

FEEDING PREFERENCES OF THE MONKEY MIA DOLPHINS: RESULTS FROM A SIMULTANEOUS CHOICE PROTOCOL

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ABSTRACT

The semiwild beach-feeding bottlenose dolphins (*Tursiops aduncus*) of Monkey Mia, Western Australia, provide an unparalleled opportunity to examine prey preference of this species. In a series of binary-choice feeding experiments, we took advantage of the animals' willingness to be fed by hand, to explore their preferences for fish species, size, and state (freshly caught or previously frozen). At the end of each beach visit, each dolphin was provided with a pair of fish but allowed to eat only the first one chosen. The dolphins appeared indifferent among the three species of fish offered to them (yellowtail trumpeter, *Amniataba caudovittatus*; striped trumpeter, *Pelates sexlineatus*; and western butterfish, *Pentapodus vitta*), which were of similar body form and matched for mass. Overall, the dolphins showed a slight preference for the larger of two yellowtail trumpeter offered, suggesting the capability for rational choice when there was a basis for it (most likely energy in this case), although there was considerable individual variation. The dolphins did not distinguish between freshly caught and previously frozen yellowtail. The methodology we describe can be used to generate data of potential value for understanding food and habitat selection of wild dolphins, and for modifying management practices for semiwild dolphins at Monkey Mia and elsewhere.

Key words: food preference, choice behavior, prey and habitat selection, feeding regimes.

Information on the diet of bottlenose dolphins (*Tursiops* spp.) in the wild has been reported many times in the literature, usually on the basis of stomach contents analysis from stranded or bycaught individuals (*e.g.*, Barros and Odell 1990,

Cockcroft and Ross 1990, Barros and Wells 1998, Blanco *et al.* 2001, Santos *et al.* 2001). However, seldom are there sufficient data on prey availability at the time of the observations to say much about prey preference, *i.e.*, the consumption of some prey types disproportionately more often than they are encountered. One exception is provided by Corkeron *et al.* (1990), who hand-fed *T. truncatus* off the stern of a prawn trawler in Moreton Bay, Queensland, and concluded that the dolphins exhibited preferences for certain fish species. Information on preference is valuable in several contexts, including the design of captive or semiwild feeding regimes and the suitability ranking of habitats which differ in the prey species available there.

Prey preferences of captive dolphins can be readily determined, but these may have little relevance to wild animals, owing to training effects of various sorts. And as noted above, preference is difficult to measure in the field because of the difficulty of measuring prey encounter rate and diet simultaneously. The beach-feeding dolphins (*T. aduncus*) of Monkey Mia, being semiwild, provide a unique opportunity to measure prey preference. These animals have been fed locally abundant fish, at the beach, for at least 20–25 yr, depending on the individual (Connor and Smolker 1985), yet still do the majority of their own foraging (~80%) offshore. The current study took advantage of this situation to examine prey preference by simultaneously presenting the dolphins with pairs of fish differing in some way, and recording their choice.

Prey preference can be measured along several axes. Here we report the dolphins' choices: (1) among three locally common fish species, (2) among fish of three different size classes, and (3) between freshly caught fish and those previously frozen. Results of the first two sets of experiments are potentially relevant to understanding diet and habitat choice in the wild, while those of the third may have value in the design of appropriate feeding protocols for this and similar semiwild dolphin populations.

METHODS

General Choice Test Protocol

The general protocol was the same for all of the experiments reported here. During a regular visit to the beach at Monkey Mia, one or more dolphins would be presented with a pair of fish held by one of the authors, another Ranger, or a volunteer. All the dolphins could be fed simultaneously to prevent interference with one another's feeding. The pair of fish was always presented at the end of the beach visit, when the dolphin was allowed to consume only one more to reach its predetermined quota for that visit or that day (the dolphins sometimes visit up to three times a day but, in total, are fed only 15%–25% of their estimated daily food requirement, *i.e.*, 2 kg per day and no more than 750 g per feed).

