

The Biology of Traditions

Models and Evidence

Edited by

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Like mother, like calf: the ontogeny of foraging traditions in wild Indian ocean bottlenose dolphins (*Tursiops* sp.)

9.1 Introduction

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In this chapter, we identify aspects of delphinid socioecology and life history that relate to the probability and utility of socially aided learning. We also present new findings from our on-going research with dolphins at Shark Bay, Australia that address the possibility that the acquisition of specialized foraging techniques by young dolphins is aided by their affiliation with their mothers and, thus, may be viewed as likely traditions. Studies of bottlenose dolphins (*Tursiops* spp.) in captive and field settings over the last four decades indicate that this genus shows remarkable plasticity and convergent features with primates. Similar to primates, bottlenose dolphins have a long period of dependency and juvenile development (Mann *et al.*, 2000), large brains for body size (Marino, 1998; Ridgway, 1986), complex alliance formation (Connor *et al.*, 2000a), and social learning (reviewed in Janik, 1999; Janik and Slater, 1997; Rendell and Whitehead, 2001). Unlike nonhuman primates, bottlenose dolphins also show vocal learning in call production (Janik and Slater, 1997, 2000; see also Ch. 8); they produce individually distinctive "signature whistles" (Sayigh *et al.*, 1995, 1999; Tyack, 2000) and can also match each other's whistles in natural contexts (Janik, 2000).

Recently, several cetacean biologists have claimed that cetaceans have culture (Deecke, Ford, and Spong, 2000; Noad *et al.*, 2000; Rendell and Whitehead, 2001; Whitehead, 1998). The strongest evidence for social learning comes from bottlenose dolphins studied in captive settings (reviewed by Rendell and Whitehead, 2001). Field data are weaker, but the best field evidence for social learning is in the acoustic domain (e.g., see Deecke *et al.*, 2000; Janik and Slater, 1997; Noad *et al.*, 2000); evidence for

social learning of gestures and motor movements has been limited to captive studies of bottlenose dolphins (Janik, 1999).

In this chapter, we intentionally do not use the term "culture," nor do we address whether this term accurately describes cetacean intraspecific behavioral variation (but see Mann, 2001). Where appropriate, we use the terms *social learning* and *tradition* (as defined by Fragaszy and Perry in Ch. 1). Our goals are to assess the role of maternal social influence in producing variation in Shark Bay bottlenose dolphin foraging techniques, and to show that such questions can be addressed in wild cetaceans (see Rendell and Whitehead, 2001).

Foraging presents an appropriate avenue for investigating social learning and traditions in cetaceans. First, bottlenose dolphins exhibit a diversity of foraging techniques both within and between populations (Connor *et al.*, 2000a; Shane, 1990). Second, foraging specializations within the Shark Bay dolphin population have been identified (e.g., Connor *et al.*, 2000b; Smolker *et al.*, 1997). Intrapopulation variation may provide the means for evaluating the role of experiential factors in behavioral development. Third, detailed long-term study of the Shark Bay population of bottlenose dolphin behavior and ecology allows us to identify matrilineal patterns of foraging, the ontogeny of foraging among calves, and foraging patterns of the larger population.

Much of the literature regarding primate foraging techniques is based on different methods of manipulating or processing food items (e.g., Chs. 10–13). Bottlenose dolphins cannot easily manipulate prey (except to beat it with their tails or on the water surface, or to break the fish on the seafloor). Rather, they vary in hunting technique rather than processing. For example, many of the foraging strategies identified in the bottlenose dolphins of Shark Bay are characterized by distinct dive or surfacing patterns (see Tables 9.1 and 9.2). Because most foraging occurs several meters below the surface of the water, we describe the most overt distinctions between foraging types. More subtle characteristics are difficult to observe and to identify reliably.

9.1.1 Flexibility in foraging

Although bottlenose dolphins have been characterized as catholic, opportunistic hunters that feed predominantly on fish, cephalopods, and crustaceans (e.g., Corkeron, Bryden, and Hedstrom, 1990; Cockcroft and Ross, 1990; Connor *et al.*, 2000b), and occasionally stingrays, sharks, eels, and mollusks (J. Mann, personal observation; Mead and Potter, 1990),

Table 9.1. Twelve types of foraging strategy used by bottlenose dolphins

Foraging strategy	Characteristics
Bird milling	Dolphins are surfacing within or around a tight feeding group of cormorants (and usually pelicans); this typically occurs in shallow water (< 4 m)
Leap and porpoise feeding	Dolphins are multidirectional (milling) and leaping continuously within an area, which may be relatively small or spread out over as much as a kilometer. This activity usually occurs in closely spaced bouts with abrupt starts, stops, and changes in direction. The group as a whole is often travelling rapidly
Bottom grubbing	Dolphin sticks its beak to the seafloor or sea grass to ferret something out while in a vertical position. This can only be viewed in shallow water. Regular dive types characterize surfacing
Milling	Dolphin forages and changes direction with virtually every surface and breath; breathing intervals tend to be irregular
Tail-out/peduncle dive foraging	The predominant dive types during foraging include tail-out or peduncle dives (Table 9.2). Dolphins typically stay submerged for 1-3 minutes after a tail-out or peduncle dive; once surfacing, they typically take 1-12 breaths before diving again
Rooster tailing	The predominant dive type during foraging is a rooster tail, which is a kind of fish chase with a fast swim along the surface of the water in which a sheet of water trails off the dorsal fin; After the rooster tail, the dolphin dives to the bottom, often back-tracking the direction of the fast swim
Sponge carrying	Dolphin forages wearing a sponge on its rostra while doing tail-out dives and staying down in the water for 2-3 minutes (Smolker <i>et al.</i> , 1997). The dolphin also tends to change directions often. This occurs almost exclusively in channels 8-12 m
Snacking	Characterized by a belly-up chase and capture of fish trapped at the surface. Calves typically have prolonged circular belly-up swims during the fish chase; adult snacking tends to be brief
Trevally hunting	Begins with tail-out diving, but once the trevally (always golden trevally (<i>Gnathanodon speciosus</i>)) is located, there are directed leaps after the fish. The fish is then processed in a particular way (see text)
Beaching	Shallow-water feeding involving chasing fish close to the shore-line such that the ventrum is on the seafloor or beach; fish are often trapped onto the shore, with the dolphin launching partially or fully out of the water onto the beach. The dolphin turns sharply to return to the water head first
Boat begging	Dolphin approaches stationary or slow-moving boats within 1-2 m and opens jaw or brings the head out of the water
Provisioning*	Dolphin receives fish handouts (chawed, dead fish) from humans standing in shallow water

Calves are not provisioned, so the category "provisioning" was excluded from data analysis. Further, all observations in the present study were conducted away from shore, where provisioning does not occur (although a few dolphins beg from boats).

