



the
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FROM SOCIAL LEARNING TO CULTURE:

INTRAPOPULATION VARIATION IN

BOTTLENOSE DOLPHINS

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Introduction

A colleague studying sharks in Australia was once asked by a tourist, "We *know* we can commune with dolphins, but can you commune with sharks?" It is a common perception that the cognitive abilities and social complexity of bottlenose dolphins (*Tursiops* spp.) rival those of any other nonhuman animal. If prompted, laypersons are likely to report that dolphins have language, communicate with people, teach their offspring to hunt, baby-sit each other's offspring, rescue stranded people from the sea, and defend people from sharks. Although such statements are both anthropomorphic and hyperbolic, some are, perhaps surprisingly, partially rooted in real data.

Bottlenose dolphins have been called our cognitive cousins because they exhibit an impressive array of cognitive skills rarely observed outside the great apes. These include passing the controversial, but widely applied, Gallup test of mirror self-recognition (Reiss and Marino 2001), program-level imitation (Tayler and Saayman 1973; Roitblat 1988, 1991), language-like skills (reviewed in Herman 2002a), vocal learning (common in birds, but relatively rare in mammals; Janik and Slater 1997), mental representation (e.g., cross-modal representation of echoic and visual information; Harley et al. 2003), metacognition (Smith et al. 2003), exceptional memory (Mercado et al. 1998), behavioral innovation (Herman 2002a), and tool use with marine sponges (Smolker et al. 1997; Mann and Sargeant 2003; Krutzen et al. 2005). Although such abilities are not restricted to hominoids and bottlenose dolphins (tool use, for example, has been documented in more than 30 avian species [Tebich et al. 2001; Lefebvre et al. 2002; Kenward et al. 2005], primates [e.g., van Schaik et al. 1999, 2003b; Whiten et al.

1999; Fragarzy et al. 2004], elephants [Hart et al. 2001], and others [Hall and Schaller 1964], among others), they do push the boundaries for known capabilities of nonhuman animals and blur the constantly shifting line distinguishing *Homo sapiens* from all other animals.

In this chapter, we will discuss whether dolphins have culture, which is a hotly debated behavioral trait often considered a hallmark of being "human." We will also investigate the interplay between social learning and individual specialization in foraging, a relationship important in understanding our study population of bottlenose dolphins in Shark Bay, Western Australia, where matrilineal traditions help create a patchwork of foraging tactics.

Defining Culture

An immediate challenge to determining which species have culture is providing a definition of culture that is biologically meaningful, does not inherently prevent or require attributing culture to particular species, and is widely acceptable to a diverse community of scientists (Laland and Hoppitt 2003). Although recognizing some simple requirements for a satisfactory definition is easy, finding a definition that meets those requirements is not (e.g., Heyes and Galef 1996; Rendell and Whitehead 2001 and peer commentaries). We agree with others that a definition encompassing social learning broadly is more useful than one restricted to certain social learning mechanisms (e.g., teaching, imitation) (e.g., Laland and Hoppitt 2003), and such a definition would capture many human cultural behaviors arising from diverse mechanisms of social learning (e.g., Henrich and Boyd 1998), while permitting comparisons across taxa. Of commonly used definitions that center on social learning, many consider culture as any information or behavior that develops through social learning (e.g., Boyd and Richerson 1996), or further stipulate that it be shared by a population, "subpopulation," or "groups" (e.g., Rendell and Whitehead 2001; Laland and Hoppitt 2003). The former approach would designate any socially learned behavior as "culture," and the latter does not clarify what constitutes a subpopulation or group. Thus, these definitions potentially label all socially learned behaviors (even those shared by two individuals) as "culture" because, technically, socially learned behaviors must be shared by at least two individuals *and* two individuals arguably compose a subgroup.

Consider a case in which an individual learns its mother's hunting behavior, but then no longer associates with her after weaning. Consequently, mother and offspring are the only two individuals in the population engaging in the hunting technique. Would these two individuals comprise a culture? We suggest that most behavioral scientists would be disinclined to label two individuals that share a single socially learned behavior as a distinct "culture," regardless of whether those individuals were humans or nonhumans. The issue of the minimum group size required for culture has rarely surfaced in discussions of animal cultures because intrapopulation variation in socially learned behaviors is typically quite low in populations studied. As we shall discuss, many putative cultural behaviors of bottlenose dolphins, particularly foraging behaviors, are not common to an entire population, but rather to subgroups within populations. Thus, the degree to which a socially learned behavior is shared exists on a continuum, ranging from only two individuals to an entire population. Such intrapopulation variation presents challenges to many current definitions of culture and suggests that more consideration is necessary to determine whether there is any reason to demarcate steps along the continuum. For example, information about group identity or social affiliation may be most likely to be shared by large proportions of a population and may differ *qualitatively* from behaviors with other functions. In fact, some argue that, consistent with use of the term "culture" in studies of human behavior, the term should be reserved for socially learned behaviors that perform social functions, such as promoting shared values or group identity (Premack and Hauser 2001; Henrich and McElreath 2003; Castro and Toro 2004; Tomasello et al. 2005).

We consider socially learned behaviors as points along a continuum (Figure 7.1), in which a higher tendency for the behavior to provide shared benefits for individuals results in more individuals engaging in the behavior. Because socially learned behaviors that provide social identity, communicative, or affiliative functions are generally considered essential to human culture and are more likely to be widespread among individuals, we view these as qualitatively different from behaviors with other functions and therefore consider them cultures. Although social functions are harder to identify in nonhuman animals, this definition does not exclude nonhuman animals from having culture, but remains consistent with the term's traditional use. Therefore, we will discuss the evidence for socially learned behaviors in bottlenose

dolphins, but will reserve the term "culture" for those behaviors that likely function to promote group identity, affiliation, and/or social cohesion.

