

# Cultural transmission of tool use in bottlenose dolphins

Michael Krützen<sup>\*†</sup>, Janet Mann<sup>‡</sup>, Michael R. Heithaus<sup>§</sup>, Richard C. Connor<sup>¶</sup>, Lars Bejder<sup>||</sup>, and William B. Sherwin<sup>\*</sup>

<sup>\*</sup>School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney NSW 2052, Australia; <sup>†</sup>Departments of Biology and Psychology, Georgetown University, Washington, DC 20057; <sup>§</sup>Department of Biological Sciences, Marine Biology Program, Florida International University, North Miami, FL 33181; <sup>¶</sup>Department of Biology, University of Massachusetts, North Dartmouth, MA 02748; and <sup>||</sup>Department of Biology, Dalhousie University, Halifax, NS, Canada B3H 4J1

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**In Shark Bay, wild bottlenose dolphins (*Tursiops* sp.) apparently use marine sponges as foraging tools. We demonstrate that genetic and ecological explanations for this behavior are inadequate; thus, “sponging” classifies as the first case of an existing material culture in a marine mammal species. Using mitochondrial DNA analyses, we show that sponging shows an almost exclusive vertical social transmission within a single matriline from mother to female offspring. Moreover, significant genetic relatedness among all adult spongers at the nuclear level indicates very recent coancestry, suggesting that all spongers are descendants of one recent “Sponging Eve.” Unlike in apes, tool use in this population is almost exclusively limited to a single matriline that is part of a large albeit open social network of frequently interacting individuals, adding a new dimension to charting cultural phenomena among animals.**

culture | *Tursiops* sp. | social learning | tradition

The presence of culture within animal societies is a matter of considerable debate (e.g., 1–3). Among biologists and an increasing number of anthropologists, there is general consensus that an inclusive definition of culture should reflect a continuity between animals and humans (4). Here, we argue that the by far most parsimonious explanation for the first case of tool use in bottlenose dolphins (5) is that it is socially learned and transmitted. It is known that bottlenose dolphins are highly imitative and capable of social learning, both in the wild and in captivity. We show that ecological explanations for the observed behavioral pattern are inadequate and present genetic and long-term behavioral data showing that genetic explanations are extremely unlikely.

A behavioral trait is considered to vary culturally if it is acquired through social learning from conspecifics (6) and transmitted repeatedly within or between generations (7). Strong evidence for the existence of culture in animals comes from comparative long-term field studies of primate communities (1, 2), suggesting that there is significant cultural variation between populations for different behaviors. A study of six chimpanzee (*Pan troglodytes*) communities with no geographic overlap identified >39 behavioral patterns that were found in only some of the communities studied. Fifteen of these patterns were directly related to foraging and involved tool use (sensu 8), such as probing of vegetation to gather ants (9) or the use of stone hammers and anvils to crack nuts (10). Material culture also has been described in orangutans (*Pongo pygmaeus*) from six different sites on Sumatra and Borneo, where there was significant geographic variation among 19 “very likely cultural variants,” four of which involved tool use (2). In both studies, ecological explanations for the variation found between sites could be discounted. No conclusive evidence of social learning in the wild was presented, but claims for cultural transmission were further corroborated by additional evidence favoring the inference of social learning such as intense visual attention by offspring to the expert actions of their mothers and experimental evidence showing that captive apes will learn tool use observationally.

In wild populations, it is difficult to identify the transmission of a behavior based on social or observational learning. In cetaceans, this problem is exacerbated because of the habitat they live in and the limited observational opportunities. Therefore, we chose to adopt the approach suggested by Whiten *et al.* (1), which hinges on dismissing alternative explanations for the observed behavior, in particular ecological and genetic ones (3, 11).

