A functional paradigm for evaluating culture: An example with cetaceans

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Abstract  Nonhuman culture was first considered in nonhuman primates because they are genetically similar to humans. However, evolution is not progressive and therefore many species may occupy niches that favor socially transmitted, group specific behavior. Not surprisingly, evidence for culture has accrued in several taxonomic groups, including cetaceans. If culture is an adaptation, it is imperative we understand the factors that favor its formation. Understanding the evolutionary origin of culture will allow for a wider range of species to be studied, including those that are difficult to test in the laboratory. I propose a broad-based functional paradigm for evaluating nonhuman culture; based on the idea that while not all cultural behaviors may garner fitness benefits to the individual, the ecological and social environments in which cultural behaviors evolved must have favored the physical attributes and social learning capabilities that allow for cultural formation. Specifically this framework emphasizes the relationships between social learning, ecology, social systems, and biology in relation to culture. I illustrate the utility of the functional paradigm with evidence from the cetacean group, while setting the stage for a stringent species by species analysis. By means of contextualizing culture, the Functional Paradigm can evaluate a species’ potential to exhibit culture and can investigate potentially cultural behaviors [Current Zoology 58 (2): 271–286, 2012].

Keywords  Nonhuman culture, Social learning, Evolutionary function, Cetaceans

There is no denying the complexity of human culture. However, focusing on an anthropocentric definition of culture occludes evidence of culture in other species. Some bottlenose dolphins Tursiops truncatus use sponges as specialized feeding tools (Smolker et al., 1997), sperm whales Physeter macrocephalus form groups that define feeding and movement patterns (Whitehead and Rendell, 2004), and killer whale Orcinus Orca groups share stable and unique vocalizations (Ford, 1991; Strager, 1995; Yurk, 2002). From Darwin’s perspective these differences between humans and animals are a matter of degree, not kind. Nonetheless, without a concrete understanding of the origin of cultural behavior, we cannot assume that similar evolutionary pressures created culture across a variety of taxonomic groups.

This paper serves as a preliminary step towards creating a framework for evaluating the evolutionary influences on cultural behavior. While many have advocated for a broader view on culture (Marler, 1996; Kamil, 1998; Fragaszy and Perry, 2003), sought to understand the biological precursors of culture (Fragaszy and Perry, 2003) and explored the precursors of cultural behavior across the animal kingdom (Bonner, 1980), a cohesive view of the dynamic forces that favor group specific behavior has yet to be explored. This interdisciplinary schematic allows species from a wider range of taxonomic groups to be included in the cultural discussion, including species that are difficult or impossible to study in the laboratory.

A serious objection to adopting an evolutionary perspective on culture is that cultural variants may be neutral or even maladaptive (Boyd and Richerson, 1985; Laland and Williams, 1998; see also Lachland and Slater’s “culture trap”, 1999). While specific cultural behaviors may not have adaptive value, the biological capacity to learn from conspecifics and maintain a behavior within a group must have arisen due to fitness benefits (Bonner, 1980). Therefore, even if culture is a byproduct of selection, the cognitive mechanisms, life histories, and social structures that facilitate its formation must have been favored at some point over evolutionary time.

1 Studying Culture

1.1 Why we need the functional paradigm

The study of nonhuman culture is plagued by confusion over nomenclature and the fundamental debate
whether human and nonhuman culture should be considered together (see Laland and Galef, 2009, for a concise historical perspective on the debate.). Most definitions of culture share several core characteristics: culture is comprised of behaviors, those behaviors are shared by groups of individuals, and social learning plays a role in the transmission of those behaviors (Rendell and Whitehead, 2001; Laland and Janik, 2006). Disagreement stems from the defining details: behavioral differences must not result from genetic or environmental variability (Morgan, 1900; Menzel et al., 1972, Mainardi, 1980; Galef, 1992; Whiten and Ham, 1992), or behaviors are cultural only if they are transmitted by imitation or teaching (Galef, 1992). Additionally, “culture” is sometimes said to be comprised of multiple “traditions” (Boyd and Richerson, 1985; Fragaszy and Perry, 2003; Whiten and van Schaik, 2007). Yet, this division is not clear because definitions of “tradition” vary as much as definitions of the word “culture”, and often overlap with similar meaning. Traditions can be socially transmitted information that must persist over several generations (Mundinger, 1980; Cavalli-Sforza and Feldman, 1981, Whiten et al., 1999), or simply persist for some time (Fragaszy and Perry, 2003). For the purpose of this framework, “culture” and “tradition” will be considered interchangeable, for the reasons stated below.

Dividing human and nonhuman culture into discrete phenomena masks many of the similarities between the two. The assumption that animals cannot modify culture as humans do, i.e. “ratchet” culture ( Tomasello et al., 1993), has served as justification for their separation. However, this assumption has been partially dismantled by evidence that zebra finches can ratchet song culture (Fehér et al., 2009), and dolphins can produce one of the processes involved in ratcheting; i.e. process-orientated imitation (Herman, 2002). The theory that animals lack social motivation to maintain culture has also generated objections to nonhuman culture (Tennie et al., 2009), however there is evidence of social conformity in humpbacks (Noad, et al., 2000), and orcas (Yurk et al., 2001). The accretion of nonhuman evidence indicates why separating human from nonhuman culture creates a false dichotomy and is unproductive to understanding the roots of culture.