Foraging behaviors are often designated as cultural because of the role social learning frequently plays in their development. Socially learned foraging behaviors may be particularly common because foraging skills are closely tied to fitness, and social learning can increase the efficiency of behavioral development (Laland 2004). The usefulness of learned foraging behaviors, however, depends on exposure to appropriate environmental contexts and should be widely shared only when individuals forage cooperatively, forage in groups, or forage in similar habitats that enable them to exploit similar resources. In the former cases, affiliative or cohesive functions are likely to be involved.

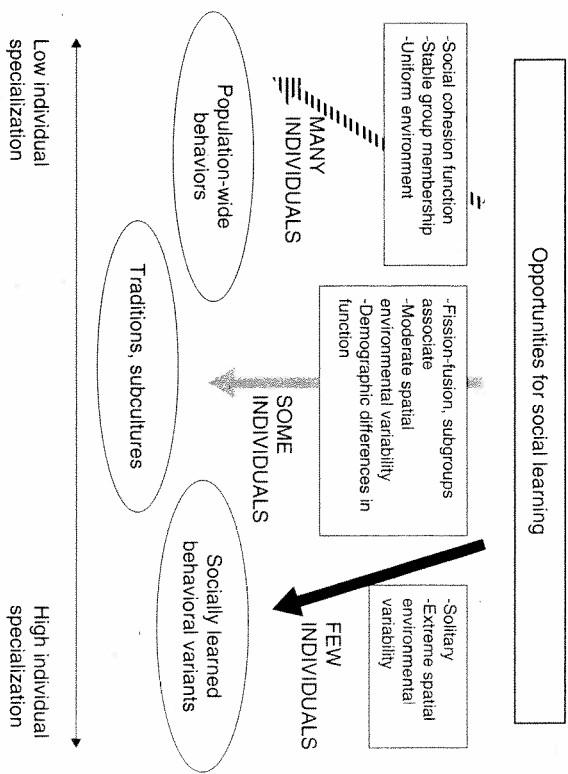


Figure 7.1 Model of how opportunities for social learning and shared function determine the frequency of a socially learned behavior in the population. Social learning opportunities are filtered through shared function to produce the incidence of a behavior in the population, with effects of differences in age and sex superimposed on the entire system. The striped and gray arrows represent pathways that favor horizontal and vertical transmission, respectively.

For animals that engage in relatively little group foraging, the degree to which a socially learned foraging behavior is shared should be driven by habitat similarity and access to similar prey items. Identifying the functions of socially learned behaviors in their ecological and social contexts should increase our understanding of (1) patterns of transmission (vertical, oblique, and horizontal patterns of social learning; see Cavallini-Sforza et al. 1982); (2) the frequency of the behavior within a population; (3) the extent of individual specialization; and (4) whether the behavior serves a social function, i.e., is cultural (Figure 7.1).

Several factors influence whether social learning occurs and the patterning of information transmission within a population. First, individuals must have opportunities to acquire information from others. The degree of social tolerance within a population can significantly affect the probability of social learning (Coussi-Korbel and Fragaşy 1995; Boesch and Tomasello 1998; van Schaik et al. 1999; van Schaik 2003) by allowing individuals opportunities to observe the behavior of others in the group or the products of their behavior. Although social learning can occur when animals do not directly interact, as in local and stimulus enhancement, stable, egalitarian social groups should provide more social learning opportunities than unstable or hierarchical groups by allowing behavioral coordination in time and space (Coussi-Korbel and Fragaşy 1995). Highly despotic groups have fewer opportunities for social learning because individuals are prevented from closely attending to each other's actions (Coussi-Korbel and Fragaşy 1995; van Schaik et al. 1999).

Once opportunities for social learning are available, the spread of socially learned behaviors will depend on the adaptive value of the behavior and environmental variation (Figure 7.1). Although maladaptive information can be transmitted (e.g., Laland and Williams 1998; Giraldau et al. 2002), long-lasting persistence of a socially learned behavior both in individuals and in populations is likely to depend on its usefulness to individuals that have acquired it from others (Galef 1995). For example, pinecone stripping in black rats (Aisner and Terkel 1992) and teaching of prey handling in meerkats (Thornton and McAuliffe 2006) provide clear benefits to naive foragers. Opportunities for social learning and behavioral function also have implications for the patterns of transmission that would be favored (Figure 7.1). Different types of information have different values depending on social structures and ecological heterogeneity. Socially learned behaviors that perform a social role are likely to result in population- or group-wide cultures as a result of oblique or horizontal

transmission (e.g., Whiten et al. 2005), even if individuals are largely solitary. For example, group-specific vocal communications in sperm whales (*Physeter macrocephalus*) are shared and enable maintenance of the social group (Rendell and Whitehead 2003), and motor behaviors such as hand-clasp grooming in chimpanzees (*Pan troglodytes*) may help strengthen bonds among members of a community even though some individuals spend significant amounts of time alone (Nakamura and Uehara 2004). Capuchins (*Cebus capucinus*) show substantial variation in social behaviors at different sites, from hand sniffing to social games (Perry et al. 2003a). These would qualify as cultures by our definition. However, socially learned behaviors that do not function primarily to maintain social cohesion (such as foraging) may still be widely shared, provided that individuals experience the same habitat either because resources are spatially uniform or the social group travels together (Figure 7.1).

