CALF INSPECTIONS OF FISH CATCHES IN BOTTLENOSE DOLPHINS (*TURSIOPS* SP.): OPPORTUNITIES FOR OBLIQUE SOCIAL LEARNING?

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In recent years, the study of social learning and culture in wild cetaceans has visibly increased (Rendell and Whitehead 2001, Mann and Sargeant 2003, Krützen *et al*. 2005). Some of the best evidence for some type of social learning in wild cetaceans comes from studies of vocal traditions in killer whales (Deecke *et al*. 2000, Yurk *et al*. 2002), song change in humpback whales (Noad *et al*. 2000), coda dialects in sperm whales (Rendell and Whitehead 2005), whistle convergence in bottlenose dolphins (Smolker and Pepper 1999, Watwood *et al*. 2004), and foraging behaviors in bottlenose dolphins (Mann and Sargeant 2003, Sargeant *et al*. 2005). The mechanisms (*e.g.*, local enhancement, imitation) of social transmission have received very little attention, largely because this requires well-controlled experiments, compounded further by the difficulties in studying marine mammals. In a broader sense, determining whether transmission is vertical (parent to offspring), oblique (older to younger), or horizontal (laterally to peers or similar age classes), even without precise determination of mechanisms, offers insights into the ecological and social demands of a species. For example, horizontal transmission of song types in humpback whales is consistent with the proposed competitive function of song (Noad *et al*. 2000, Cerchio *et al*. 2001), and the context of pod-specific calls in killer whales suggests that calls promote cohesiveness (Miller *et al*. 2004). To date, our work on Shark Bay bottlenose dolphins (*Tursiops* sp.) suggests that vertical transmission of foraging types from mother to calf are commonplace (Mann and Sargeant 2003), but other forms of transmission may also occur (Sargeant *et al*. 2005). We argue that habitat heterogeneity and bisexual philopatry favors vertical transmission, especially for daughters who, more than sons, maintain a range similar to the mother's (Krützen *et al*. 2004). For

example, sponge carrying, where dolphins use marine sponges on their rostra to aid in finding prey, is transmitted through matrilines almost exclusively (Krützen *et al*. 2005). Here, we present evidence suggesting that calves seek exposure to prey caught by older non-mother individuals, but the converse is not true. Older individuals show little interest in what younger dolphins catch.

For years, Shark Bay researchers have noticed that dolphins sometimes closely follow an individual that has caught a fish. These close inspections resemble "begging" behaviors seen in a variety of mammals (*e.g.*, primates, canids), but fish are never shared, even between mother and calf. Food sharing may be unlikely to evolve in small delphinids because they typically catch small preys that are swallowed whole. Even when very large fish are caught that take an hour or more to break up, the calf does not take any of the floating pieces of fish (Mann and Sargeant 2003). This contrasts with killer whales (Hoelzel 1991, Baird and Dill 1996, Guinet *et al*. 2000) Q1 and a variety of social carnivores that routinely share prey, especially between mother and offspring (*e.g.*, Fanshawe and Fitzgibbon 1993, Packer and Pusey 1997, Vucetich *et al*. 2004). Fish inspections then, defined as remaining <2 m to a dolphin that has a fish in its mouth, are unlikely to be "requests" for food. The inspections are obvious and distinct from typical social groupings in that dolphins are typically dispersed during foraging (*e.g.*, Mann and Watson-Capps 2005), but following the fish catch, one or more dolphins rapidly (<0.5 min) approaches the dolphin that caught the fish. If the one that caught the fish continues swimming, then the inspectors stay very close (typically <1 m), with their head(s) near the prey item. Inspectors do not adopt echelon or calf position typical of calves (Mann and Smuts 1999), but are clearly oriented to the fish itself. If the fish owner remains stationary (hanging at the surface) with the fish in its mouth, then inspectors commonly form a star or semi-star formation around the fish, with their heads close to the fish. If the fish owner begins to break up the fish, the inspectors keep circling and diving down near the prey, but again, never touch pieces that are floating close to their rostra.

Our current study was based in Shark Bay, Australia, where a long-term mother–calf dolphin study was established in 1988 using focal follow methods (Mann 1999, Mann and Smuts 1999). From 1988 to 2003, 97 focal calves and their mothers were observed for 2,160.1 h; 1,021 definite fish catches were recorded for the focal calf, mother, or another group member. Group composition, defined as any dolphin within 10 m of any group member, was recorded every minute or 5 minutes. For the fish-catch data set, available group members included any dolphin that was in the group over the last 5 min. Although any group member might have foraged, we recorded focal maternal and calf foraging systematically (point, predominant, and continuous sampling; see Mann 1999), and fish catches by other group members were noted *ad lib* (as often as possible). All instances (all-event sampling) of fish inspections were described, regardless of whether or not the focal mother–calf pair was involved, because these are highly salient events. The proportion of individuals in each age–sex class was defined for each fish catch (calves <4 yr, juvenile females 4–11 yr, juvenile males 4–13 yr, adult females ≥12 yr, adult males ≥14 yr). Information about the size or species of fish and behaviors around the fish were noted whenever possible. Of 1,021 fish catches, 496 (48.6%) were by focal calves, 350 (34.3%) were