Additional controversy focuses on how cultural behaviors are transmitted. By definition, cultural behaviors (or traditions) must be transmitted through some form of social learning (Mundinger, 1980; Cavalli-Sforza and Feldman, 1981; Rendell and Whitehead, 2001; Fragaszy and Perry, 2003; Laland and Janik, 2006). If social learning is simply defined as changes in behavior as a result of observation or interaction with a conspecific (Box, 1984; Galef, 1988; Heyes, 1994), many animals are social learners. For example, guppies can learn travel routes from others (Laland and Williams, 1997; 1998), archer fish may imitate (Schuster et al., 2006), and rats gain information from conspecifics about food preferences and foraging techniques (Laland and Plotkin, 1992). However, the categories of social learning are not straightforward, nor can they be organized neatly into a hierarchy of complexity (Heyes, 1994). Imitation and teaching are assumed to be the most cognitively taxing (Galef, 1992), even though the cognitive mechanisms behind social learning are still not understood.

Imitation has been proposed as a crucial transmission mechanism for cultural learning (Mundinger, 1980; Whiten, 1989; Tomasello, 1993, Galef, 1992). Historically this was used as justification for denying nonhuman culture because imitation and teaching were not considered in animals until recently. So much so that the concept of imitation recently lacked a coherent theoretical framework (Heyes, 1993), and teaching was not considered in reviews of social learning (Heyes, 1994). However, the literature on imitation and teaching in many species continues to grow, threatening the idea that imitation and teaching are “advanced”. Additionally, there is insufficient evidence that humans always use imitation, and teaching in transmitting our own culture (Boesch, 2001). Finally, imitation does not support sufficient fidelity to explain the stability of cultures (Claïdière and Sperber, 2010). Therefore, limiting culture by imposing a hierarchy of social learning types denies the full scope of culture and is irrelevant for the mechanisms that maintain culture.

Social learning is not inherently more advanced than asocial learning because they share the same neural substrate, and differ solely by the context in which the learning takes place (Fragaszy and Perry, 2003). Social and asocial learning are not mutually exclusive, nor do they act in conflict of each other (Heyes, 1994), because social learning is correlated with overall greater learning capacities (Reader, 2003). Because the neural mechanisms behind the forms of social learning are unknown, any assessment of their cognitive load is purely theoretical at this point. Potentially, therefore, all types of social learning could contribute to culture.

The definition of culture adopted by this paradigm allows for the inclusion of taxonomic groups that would otherwise be ignored by excluding nonhuman animals or imposing a hierarchy of social learning. Therefore, a
definition of tradition, “a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning” (Fragaszy and Perry, 2003), will be used to define culture, as has been done before (Laland and Hoppitt, 2003).

1.2 Proposal for a WIDER paradigm

Separating human and nonhuman culture and assuming a hierarchy of social learning types impedes the study of culture while demonstrating the need for a broad and evolutionarily relevant conception of culture. Efforts have been made to analyze human and nonhuman culture together. According to Bryne and colleagues (2004), culture is not formed nor defined by one element, but each species has its own unique “package” of six different and broadly applicable definitions (Bryne et al., 2004). Putting this perspective into an evolutionary framework allows for an understanding of the unique environment that has shaped behavior at the individual level to create each species’ “package”. This paper reviews the interdisciplinary factors that would contribute to culture and classifies them into one of four dynamic and interacting categories: social learning, ecology, social system, and biological predispositions (see Fig. 1).

The following discussion will explain the origin of the Functional Paradigm and will outline how to apply it at the individual and behavioral level with examples from cetaceans. Using a notoriously difficult to study taxonomic group demonstrates the full implications of the framework.

2 The Functional Paradigm

2.1 Social learning

By definition cultural behaviors are transmitted by social learning. Therefore, the first concern of the Functional Paradigm is to identify if an individual of a species can interpret social cues and learn from them. This may be answered through both laboratory and field studies, and must consider all forms of social learning. Species that cannot learn socially should be excluded from the discussion of culture. Since social learning may be better predicted on a trait by trait basis (Laland and Kendal, 2003), specific behaviors must be considered. Candidate behaviors include those that are found repeatedly among individuals of a community (Whiten et al., 1999) or those that differ in rate or intensity between communities (Whitehead, 2008). Evaluation of the transmission mechanisms of a specific behavior must occur in an ecologically valid setting. Simply because a species has the capacity to learn socially does not mean that they do in the context of a specific behavior.

Identifying social learning is a demanding task because it may be evoked too easily and wrongly used to explain behavioral differences between populations (Galef, 1992; Heyes, 1993; Tomasello et al., 1993; Laland and Hoppitt, 2003; Laland and Janik, 2006). We cannot judge sociality—a gregariousness between individuals of the same species, as defined by Deputte (2000)—as evidence of social learning. Moreover, observed learning might result from individual learning in a social context (Kuczaj, 2001), and stable differences in behavior between groups may be a reflection of what each group encounters in its lifetime (Schiel and Huber, 2006).