When a population is subdivided such that smaller subgroups (e.g., matriline) preferentially associate and have similar patterns of habitat use in a patchy environment, vertically transmitted "traditions" (*sensu* Fragaşy and Perry 2003b; Perry et al. 2003a) may be common, a situation that may characterize foraging traditions in bottlenose dolphins. Further along the continuum of sociality, primarily solitary individuals in a patchy environment may learn socially, but large groups of individuals are unlikely to share socially learned traits. Thus, spatial environmental heterogeneity has clear implications for modes of transmission (horizontal, vertical, oblique) and for how widespread a behavior should be based on the probability that individuals will share the same environment (Figure 7.1). Similar effects of temporal environmental variability on transmission mechanisms have been addressed previously (Laland et al. 1996; Laland and Kendal 2003).

Factors promoting individual differences in the development of socially learned or cultural behaviors are not limited to ecological heterogeneity. Life-history strategies may promote mechanisms that favor age and sex differences in socially learned behaviors. For example, biases to learn from a model similar to oneself would result in more copying of mothers by daughters than by sons, even if mothers and offspring of both sexes spend considerable time together, as we suggest for dolphins (Mann and Sargeant 2003) and as has been suggested for chimpanzees (Lonsdorf et al. 2004). Behavioral patterns specific to juveniles may also develop because of morphological traits (e.g., size) or social structure (e.g., dominance hierarchies).

Cultural explanations are often invoked by cetologists and primatologists when individual variation is partially accounted for by association (social preferences). In such cases, researchers rarely consider how habitat heterogeneity and niche partitioning may also explain individual and subgroup variation. Vertically transmitted traditions, for example, may help explain matrilineal patterns of behaviors within single populations, but habitat biases may be equally important because association and habitat use are invariably correlated. In particular, individual specialization, when individuals exploit narrower niches than the population (Bolnick et al. 2003) and consequently differ from one another in niche use, becomes important to understanding cultural and social learning differences within populations (Figure 7.1). Individual specialization has a long history of research in the fields of ecology and evolutionary biology (reviewed by Bolnick et al. 2003), but has thus far received relatively little attention in the context of culture (but see Estes et al. 2003; Tinker 2004). We argue at the end of this chapter that individual specialization contributes critically to defining and understanding patterns of social learning in a given population.

Identifying and Measuring Social Learning

Most definitions of culture depend, at the very least, on demonstrations of social learning. Thus, methods used to study culture in populations of wild animals typically use social learning as the key criterion. At present, the method most commonly used to identify social learning is the "group contrast method" (Fragaszy and Perry 2003b; also called the "method of elimination" [van Schaik 2003] and the "ethnographic method" [Laland and Janik 2006]), which has been applied to chimpanzees (Boesch et al. 1994; Whiten et al. 1999), orangutans (*Pongo pygmaeus*) (van Schaik et al. 2003a), bottlenose dolphins (Krützen et al. 2005), and other cetaceans (Rendell and Whitehead 2001). Originally, the group contrast method was used to identify behaviors that varied between sites when such variation could not be explained by ecological or genetic differences (e.g., Boesch et al. 1994; McGrew et al. 1997; Whiten et al. 1999). More recently, the group contrast method has been employed to identify cultural patterns within populations when individuals differ in their behavioral repertoires (e.g., van Schaik et al. 2003b; Krützen et al. 2005).

Although the group contrast approach has succeeded in extending the cultural debate to nonhuman animals, the approach is undermined by at

least two major weaknesses. First, the group contrast method requires exclusion of ecological and genetic explanations of behavioral variability, a task equivalent to proving the null hypothesis (Fragaszy and Perry 2003b). Relatively few studies collect sufficiently detailed ecological or genetic data before dismissing these factors as important. Second, attempting to find a single explanation for complex behavioral patterns and divorcing behaviors from their ecological context conflicts with basic tenets of ethology (Tinbergen 1963). Many behavioral variants are likely to be correlated with ecological differences, making it both conceptually and practically impossible to eliminate the role of ecological factors in producing behavioral differences between populations. Many behaviors discussed as possible cultural variants involve foraging (e.g., Rendell and Whitehead 2001; Fragaszy and Perry 2003a), a task critically tied to ecology. Thus, the group contrast method may either underestimate or overestimate the actual frequency of social learning in wild animals. The method helps identify areas for investigation, but in the end, finding ecological contributions to a behavior does not rule out social learning, and ruling out ecological contributions may be both extraordinarily difficult and unnecessary for the study of social learning.

Several promising alternative approaches to identifying the occurrence of social learning in wild animals have been proposed, although some approaches are similar to the group contrast method in that they require behavioral variation to tease apart mechanisms and may therefore underestimate the frequency of social learning. These techniques include: (1) use of transmission chains and diffusion curves (Day et al. 2001; Laland and Kendal 2003), (2) correlations between association and behavioral similarity (Perry et al. 2003b), (3) field experiments (Humble and Matsuzawa 2002; Reader et al. 2003; Galef 2004), (4) comparison of field data to experimental work on captive populations (Terkel 1996) or theoretical models (Laland and Kendal 2003; Dewar 2003, 2004), and (5) use of multifactorial models that measure the contributions of multiple factors to behavioral development and avoid the concept of exclusion (Sargeant 2005). Finally, with the exception of a few studies (e.g., pinecone stripping in black rats (*Rattus rattus*) [Aisner and Terkel 1992], termite fishing in chimpanzees [Lonsdorf et al. 2004], food processing in orangutans [Russon 2003], and prey handling in meerkats [Thornton and McAuliffe 2006]), behavioral development has received scant attention in field studies, although understanding development is critical to establishing ecological and social contexts for socially learned behaviors. Researchers are also

moving beyond the question of whether animals have culture to the functional questions about social learning and its transmission mechanisms (e.g., "social learning strategies"; see Laland 2004). We have used correlations between association and behavioral similarity, multifactorial methods, and developmental approaches to investigate the diverse foraging tactics of dolphins in Shark Bay, Western Australia (Mann and Sargeant 2003; Sargeant 2005; Sargeant et al. 2005; Sargeant et al. 2007).