Table 9.2. Definition of surface and dive types associated with foraging

Dive type	Description
Tail-out dive	Deep dive, flukes out of the water
Peduncle dive	Peduncle or tail-stock arched at dive, flukes partially submerged
Rooster tail	Not really a dive type; more a kind of fish chase. A fast swim along the surface in which a sheet of water trails off of the dorsal fin. Following this type of swim, the dolphin descends rapidly, often opposite to the direction of the swim
Rapid surface	A rapid surface in which the dolphin maintains a horizontal posture and the dolphin's ventrum does not clear the water surface
Porpoise	A rapid surface in which the dolphin maintains a normal horizontal posture but the entire ventrum does not clear the water surface at once; the dolphin's entire body does leave the water surface in the course of the dive
Leap	A rapid surface in which the dolphin maintains a normal horizontal posture and the dolphin completely clears the water surface
Regular dive	The dolphin sinks down at the end of a breath series without arching the peduncle or raising the flukes out of the water. Regular dives are typical of infants
Humping surface	A normal speed surface in which the dolphin "humps up" its posterior half to break its forward motion as it descends. Often seen when dolphins are driving or pursuing a fish school in shallow water but also seen in aggressive contexts
Fast swim	A dolphin rapidly accelerates and/or swims fast along or below the water surface

a number of distinct population-specific foraging techniques have been described. These include sponge carrying to ferret prey from the sea floor (Smolker *et al.*, 1997; Fig. 9.1); corkscrewing into the sand after fish (Rossbach and Herzing, 1997); belly-up chasing of fish at the surface (Bel'kovich *et al.*, 1991; Mann and Smuts, 1999); strand feeding on mud-banks in Portugal (dos Santos and Lacerda, 1987), Georgia and South Carolina, USA (Hoese, 1971; Petricig, 1993), and on beaches in Shark Bay, Australia (Berggren, 1995; Fig. 9.2); stunning or killing fish with a tail-hit (Shane 1990; Wells, Scott, and Irvine, 1987); or tail-whacking the water surface to scare up fish (Connor *et al.*, 2000b). As a coastal cosmopolitan species, bottlenose dolphins have also learned to take advantage of human activity. For example, bottlenose dolphins have learned to feed on fish drawn to a garbage barge and were predictably found based on the schedule of the garbage barge (Norris and Dohl, 1980). They follow shrimp trawlers (e.g., Caldwell and Caldwell, 1972; Corkeron *et al.*, 1990; Leatherwood, 1975; Norris and Prescott, 1961) and steal bait from lines or crab pots (Noke and Odell, 1999). In Laguna, Brazil, fishermen and

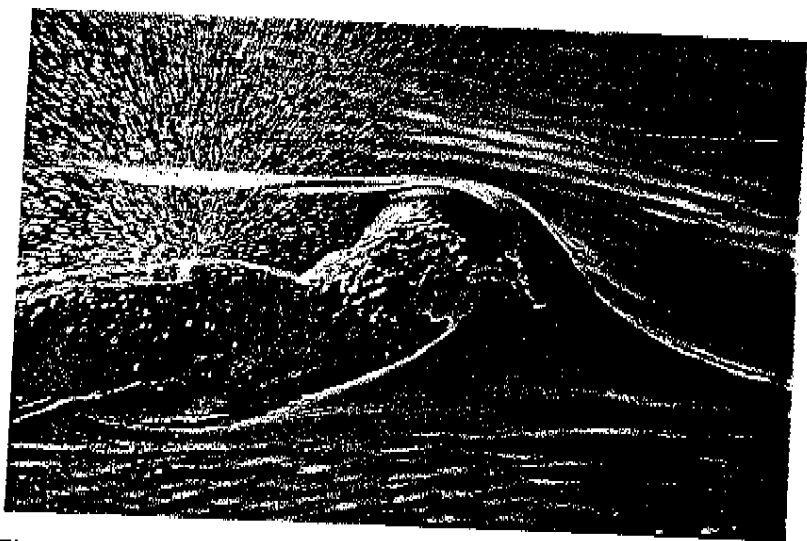


Fig. 9.1. Photograph of "Original Spongemom", who was observed sponging in the late 1980s and continues to carry sponges in 2001. Her surviving offspring, Grunge, still carries a sponge, two years after weaning, at age five.

dolphins appear to net mullet cooperatively, with the dolphins herding the fish into the nets and feeding easily off the remains (Pryor *et al.*, 1990). Historical accounts of Australian aboriginal cooperative fishing with dolphins have also been reported (Corkeron *et al.*, 1990). Provisioned females in Monkey Mia, Shark Bay, Australia beg for fish from boats and tourists (Connor and Smolker, 1985; Mann and Smuts, 1999). The Monkey Mia and Laguna "traditions" have continued across at least three generations.

Although these studies describe foraging strategies that differ between populations, in Shark Bay, the intrapopulation variation is remarkable and distinguishes Shark Bay bottlenose dolphins from other populations and species studied to date. In particular, individual females and their offspring have distinctive foraging strategies ranging from one to seven foraging types out of the 11 that we have studied and 13 that have been documented at our field site (Table 9.1). For example, one technique, sponge carrying, is clearly a form of tool use and is restricted to a limited number of animals (Fig. 9.1).

9.1.2 Is the duration of lactation related to calf foraging skill?

It is clear that dolphins are precocious and well developed at birth but maintain a long period of dependency. Bottlenose dolphins typically