Despite the difficulties, there are a variety of experimental tests available that aim to identify a type of social learning in the laboratory. However, it is often difficult to isolate which type of social learning is being utilized to solve a behavioral task (Hoppitt and Laland, 2008). Using the definition of culture that this framework employs, the differences between social learning types are inconsequential because all could potentially contribute to culture. Therefore the extensive list of methods given by Hoppitt and Laland (2008) are all relevant to identifying whether a species has the ability to learn socially. A separate set of techniques exist for determining social learning outside of the laboratory (Kendal et al., 2010). Care must be taken to distinguish between those techniques that introduce a new behavior and therefore test a group’s capacity for social learning and those that assess an existing, potentially cultural behavior. Additionally many of the methods are limited in their applicability across contexts and vary in the type of data needed for an assessment of social learning. For example, the Cue Reliability Approach (Dewar, 2003) determines a cost/benefit ratio for individual social learning, but only applies to situations where an individual must classify a
stimulus or tactic as safe or harmful, and a classification error is costly. Meanwhile the Option Bias Method (Kendal et al., 2009) is useful for identifying social learning of a novel behavior, but cannot be used to analyze existing cultural candidates like movement patterns. While this list represents an accumulation of many years of progress on the topic, there is still the need for continued exploration into reliable identification methods that can be applied across behaviors.

Regardless of the identification method, applying broad and conceptually testable definitions of social learning processes allows a greater range of species to be included in the cultural discussion. Heyes’s (1994) definition of imitation—an observer performing a topographically matching behavior acquired from a demonstrator—eliminates the questionable role of goal-directedness and perspective taking in imitation. The Caro and Hauser (1992) definition of teaching—in which an at-cost behavior for the demonstrator produces accelerated learning in the observer—eliminates anthropomorphic limitations that require a Theory-of-mind. Focusing on humanistic conceptions of social learning limits our understanding of behavior and ignores behaviors with different proximate mechanisms whose end result is a behavioral copy (Heyes, 1994) or the facilitation of learning (Hoppitt et al., 2008).

While identifying social learning is crucial to identifying culture, it only explains the transmission of cultural behaviors. Other aspects of a behavior such as the source, the ecological setting, the content, and the reward from performing it contribute to the formation of a cultural tradition (Claïdière and Sperber, 2009). Therefore the contextual details that would favor social learning must be examined when assessing species and specific behaviors.

### 2.2 Ecology

There is no consensus on the precise environment that would favor social learning, due in part to the way environmental change is measured. When measured in a general way, an environment that is highly stable does not favor learning because species would have time to evolve appropriate adaptations. Therefore, a degree of change or heterogeneity is necessary to make any type of learning adaptive. In an environment that is changing too quickly, asocial learning is favored because socially learned behaviors may be outdated or inappropriate, making an environment with an intermediate rate of change optimal for social learning (Laland and Kendal, 2003). Others argue that social learning would be favored in stable environments because it is more likely that an observing individual will occupy a similar environment to the one their behavioral model experienced (Boyd and Richerson, 1988; 1996). Through both perspectives, learning from conspecifics becomes advantageous in environments where individual learning is costly or inaccurate, or when social learning permits an individual to acquire behaviors that increase fitness (Boyd and Richerson, 1988; Mann and Sargeant, 2003; Laland, 2004).

When environmental variation is considered spatially, an environment that changes over short distances would cause pressure for culture because groups would be forced to move considerably and adapt to different conditions (Rendell and Whitehead, 2001). In such environments, behavioral flexibility and cultural transmission of feeding strategies would be favored for species with low travel costs and reduced territorial restrictions (Knight, 2001) because they encounter more varieties of habitat. When considered temporally, over the period of an individual’s lifetime, incidents of severe weather may also favor culturally retained memories of such events (Barrett-Lennard, 2001).

Whether the ecosystem preferentially selects for social learning depends upon each species’ unique relationship with its environment. A species’ generational rate, the distribution of their prey, whether they can transmit information vertically and horizontally, and the size of an animal’s home range (Laland and Kendal, 2003) all contribute to that relationship. For example, habitat complexity based on the ecology of available foods may contribute to larger brains and greater levels of social complexity in spider monkeys *Ateles geoffroyi*; two factors that promote social learning. Meanwhile, howler monkeys *Alouatta palliate* that inhabit the same area of forest experience it differently and have not responded the same way (Milton, 1988).

An intriguing theory linking the environment to the evolution of cultural practices proposes that culture itself may modify the environment. Niche construction—otherwise known as behavioral drive (Wilson, 1985), or ecosystem engineering (Jones et al., 1994)—is a mechanism by which species alter their environment through their metabolism, and/or behavior to modify natural selection pressures (Odling-Smee, 2003). Cultural niche construction in human models amplifies these effects, by influencing a species’ rate of evolutionary change (Laland et al., 2000; Laland et al., 2001). This same process may exist to a lesser degree in other species that use culture to exploit unoccupied niches (Rendell et al., 2011), such as the sponging behavior of...
2.3 Social system

Social structures are a product of the selective forces of the ecological environment in the form of predation, and the spatial and temporal distribution of food and resources (Wilson, 1975; Eisenberg, 1981). Importantly, though, social structure may not optimize the fitness of the population because it operates and forms under the decisions of individuals (Whitehead, 2008). What forms of social structure make social learning favorable for individuals?