Evidence for Social Learning in Wild Bottlenose Dolphins: When Is It Culture?

On the basis of life-history characteristics, social patterns, and ecological environments, bottlenose dolphins have been considered likely candidates for socially learned and cultural behaviors. They are large-brained (Marino 1998) and capable of vocal (Janik and Slater 1997) and motor imitation (Herman 2002b). Although dolphin foraging is generally solitary, dolphin calves often accompany their foraging mothers, remaining within meters of her, and therefore have many opportunities for social learning before they are weaned at 3 to 6 years of age (Mann et al. 2000). Delayed weaning offers calves years of exposure to the behaviors of their mothers as well as time to practice them. Dolphin females, in general, are rarely aggressive (Scott et al. 2005) and tolerate close inspection of captured prey by others (Mann et al. 2007). Such high social tolerance allows the close proximity thought to favor social transmission (Cousi-Korbel and Fragaszy 1995; van Schaik et al. 1999). Furthermore, calves begin foraging independently at 3 months of age and thus experience several years of overlap between closely observing their mothers' foraging behaviors and developing their own foraging skills. Because of the calves' uniquely high degree of exposure to their mothers' actions, matrilineal-transmission of foraging tactics and other behaviors seems probable and may be an adaptive strategy allowing quicker and more efficient behavioral development than individual learning alone (e.g., Laland 2004). Dolphins are top predators in a patchy marine environment, and consequently fitness may be determined largely by food acquisition, especially in females. Thus, social learning from foraging mothers may be favored by natural selection. Calves may also learn social behaviors from a variety of others while still in their mothers' care because mothers constantly change their social companions (Gibson and Mann 2008a,b).

Evidence for social learning and possibly for culture in bottlenose dolphins comes from three main sources: (1) strong experimental evidence of vocal learning and whistle convergence in wild animals; (2) inter- and intrapopulation behavioral variation seemingly without genetic or ecological explanation; and (3) correlations between degree of association and behavioral similarity. In some cases, there is evidence for culture when socially learned behaviors seem to aid in social cohesion. However, most candidates for social learning in bottlenose dolphins involve foraging, where social functions are less apparent. Such functions may be present, but little effort has been devoted to identifying them, and supporting data are lacking. For example, do sponge carriers (described below) preferentially associate or cooperate with each other (controlling for habitat use and kinship) rather than with non-sponge carriers?

Vocal Learning

Dolphins are clearly capable of vocal imitation, although not all vocal imitation is cultural. For example, dolphins may mimic the whistles of conspecifics (Tyack 1997; Tyack and Sayigh 1997; Janik 2000b), a behavior that involves social learning but would not constitute culture because the whistles are copied only at that instant and the mimicry is ephemeral. The stability of socially learned behavior is often considered or implied as a necessary condition for culture. Whistles may be used to communicate specific contexts (e.g., food over here; Janik 2000a) and to carry identity information (Janik et al. 2006), but generally are not consistently shared by a subpopulation. However, convergence of whistle types among allied males (Smolker and Pepper 1999; Warwood et al. 2004) seems to qualify as culture because the whistle types are consistently used, shared by a subpopulation, and are likely to promote social cohesion and group identity within alliances.

The largest delphinid, the killer whale (*Orcinus orca*), exhibits clear examples of vocal culture, with pod-specific dialects (Ford 1991; Deecke et al. 2000; Yurk et al. 2002) and interclan (but not intercommunity) whistle similarity (Riesch et al. 2006) that is believed to be used to maintain group cohesion (Miller et al. 2004). While similar vocal cultures have not been identified in dolphins, alliance-specific whistles can be considered cultural and suggest some continuity between socially learned behaviors shared by a few individuals and those shared by large subpopulations or entire populations.

Interpopulation Variation in Motor Behaviors

Motor and even program-level imitation has been documented in captive bottlenose dolphins (e.g., Tayler and Saayman 1973; Bauer and Johnson 1994; Heriman 2002a), providing a basis for inferring that dolphins are capable of socially learning motor behaviors in the wild. Although no comprehensive survey of interpopulation variation in bottlenose dolphins similar to Whiten and colleagues' (1999) analysis of chimpanzee behaviors has yet been published, preliminary evidence suggests that the group contrast method may help identify candidates for socially learned behaviors. Diverse foraging behaviors have been reported in the literature, some of which appear distinctive either to particular populations or to subgroups within a population (e.g., Shane 1990; Connor et al. 2000; Nowacek 2002; Mann and Sargeant 2003; Gazda et al. 2005; Sargeant et al. 2005). For example, use of sandy beaches and estuarine mudflats to isolate and capture fish has been documented in several populations (reviewed by Silber and Fertl 1995; Sargeant et al. 2005), but not in other populations living in areas where dolphins have access to habitats favoring these techniques. Sponge carrying, a foraging tactic in which marine sponges are worn over the beak and presumed to act as tools, has been documented only in bottlenose dolphins of Shark Bay (Smolker et al. 1997). An exclusively genetic cause for such complex motor behaviors is unlikely (Krützen et al. 2005), and beaches and sponges are common to many delphinid habitats. However, as suggested by our critique of the group contrast method, inferences as to the roles of genetic and environmental variability in producing behavioral variability must be made with caution.

