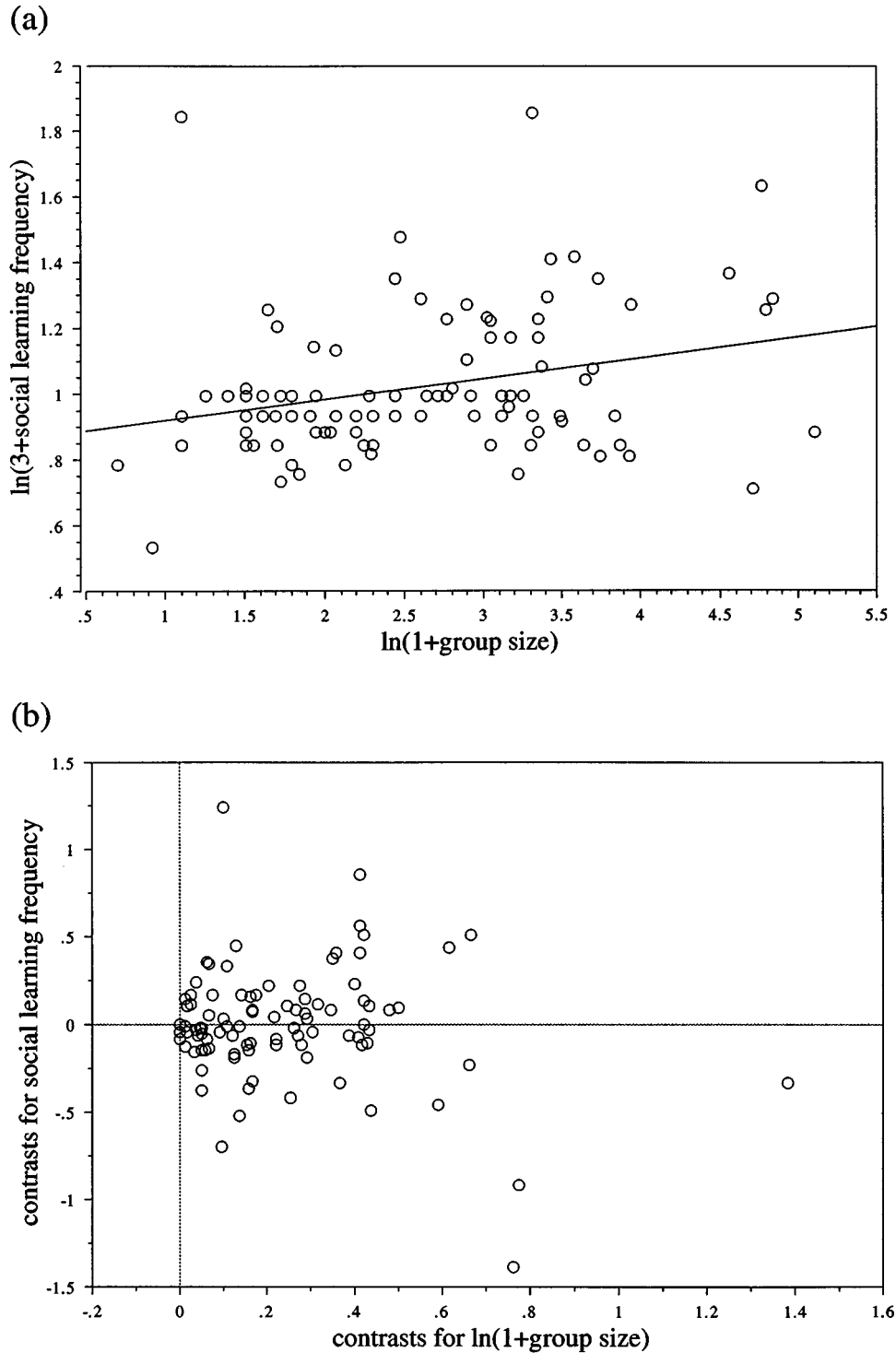


Figure 1 (Reader & Lefebvre). Social learning frequencies and social group size in non-human primates. (A) The raw data, with each point representing one species ($r^2_{\text{adj}} = 0.06$, $F_{1,103} = 7.33$, $p < 0.01$). (B) Independent contrast data ($r^2_{\text{adj}} = 0.00$, $F_{1,92} = 1.01$, $p > 0.1$). Frequencies are corrected for research effort by taking residuals from a natural log-log plot through the origin of social learning frequency against research effort. From Reader (1999).

et al. 1996; Roper 1986). Relevant to this discussion are the social (or Machiavellian) intelligence hypotheses (Byrne & Whiten 1988; Flinn 1997; Humphrey 1976; Jolly 1966; Whiten & Byrne 1997), which argue that the large brains of primates evolved as an adaptation to living in large, complex social groups. Social learning is often described as a core aspect of such social intelligence (e.g., Byrne & Whiten 1997).

What is the evidence for a link between social living and social learning? In birds, Templeton et al. (1999) found that the more social pinyon jay is better at social learning than individual learning, whereas the less social Clark's nutcracker performs similarly in both tasks. Templeton et al. (1999) argue that this supports the hypothesis that social learning is an adaptive specialization to social living. To our knowledge, this is the only study to show such a

relationship after controlling for the possible confound of species differences in individual learning. Balda et al. (1997) describe a link between social structure and observational learning in corvids, but Lefebvre (2000) notes that the interspecific differences reported by Balda et al. (1997) parallel those found by Olson et al. (1995) on a nonsocial, nonspatial task, which may provide an alternative account for the results if individual learning is a confound. Similarly, interspecific variation in social learning parallels variation in individual learning and degree of urbanisation in the five Passerine species studied by Sasv ari (1979; 1985) and the two Columbidae species studied by Lefebvre et al. (1996). There is thus currently little comparative evidence that social learning is an adaptive specialisation to particular environmental demands in birds (Lefebvre & Giraldeau 1996), beyond the study of Templeton et al. (1999).