Basic components of sociality, such as gregariousness and tolerance, promote social learning (Coussi-Korbel and Fragaszy, 1995; van Schaik, 2003). Social species have been predicted to use social learning more often than solitary species (Lee, 1991; Lefebvre et al., 1996; Lefebvre and Giraldeau, 1996; Reader and Lefebvre, 2001). However, group size alone is not correlated with a higher frequency of social learning, and a measure of social complexity may better predict social learning (Reader, 2003). A complex social environment has been suggested to select for social intelligence and also been used to explain the evolution of general intelligence as a side-effect (Byrne, 1997; Humphrey, 1976). However, the “Social Intelligence Hypothesis”, or theory of “Machiavellian intelligence” is still under scrutiny because—as suggested by Fitch et al. (2010)—unforeseen levels of intelligence are seen in solitary species such as the octopus (Fiorito and Scotto, 1992), and red-footed tortoise (Wilkinson et al., 2010). Nonetheless, the idea that social organization may be connected with cognitive capabilities is highly relevant when considering the evolutionary origin of culture in species with complex social structures.

While there are statistical methods available for determining the complexity of a social system (Whitehead, 2008), “complex” is not an operationalized term. De Waal and Tyack (2003) define complex societies as those that are stable over time, individualized, and may be characterized by the propensity for the behavior and survival strategies. In contrast, unstable social groups, such as fission-fusion systems, are often assumed to be complex because they require higher levels of behavioral flexibility. However, fission-fusion structure may simply be a correlate of advanced cognition, as it could result from several evolutionary trajectories (Aureli et al., 2008). Instead of ending superior cognition to all species with high fission-fusion dynamics, it is best acknowledged that social structure is an adaptation to a variety of ecological and biological necessities that differ for each species. The same applies for social systems such as monogamy that are assumed to be simple because the details of relationship maintenance may contribute to unexpected complexity (Emery et al., 2007).

Aside from the influence of social complexity, culture could prove adaptive if it occurs within groups of related individuals. The selective advantage of maintaining culture—the type which offers a fitness benefit (an adapted category of Bryne et al., 2004)—for an individual within a group of relatives is clear since any advantages associated with efficient information transmission increases indirect fitness.

Matrilineal groups may favor culture, yet culture may have unique genetic consequences when groups are divided along female lines. “Cultural hitchhiking” may be the reason behind the presence of low levels of diversity of mtDNA in sperm whales, killer whales, pilot whales and possibly narwhals (Whitehead, 1998; 2005). A theory previously only applied to humans (Feldman and Laland, 1996), cultural hitchhiking—a form of gene-culture co-evolution—is analogous to genetic hitchhiking where neutral neighboring genes are passed along due to the fitness benefits of others. Genes and culture may also interact within matrilineal groups if female genes are selfishly passing on culture as a way to limit the genomic imprinting effects of males (Brown, 2001). Through this theory, culture could mediate genomic
conflict in favor of the mother. As of now, all of these theories are controversial but stress the wide-ranging evolutionary implications of social systems.

Classifying social systems is not a simple task; therefore, the first step in evaluating their role in mediating cultural behavior is to identify the details of the species’ social structure. Whitehead (2008) outlines methods for assessing social structure given varying levels of sampling difficulty. Apart from sheer complexity, family groups, mother/infant interactions, and relationship maintenance should be considered. Second, the system’s propensity for social learning can be assessed by analyzing its potential benefits within the kin organization and social structure. With a deeper understanding of the pressures put on the individual from the social system, a cultural candidate can be evaluated by investigating how the social system may facilitate the transmission and maintenance of the behavior.

2.4 Biology

Biological attributes such as advanced cognition, long lifetimes, and extended infant care are suggested to favor social learning (Roper, 1986). These attributes evolved in response to the social and ecological environment and potentially indicate selection for culture. For instance, an increase in social interactions increases an individual’s cognitive load, selecting for a larger brain over time (Eisenberg, 1981), including an enlarged neocortex (Bryne, 1995). In environments with patchy resources, selection will favor an increase in the amount of life span young spend in social learning situations (Eisenberg, 1986). And certain mating and dispersal patterns may increase the relatedness of females to a group as they age, making post-reproductive investment advantageous (Johnstone and Cant, 2010). The functional significance and evolutionary origin of these traits will be considered below. However, biological attributes that could facilitate cultural formation vary depending upon the species and should not be limited by these examples. Theoretically, traits such as distinctive coloration that divides social groups, or a finely tuned vocal organ that produces complex song could promote culture.

Increased brain size is noteworthy because the brain is metabolically expensive, and neurogenesis is extremely conservative across all mammals (Finlay, Darling, and Nicastro, 2001). Therefore, larger brains and the expansion of neural circuits should have some functional significance for the individual (Bryne, 1995). Innovation and social learning require increases in brain size as they evolve (Wilson, 1991). Following this logic, there is a significant positive correlation between absolute brain volume and social learning (Fragaszy and Perry, 2003). Additionally brain size is important because brains and behavior co-evolved in a general way, rather than evolving specific structures for unique behaviors (Fragaszy and Perry, 2003). Therefore relatively large brains should correlate with behavioral flexibility and social sophistication (two correlates of social learning), regardless of their evolutionary history.