Interpreting behavioral differences among populations of bottlenose dolphins presents additional concerns. First, without a systematic survey based on complete reports of observed behaviors and not solely on published findings, it is not clear how many behaviors are limited to particular populations. Second, even if such a survey were to be conducted, it is unclear whether all observers are studying the same species (Laland and Janik 2006). The phylogenetic status of *Tursiops*, *Senella*, and other genera in the Delphinidae family remains unresolved (LeDuc et al. 1999), and therefore we refer to our own study population as *Tursiops* sp. (M. Krützen, unpublished data).

Intrapopulation Variation in Motor Behaviors

Within-population variation is well established in bottlenose dolphins and is exemplified by the foraging tactics of dolphins in Shark Bay. Sponge carrying is exclusive not only to Shark Bay, but also to a specific subset of the Shark Bay population (Mann and Sargeant 2003), most of whose members belong to the same matriline (Krützen et al. 2005). Dolphins in other populations also exhibit individual or subgroup variation in behavior. For example, only one of two sympatric communities of bottlenose dolphins in Moreton Bay, Australia, feeds on scraps thrown from trawlers (Chivers and Corkeron 2001); social groups of dolphins in Cedar Key, Florida, differ in their use of a group foraging technique (Gazda et al. 2005); and individual differences in a variety of techniques used to catch fish have been documented in Sarasota, Florida (Nowacek 2002).

The group contrast method has been applied to such intrapopulation variation, taking advantage of the fact that individuals within populations may be less likely to have substantial genetic or ecological differences than members of different populations (Krützen et al. 2005). However, critics of the group contrast method will note that there may be genetic or environmental differences among subpopulations, and studies of intrapopulation variation do not necessarily provide significantly stronger evidence of culture than studies of interpopulation variation. For example, sponge carriers are closely related to each other (Krützen et al. 2005), and sponge carrying is correlated with increased use of deep channels where sponges grow in high density (Sargeant et al. 2007).

Correlations between Foraging Similarity and Association

The strongest support for socially learned behaviors in wild bottlenose dolphins is based on correlations between measures of association and the use of particular foraging tactics. With this approach, ecological differences need not be fully excluded, but can be added to statistical models, provided sufficient variation exists to tease apart contributions of ecology and association. Such disassociation of ecology and propensity is most easily accomplished by examining both parent-offspring similarity and offspring behavioral development in species where offspring receive substantial parental care after birth (Aisner and Terkel 1992; Guiner and Bouvier 1995; Estes et al. 2003).

Several anecdotal studies of bottlenose dolphins describing unusual foraging behaviors suggest that vertical transmission from mothers to

offspring may be important in the development of young. For example, Nowacek (2002) reported that two relatively rare foraging tactics of bottlenose dolphins in Sarasota (fish whacking [whacking fish with tail flukes] and kerplunking [smacking tail flukes down onto the water's surface]) were used solely by a few mothers and their offspring. However, the most comprehensive study of matrilineal transmission of bottlenose dolphin foraging tactics has been our work in Shark Bay (Mann and Sargeant 2003), which we now discuss in greater detail.

Cultures and Traditions in Bottlenose Dolphins of Shark Bay

Factors Influencing Foraging Development

A bottlenose dolphin born in Shark Bay has much to learn, if it is to survive and reproduce. Forty-four percent of calves do not survive to 3 years of age, and 29 percent of adult females did not successfully wean young over a 10-year period (Mann et al. 2000). Access to food (Mann et al. 2000; Mann and Watson-Capps 2005) and predation by large tiger sharks (*Galeocerdo cuvier*) (Mann and Barnett 1999) are important in determining both calf survival and female reproductive success. Predation pressure may also act indirectly, causing habitat shifts that affect foraging (Heithaus and Dill 2002, 2006).

Bottlenose dolphins are well known for their diverse diets, consuming dozens of species of fish, as well as various cephalopods (squid, octopus) and crustaceans (shrimp, crabs) (Mead and Porter 1990; Barros and Wells 1998; Gannon and Waples 2004). Given the myriad highly mobile prey species and antipredator tactics dolphins must overcome, it is likely that dolphins must learn which species and foraging tactics are appropriate.