The pair of fish was held below the water surface while the feeder faced the dolphin, trying to keep the two fish equidistant from its rostrum; sometimes this required the feeder to back up, forcing the dolphin to swim toward the pair of fish. Once the dolphin made a clear choice and took one fish, the extra fish was put out-of-sight and the feeding session ended. Some preliminary training trials (12–20 per dolphin in 1994, 5–6 per dolphin in 2001) were required for the dolphins to learn that this second fish was not available to them. We believed that this would put a premium on the dolphin's making an appropriate choice and increase the likelihood of their doing so. The dolphins learned the procedure quickly and, in

most cases, departed of their own volition immediately following the fish pair presentation.

The fish species and size trials were conducted between October 1994 and February 1995 on the four beach-feeding female dolphins (Holey Fin, Surprise, Puck, and Nicky). The fresh-frozen fish comparisons were carried out in October 2001; only three dolphins were used, as Holey Fin had died in the interim (Connor *et al.* 2000b, fig 4.2). All trials were conducted between 0810 and 1550 on days when nearshore wave action was not extreme. The feeder made note of whether the dolphin looked at both fish prior to her choice, echolocated (obvious in only 12 of 360 trials), or showed any reluctance to swallow, or other unusual behaviors.

Fish Species Choice

This experiment was performed to test the hypothesis that bottlenose dolphins prefer some prey species to others, perhaps due to differences in caloric value or specific nutrient content. Pairwise trials were conducted using three locally abundant fish species, yellowtail trumpeter (henceforth YT; *Amniataba caudovittatus*, Teraponidae), striped trumpeter (ST; *Pelates sexlineatus*, Teraponidae), and western butterfish (BF; *Pentapodus vitta*, Nemipteridae). These species were chosen because they have a similar fusiform body shape, and thus similar handling time. All three species are known to be eaten by the local dolphins¹ and are normally fed to the dolphins at the beach when available, BF less commonly than the others. There was no *a priori* reason to expect the dolphins to prefer one species over the other.

Each of the four dolphins was presented with 45 pairs, 15 of each combination (*i.e.*, YT with ST, YT with BF, ST with BF). Length-weight relationships were calculated for a sample of 30 individuals of each species (Fig. 1), and were used to select fish lengths that ensured approximately equal masses for the two fish on offer, and were similar to those of fish normally fed to these dolphins. Fish (all previously frozen and then thawed) were measured (fork length) to the nearest 0.5 cm, both for the length-weight regressions and the experiment itself. Fish presented to the dolphins ranged in length from 15 to 19.5 cm.

The 45 trials were run in 15 blocks of three (one of each pair type, in random order within the block); the order of these trials was the same for each dolphin (with a few exceptions). The species in the feeder's left hand was decided by a coin toss for each trial, and again was the same for all four dolphins. Since dolphins did not always visit the beach together, nor always get tested simultaneously (*e.g.*, Surprise was not fed for two weeks after giving birth, part way through the experiment), identical trial numbers were conducted on different days for each animal; *i.e.*, trials quickly got out of synchrony across dolphins.

Fish Size Choice

The experiment used only previously frozen YT of three size classes: small (henceforth S; 15.5–16.5 cm), medium (M; 17.5–18.5 cm), and large (L; 19.5–20.5 cm). The average masses of these size classes (from the regressions in Fig. 1) were 73, 100, and 134 g, respectively. The *a priori* expectation was that, since handling

¹ Personal communication from Dr. Michael Heithaus, National Geographic Society, Washington, DC, 6 December 2002.