The fitness benefits of prolonged infant dependency must outweigh the potential costs from predation during that time. Although social structure may lessen predation risk, (as has been theorized for sperm whales, Connor and Mann, 2006), prolonged juvenile development must still provide fitness benefits. Prolonged mother-infant associations may allocate more time for social learning and facilitate the formation of culture.

Menopause does not occur simply because of longevity. Other long lived mammals remain reproductively active throughout their lives; as Johnstone and Cant (2010) point out, elephants breed into their 60’s (Moss, 2001) and baleen whales can breed into their 90’s (Mizroch, 1981). The grandmother hypothesis—originally devised for explaining menopause in humans—proposes that menopause is highly adaptive when older females serve as a source of information that significantly increases the fitness of her kin (Boran and Heimlich 1999; Norris and Pryor 1991). When viewed as a form of kin selection (Williams 1957; Hamilton 1966; Hawkes et al., 1998), menopause could serve an equally important function in species beyond humans given they have the capacity to pass on information.

3 Example with Cetaceans

In practice the functional framework should be applied one species at a time to truly map each species’ unique evolutionary context. However, for the sake of discussion, I will bring in examples from several species to highlight the flexibility of the framework. The method for utilizing this paradigm is outlined in Table 1 and a species-specific application of the paradigm is outlined in Table 2.

3.1 Can cetaceans learn socially?

The bottlenose dolphin T. truncates has been the primary subject of most cognition and social learning studies because experiments with large cetaceans are extraordinarily challenging. There is robust evidence that bottlenose dolphins can understand the referential meaning of gaze. Captive dolphins can pick up gaze following through informal interactions with humans.
Table 1  Analyzing the cultural potential of a species and a specific behavior

<table>
<thead>
<tr>
<th>SPECIES LEVEL</th>
<th>BEHAVIORAL LEVEL</th>
</tr>
</thead>
<tbody>
<tr>
<td>SOCIAL</td>
<td></td>
</tr>
<tr>
<td>LEARNING</td>
<td>(1) Can they learn socially?</td>
</tr>
<tr>
<td></td>
<td>- Consider all types of social learning</td>
</tr>
<tr>
<td>ECOLOGY</td>
<td>(1) How variable is it?</td>
</tr>
<tr>
<td></td>
<td>- Consider spatial and temporal rates of change, home range, travel patterns and prey distribution</td>
</tr>
<tr>
<td></td>
<td>(2) Could social learning offer reliable information related to survival?</td>
</tr>
<tr>
<td>SOCIAL</td>
<td>(1) What are the details of the social structure?</td>
</tr>
<tr>
<td>SYSTEM</td>
<td>- Consider complexity, kin organization and relationship maintenance</td>
</tr>
<tr>
<td>BIOLOGY</td>
<td>(1) Are there biological traits that may indicate selection for culture?</td>
</tr>
<tr>
<td></td>
<td>(2) What are the evolutionary origins of these traits?</td>
</tr>
</tbody>
</table>

Table 2  Initial evaluation of killer whales *Orcinus orca* and their group-specific calls through the Functional Paradigm

<table>
<thead>
<tr>
<th>Orcinus orca</th>
<th>Group-specific vocalizations</th>
</tr>
</thead>
<tbody>
<tr>
<td>SOCIAL</td>
<td></td>
</tr>
<tr>
<td>LEARNING</td>
<td>(1) Yes.</td>
</tr>
<tr>
<td></td>
<td>- Vocal learners.</td>
</tr>
<tr>
<td></td>
<td>- Observations of imitation in captivity (a), the wild (b), and of teaching (c).</td>
</tr>
<tr>
<td></td>
<td>* Experimental studies are needed.</td>
</tr>
<tr>
<td>ECOLOGY</td>
<td>(1) See section 3.2.</td>
</tr>
<tr>
<td></td>
<td>- Orcas hunt various food types according to group membership: all types are patchily distributed, may make group hunting adaptive.</td>
</tr>
<tr>
<td></td>
<td>(2) Yes.</td>
</tr>
<tr>
<td></td>
<td>- Hunting strategies would be easier to learn socially than individually and offer obvious fitness benefits.</td>
</tr>
<tr>
<td>SOCIAL</td>
<td>(1)</td>
</tr>
<tr>
<td>SYSTEM</td>
<td>- Close matrilineal groups often associate in larger pods and pods sometimes with large clans.</td>
</tr>
<tr>
<td></td>
<td>- Young live with their mothers throughout life.</td>
</tr>
<tr>
<td></td>
<td>- Males mate with females from other pods.</td>
</tr>
<tr>
<td></td>
<td>* More research is needed on relationship maintenance.</td>
</tr>
<tr>
<td>BIOLOGY</td>
<td>(1)</td>
</tr>
<tr>
<td></td>
<td>- 2.57 EQ (d)</td>
</tr>
<tr>
<td></td>
<td>- Menopause (e),</td>
</tr>
<tr>
<td></td>
<td>- Low levels of mtDNA diversity. (f).</td>
</tr>
<tr>
<td></td>
<td>(2) See section 3.4.1.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Orcinus orca</th>
<th>Group-specific vocalizations</th>
</tr>
</thead>
<tbody>
<tr>
<td>SOCIAL</td>
<td></td>
</tr>
<tr>
<td>LEARNING</td>
<td>(1) Yes.</td>
</tr>
<tr>
<td></td>
<td>- Calves learn group calls.</td>
</tr>
<tr>
<td></td>
<td>- Family groups may facilitate learning by increasing the use of group-specific calls for the first two weeks after birth (g).</td>
</tr>
<tr>
<td>ECOLOGY</td>
<td>(1)</td>
</tr>
<tr>
<td></td>
<td>- Foraging orcas must separate hundreds of meters—outside the reliable sight range in water—and group specific calls can occur across long distances</td>
</tr>
<tr>
<td></td>
<td>(2)</td>
</tr>
<tr>
<td></td>
<td>- Calls could maintain proximity (h).</td>
</tr>
<tr>
<td></td>
<td>(3)</td>
</tr>
<tr>
<td></td>
<td>- This allows effective foraging across larger distances</td>
</tr>
<tr>
<td>SOCIAL</td>
<td>(1)</td>
</tr>
<tr>
<td>SYSTEM</td>
<td>- Call repertoires are maintained over generations, and certain calls change more rapidly than others (i).</td>
</tr>
<tr>
<td></td>
<td>- Pod-specific calls could make inter-pod communication more efficient, and strengthen group membership (j).</td>
</tr>
<tr>
<td></td>
<td>- Could help avoid inbreeding (k)</td>
</tr>
</tbody>
</table>