In nonhuman primates, social learning frequencies have been estimated for 105 species by collecting reports of social learning from the published literature (Reader 1999; Reader & Laland 1999b). Mean social group size and social learning frequency correlate weakly when species are treated as independent data points, but when phylogeny was taken into account using independent contrasts this relationship was no longer significant (Fig. 1). Inclusion of relative executive brain size as an independent variable, the exclusion of the unusual orang-utan and the exclusion of captive studies and data where a human influence was suggested all produced similar findings. Hence we have no evidence for a correlation between group size and social learning frequency in nonhuman primates, once phylogeny or relative brain size are taken into account. However, it is also plausible that social group size may be a poor or inexact measure of social complexity, and that a better measure of social complexity would reveal an association with social learning.

Some authors view non-imitative forms of social learning as a subcategory of individual or asocial learning, perhaps sharing similar psychological mechanisms and neural substrates, and predict that social learning will co-vary with general behavioural plasticity (Galef 1992; Heyes 1994b; Laland & Plotkin 1992). Thus social learning per se may not be an adaptive specialisation, and selection for individual learning may also increase the propensity to socially learn. Others view asocial learning and social learning as different, domain-specific, special-purpose adaptive mechanisms (Giraldeau et al. 1994; Tooby & Cosmides 1989), with some authors suggesting or assuming a trade-off between these two abilities (e.g., Boyd & Richerson 1985; Rogers 1988). If the first group of authors are correct, a search for selection pressures specifically effect social learning may be misguided, and we may do better by focusing on the evolution of individual learning or general behavioural plasticity.

We have poor evidence at present that social learning is an adaptive specialisation to social living. It may be that, in cetacea, a reliance on social learning has more to do with feeding ecology than with social structure. Though there is an obvious confound in that the four cetacean species providing the best evidence for social learning are also the best studied, it is notable that all these species rely on diverse prey types and are partly carnivorous. Alternatively, if all cetacea are shown to exhibit similar social learning propensities, this may have more to do with common ancestry (that is, phylogeny), than the ecological explanations discussed by R&W. Like the target article authors, we urge researchers to study social learning in this interesting group, since data on social learning frequencies will allow tests of competing theories of foraging ecology, sociality, phylogeny, cognitive capacity, and dependence on parental care for the evolution of social learning.

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Can culture be inferred only from the absence of genetic and environmental actors?

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Abstract: Rendell & Whitehead's minimalist definition of culture does not allow for the important gaps between cetaceans and humans. A more complete analysis reveals important discontinuities that may be more instructive for comparative purposes than the continuities emphasized by the authors.

Although Rendell and Whitehead (R&W) choose a rather straightforward definition for culture, we think that this concept is insufficiently discussed in the target article. However, instead of debating about whether cetaceans have or have not a culture, we would rather like to concentrate in our commentary on the possible differences between cetacean culture and human culture.

A distinction is made by linguists and cognitive psychologists between performance and competence (Chomsky 1965). While performance refers to observable behaviors (e.g., spoken language as we hear it), competence refers to the set of rules and operations that make performance possible. This distinction can also be useful to critically examine R&W's approach because these authors seem to allude only to performance in discussing animal culture. We would like to focus on the interest of bringing up such distinctions in relation to culture in order to fully understand the nature and consequences of attributing a form of culture to cetaceans.

We start by pointing out some of the features that are associated with culture, in its full human sense. First of all, a single process of information transmission such as imitation cannot solely define culture. In this respect, and notwithstanding the controversies surrounding the definition of imitation (e.g., Galef 1998b), many animal species and even invertebrates such as octopuses (Fiorito & Scotto 1992) show evidence of fast learning by observing conspecifics performing a specific action. Now, would it be sufficient to state from this finding that octopuses have a culture? Certainly not. Concerning the definitions of cultural behaviors (e.g., R&W's Table 1), we note that all these definitions rely on some sort of social behavior (learning, modification, etc.), with or without reference to its likely mechanism (namely, some form of imitative behavior). But surprisingly, the proposed definitions do not mention competencies or processes related to culture for the organisms possessing it. In humans, some crucial features appear to be linked to culture either as necessary components or as by-products. Thus, language and more generally symbolic and intentional systems probably constitute the main features of human culture. But culture is hard to conceive outside a process of accumulation and complexification of knowledge over generations (e.g., Donald 1991; Tomasello & Call 1997). A starting point of culture is the establishment of social rules that have a commonly defined and conventionalized medium for which language is likely to be the best candidate. Moreover, it is likely that culture is organized as an autonomous system and thus presents similarities with linguistic organization. Each relation within this system is tied to other relations. In humans, this system has become independent from biology in such a way that the constraints acting for stabilization or for changes in a given culture are internal; and these features no longer require a parallel evolution of natural or genetic environments.

Let us briefly consider what could be equivalent in cetacean culture to the devices we just mentioned. First, according to R&W's minimalist definition, culture appears as soon as the behavioral repertoire is sufficiently broad to respond to environmental changes. From then on, a given species can develop specific traditions because learning abilities are flexible enough to