In Shark Bay, Western Australia (113°45'E, 25°48'S), a longitudinal study of bottlenose dolphins has been conducted since 1984. Previous genetic studies using both nuclear and mitochondrial markers have shown that all animals in our study area, comprising the Eastern Gulf of Shark Bay, are part of the same population (12) and interbreed (13). Within this population, as many as 11 different tactics related to foraging have been identified (14), exhibiting a diversity comparable with that of chimpanzees and orangutans. The only tactic involving tool use is sponging (Fig. 1), which has been observed in 15 of 141 known mothers in the Shark Bay population (14) and at least 7 offspring. In sponging, a dolphin breaks a marine sponge off the seafloor and wears it over its closed rostrum to apparently probe into the substrate for fish (5, 14). Sponging is significantly sex-biased to females (14), making it comparable with sex differences in learning tool use in chimpanzees (15). In dolphins' early development, which is critical for acquiring foraging skills, both males and females spend the same time with their mother (16), but all but one of the adult spongers observed to date are female, and male offspring of spongers have not been shown to take up sponging (14). It was previously suggested that sponging is a tradition (3, 14) but that more detailed genetic data are needed, which this paper provides.

Ecological data show that sponging is mainly, but not exclusively (5, 14), confined to deep-water channels ( $\geq 8$  m) (Fig. 2). At least four nonsponging females regularly forage in at least one of these channels without using a sponge (14), strongly indicating that both spongers and nonspongers use the same habitat for foraging. Males also are regularly seen foraging in all sponging channels (R.C.C., unpublished data), ruling out the possibility that the occurrence of sponging is due to ecological differences alone.

Given the recent findings in New Caledonian crows (*Corvus moneduloides*) (17), we examine the possibility that the behavior is transmitted genetically as a single-locus trait, such as the “green-beard” locus in red fire ants (*Solenopsis invicta*) (18). Possible genetic influences on such behavior also include polygenic inheritance. If genetic inheritance of sponging could be discounted, then it seems highly likely that sponging is culturally transmitted mainly within a matriline, i.e., daughters learn this behavior from their mothers. This social transmission would add

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<sup>†</sup>To whom correspondence should be sent at the present address: Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland. E-mail: michael.krutzen@aim.unizh.ch.

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**Fig. 1.** Wild bottlenose dolphin foraging with marine sponge (photograph by M.R.H.).

an interesting new dimension to the mapping of cultural phenomena among animals by showing that unlike in apes, tool use in this population of bottlenose dolphins is limited almost exclusively to the social transmission within a matriline that is part of a larger population.

Members of a matriline should share mitochondrial DNA haplotypes, but what is expected of bi-parentally inherited nuclear DNA variants? Under random mating, the nuclear coancestry coefficient among noninbred individuals of the same matriline is expected to rapidly approach zero, because the number of alleles that are identical by descent shared by two individuals is expected to halve every generation. Thus, if the shared mitochondrial haplotypes derived from very ancient coancestry, nuclear relatedness of spongers should not be above population average. In contrast, if there is recent coancestry, nuclear genes also should show high relatedness. Moreover, there are two possible reasons for recent coancestry: (i) that the behavior is genetically inherited or (ii) that it is culturally transmitted between relatives. Previous genetic analyses showed

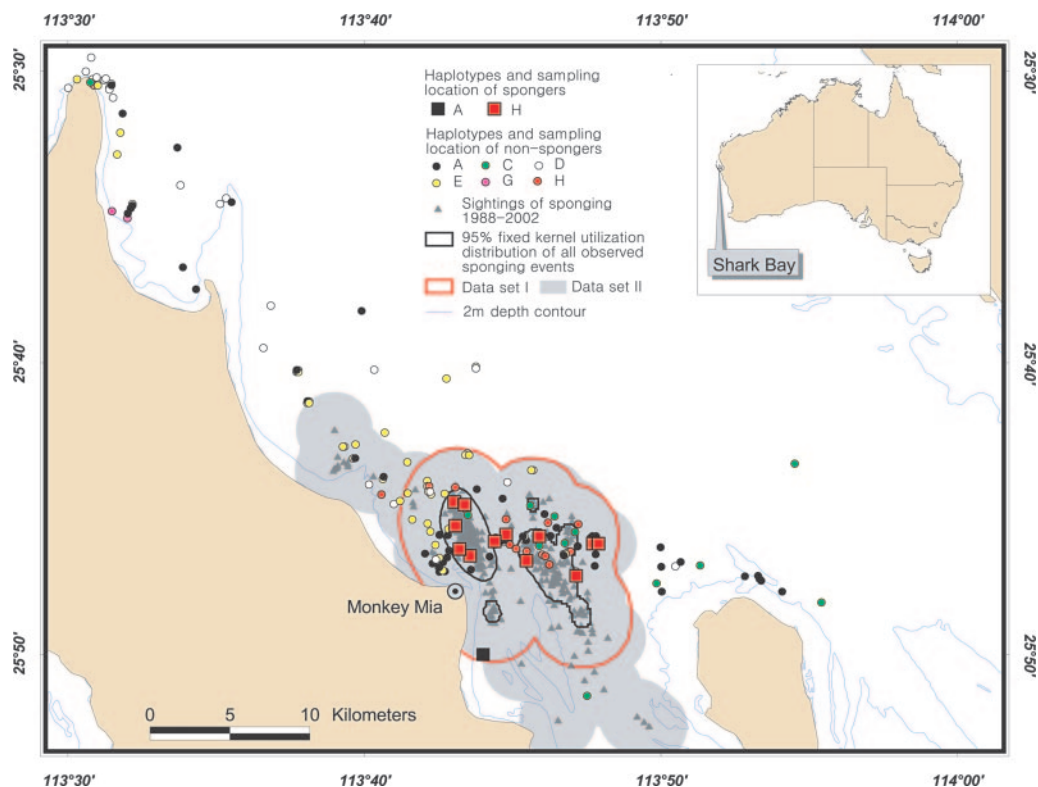
that random mating can be assumed for the Shark Bay population (12). Hence, if the relatedness levels among all spongers were significantly above the population average, then it would be likely that sponging was a fairly recent invention.