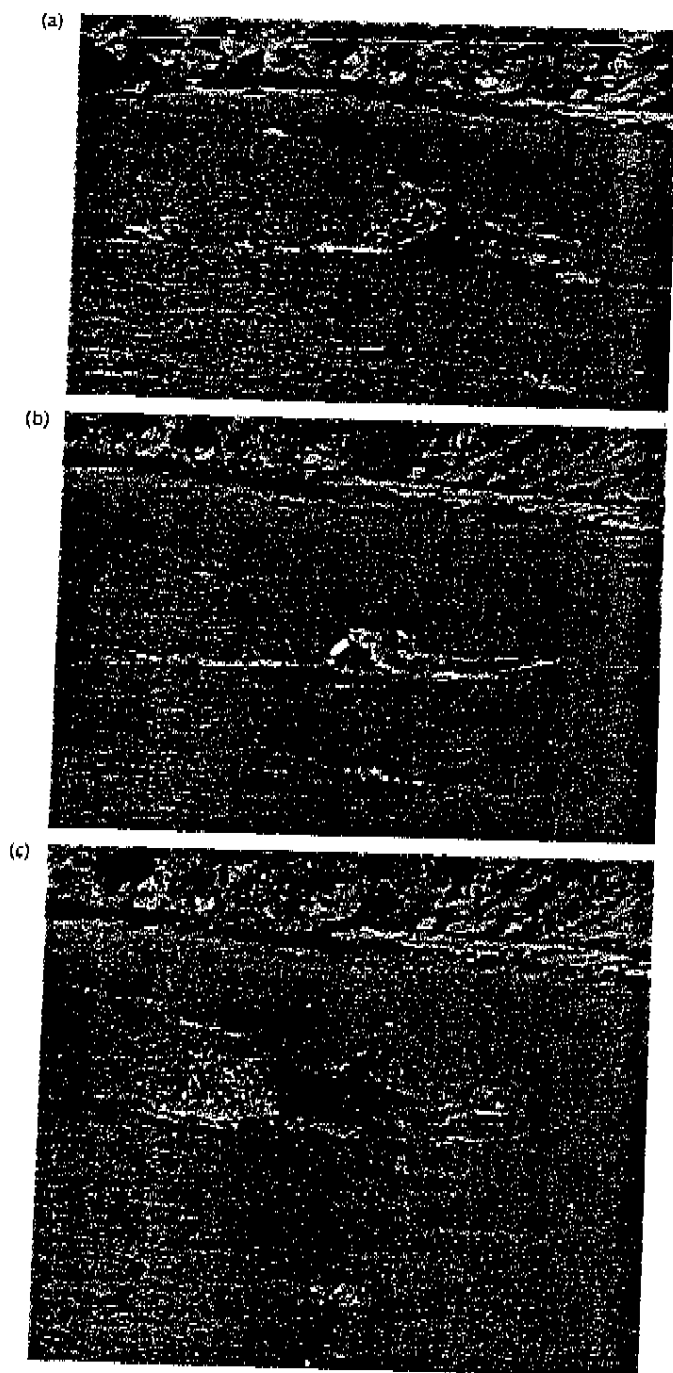


Fig. 9.2. Photograph of beaching behavior (triple sequence): an adult female, Rhythm, lunges out of the surf (a), catches a mullet (b), and turns back into the water (c).

nurse for three to six years in Shark Bay (Mann *et al.*, 2000). A calf must be able to forage successfully before being completely weaned. Learning to forage appears to be a slow process, warranting the overlap between nursing and foraging for the first years of life. This contrasts with most mammals, where independent foraging does not begin until late lactation. Compared with toothed whales, baleen whales have shorter periods of maternal investment, less overlap between nursing and calf foraging, and fewer, less-complex feeding strategies (e.g., Clapham, 2000; Whitehead and Mann, 2000).

Johnston (1982) proposed that parental investment is likely to be intensive and prolonged for species with complex foraging skills (high dependence on learning). Although this seems likely, we suggest that social learning would reduce the mother's lactation costs by decreasing the period of nursing or by increasing the overlap of nursing and foraging. A longer period of dependence allows for the infant to learn specialized foraging skills from its mother or on its own while still nutritionally dependent on and protected by her. Dolphin calves maintain roughly the same home ranges as their mother after weaning (Mann *et al.*, 2000); a similar habitat would favor similar hunting strategies. Thus, selection should favor social learning from the mother. Consistent with this hypothesis, Laland and Kendal (Ch. 2) propose that moderately low environmental variability will favor vertical transmission.

Unlike carnivores (e.g., felids, canids, mustelids) and primates, cetacean mothers generally do not share prey with young. One exception is the killer whale, where prey sharing between mother and offspring has been well documented (Baird, 2000). Despite several thousand hours of observation of bottlenose dolphin calves in Shark Bay by J. Mann, prey sharing has not been observed. Nevertheless, calves seem quite interested in fish caught by other individuals. They frequently approach and inspect prey caught by others and will sometimes travel tens of meters to observe (unpublished data). Even with the fish or pieces of the fish floating in the water, calves have never been observed taking fish caught by another.

9.1.3 Dolphin social structure and foraging strategies

Because bottlenose dolphins live in a fission-fusion society with flexible group membership (Smolker *et al.*, 1992) and travel costs are low (Williams *et al.*, 1992; Williams, Friedl and Haun, 1993), dolphins can likely enjoy the benefits of group living without the costs of direct feeding competition (Connor *et al.*, 2000a). Individuals have the opportunity to associate in a

number of small groups or to travel alone, allowing individuals to benefit from the group structure as well as from individual foraging success. Although most hunting is a solitary affair, schooling fish may attract groups and individual dolphins may benefit by collective balling of fish. We predict that some of the group-foraging techniques (feeding on large schools) are more widely shared (less specialized) across individuals, as large prey patches may attract all dolphins more readily.

Males and females differ in their social affiliations. Females, especially those with calves, are usually in larger groups than are males (Scott, Wells, and Irvine, 1990), although group size is variable. Some females remain fairly solitary while others are quite social (Mann *et al.*, 2000). Females tend to associate with their mothers after weaning; males do not disperse, but they do form coalitions with other males within the community (Connor *et al.*, 2000a; Wells *et al.*, 1987). Sons are weaned at an earlier age than daughters (Mann, 1998); consequently, daughters have a longer time to learn specific foraging skills from their mothers and could be expected to have a higher degree of similarity with their mothers for the specialized types of foraging. There is also a difference in the movement patterns between the sexes, with the females covering smaller areas than males (Bearzi, Notarbartolo-Di-Sciara, and Politi, 1997). The differences in social affiliation and use of space for male and female dolphins suggest that there may also be differences in foraging techniques and degree of specialization, with females more likely than males to acquire specialized techniques.

Female dolphins spend, on average, 19–36% of the daytime foraging. Their hunting strategy and choice of habitat are likely to affect their fitness. Shallow-water habitats in Shark Bay are associated with higher female reproductive success than deep-water habitats (Mann *et al.*, 2000), possibly because of differences in food density (Heithaus and Dill, 2002) or in fish species or distribution.

9.1.4 Research questions

In the following sections, the study of Shark Bay dolphins is used to examine foraging techniques and their dissemination. Three specific areas are discussed.

1. The diversity and distribution of foraging techniques used by mothers and their calves are examined, specifically to identify foraging techniques shared widely by members of the population and techniques that are more specialized (restricted to a few members).

2. Associations between the foraging strategies used by mothers and their calves are determined to see if similarities in foraging technique between mothers and calves increases with the calf's age.
3. The evidence that some specialized foraging techniques qualify as "traditions" (Ch. 1), passing from one generation to the next via vertical social transmission, is outlined. Widely shared (generalized) foraging techniques may also be socially influenced, but it will be more difficult to document their status as traditions *per se*.

9.2 Methods

9.2.1 Background and field site

The study incorporated a 130 km² area east of the Peron Peninsula, which bisects Shark Bay (25° 47' S, 113° 43' E), Western Australia. A longitudinal field study was established in 1984 (Connor and Smolker, 1985). By 2000, over 600 dolphins had been identified and 200 animals were sighted regularly. Dolphins are identified by their fin shape, nicks, and other natural markings. Calves have been sexed using views of the genital region. A mother-calf study was initiated in 1988 by Janet Mann and Barbara Smuts. Observations of mothers and calves by the former has continued for two to six months every year since, except 1995.