Sources: (a) Bain, 1986; (b) Ford, 1991; (c) Guinet & Bouvier 1995; (d) Marino, 2006; (e) Olesiuk, Bigg, & Ellis, 1990; (f) Whitehead, 1998; 2005; (g) Weiss et al., 2006; (h) Ford et al., 2000; (i) Yurk et al., 2002; (j) Ford, 1989; (k) Sayigh et al., 1990; Ford, 1991; Barrett-Lennard, 2000.
(Herman et al., 1999, 1993; Herman and Uyeyama, 1999; Pack and Herman, 2004; Tschudin et al., 2001); suggesting that they possess mechanisms for shared attention that need not be developed through formal training. They can interpret both static and dynamic gaze almost flawlessly, even in novel situations in the first set of trials (Herman, 2004), eliminating the possibility that they used an arbitrary stimulus response.

Overall, bottlenose dolphins have been classified as “imitation generalists”. They can imitate actions, both known and novel, that are performed by conspecifics (Xitco, 1988; Xitco et al., 1998); Bauer and Johnson, 1994), humans, and themselves. They can imitate to order (Harley et al., 1998; Xitco 1988), and produce delayed imitation, (Kuczaj et al., 1998; Richards, 1986; Richards et al., 1984; Herman and Pack, 2001). A high fidelity of imitation is necessary for any behavior to spread accurately (Heyes, 2009; Huber et al., 2009), and dolphins are more accurate at producing behavioral copies of the Do-as-I-Do behaviors (Herman, 2002) than apes are (Custance et al., 1995), despite greater anatomical differences from humans.

There have been numerous studies on wild cetaceans, documenting their mimicry and synchronous behavior. It has been suggested that the innate capabilities of dolphins for synchronous behavior reflect a precursor to true imitative abilities that develop later in life (Fellner, 2006). In wild settings, dolphins have been observed copying each other’s signature whistles (Janik, 1997; 2000). While the large body of evidence from captivity must be interpreted with caution—because the subjects are highly enculturated—field observations of dolphin imitation suggest that this capacity could be employed in social contexts as a form of social learning.

Preliminary field evidence for cetacean teaching comes from a study on the Atlantic spotted dolphin Stenella frontalis, in which nursing females significantly changed their hunting/feeding behavior when their calves were observing them (Bender et al., 2008). The authors did note however, that the data does not yet deserve the full ‘teaching’ label because it is unknown whether or not the mother’s behavior accelerated the calves’ learning.

In order to make similar conclusions about social learning capabilities across cetaceans, evidence is needed in other species with the same level of scientific scrutiny under which dolphins have been tested (Day, 2001). Outside of dolphins, the only research on imitation and teaching stems from behavioral observations. For example, bowhead whales Balena mysticetus have been seen apparently imitating conspecific calls (Clark, 1990), sperm whales have been reported to match their “codas” to arbitrary click rates (Backus and Schevill, 1966), and captive orca imitation has been reported (Bain, 1986), as well as interpod mimicry in the wild (Ford, 1991). Because of the difficulties in experimentally testing imitation in larger cetaceans, the strong laboratory evidence from bottlenose dolphins may be the only link between field observations and conclusions about their imitative abilities.

3.2 How variable is their environment?

The relative rate of stability and the relative rate of instability of the marine environment have been proposed separately to support the formation of culture in cetaceans. This confusion partially stems from the different ways that environmental change can be measured. The stable marine environment lends itself to the development of social learning (Thomas, 2001) because the heat capacity of the ocean lessens temperature variability over short time scales (Steele, 1985; 1991) and the atmosphere and ocean work as one system to reduce variability over long time scales (Steele, 1991). However, when the rate of change is considered as a function of spatial makeup, it has been proposed that the marine environment is actually less stable than the terrestrial one because habitats change quite rapidly over short distances. Cetaceans low travel costs and few territorial restrictions would amplify the amount of spatial variability they experience, favoring culture (Whitehead, 1998; Rendell and Whitehead, 2001). Temperature and spatial variability are inseparable elements of the environment; therefore cetaceans would have experienced more varieties of habitat but less variability in temperatures when they adapted to the marine environment.