## Materials and Methods

**Behavioral Observations.** Both spongers and nonspongers were identified by using *one-zero* sampling methods (19) during 9,029 boat surveys with 14,447 different sightings, which were opportunistically conducted off Monkey Mia in the Eastern Gulf of Shark Bay (Fig. 2) between 1988 and 2002. Unusual behaviors, such as sponging, were recorded separately during the surveys, and the individual performing the behavior was identified by using a photographic database containing >850 different individuals.

**Genetic Analysis.** Genetic data were obtained from biopsy samples (20) of 185 individually identified dolphins (Fig. 2), 13 of which were adult spongers (Table 2). Each individual was genotyped for 12 hypervariable microsatellite loci (12), a genetic marker that is bi-parentally inherited. Additionally, a 355-bp segment of the maternally inherited control region of mtDNA was sequenced to obtain mtDNA haplotypes for each dolphin (12).

**Statistical Analyses.** The analysis was limited to the most conservative possible delineation of a randomly breeding group. Such conservatism reduces the chance of obtaining a high relatedness of spongers simply because the analysis includes many animals that would have little chance of interbreeding with them. Two different ways of limiting the data were tried, creating data sets 1 and 2, both of which included not only dolphins from the sponging area, but also close neighbors. Dolphins sampled in proximity to the sponging area were included because they have a high likelihood of having been exposed to a sponger and/or sponging behavior in their lifetime (i.e., they are familiar with sponging), and they also were potential mating partners to spongers. Data set 1 was produced by



**Fig. 2.** Distribution of mtDNA haplotypes and sampling locations of spongers and nonspongers.

**Table 1. Individual characteristics of spongers**

Individual, ID code	Sex	MtDNA haplotype	No. of sightings with sponge (%)	No. of years observed sponging	Known offspring, sex, sponger
CKY	F	H	14 (35.7)	2	SPZ, U, U
ANT	M	H	49 (30.6)	6	
RUF	F	H	9 (33.3)	4	
RSH	F	H	9 (33.3)	2	RAW, U, U
MOO	F	H	28 (21.4)	2	IND, F, Y; KOK, U, Y
SPE	F	H	36 (41.7)	4	
BUS	F	A	21 (42.9)	6	
WOB	F	H	16 (31.3)	1	
DEM	F	H	154 (52.0)	9	DOD, U, Y
KIT	F	H	87 (71.3)	7	
BYT	F	H	137 (56.2)	12	PIE, F, Y; BIN, M, once
SPO	F	H	34 (35.3)	5	GRG, F, Y
GUM	F	H	64 (20.3)	8	MUM, M, N; GOO, F, once; GMP, F, U

M, male; F, female; U, unknown; Y, yes; N, no.