Since the early 1960s, 6 to 11 dolphins (at a time) have been provisioned by tourists and fishers at a small fishing camp, turned resort, called Monkey Mia. Since the mid-1980s, the feeding has been controlled and monitored by rangers currently employed by the Department of Conservation and Land Management (CALM) of Western Australia. Since 1995 feeding from boats has been firmly restricted by CALM although it still occasionally occurs. At present, three adult females (Nicky, Puck, and Surprise) and their offspring visit the Monkey Mia beach up to three times per day and receive up to 2 kg of fish per day. To discourage dolphins from spending too much time near the provisioning area, no dolphins are fed after 1 p.m. Nicky, Puck, and Surprise visit daily, with only a few absences per annum. During their visit, the mothers remain in shallow water near people and make frequent contact with the rangers until the feeding, which occurs approximately 30–60 minutes after their arrival at the beach. Calves typically remain in deeper water until the feed is over. The dolphins leave almost immediately after each feeding.

Offshore focal observations involved following individual animals in small boats (4–5 m dinghies equipped with 6–45 hp motors) for up to

Table 9.3. Observation record for dolphin calves at each age

Age class	Calf age (months)	Total focal calf observation minutes (hours)	No. Days observed	No. calves with focal data
Newborn	0-3	4721(78.68)	41	6
1st year	4-11	20931(348.85)	119	34
2nd year	12-23	21247(354.12)	135	35
3rd year	24-35	14534(242.23)	93	25
4th year	36-47	11192(186.53)	67	11
5th year	48-59	3617(60.28)	25	4
6th year	60+	566(9.43)	4	1

10 hours at a time (Smolker, Mann, and Smuts, 1993; Mann and Smuts, 1998). Observers typically remained < 50 m from the mother or calf. Between 1996 and 1998, and during 2000 field seasons, two boats, a 5 m fiberglass dinghy and a 10 m catamaran (*Nortrek*) were used for observations and acoustic recordings and localization. When mother and calf were together (< 10 m), only one boat stayed with the focal pair. When separated (> 10 m), one boat would stay within 100 m of each member of the dyad. *Nortrek* typically remained > 50 m from the mother or calf.

9.2.2 Subjects

The study, conducted between 1989 and 2001, incorporated 1280.1 hours of focal observations on 58 calves (18 males, 22 females and 18 of unknown sex) born to 37 mothers. We used 1781 calf and 3020 maternal foraging bouts for these analyses. Of the 37 mothers in the current sample, five visit (or visited) the provisioning beach. The remainder, to our knowledge, have had no contact with humans. The data include information about the infant's and mother's time spent foraging overall, the types of foraging, the dive type, the depth, and group membership. "Group" is defined using a 10 m chain rule: any animal that is within 10 m of any animal within the group is in the group. The total number of hours observed for the calves at each age is detailed in Table 9.3. The approximate date of birth of the infant is known for most subjects.

9.2.3 Focal sampling

Data were collected with a focal-animal procedure using several different observational methods including continuous, scan, and point sampling (Altmann, 1974; Mann, 1999). In addition to boat-based observations,

similar focal methods were applied during five days of shore-based observations from cliffs and beaches of Point Peron to study the "beaching behavior". For follows from Point Peron, we also sampled the mother's and the calf's distance from the beach every minute and during beaching events.

Activity data were gathered using continuous or point sampling, with duration and/or frequencies of behaviors maintained in the sampling record. This method was used to record the duration of foraging (bout length and frequency) and dive types (frequency). Every 5 minutes we measured water depth (using a depth sounder); water depths were further classified as shallow (≤ 4 m), moderate (4–7 m), and deep (> 7 m). Group composition for mother and calf were determined every minute (post-1996) or every 5 minutes (pre-1996). Latitude and longitude were determined every 15 or 30 minutes using the Magellan Pro-Mark X or (pre-1996) using compass bearings on landmarks.

Foraging was recorded when there was reasonable evidence that the animals were actually searching for, catching, processing, and eating prey. Foraging is a regular and more or less exclusive search for prey. It is difficult to diagnose because foraging occurs below the surface and is not always successful. Further, successful prey capture often eludes observers since prey are typically swallowed whole immediately. Specific types of foraging were identified and given names, as listed in Table 9.1, although in some cases, the foraging type was defined *post hoc* based on absence or presence of defining features. *Post hoc* coding was done "blind" to dolphin identification. Foraging that could not be classified was placed in a generic category of "foraging". Foraging types were determined, in part, by dive types, which are indicated in Table 9.2.

9.2.4 Data reduction and analysis

A foraging bout was defined as each onset and offset of foraging. When point sampling was used, or if it was impossible to determine the exact time of onset or offset, the midpoint between point samples was used as the onset or offset. Each bout was classified as a type in Table 9.1. Percentage time foraging for each calf for each age class observed was determined by dividing the total minutes foraging that year by the total time observed that year. Similarly, the rate of foraging (bouts per hour) was determined by dividing the number of foraging bouts by the total time observed. For all calves that foraged ($n = 51$), percentage of foraging bouts by type was determined overall for each calf and for each age class

by dividing the number of bouts of foraging type by the total number of foraging bouts.

Chi-square (Yates corrected) analysis was used to determine the association between mother and calf in foraging types in two ways. First, each mother and calf was coded according to whether or not they engaged in a specific foraging type. Some pseudoreplication was inevitable given that 13 of 37 mothers had more than one calf in the sample. Seven calves were not used in this analysis because they did not forage; in one case, the mother was not observed foraging. If the foraging type was not indicated or could not be coded using descriptions of dive types and other information, these cases were excluded from the "foraging type" analyses but included in time budgets and bout rates. Second, each mother and calf pair was coded according to the calf's age. For this analysis, the earliest year was used to characterize each mother's foraging type(s) (first year of her calf's focal data). The calf's foraging type(s) was coded for subsequent years (see Table 9.1). This way, independent datasets were obtained for mothers and calves. Hence, this analysis is more conservative because foraging similarity could be demonstrated across years. The Fisher exact test (two-tailed) was used for this analysis because the expected values for cells were less than five. The second analysis reduced our sample size to 31 mother-calf pairs because some calves were only observed in one year.

9.3 Results and discussion

9.3.1 Diversity of foraging types

Twelve foraging types were identified in this study and the distribution and mother-calf similarity of 11 were analyzed (provisioning was excluded). The mothers' predominant (most common) foraging type was tail-out/peduncle dive foraging (Fig. 9.3). The calves' predominant foraging type was snacking, followed by tail-out/peduncle dive foraging. Most mothers and calves used only a few of the foraging types available (Fig. 9.4).