Marine predators must hunt abundant but patchy schools of fish; prey patterns that may explain why group foraging strategies may have evolved (Barrett-Lennard et al., 2001; Laland and Kendal, 2003). Again, a species by species analysis of the effects of prey distribution must be considered because prey type also may have contributed to variability within the cetacean order. For example, humpback whales have

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fewer, less-complex feeding strategies as well as shorter periods of maternal investment and calf dependence than certain delphinid species (Clapham, 2000; Whitehead and Mann, 2000) and seek very different albeit patchily distributed prey.

Cooperative feeding strategies within cetaceans that merit evolutionary analysis at the behavioral level include: bubble net feeding in humpback whales (Jurasz and Jurasz, 1979; Hain et al., 1982), use of the water surface to catch prey in dusky dolphins (Wursig and Wursig, 1980), and ‘strand feeding’ by bottlenose dolphins (Leatherwood, 1975; Petricig, 1995). These behaviors exploit prey more effectively than lone foraging; therefore they potentially offer fitness benefits.

### 3.3 What are the details of their social structure?

Several cetacean species clearly illustrate the inability of the fission-fusion label to describe the details and complexities of social organization. The social system of sperm whales (Mesnick, 2001), bottlenose dolphins (Connor et al. 1998), and humpback whales (Clapham, 1993) have all been labeled “fission-fusion”, yet, the dynamics of each species vary markedly. Female and immature male sperm whales form long-lasting units and often aggregate in temporary groups preferentially with members of their own acoustic clan (Rendell and Whitehead, 2003). The social structure of bottlenose dolphins is characterized by stable male alliances, a network of flexible female relationships (Connor et al., 2000a; 2000b; Connor and Mann, 2006), and a hierarchy that is one of the most complex in the mammalian world (Connor et al., 2000a). Meanwhile, humpback whales form loose fission-fusion groups (Clapham, 1993) but show neither the group specific vocalizations of sperm whale groups nor the hierarchical organization of bottlenose dolphins. Because the character of social complexity is different in each of these systems, culture and its mechanisms would have unique functions in each; producing distinctive fitness consequences.

The evolutionary interplay of a social system at the individual level should take into account its relationship with that species’ ecology and biology. For example, most large cetaceans, such as sperm whales, are not affected by predators as adults, but their young are vulnerable and need protection. Predation pressures may therefore explain alliances between sperm whales that allow for alloparenting while mothers dive deeply in search of food (Connor and Mann, 2006). Sociality would also be favored over evolutionary time if the patchy distribution of food has made cooperative feeding methods adaptive. Membership in sperm whale groups is based on coda vocalizations and specific membership also determines feeding patterns. Marcoux, Rendell, and Whitehead (2007) tracked several sperm whale groups and used defecation rates as evidence of feeding success, finding different rates of success for different groups depending on environmental conditions. Therefore, it is clear that social groups play a role in mediating feeding behavior and movement patterns; both forms of niche construction that can have implications for fitness. Analysis at the behavioral level, choosing coda vocalizations for example, would analyze how the social structure facilitates the behavior and vice versa. Experimental tests are needed to fully prove that groups are formed via cultural associations; however, framing coda vocalizations in an evolutionary perspective shows how group traditions could be adaptive for sperm whales in changing environments.

### 3.4 Is there evidence for costly biological traits?

Certain cetaceans have large brain-to-body ratios, otherwise known as encephalization quotients (EQ), and life histories which are costly to the individual. Human’s EQ is roughly 7.0—while 1.0 corresponds to the ratio predicted for a mammal—and four species of dolphins have the next highest ratio with 4.14 to 4.56 (Marino, 2002) or roughly double that of chimpanzees and orangutans (Ridgway, 1986). In addition, a prolonged period of development in infancy (Connor et al., 2000a) and the evolution of menopause in some cetaceans also points to a biological need for extended care and perhaps to pass on knowledge (Rendell and Whitehead, 2001).

While closely related species may be utilized to form initial conclusions about the evolution of a trait, final analyses should look at the unique evolutionary trajectory of a species. For example, a general analysis of cetacean evolution may be useful, but brain size is not consistent across cetaceans, with as much variety between two species of similarly sized odontocetes (toothed whales) as there are between humans and great apes (Connor and Mann, 2006). A detailed investigation into the origin of any trait must be conducted before conclusions can be made about its evolutionary contribution to cultural behavior.

There are several hypotheses surrounding the origin of large brains in cetaceans. They may have evolved as an adaptation to the aquatic environment, as a byproduct of diet, as a tool for echolocation, or as a response to a complex social structure. Each of these possibilities will be explored below. Extra gilial cells and a larger overall body size may have evolved to allow cetaceans maintain...
heat effectively in cooler temperatures (Manger, 2006). However, Marino and colleagues (2007) refute this claim because odontocete bodies actually decreased in size, and were already above the body size threshold that would respond to temperature with increased size (Downhower, 1988). Additionally, an analysis of brain size in extant cetaceans (values obtained from Slijper, 1979) shows, that mysticetes (baleen whales) did not respond to the cooling temperatures by evolving larger brains, despite occupying the same cooling aquatic environment, indicating that other factors promoted brain growth in odontocetes.