calculating a fixed kernel utilization distribution (21) from all location points where sponging had been observed (Fig. 2), by using the Animal Movement Analysis add-in (22) in ARCVIEW 3.3 (Environmental Systems Research Institute, Redlands, CA). A buffer was then created around the 95% kernel at a distance of 3.17 km (Fig. 2), which represents the radius of the average circular home range of a female bottlenose dolphin in Shark Bay (23). Data set 1 included animals sampled within the kernel and the buffer zone. Data set 2 was produced by creating a buffer at a distance of 3.17 km around the location points where sponging had been observed. This method is slightly less conservative because it does not take into account the probability distribution of the location points. The hypothesis that there is a nonrandom association between haplotype and sponging behavior was tested by using a resampling simulation. Twelve females and 1 male were resampled with replacement 10,000 times for data sets 1 and 2, and the number of occasions on which the resampled average proportion of spongers with the same haplotype exceeded the observed was counted. Pairwise relatedness among individuals that were sampled within the area of data sets 1 and 2, excluding known offspring of spongers (Table 1) and those of other females, was calculated from the 12 microsatellite loci by using RELATEDNESS 5.08 software ([www.gsoftnet.us/GSoft.html](http://www.gsoftnet.us/GSoft.html)) (24). Sponger status was randomly assigned 10,000 times to 12 females and 1 male among all 112 and 130 individuals for data sets 1 and 2, respectively. Significance was applied by counting the number of occasions on which the observed mean relatedness among all spongers was exceeded by the randomized mean.

**Exclusion of Genetic Explanations.** There are several possible modes of genetic inheritance that might explain the presence or absence of a behavioral trait in certain individuals. We used a combination of long-term behavioral and genetic data to test whether sponging

might be transmitted genetically by evaluating 10 different modes of genetic inheritance and expression patterns for their agreement with the data both on a family and population level. We also assessed whether the nonrandom (i.e., assortative) mating based on the phenotype between spongers and nonspongers might explain the observed transmission patterns of sponging; although it appears unlikely, assortative mating could possibly reduce recombination between multiple loci that determine a trait, and thus enhance the trait's transmissibility and variation between lineages. The number of occasions a sponging female was consorted by either non-sponging or the one sponging male between 2001 and 2004 was determined using focal data from an ongoing study of alliance affiliation of >100 males. Consortships are conducted by pairs or trios of males and are the only recognized mating strategy in Shark Bay (25, 26). A consortship was recorded if a pair or trio with a single female was observed for 1 h or on two consecutive surveys separated by more than 1 h, or if there was evidence of aggression toward the female (25, 26). Because assortative mating is expected to lead to a decrease of heterozygote genotype frequencies among the progeny (27), we investigated this possibility by calculating  $f$  (28), which is an estimator of the inbreeding coefficient  $F_{IS}$  (29) among all spongers, using FSTAT 2.9.3 software ([www.unil.ch/izea/software/fstat.html](http://www.unil.ch/izea/software/fstat.html)) (30).

## Results

We sampled 13 of the 15 documented adult spongers (Table 1). Among all sampled individuals, six of the eight different haplotypes common in Shark Bay occur in our study area (Fig. 2 and Table 2). Only one of the regular spongers is male, and all but one sponger share the same haplotype H (Table 1), which in the broader sample is found in 11.35% of all females, and 5.41% of all males (Fig. 2 and Table 2). We found a significant non-random association between haplotype and sponging ( $P < 0.001$

**Table 2. Haplotype distribution within study area and for both data sets**

Haplotype	Study area (12)		Data set 1		Data set 2	
	Males (%)	Females (%)	Males (%)	Females (%)	Males (%)	Females (%)
A	30 (16.2)	37 (20.0)	19 (17.0)	24 (21.3)	21 (16.2)	25 (19.2)
C	9 (4.9)	5 (2.7)	5 (4.5)	4 (3.6)	6 (4.6)	4 (3.1)
D	8 (4.3)	19 (10.3)	3 (2.7)	3 (2.7)	3 (2.3)	4 (3.1)
E	27 (14.6)	17 (9.2)	14 (12.5)	11 (9.8)	21 (16.1)	16 (12.3)
G	0	2 (1.1)	0	0	0	0
H	10 (5.4)	21 (11.4)	10 (8.9)	19 (17.0)	10 (7.7)	20 (15.4)
Total	84	101	51	61	61	69