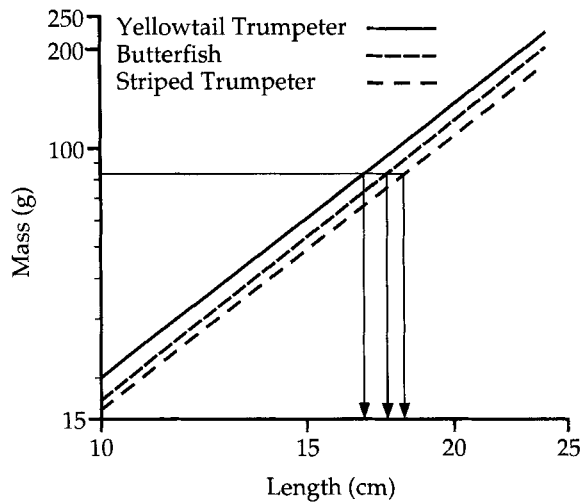


Figure 1. Length-mass relationships for the three types of fish used in the species choice experiment (based on $n = 30$ for each). The perpendicular lines to the axes show how different lengths for the three species can be selected to produce the same mass. The best fit regressions were: yellowtail trumpeter $\ln W = 2.74 \ln L - 3.31$ ($r^2 = 0.95$); striped trumpeter $\ln W = 2.72 \ln L - 3.47$ ($r^2 = 0.94$); butterfish $\ln W = 2.77 \ln L - 3.51$ ($r^2 = 0.95$).

times were minimal, the dolphins would prefer $L > M > S$ for energy reasons. We are assuming that mass is a good proxy for caloric value. There was no evidence that any size class was reproducing, so the presence of gametes is unlikely to have caused differential nutrient levels. This experiment therefore serves as a check on whether the dolphins' choices are rational and transitive (*i.e.*, if L is preferred to M and M to S , then L should be preferred to S).

As in the species preference experiment, 45 trials were conducted (15 per size-pair) on each dolphin, in blocks of three (one of each pair in random order), with the fish in the left hand determined by a coin toss. And as in that experiment, each dolphin experienced the 45 trials in the same order (with rare exceptions), but not on the same days.

Fresh-Frozen Fish Choice

In all of the above experiments (and in their regular feedings) the dolphins were presented with previously frozen, and thawed, fish. Even though most of these fish would have been frozen within 8 h of capture, freezing may cause tissue breakdown and protein denaturation, with consequent changes to texture, flavor, and nutritional value (Wheaton and Lawson 1985). It was therefore expected that the dolphins might distinguish fresh from previously-frozen fish and exhibit a preference for the former. Fresh fish were caught by hook and line immediately adjacent to the feeding area, and kept on ice for 1 d (41 of 60 trials) or 2 d (19 trials) before use.

This experiment was conducted from 28 September to 12 October 2001 on the three remaining dolphins. Over that period each animal was presented with 20

Table 1. Fish species choices by the Monkey Mia beach-feeding dolphins. Each pair of fish species (BF = western butterfish, ST = striped trumpeter, and YT = yellowtail trumpeter) was presented 15 times to each of the four female dolphins. There was no significant preference demonstrated by any of the dolphins (or all pooled) for any species of fish presented (all $\chi^2 < 1.0$, $P > 0.30$).

| Dolphin | Choice in pairs | | | Number eaten | | |
|-----------|-----------------|-------|-------|--------------|----|----|
| | BF/ST | YT/BF | YT/ST | BF | ST | YT |
| Holey Fin | 5/10 | 7/8 | 8/7 | 13 | 17 | 15 |
| Surprise | 8/7 | 9/6 | 10/5 | 14 | 12 | 19 |
| Puck | 6/9 | 7/8 | 9/6 | 14 | 15 | 16 |
| Nicky | 7/8 | 7/8 | 6/9 | 15 | 17 | 13 |
| Overall | 26/34 | 30/30 | 33/27 | 56 | 61 | 63 |

fresh-frozen pairs of YT, matched for length (ranging from 16 to 19.5 cm). The hand holding the frozen fish was determined at random, and independently for each dolphin, and the feeder was unaware of which fish had been previously frozen. In all other respects the protocol was identical to the 1994–1995 experiments already described.