The number of techniques employed ranged from one to seven for mothers and calves. This variable was significantly correlated for mother and calf (Pearson $r = 0.66$; $p < 0.001$; $n = 51$). That is, mothers who engaged in multiple foraging types had calves who tended to do the same. However, the number of foraging tactics used by mothers strongly correlated with the number of hours she was observed (Pearson $r = 0.71$;

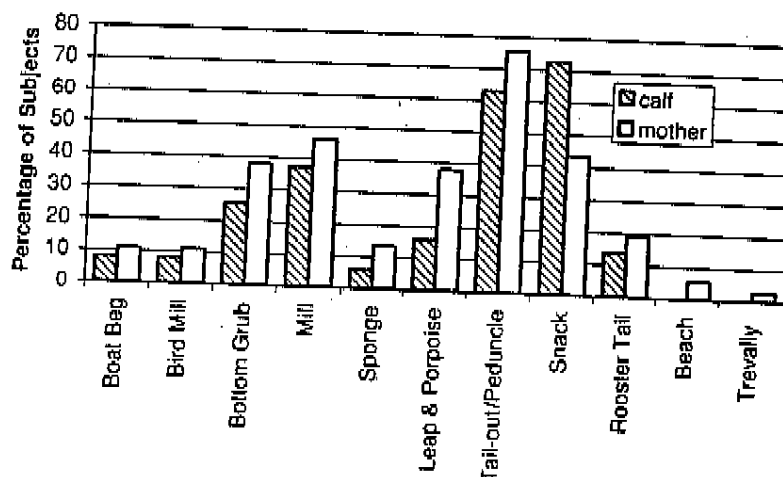


Fig. 9.3. Proportion of mothers and calves engaging in different foraging types. The predominant foraging tactics used were tail-out and peduncle dive foraging, milling, and snacking (especially for calves). Only a few subjects engaged in behaviors deemed "traditions".

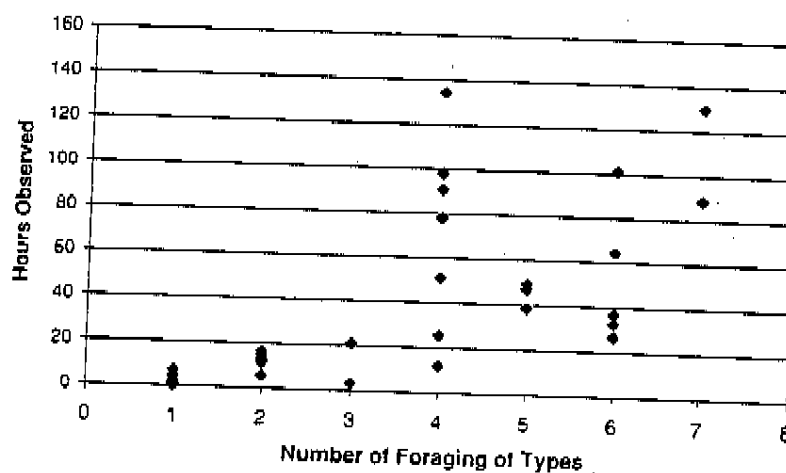


Fig. 9.4. Correlation between the number of maternal foraging types per female and observation hours (Pearson $r = 0.711$; $p < 0.01$; $n = 33$). Females who were observed for more hours exhibited more foraging types, but some females who were observed 50 hours or more still exhibited only four types. The two females who exhibited the most foraging types were provisioned. Provisioning has been associated with innovation and behavioral flexibility at other mammalian research sites (Ch. 10).

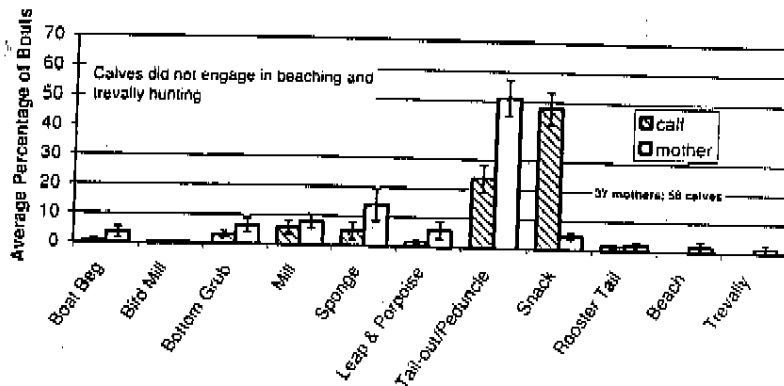


Fig. 9.5. Average proportion of bouts by foraging type across all subjects. This shows the mean proportion (\pm SE) of foraging types mothers and calves engaged in. Tail-out and peduncle dive foraging clearly made up the greatest proportion of foraging bouts, averaging approximately 51% for mothers. For calves, snacking clearly was the predominant foraging type, averaging 49% of calf foraging bouts.

$p < 0.01$; $n = 33$) and this variable accounted for 50% of the variance in diversity of foraging types in mothers (Fig. 9.4). Across mother-calf pairs, the average proportion of foraging bouts by type illustrates the preponderance of snacking for calves and tail-out and peduncle dive foraging for mothers and calves. Other types of foraging occurred at low rates across our sample, although they may represent a high proportion of an individual mother's foraging bouts (see Fig. 9.5).

9.3.2 Development of foraging in calves

Calves increased both bout rate and proportion of time foraging with age (Fig. 9.6). *Post hoc* comparisons revealed significant differences between the newborn period (birth to three months) and the third year, and between the first and third year. The dip in foraging rate and percentage time foraging during the calf's fourth year is not significant. Calves did not forage (chase and catch fish) during the first three months. Maternal foraging did not significantly change as a function of calf age.

Among the 34 calves observed in the first year, all foraging types were observed except beaching, trevally hunting, and sponge carrying. Milling and snack foraging were first observed at 3.4 months of age. Leap feeding was first observed at 6.4 months. At seven to eight months, four foraging types were observed: boat begging, bird milling, rooster tail and tail-out/peduncle dive foraging. Calves have not been observed beaching or

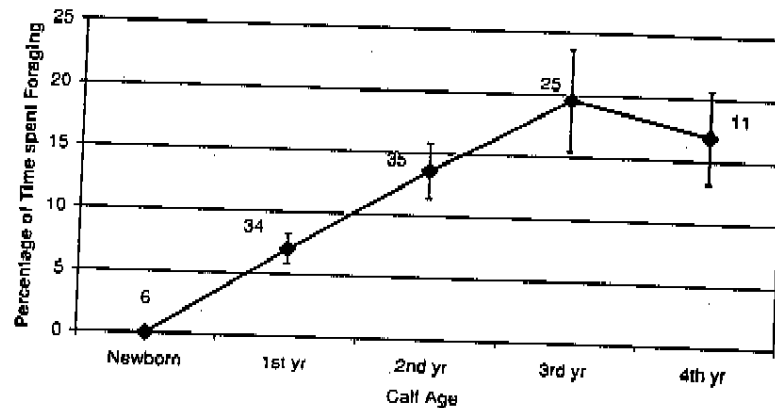


Fig. 9.6. The mean percentage of time calves spent foraging from the newborn period (0–3 months) until their fourth year. Sample sizes are indicated above the average. Calves increased the proportion of time and rate of foraging with age and no calves foraged during the newborn period. (Forage rate (bouts per hour): Kruskal–Wallis = 16.68; $p = 0.002$; Bonferroni post-hoc pairwise comparisons for newborn versus third year, $p < 0.016$; first versus third year, $p = 0.006$. Percentage time calf foraging: Kruskal–Wallis = 23.87, $p < 0.001$; Bonferroni post-hoc pairwise comparisons for newborn versus third year, $p = 0.016$; first year versus third year, $p = 0.006$.)

trevally hunting up until their third year (no fourth year observations have been conducted for calves born to mothers who engage in these behaviors). Sponge carrying was first observed at 20 months for one calf (Grunge), and at 31 months for another (Demi). The third calf was only observed during the fourth year of life and was already sponge carrying. Both Demi and Grunge have continued to sponge carry after weaning (Fig. 9.1).