Multiple factors are likely to influence the development of calf foraging tactics (Figure 7.2). At the most basic level, the calf's foraging behavior will be directly influenced by the prey available in its habitat, and foraging appears to involve a period of learning. Dolphins do not forage immediately after birth, but are 3 to 4 months of age when they consume their first prey (Mann and Sargeant 2003). In the first few months of life, calves engage in what appears to be "practice" foraging, chasing and biting blades of seagrass (Mann and Smuts 1999). Calves spend most of their foraging time engaging in belly-up fish chases near the water surface, a behavior that we call snacking (Mann and Sargeant 2003). Snacking is not restricted to specific habitats and allows a young calf to hone

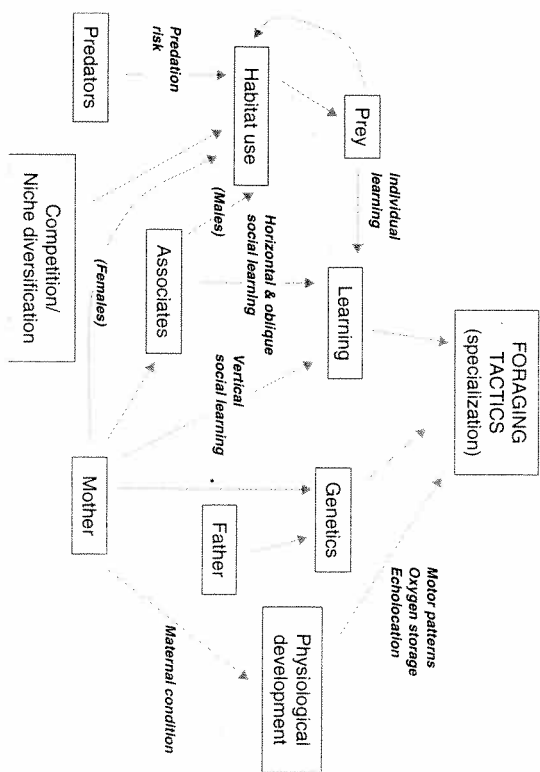


Figure 7.2 Factors likely to influence calf foraging development in bottlenose dolphins.

its hunting skills regardless of maternal habitat and prey distribution (Sargeant et al. 2007). However, snacking declines with age, and the calf must develop additional foraging tactics that are appropriate to its habitat, which is largely determined by its mother's foraging patterns (Mann and Sargeant 2003).

Newborn dolphins in Shark Bay spend, on average, more than 96 percent of their time within 10 meters of their mothers, although the amount of time they spend near their mother decreases as they mature (Mann and Smuts 1999). Calves eventually spend an average of 10 to 20 percent of their time further than 10 meters from their mothers (Mann and Watson-Capps 2005) but continue to associate closely with their mothers until weaning (Mann et al. 2000). Although out of visual range when separated by a few meters, calves and mothers can be in acoustic contact and receive foraging information during long-distance separations (Smolker et al. 1993). Post-weaning, females tend to stay in the same areas as their mothers, and males range slightly farther than females (Krützen et al. 2004b). However, into adulthood, the home ranges

of both sexes continue to overlap with that of their mother. That is, none of the 56 male or female offspring we have monitored from birth to adulthood (with birth records since 1982) has completely left their mother's home range. Males form alliances to gain reproductive access to females (Connor et al. 1992), and thus the habitat use of juvenile and adult males may be more closely tied to that of their male associates than to that of their mothers. Habitat use may also be affected by intraspecific competition and prey availability, as dolphins forage predominantly in habitats that provide sufficient energetic benefits. Predation risk from tiger sharks is also known to influence habitat use of dolphins at multiple spatial scales (Heithaus and Dill 2002, 2006).

Foraging abilities and prey preferences could also be influenced by genetic traits inherited from either parent, by physical condition, and by physiological development. Oxygen stores in both blood and muscle are lower in calves than in adults, which could limit calves' diving abilities (Noren et al. 2001, 2002). Furthermore, maternal condition may be an important determinant of calf condition and development, and our data suggest that calves in better condition spend more time foraging than do calves in relatively poor condition (Mann and Watson-Capps 2005).

Opportunities for the social learning of foraging tactics may result from a calf's interaction with its mother or other associates (Mann et al. 2007) and may allow for any number of social learning mechanisms, including local enhancement via habitat selection. In sum, a calf's use of a foraging tactic is the result of a complex interaction of ecological, genetic, social, and developmental (age, sex) factors (Figure 7.2).

Population-wide Cultures

Many of the diverse behaviors often thought to be socially learned by bottlenose dolphins are not common to all or even to most members of a population. Bottlenose dolphins have a fission-fusion social structure in which group compositions are very fluid and change as often as several times an hour (Smolker et al. 1992; Connor et al. 2000). Within such a fission-fusion society, there are no fixed groups, but rather frequent temporary interactions with some individuals preferentially associating with one another. Individual variation in behavior is common, and many behaviors are linked to matriline or subgroups within a population. However, some behaviors might qualify as population-wide cultures, including patterns of alliance formation (Connor et al. 1992).

In Shark Bay, several levels of alliance formation have been documented (Connor et al. 1992, 2000). Males form tight associations with one or two other males (first-order alliances) and work together to "herd" cycling females (Connor et al. 1992). Most males of prime reproductive age in Shark Bay form alliances (Connor et al. 2000), and males in alliances are more likely to father offspring than nonallied males (Kritzen et al. 2004a). First-order alliance formation has been reported at three additional sites (Sarosora Bay, Florida, USA; Wells 1991, Owen et al. 2002; Port Stevens, Australia; Möller et al. 2001; Bahamas: Parsons et al. 2003), but not at others (Moray Firth, Scotland; Wilson 1995; New Zealand; Lusseau and Newman 2004).

Second-order alliances (alliances of alliances) have been reported only in Shark Bay. Still, a major difficulty in comparing across sites is that both observation conditions and intensity of observation differ markedly from one site to another. However, some very obvious behaviors, such as in-air head butts where two males leap toward each other and hit heads in air (much like head-to-head ramming in male ungulates), have been observed in New Zealand (Lusseau 2003), but not reported elsewhere. Patterns of alliance formation and specific agonistic behaviors (e.g., head butting) seem to qualify as cultural if they are socially learned and serve important social functions.