RESULTS

Hand Preference

In the 1994–1995 experiments on species and size choice, the dolphins showed a strong preference for whichever fish was offered in the feeder's right hand, *i.e.*, on the dolphins' left. Holey Fin took this fish in 57 of the 90 trials, Surprise 54 times, Puck 60 times, and Nicky 66 times. Overall, the dolphins showed a nearly 2:1 preference (237:123) for the fish on their left; this was accounted for in the analyses by considering this ratio as the prediction from a null hypothesis of no choice. Thus, the expected number of a prey type eaten in any given pairing was calculated as: the number of times that prey type was presented in the right hand times the observed preference for that hand (0.66), plus the number of times it was presented in the left hand times the preference for that hand (0.34). This was done for both prey types in the binary choice pair (*e.g.*, L *vs.* S) and the expectations compared to the observed numbers eaten with a Chi-square test.

In the 2001 trials, hand preference was inconsistent across dolphins (see below), so a somewhat different sort of analysis was required. Rather than using a single pooled hand preference ratio to calculate the expected numbers of fresh and frozen prey eaten, a separate expectation was used for each of the three dolphins.

Fish Species Choice

Equal numbers (30) of all three fish species were presented to each of the four dolphins. Overall they chose 56 BF, 61 ST, and 63 YT, and no individual showed a preference for any of the species presented to them (Table 1; all $\chi^2 < 1.0$, $P > 0.30$). It is possible that a preference for a particular species in one comparison (*e.g.*, YT over BF) is balanced by avoidance in another (*e.g.*, ST over YT), but

Table 2. Fish size choices by the Monkey Mia beach feeding dolphins. Each pair of fish sizes (Small, Medium, and Large) was presented 15 times to each of the four female dolphins. For each hypothesis tested, the last three columns present χ^2 and P values; NS means non-significant).

| Dolphin | Choices in pairs | | | No. eaten | | | Preference hypothesis | | |
|-----------|------------------|-------|-------|-----------|----|----|-----------------------|---------------------|---------------------|
| | M/S | L/M | L/S | S | M | L | $M > S$ | $L > M$ | $L > S$ |
| Holey Fin | 8/7 | 9/6 | 8/7 | 14 | 14 | 17 | 0.215 NS | 0.002 NS | 0.016 NS |
| Surprise | 9/6 | 8/7 | 13/2 | 8 | 16 | 21 | 0.689 NS | 0.106 NS | 4.442 $P < 0.05$ |
| Puck | 7/8 | 13/2 | 14/1 | 9 | 9 | 27 | 0.106 NS | 2.859 $P < 0.10$ | 6.685 $P < 0.05$ |
| Nicky | 8/7 | 13/2 | 11/4 | 11 | 10 | 24 | 0.215 NS | 2.508 NS | 1.323 NS |
| Overall | 32/28 | 43/17 | 46/14 | 42 | 49 | 89 | 1.082 NS | 1.890 NS | 8.231 $P < 0.05$ |

pairwise comparisons between the species also indicated no species preference ($P > 0.05$), after correction for hand preference as described above. This was true both for the overall data and the results for individual dolphins.

Fish Size Choice

It is clear by inspection of the raw choice data (Table 2) that three of the dolphins exhibited some preference for the larger of the two fish presented to them, and that this preference was most obvious when the fish differed most in length and mass, *i.e.*, the L and S pairing. One dolphin (Holey Fin) exhibited no size preference. Pairwise statistical comparisons between fish sizes, separately for each dolphin, and taking hand preference into account, bear out these conclusions. However, the observed preferences were generally weak, and the pooled results are clearly dominated by the data for Puck. For the most part, choices were transitive, although Nicky preferred L to M, but not M or L to S.