Snacking, the most common calf foraging behavior, declined with calf age, suggesting that calves increase nonsnack foraging tactics with age. Snacking is also the first type of foraging to appear developmentally and is practiced in the newborn period (Mann and Smuts, 1999).

9.3.3 Correspondence between maternal and calf foraging style

Mother–calf similarity in foraging was evident for nearly all foraging types, with calves almost exclusively engaged in techniques used by their mothers. With the exception of snacking, there were only five cases where calves engaged in a foraging type not seen in their mothers. Three of those cases were calves born to sponge-carrying females, and the calves were not (yet) sponging themselves. One case was Whoops, offspring of the “trevally hunter” Wedges. The remaining case referred to a single bout of leap and porpoise feeding by a calf. The biggest difference between

mothers and calves related to snack foraging. Eight calves snacked, although their mothers did not. In contrast, mothers engaged in two foraging techniques not observed in calves, beaching and trevally hunting.

9.3.3.1 Boat begging and its relationship to provisioning

Boat begging typically occurred near shore when boats were stationary (fishing) or on return from fishing trips. Average water depth of boat begging was 3.07 ± 0.15 m; four focal calves and four of five provisioned mothers engaged in boat begging.

All calves in the database that engaged in boat-begging behavior had mothers who were provisioned. One calf born to a nonprovisioned female (and not included in this dataset) was observed begging from a boat once. This calf spent the majority of his time associating with provisioned mothers and their calves (unpublished data). No nonprovisioned mothers begged from boats. In addition, one provisioned mother did not beg at boats and neither did her two calves. Boat begging is significantly associated between mothers and calves (chi-square Yates corrected = 16.92; $p < 0.001$; $n = 51$ calves). If the presence or absence of boat begging in the mother's first year of observation is compared with subsequent years of calf observation, the association between mothers and calves is weaker but approaches significance (Fisher exact test, $p = 0.060$, $n = 31$ calves). Most begging by calves occurred close to the mother, when she too was begging at the boat (average distance was < 10 m). The only calf who was provisioned (by CALM) did the most begging (84% of all calf begging bouts, at a rate of 0.5 per hour), whereas the three nonprovisioned calves of provisioned mothers begged at low rates of 0.009–0.117 per hour. The sole provisioned calf became dependent on provisioning and this was probably the cause of his death at the age of four years.

The association patterns and foraging techniques of the offspring of provisioned females indicate why foraging traditions may be more likely to be transmitted to daughters than to sons. The two nonprovisioned sons of provisioned females (now aged 6 and 13 years) rarely visit the provisioning area. In contrast, the four daughters of provisioned females (now aged 7, 9, 25, and 26 years) frequently visit the provisioning area with their mothers, and all but the youngest have been offered and have accepted fish handouts after being weaned. Although the sample is small, these observations are consistent with the pattern away from the beach, which is that mother-son association declines after weaning and likely inhibits sharing of foraging tactics that require small and specific habitats such as the

provisioning beach. This pattern would reinforce foraging traditions for daughters that were limited to specific areas but would work against sons adopting their mothers' specializations (Peron beach, Monkey Mia beach, channels).

9.3.3.2 Bird milling

Large groups of pelicans (*Pelecanus conspicillatus*) and pied cormorants (*Phalacrocorax varius*) gather in shallow water and co-feed with bottlenose dolphins, typically in shallow water < 4 m (average depth of bird milling 3.51 ± 0.56 m). The surfacing patterns and numbers of dolphins attracted to bird-milling groups suggest that they are foraging on large schools of fish. However, not all individuals are attracted to bird-milling groups. In contrast to "leap and porpoise foraging", (see below), dolphins do not travel a kilometer or more to join bird-milling groups. Bird milling was seen in four (8%) of focal calves and four (11%) of focal mothers. All calves who engaged in bird milling had mothers who did so. The behavior is strongly associated for mother-calf pairs (chi-square Yates corrected = 16.93; $p < 0.001$; $n = 51$ calves). The presence or absence of the mother's bird milling in the calf's first year of observation compared with calf's bird milling in subsequent years indicates no relationship (Fisher exact test, $p = 1.0$, $n = 31$ calves). However, this type of foraging is infrequent, making up only 0.6% of calf foraging bouts and 0.6% of maternal foraging bouts.

9.3.3.3 Bottom grubbing

Grubbing in the sea grass or seafloor to ferret out fish probably occurs in all habitat types, but observers can only be certain of bottom grubbing in shallow water, when the behavior can be clearly seen. Fourteen females (38%) and 13 calves (25%) use this foraging technique, typically in 2.9 ± 0.11 m of water. One calf bottom grubbed, although his mother was not observed doing this behavior. Bottom grubbing was strongly associated for mother-calf pairs (chi-square Yates corrected = 7.96; $p = 0.005$; $n = 51$ calves). This association remained significant when the mother's first year of bottom-grub foraging was compared with her calf's bottom grubbing in subsequent years (Fisher exact test, $p = 0.008$; $n = 31$).

9.3.3.4 Milling

Milling, surfacing repeatedly in different directions, involves feeding on schooling fish (mid-water). This behavior occurs in both shallow and

deep water (average depth 4.73 ± 0.21 m). A large proportion of mothers (46%) and calves (37%) engaged in mill foraging and there was significant mother-calf similarity (chi-square Yates corrected = 6.50; $p = 0.011$; $n = 51$ calves). When the mother's mill foraging was compared in her first year of observation with that of the calf's subsequent years, the relationship approached significance (Fisher exact test, $p = 0.056$; $n = 31$). This foraging technique ranked third in proportion of subjects using the technique and may be considered a generalized or widely shared foraging tactic.