Perhaps certain cetaceans could afford large brains because their high energy diet could support them. Interestingly, cetaceans have a higher metabolic rate than similarly sized land mammals (Ridgway and Patton, 1971), which would be supported by their high protein diet (Ridgway, 1986). The energy rich diet of dolphins in comparison to the grazing manatee, with a much lower EQ, illustrates how diet could have facilitated the metabolically expensive large brain (Connor and Mann, 2006). However, while diet may explain how it was possible for large brains to evolve, it does not explain why they increased in size.

Conceivably, the large brains of certain odontocetes are attributable to the physiological demands of echolocation (Jerison, 1986; Ridgway, 1986). Auditory structures are large in the dolphin brain (Breathnach, 1960; Ridgway, 2000), however, evidence is lacking that other enlarged parts of the brain, such as the cerebral cortex are used for auditory processing (Pabst et al., 1999). Additionally, several species of echolocating odontocetes lack high EQ’s, (data obtained from Marino (2006)) thus other factors must contribute to brain size as well.

Another theory proposes that complex social organization necessitated larger brains (Eisenberg, 1981) because a high encephalization quotient is correlated with pod size in dolphins (Marino, 1996). Evidence for this theory stems from specific brain structures as well. The ratio of neocortex to brain size in dolphins lies between humans and chimpanzees, with values closer to us (Tschudin, 1999), and in cetaceans, relative neocortex size is positively correlated with social group size (Connor et al., 1998, Tschudin et al., 1996). Because cetaceans evolved in a marine environment, their bodies adapted to different conditions than terrestrial animals. Therefore cognitive similarities between primates and cetaceans are evolutionary convergent (Marino, 2002) and universalities in brain function must not be assumed. Despite that the dolphin neocortex is the most convoluted in the animal world (Elias and Schwartz 1969; Marino, 2007), it is relatively thin and its neuronal characteristics mirror that of a primitive mammalian brain (Huggenberger, 2008). However this organizational structure may have simply been the result of an alternative evolutionary solution to improve brain performance; supporting an increase in cortical size instead of an increase in complexity (Huggenberger, 2008; Hof and van der Gucht, 2007; Marino et al., 2007). This evolutionarily analogous solution would still allow odontocetes to exploit a new prey niche with echolocation while supporting the brain structures necessary for social communication and complex group feeding.

The debate about the origins of large brains in cetaceans demonstrates why the diversity within cetaceans cannot be explained by one theory alone and that diet, echolocation and a complex social structure all may have contributed to their evolution. Whatever combination of factors caused an increase of EQ in several cetacean species, it did so on a rapid timescale; at a pace just lagging behind the pattern of human brain evolution (Marino, 2002). Because the EQ for archaeocetes was low (Marino et al., 2000), this evolutionary trajectory suggests that a larger brains must have been extremely favorable at one time. However, these evolutionary changes did not occur in isolation and are correlated in odontocetes with social competition (Huggenberger, 2008; Connor, 2007) and a lengthened life span (Lefebvre et al., 2006). Apart from longevity and prolonged infant care (Herman et al. 1994; Marten and Psarakos, 1995; Tyack 1986), certain cetaceans also display senescence; a rare physical attribute that may indicate selection for culture. The fact that killer whales (Olesiuk, Bigg, and Ellis, 1990), pilot whales (Marsh and Kasuya, 1984; 1986) and possibly sperm whales (Marsh and Kasuya, 1986; Whitehead, 2003) have menopause demonstrates that there is value in older, non-reproductive females within their social organization. The unique dispersal patterns

of certain cetaceans allow for an increasing ratio of relatedness of females to the group as they age, favoring the investment of energy by post menopausal females (Johnstone and Cant, 2010). Their investment is especially potent given their social learning skills could confer both direct benefits (Baird, 2000) and the transfer of information (Connor et al., 2000a; Whitehead and Mann, 2000; McAuliffe and Whitehead, 2005; Rendell and Whitehead, 2001) to their social group. There is no denying that older individuals are tolerated in orca groups, a puzzling behavior if there were not value in having non-reproducing elders around (Bigg et al., 1990).

4 Conclusion

Studying nonhuman culture and its mechanisms could potentially help us understand the evolution behind our own culture without retroactively assuming its basis (Knight, 2001). However, the search for culture in species that are difficult to study is often left to estimates of plausibility (Laland and Hoppitt, 2003) than sound science, and efforts even dismissed as futile (Premack and Hauser, 2001). This framework will help guide judgments about whether cultural candidates are indeed cultural and offer an alternative to abandoning the cultural search. The key to this model is that the four aspects that contribute culture have not contributed equally in every case; instead a unique combination of factors has facilitated each cultural example. This does not eliminate the need for experimental tests to validate that behaviors are socially transmitted, but provides a context in which cultural candidates from numerous taxonomic groups can be discussed. Overall this is a work in progress; continued study and future innovations will embellish this theory with growing examples and quantitative measures. In particular, universal measurements for evaluating environmental change and new field techniques for identifying social learning need to be developed. For cetaceans, details about the social structure of more species are desperately needed. Analysis of other taxonomic groups using this paradigm will highlight areas where more species-specific study is needed.

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