Fresh-Frozen Fish Choice

The dolphins expressed no preference for fresh over frozen fish ($P > 0.05$; Table 3). Two of the dolphins showed a strong preference for the hand in which the fish was presented: in this case Surprise took the fish in the right hand 18 of 20 times, while Nicky showed an equally strong bias (18/20) for the left hand. Puck showed no hand bias (8 right: 12 left), but also no fish preference (9 fresh: 11 frozen). The expected fresh:frozen ratio (based on the null hypothesis of no preference, the slight observed left hand bias, and the fact that by chance the fresh fish was in the right hand 13 of 20 trials) can be calculated as 9.4:10.6, obviously indistinguishable from the observed ratio for Puck. Expected fresh:frozen ratios for Surprise and Nicky lead to the same conclusions (Table 3). Looking only at those trials in which the animals showed what the feeder considered a "definite choice" (being attentive to both fish) gave the same results.

Table 3. Fresh-frozen fish choice experiment. For no dolphin does the observed proportion of fresh fish chosen differ from the proportion predicted; see explanation below.

| Dolphin | A P_{RH} | B $P_{FRE/RH}$ | A \times B | C P_{LH} | D $P_{FRE/LH}$ | C \times D | PropFRE _{pred} (A \times B) + (C \times D) | PropFRE _{obs} | χ^2 | P |
|----------|---------------|-------------------|--------------|---------------|-------------------|--------------|--|------------------------|----------|------|
| Surprise | 0.9 | 0.4 | 0.36 | 0.1 | 0.6 | 0.06 | 0.42 (8.4/20) | 0.30 (6/20) | 1.182 | >0.2 |
| Puck | 0.4 | 0.65 | 0.26 | 0.6 | 0.35 | 0.21 | 0.47 (9.4/20) | 0.45 (9/20) | 0.032 | >0.8 |
| Nicky | 0.1 | 0.35 | 0.035 | 0.9 | 0.65 | 0.585 | 0.62 (12.4/20) | 0.65 (13/20) | 0.076 | >0.7 |

Key to columns:

A: proportion of trials in which the dolphin chose the fish in the feeder's right hand (RH).

B: proportion of trials in which the fresh fish was in the RH.

A \times B: expected proportion of trials the fresh fish would be chosen when offered in the RH.

C, D, and C \times D: same as previous three columns, but for fish in the feeder's left hand (LH).

DISCUSSION

Animal foraging behavior is best thought of as a series of strategic decisions: where to forage (at various scales, from the landscape to the local patch), which hunting tactics to employ, and what prey types to search for, attack, and ingest. Some of these issues have previously been examined in the bottlenose dolphins of Shark Bay. Thus, their decisions regarding where to forage depend on seasonally varying spatial patterns of fish availability and predation risk (Heithaus and Dill 2002), and different foraging tactics are employed in particular situations (e.g., Smolker *et al.* 1997, Connor *et al.* 2000a). In this paper we are concerned only with decisions having to do with targeting and consuming particular prey species within a chosen foraging patch, and thus have extracted this component from the rest of the foraging process.

A large body of theoretical and empirical evidence (Stephens and Krebs 1986) supports the conclusion that, all else being equal, animals should prefer the prey types which provide the greatest net energy return per unit time spent handling ("profitability"). Because most of their foraging takes place underwater, it is difficult to test this hypothesis for wild cetaceans in the field. The beach-feeding dolphins at Monkey Mia provide an opportunity to do so, using semiwild individuals. Although they are habituated to humans, these dolphins still do most of their own foraging offshore and are expected to have retained the ability to choose prey efficiently in an energy-wise sense.

The purposes of this experiment were twofold: (1) to determine whether simultaneous choice experiments could be used to measure dolphin prey preference; and (2) to assess the prey species, size, and condition preferences of the beach-fed dolphins at Monkey Mia. It is clear from the results that the methodology holds promise for measuring dolphin prey preference.

The dolphins appeared indifferent to fish species of equivalent body shape and mass. Either they could not distinguish between them, or did not care to do so; these alternatives cannot logically be distinguished when a choice test produces a null result. However, observations of these same dolphins refusing, at one time or another, virtually every local species of fish (including the three tested here) during their regular feedings suggests that they can be sensitive to fish species under some circumstances. Thus, it is unlikely that the findings of no preference were due to these semitame dolphins having lost the ability or the incentive to feed in a discriminatory fashion.