9.3.3.5 Sponge carrying

Sponge carrying, the only known example of tool use in any wild dolphin or whale, was observed in five adult females (14%) and three of their calves in this dataset. Of 141 identified mothers in the Shark Bay population, 15 (11%) carry sponges. All five sponge carriers use this foraging technique almost exclusively (100, 100, 96, 90, and 75% of their foraging bouts, respectively) and tend to forage in specific deep water channels (> 8 m). Sponge carrying shows a clear female bias. Of 25 sexed animals known to carry a sponge at least once, 20 are female. Only one of the males that carried a sponge is an adult. Out of our total population of sexed animals, (192 females, 166 males), females were more likely to carry sponges than males (chi square Yates corrected = 7.52; $p = 0.006$; $n = 358$).

The occurrence of sponge carrying is clearly associated for mothers and calves (chi-square Yates corrected = 15.73; $p < 0.001$; $n = 51$ calves), and relationship between the presence or absence of the mother's sponge carrying in the first year of observation and her calf's sponge carrying in subsequent years approaches significance (Fisher exact test, $p = 0.065$, $n = 31$). Of the three calves observed sponge carrying in our focal sample, two were sexed as female. The sex of the third calf was not known. Of the three calves who did not carry sponges (although their mothers did), one died in the second year (too early to begin sponge carrying), another (not sexed) began sponging in the fourth year of life (after the analyses described here were completed). The third, a male, was observed sponge-carrying once postweaning.

The strong female bias in sponge carrying could be related to several factors. First, since sponge carrying occurs mainly in deep channels, male offspring may be unable to maintain such a specialized technique and still range widely enough to herd adult females (see Smolker *et al.*, 1997). Further, males might be unable to find other sponge-carrying males and thus maintain the behavior with their alliance partners. As yet, we

know of no dolphins who became "spongers" who were not born to sponge carriers. Some males born to spongers have been observed carrying sponges, but only on a few occasions. It is unclear what developmental mechanisms might inhibit males from sponge carrying before weaning.

Sponge carrying appears latest developmentally, in the second rather than first year of life. This may be because of its difficulty, involving long dives (typically 2-3 minutes) to tear off and hunt with sponges along the seafloor. Calves under one year of age are capable of remaining submerged for 3 minutes, but this diving pattern may be difficult to maintain, or conduct appropriately, while wearing a sponge. Alternatively, the prey may be quite difficult to catch, with or without a sponge. We doubt that the prey are difficult to process, since females appear to swallow these quickly, rarely bringing prey to the surface.

As mentioned above sponge carrying tends to occur in deep channels (8-12 m), but not exclusively, and sponge carriers occasionally sponge in other areas. Further, many dolphins regularly forage in the same channels without sponging. Four of our focal females regularly used the "sponge channels" but did not sponge. Thus, the behavior does seem largely habitat specific, but use of channel habitats is not sufficient to explain the development of this foraging tactic. Recent genetic data (Krützen *et al.*, unpublished) suggest that nearly all spongers share the same mitochondrial DNA haplotype, which is rare in the rest of the (nonsponging) population. This lends further support to the suggestion that sponge carrying is transmitted through matriline. It is unclear why other dolphins do not, at least occasionally, try to sponge. Perhaps there is some 'sensitive period' during which exposure to foraging is most likely to lead to a young dolphin acquiring similar practices.

9.3.3.6 Leap and porpoise foraging

Leap and porpoise foraging typically attracts dolphins from large distances (several kilometers) to feed on large schools of fish. Even sponge-carrying females drop their sponges and travel some distance to join leap-foraging groups. Dolphins do not appear to "specialize" in this technique; rather they take opportunistic advantage of large schools that periodically occur in the bay. More than a third of mothers (38%) and 16% of calves (Fig. 9.3) engaged in leap and porpoise foraging. Leap and porpoise foraging occurs at variable depths (4.62 ± 0.28 m), typically in moderate or deep water (> 4 m). This behavior was not associated for mothers and calves (chi-square Yates corrected = 1.97; $p = 0.16$; $n = 51$ calves);

although calves nearly always accompanied their mothers long distances to leap-foraging groups, they did not forage in these but appeared to concentrate on tracking their mothers when so many animals (often more than 20) were present. In comparing leap feeding across years, no association between mothers and calves was found (Fisher exact test, $p = 1.0$; $n = 31$).

9.3.3.7 Tail-out and peduncle dive foraging

Tail-out and peduncle dive foraging was the most common foraging technique. It was exhibited by 76% of the mothers and 63% of the calves. This type of foraging occurs in moderate and deep water, averaging 6.75 ± 0.12 m. It is not significantly associated for mother-calf pairs (chi-square Yates corrected = 1.29; $p = 0.256$; $n = 51$). Two calves engaged in tail-out and peduncle dive foraging although their mothers did not. Both calves were born to spongers and did not sponge themselves. In comparing tail-out and peduncle foraging for the mother's first year of observation with the calf's subsequent years, no relationship was found (Fisher exact test, $p = 1.0$; $n = 31$). Tail-out and peduncle dive foraging may be considered a generalized or shared foraging tactic.

9.3.3.8 Snacking

Snacking was clearly the predominant foraging type for calves, accounting for nearly half ($48 \pm 5\%$) of all calf foraging bouts. We observed 73% of calf subjects snacking. Snack foraging was the only foraging type that calves did more often than mothers. Only 43% of mothers snack foraged and only $5 \pm 1\%$ of their foraging bouts were snacking. Eight calves snacked although their mothers did not. Most maternal snacking involved single belly-up chases of fish, rather than the repeated circular swims belly-up to chase fish that are characteristic of calves. There was a significant association between maternal and calf snacking (chi-square Yates corrected = 6.51; $p = 0.011$; $n = 51$ calves). If the mother's snacking in the first year is compared with the calf's snacking in subsequent years, the relationship approaches significance (Fisher exact test, $p = 0.059$; $n = 31$). Snacking occurs in all water depths, averaging 4.92 ± 0.22 m.

Based on the observations of newborns, who appear to practice snacking for several months before actually catching a fish (Mann and Smuts, 1999), it may be that snack foraging allows the calf to coordinate visual images (backlit when belly-up towards the water surface) and motor activity with developing echolocation skills. Dolphins see most acutely in the ventral direction. Therefore, by swimming belly-up, calves may optimize

visual and acoustic (amodal) perception. Although object play is rare in dolphins, newborn calves repeatedly belly-up "chase" and "capture" sea grass in the first months of life (Mann and Smuts, 1999). Between four and six months, calves begin capturing small minnow-sized fish, and snacking may be the easiest way for them to catch such small fish. When mothers snack, it is on much larger fish, sometimes 60 cm long (e.g., longtoms, either *Strongylura leiura* or *Tylosurus gaviaoides*). Because of the early appearance of snack foraging, its apparent "practice" with seagrass, the relative lack of snack models (especially the mother), and its predominance as a calf foraging technique, we propose that snack foraging, unlike other techniques, is predominantly individually learned. Further, snacking disproportionately declines with age. Since snacking occurs in all habitat types, the decline in snacking is unlikely to be strictly caused by habitat changes during development.