There is little evidence of population- or group-wide socially learned foraging behaviors in Shark Bay dolphins, possibly because dolphins forage in patchy habitats, usually independently of one another (Mann and Sargeant 2003), and individuals are likely to use different foraging tactics depending on the habitat they exploit. Occasionally, Shark Bay dolphins join large foraging groups and feed on aggregations of schooling fish. However, there is no clear evidence that this behavior is cultural or involves cooperation. Some cetaceans frequently feed in groups because they exploit large schools of fish or share sizeable prey (Connor 2000). For example, killer whales cooperatively hunt marine mammals (Baird and Dill 1996; Guinet et al. 2000). The number of individuals sharing a cultural foraging behavior is likely to be higher in killer whales than in bottlenose dolphins because killer whales exploit and share the same prey. Food sharing has not been observed in Shark Bay bottlenose dolphins (Mann et al. 2007), but cooperative foraging on schooling fish has been observed elsewhere (Gazda et al. 2005). Feeding on clumped prey simultaneously, even cooperatively, also makes it possible for elements of foraging to take on social meaning as well. To cooperate effectively,

individuals may engage in role specialization (e.g., Gazda et al. 2005) and communication, suggesting similarities with cultural behaviors that promote social cohesion.

Traditions and Subcultures

The majority of socially learned behaviors identified in Shark Bay dolphins involve foraging tactics that vary among individuals and are shared by frequently associating individuals, particularly members of matriline. A simple genetic cause for observed variation in foraging tactics is unlikely (see Krützen et al. 2005), although gene-environment interactions are possible.

Matrilineal transmission of sponge carrying has been indicated by both pedigree (Mann and Sargeant 2003) and genetic data (Krützen et al. 2005). However, ecological contributions are also evident, as sponge carriers make greater use of deep channels than non-sponge carriers (Sargeant et al. 2007). Overall, age, sex, maternal use of sponge carrying, and use of deep channels each appear to contribute to the development of sponge carrying in calves (Mann and Sargeant 2003; Sargeant 2005; Sargeant et al. 2007). Observational data do not allow determination of the social learning mechanisms involved in sponge carrying, and the incidence of habitat use and sponge carrying could suggest that no social contribution is required for development of the tactic. However, because maternal habitat use largely controls that of calves during their period of dependency, individual learning by calves about prey in the environment would still be a result of local enhancement.

Maternal foraging patterns also predict calf foraging behaviors in multifactorial regression models, even after large-scale patterns of habitat use are controlled for (Sargeant 2005). For some behaviors, such as mill foraging (marked by irregular surfacings with frequent directional changes) and rooster-tail foraging (rapid swims near the water's surface), use by calves is predicted by the percentage of time that their respective mothers used each tactic in statistical models that also incorporate habitat use and other factors. Two additional tactics—provisioning by humans at Monkey Mia and begging from boats—show strict matrilineal transmission and could therefore be considered as possible traditions (Mann and Sargeant 2003). Such vertical social learning of foraging tactics appears to be relatively common, but there is little evidence of other modes of transmission. Because females tend to associate with their mothers and her social network after weaning,

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matrilineal transmission of foraging tactics is likely to facilitate rapid development of foraging tactics that are successful in female calves' preferred habitats.

Calves are attracted to and inspect fish catches by adults more than the converse, suggesting that calves have opportunities to learn about prey from adults other than their mothers. Calves are exposed to foraging patterns of adults other than their mothers during approximately 4 percent of their activity budgets (Mann et al. 2007). However, most foraging behaviors used by calves are also used by their mothers, and some obvious tactics attract the attention of nonoffspring but do not result in social transmission of the tactics. Thus, despite opportunities for social learning from nonmothers, no data currently show that calves incorporate tactics learned from nonmothers into their repertoires.

In some cases, foraging traditions may involve additional social functions that have not been well studied. For example, provisioned dolphins coordinate their visits with provisioning beaches and typically arrive in unison, because feeding is not initiated by rangers until several dolphins are present. Though currently only a matter of speculation, coordinated behaviors and increased association sometimes linked to foraging traditions suggest that unidentified social functions may exist and could be an area worthy of further study.

Socially Learned Behavioral Variants

Bottlenose dolphins near the tip of Peron Peninsula in Shark Bay were first reported to chase fish along and onto sandy beaches in the 1980s. This conspicuous behavior subsequently attracted the attention of scientists, who began studying "beach hunting" in 1991. Despite observation of many dolphins in the general area, by 2004, only six adults and six calves (all born to three females engaging in the behavior) had been observed beach hunting (Sargeant et al. 2005). In fact, two beach-hunting adult females studied intensively over the course of 6 years were recorded in groups with a minimum of 25 individuals that did not beach hunt, including two females with whom the beach-hunting females had associated for at least 11 years (Sargeant et al. 2005). Thus, even though many animals are found both in appropriate habitats and associated with beach hunters, beach hunting is exceedingly rare in the population exhibiting it. However, beach-hunting females spend much more time near beaches where beach hunting is used and preferentially associate with each other (Sargeant et al. 2005).

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The four beach-hunting adult females for whom genetic data are available do not have identical mitochondrial DNA haplotypes; this rules out the possibility of strict matrilineal transmission in all cases (Sargeant et al. 2005). Thus, like the matrilineal traditions discussed earlier, beach hunting has been transmitted vertically in some cases, but may be the result of horizontal transmission or of individual learning by additional females that frequent the beaches of Peron Peninsula.