The results of the prey size experiment lend further credence to this conclusion: when there was a rational basis for choice (mass, and thus expected energy content) most dolphins did indeed exercise choice, choosing the larger of two fish if they were able to distinguish them. Small fish size differences (*i.e.*, between adjacent size categories: length, ~12%; mass, ~35%) appear difficult for the dolphins to discriminate, and one dolphin (Holey Fin) failed to discriminate at all. There is always a danger of feeder bias in experiments of this sort, particularly when the *a priori* predicted choice is so obvious. Thus, the feeder may have unconsciously biased the dolphins' choice toward the larger of the two fish, but the fact that observed preference was inconsistent, both across size pairs and across dolphins, argues against this having been a serious problem.

Holey Fin was the oldest dolphin and her behavior in the size choice experiment suggests that individual variation in prey preference among dolphins may

be significant. We had actually expected greater variation given that Puck was lactating during the 1994 experiments and Surprise was either pregnant (for the first few trials) or lactating, yet the results suggest no impact of these major life history events on choice behavior.

Obviously the fish species results cannot be extended beyond the range of species tested here, and the experiment should be repeated with a greater range of species, varying more in body shape and biochemical composition (Corkeron *et al.* 1990 suggest that lipid content may have been important in the preference for putty-nosed perch, *Polydactylus plebejus*, shown by bottlenose dolphins in Moreton Bay). Yet even our limited results may be useful in predicting habitat use of the dolphins in Shark Bay, where the present study was conducted. Heithaus and Dill (2002) have ranked the suitability of different Shark Bay foraging habitats for dolphins based on total numbers (and biomass) of fish caught there, without considering species. The present results increase confidence in the implicit assumption underlying this simplification. They also suggest that the ranking of habitat types would not be much affected by including detail on fish species, given that the three species we tested in our experiment are among the four most common species in Shark Bay (based on both angling and trap catches; for the latter, see Heithaus 2001), totalling 91.2% of numbers (ST = 76.8% [#1], BF = 13% [#2], and YT = 1.4% [#4]). Thus, the findings of prey preference experiments such as these have important conservation implications in assessing habitat suitability for bottlenose dolphins.

Despite the well-known effect of freezing on the texture, flavor, and nutritional value of fish (Wheaton and Lawson 1985), the Monkey Mia dolphins showed no preference for fresh fish over previously frozen ones. Again, it is not logically possible to determine whether they were unable to distinguish between them, or did not care to do so. Regardless, the management implication is that it is not necessary for the Monkey Mia feeding regime to be altered (at considerable cost) to include freshly caught fish. This conclusion must be tempered somewhat by the possibility that fresh fish may indeed be best for dolphins nutritionally, but they are incapable of making the distinction, never having experienced frozen fish in their evolutionary past.

The hand preference shown by the dolphins is interesting, but enigmatic. Based on the 1994–1995 study showing that dolphins had a strong preference for the fish presented on their left (*i.e.*, in the feeder's right hand) we hypothesized that this was a result of the fact that most tourists (93.5% of a sample of 400; D. Charles, personal observation) offer them the fish that way and the dolphins have come to anticipate a fish in that position. In other words, we believed that the biased choice reflected laterality in humans rather than in the dolphins, although laterality has been reported in several cetaceans, including bottlenose dolphins (reviewed in Kilian *et al.* 2000). The 2001 results confuse the picture: one dolphin (Surprise) remained strongly left-biased, one (Puck) showed no bias, and one (Nicky) switched her bias completely over the intervening 7-yr period. We currently have no explanation for this result.

Nevertheless, studies such as ours demonstrate the potential for the beach-feeding dolphins at Monkey Mia and elsewhere to contribute knowledge that may be valuable for their management and the well-being of other populations. The protocol we have described here, including the statistical procedure for correcting for side bias, may be useful for further exploring food preferences in bottlenose dolphins and other cetaceans where binary choice trials are possible.

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