by focal mothers, 171 (16.7%) were by others, and 4 (0.04%) were cases where the one with the fish was not identified. These numbers do not reflect actual rates because most fish catches are subsurface, the fish are swallowed quickly and thus not always detected even at the surface, and calves were the main focal animal. If the mother and calf separated, we stayed with the calf. Thus more catches were observed for calves, especially because mothers and calves often separate to forage (Mann and Watson-Capps 2005). In 665 fish catches, at least one other dolphin was present and could inspect the fish. For most of these cases, the fish was small and swallowed quickly. Fish inspections occurred after 55 fish catches (8.3%) when others were present. Fish size was explicitly estimated in 18 of these cases and the fish were considered large (>20 cm) in 14 (77.8%) of those. The mean duration of inspections was 4.13 ± 0.86 min. The duration depends on how quickly the fish are consumed, but lasted up to 22 min.

The group composition in those 55 cases was a measure of who was available to follow or inspect the dolphin with the fish, henceforth referred to as the "fish owner." The average group composition was $42.1\% \pm 4.3$ calves, $22.5\% \pm 3.2$ juveniles, and $34.7\% \pm 3.8$ adults. In most cases, only younger dolphins were in the fish owner's group. But for 13 of the 55 events, individuals both older and younger than the fish owner were available to inspect the fish. Thus, we coded the proportion of older and younger individuals following the fish owner relative to who was available in the group. For example, if a 7-yr-old dolphin had the fish, and there were three adults and two immatures younger than seven in the group over the last 5 min, then the proportion of older individuals available was 60% and younger, 40%. Because more than one individual could inspect the fish, the proportion of younger and older individuals that followed was compared. Younger dolphins were significantly more likely to follow the fish owner than older dolphins (Wilcoxon signed-rank test, $Z = -2.274$, $P = 0.023$, $n = 13$). Of the 55 cases of fish inspection, the owner was the mother in 23 cases, the calf in 2 cases, and another dolphin in 30 cases (13 adults, 17 juveniles). Put another way, out of all the fish catches by mother, calf, and other, inspections were most likely to occur when another dolphin caught the fish (17.5%), less likely to occur when the mother caught a fish (6.6%), and almost never when the calf caught a fish (1.3%) ($\chi_1^2 = 23.9$, $P < 0.001$ mother *vs.* other; $\chi_1^2 = 15.13$, $P < 0.001$, calf *vs.* other; $\chi_1^2 = 6.25$, $P < 0.001$, mother *vs.* other). These results might be driven by the fact that calf fish catches are smaller, but it would not explain the difference between the mother's catches and those by others in the group. However, because the mother was a focal animal, more fish catches and inspections would have been observed and noted compared to others in the group and this would bias this analysis. To determine if the focal calf was more likely to follow mother *vs.* other, we used only cases where a fish inspection occurred. Here, the focal calf was one of the "inspectors" in 78.3% of the cases when the mother caught the fish and in 93.3% of the cases that another caught the fish (Fisher's exact test, $\chi_1^2 = 1.52$, $P < 0.22$), suggesting that calves were not more likely to inspect the fish of the mother than that caught by another individual. Finally, given the focal observation time of female and male calves respectively, female and male calves were equally likely to inspect fish catches (Binomial test, $Z = 0.43$, $P = 0.66$).

How often are calves exposed to foraging by non-mothers? During calf follows in 2002, we conducted scans every 15 min, during which group composition and foraging of all group members were assessed ($n = 15$ focal calves observed for 58.5 h). Across all calves, the average proportion of time they were exposed to foraging by non-mothers was $4.0 \pm 1.97\%$. Calves were exposed to five distinct foraging types by non-mothers, most of which their mothers also exhibited.

The main finding is that young dolphins are more likely to inspect fish catches by older dolphins than the converse. Although the size of the fish may be a factor, this would not explain why older individuals would not also be interested in large fish catches. Focal calves did not show greater interest in the mother's fish than those caught by others. Although calves are exposed to maternal foraging most frequently and to foraging by non-mothers infrequently, they clearly show an interest in prey caught by non-mothers. Thus, although vertical transmission appears to be the dominant influence on calf foraging development (*e.g.*, Mann and Sargeant 2003), calves have opportunities for oblique social learning.

Over 320 species of fish have been found in Shark Bay, including dozens that are toxic or extremely difficult to consume (Hutchins 1990). Some information on consumable prey types is likely to be useful for calves, because they have little experience beyond what their mother eats. Further, because these fish inspections occurred primarily in groups, when multiple individuals were foraging near each other, the inspections provide specific contextual information (*e.g.*, schooling prey type). Opportunities to learn from experienced associates, albeit infrequent, offer both visual and acoustic-echoic information about edible prey. With age, immature dolphins increase the amount and diversity of prey (Cockcroft and Ross 1990, Gannon and Waples 2004) and develop distinct foraging repertoires (Mann and Sargeant 2003). Although both sexes surely benefit by learning about prey, repertoire expansion might be particularly more important for young males that broaden or shift habitat postweaning. Because the adult females in our study use only a subset of foraging tactics exhibited by the population (Mann and Sargeant 2003), oblique transmission may allow immature dolphins to expand their repertoire, reinforce their existing repertoire, and/or opportunistically exploit atypical prey.

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