Social Learning and Individual Specialization

Unlike many other putative cultural behaviors that tend to be common to entire populations, the behavior of bottlenose dolphins typically exhibits marked intrapopulation variation (e.g., Nowacek 2002; Mann and Sargeant 2003; Gazda et al. 2005). For example, some foraging behaviors are restricted to two individuals in a population. The underpinnings of this behavioral variation are inextricably linked to the ecological concept of individual specialization (Estes et al. 2003; Tinker 2004).

Why individuals of a population exploit different resources is a longstanding question in ecology. Such individual specialization occurs when an individual exploits a narrower niche than that of the entire population, unexplained by age or sex differences (Bohnick et al. 2003). Individuals may benefit from having narrow niches (being specialists) if there are trade-offs or costs associated with exploiting many different resources (Roughgarden 1974; Price 1987; Holbrook and Schmitt 1992), while varying from others in niche use may function to reduce competition (McLaughlin et al. 1999; Bohnick 2001; Svanbäck and Persson 2004). At more proximate levels, differences in social learning, ecology, and phenotype determine which specific resources or combinations of resources an animal uses and are therefore more directly responsible for observed individual differences in behavior than competition or trade-offs.

Social learning and individual specialization are linked in multiple, and potentially reinforcing, ways. Most directly, social learning can be a proximate cause of individual specialization (Norron-Griffiths 1967; Partridge and Green 1985; Werner and Sherry 1987; Estes et al. 2003). Models of individual specialization have suggested that cultural transmission, particularly vertical transmission, can increase the number of alternative foraging tactics in a population (Tinker 2004). For example, when individuals socially learn different ecological information through vertical transmission, individuals will subsequently differ in their resource use.

In Shark Bay dolphins, vertically transmitted foraging tactics contribute to the generation of niche variation. Thus, some calves will use sponge carrying because their mothers use it, while other calves will not develop sponge carrying but will instead mirror their own mothers' use of beach hunting. Overall, vertical transmission has contributed to both individual variation in 13 foraging tactics identified to date, and to a high degree of niche variation in the population (Sargeant 2005). Such diversity in bottlenose dolphins may reflect the coevolution of problem-solving skills, social learning ability, and behavioral plasticity that allow for rapid responses to heterogeneous and fluctuating environments. Patterns of transmission have consequences for the level of individual specialization exhibited by a population (Figure 7.1); horizontal transmission is likely to result in predominantly shared behaviors, whereas matrilineal transmission would result in greater individual specialization in the population.

Although social learning has traditionally been viewed as a proximate mechanism generating patterns of individual specialization (e.g., a dolphin calf uses sponge carrying instead of beach hunting), individual specialization can also shape patterns of social learning and culture. For example, when both increased efficiency and decreased competition result from specialization, specialized individuals utilizing untrapped niches should be favored. Such an advantage could promote the evolution of mechanisms reinforcing that niche variation, such as social learning within matrilineal or subgroups of animals that exploit similar habitats. Alternatively, individuals should conform to cultures that aid in social cohesion, and would benefit more from learning mechanisms that promote conformity and rapid spread of information (e.g., horizontal transmission). Thus, individual specialization can favor matrilineal traditions.

The concept of individual specialization is likely to aid in our understanding of culture by providing adaptive explanations for patterns of transmission and the degree of behavioral homogeneity (Figure 7.1). In short, without individual specialization, matrilineal traditions would not exist, and the adaptive benefits of modes of transmission may be tied to the benefits of individual specialization.

Summary

Although experimental data are required to identify social learning with certainty, a combination of captive and field studies strongly suggests the

existence of socially learned behaviors in bottlenose dolphins, including both population-wide behaviors and behaviors that are shared by fewer individuals (behavioral variants, traditions). We have identified several areas that need clarification. Is social function helpful in discriminating between social learning and cultures? How widespread must a behavior be to be considered a "culture?" This distinction is highlighted by the prevalence of intrapopulation variation in bottlenose dolphin foraging behaviors. According to many definitions, because all socially learned behaviors necessarily involve at least two individuals (a subpopulation), all socially learned behaviors would be considered "cultural." We suggest (Figure 7.1) that a continuum of social learning can be refined by examining the spread of socially learned behaviors in a population and that behaviors that aid in social cohesion are qualitatively different and typically more widespread. The spread of such behaviors depends on the commonality of social and ecological contexts for the behavior.

The fission-fusion social structure of bottlenose dolphins, combined with prolonged dependency, high social tolerance, and variable prey habitats, result in correlations between maternal foraging, habitat use, and the emergent foraging behaviors of calves. When individuals share behavioral traits that are caused by several factors, the group contrast method is unlikely to identify cultural traits. Multifactorial models applied to developmental data that include developmental processes and ecological and social factors should elucidate factors driving the emergence of socially learned behavior better than the group contrast method.

We also propose that attending to the adaptive functions of individual specialization can be useful in understanding the prevalence of cultural variants within populations and that individual specialization may be useful in revealing the ecological context in which socially learned behaviors are likely to emerge. For example, habitat heterogeneity can promote individual specialization via proximate mechanisms such as sex-biased learning of maternal foraging tactics. Conditions that promote individual specialization should also favor matrilineal traditions or socially learned behavioral variants rather than population-wide patterns, just as social transmission provides the proximate mechanism for individual specialization. Thus, there exists a clear interdependence of social learning and individual specialization that deserves greater attention in studies of culture and may help reunite social learning with its ecological roots.

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