9.3.3.9 Rooster-tail foraging

Seven females (19%) and seven calves (14%) rooster-tail foraged. For those seven mothers, rooster tailing made up a small to moderate proportion of their foraging bouts, ranging from 3 to 27% (chi-square Yates corrected 10.2 ± 3.9). Two of the adult females who rooster tailed were also mother and daughter. This behavior has spanned at least three generations and is significantly associated for mother and calf, with all seven rooster-tailing calves having a mother that rooster tailed (chi-square Yates corrected = 5.53; $p = 0.019$; $n = 51$ calves.) The association between rooster tailing for mothers and calves remained significant when the mother's first year was compared with the calf's subsequent years of observation (Fisher exact test, $p = 0.001$, $n = 31$). Rooster tailing usually occurs in water of shallow to moderate depth (4.23 ± 0.09 m). Because similar habitats and presumably similar prey occur throughout the bay, we would expect more dolphins to rooster tail. The complex aspect of the foraging technique is that the dolphin appears intentionally to overshoot the prey at the surface, often, but not always, back-tracking for the capture. Since a rooster-tail swim is always followed by a dive to the seafloor, it is interesting that the dolphins do not just dive immediately and pursue the fish at depth.

9.3.3.10 Beaching

Two mother-calf pairs were observed for 8.6 hours at Point Peron, just north of our main study area, specifically for their beaching behavior. These observations were conducted from cliffs and so only the foraging types used by the Peron females close to shore could be observed.

Beaching was first described by Berggren (1995) although locals have known about it since the 1980s. One of the beaching females, Reggae, has been observed beaching regularly in the period from 1991 to 2001 (J. Mann, personal observation; Berggren, 1995). The behavior pattern appears to be restricted to one to three matriline. One of Reggae's offspring beached as a juvenile (Berggren, 1995), although no one has observed dependent calves beaching. Three adult females in the current study were observed beaching fish (typically mullet, *Mugil cephalus*) on a 1 km stretch of beach. Two had calves. The calves, one in its first year and another in its third, did not stay near the mother during beaching (they were typically > 50 m from the mother) and they did not participate in any type of beaching behavior. The technique may be risky and calves are likely to be in the way.

9.3.3.11 Golden trevally hunting

One female, Wedges, engaged in trevally hunting. Wedges begins with tail-out dive foraging in deep water (over 6–7 m) and then begins a high-speed chase, always leaping (typically 3–17 leaps), to catch golden trevally (*Gnathanodon speciosus*). Once she catches the fish, she will first take several deep dives with the fish, perhaps to strike the head against the bottom (thus killing or stunning the fish). The fish, still whole, is then carried to shallow water (< 4 m). The head is broken off and the fish is eaten in shallow water. Her calf, Whoops, nurses or stays in infant position (in contact under the mother) as she carries the fish to shallow water. Once she begins breaking up the fish in shallow water, the calf moves away and forages independently, sometimes traveling several hundred meters away, but staying in shallow water to bottom grub or snack. The calf does not regain infant position for another 30–60 minutes while Wedges breaks up the trevally. (Calves are usually out of infant position for 10 minutes or less.) The calf remains 50–300 m away from the mother during the catching and eating phases but takes the opportunity to nurse or be in infant position during the carrying phase of trevally hunting. We have seen Wedges catch seven golden trevally, six during focal observations (16.4 hours of focal observation, or one trevally every 2.7 hours; 50% of Wedges' foraging bouts are trevally hunting). It takes nearly 1 hour to break up and eat fish this size. The remarkable aspect of this phenomenon is the size of the fish, which can reach up to 111 cm in length and 15 kg (Allen and Swainston, 1988). In 17 years of long-term study, no one has observed other Shark Bay dolphins catch fish this size.

9.4 Conclusions

A set of common foraging techniques and a set of individually distinctive foraging techniques can be identified for both Shark Bay bottlenose dolphin females and their calves. Tail-out and peduncle dive foraging and milling are common in both mothers and calves, and snacking is common amongst calves in particular. Nearly all females have been observed to use fewer than half the foraging techniques observed in the population. Such a high degree of intrapopulation variation in foraging style has not been documented elsewhere.

Some types of foraging strategy are restricted to a few animals (e.g., rooster tailing, boat begging, sponge carrying, trevally hunting, and beaching). No calves developed these foraging techniques unless their mothers engaged in them. Further, when the mother's first year of observation is compared with subsequent years of calf observation, similarity between mother-calf foraging types generally remained despite the small sample size (most values for $p < 0.10$). The pattern of increasing mother-calf similarity and clear examples of lifetime stability in some foraging techniques within matriline are strong evidence that these are traditions that are vertically transmitted (e.g., Demi, born to a sponger, has sponged all her life; Crooked-fin, her daughter, and grand-offspring have all been rooster tailers). Future analyses will focus more directly on the degree of similarity by examining the proportion of foraging time devoted to different techniques with age. The period of dependency, which ranges from 2.7 to more than eight years (Mann *et al.*, 2000), could be related to the complexity of acquiring specialized foraging skills, but we cannot test this directly with the current data.

9.4.1 Foraging traditions

Two types of foraging (bottom grubbing and rooster tailing) meet our stringent criteria for traditions (as defined in Ch. 1) by showing a statistically significant relationship between the mother's foraging technique during the first year of the calf's life and the calf's techniques during subsequent years. However, variation in use of at least one of these techniques may reflect variation in habitat use rather than social influence (i.e., it is only possible to observe bottom grubbing in shallow water, and mother-calf pairs share habitat types). There were also significant associations between mother and calf foraging patterns for sponge carrying and boat begging, though this could be the result of sampling biases from

simultaneous data collection on mother and offspring. It is possible that beaching and provisioning/interactions with humans are also vertically transmitted, but data on possible vertical transmission of beaching are only anecdotal (based on one mother-offspring pair), and the provisioning/human interaction data are not presented here. Six remaining foraging types (bottom grubbing, bird milling, leap and porpoise feeding, milling, tail-out and peduncle dive foraging) do not apparently require extended exposure to an adult model for their development. Further, all of these foraging techniques have been reported at other *Tursiops* spp. study sites (e.g., Connor *et al.*, 2000a; Shane, 1990), suggesting that these tactics are widely shared and social influence is relatively less important. Finally trevally hunting may be an "innovation", specific to one female.

Of the foraging techniques that could potentially be labeled "traditions", some calves and mothers are clearly exposed to these foraging types but do not engage in them. For example, Demi (a sponger) regularly associates with the majority of our focal females, but few of her associates sponge. About eight females regularly visit the provisioning area and have access to fishing boats, but they do not attempt to take fish. One female, Joy, was born to Holeyfin, a provisioned female, but avoided the provisioning beach as soon as she was weaned and has never accepted fish handouts. At the Peron beach, other animals clearly observe the beaching behavior but do not attempt it. A large number of dolphins forage in the "sponge channels", but they do not sponge. Several of our focal females regularly tail-out and peduncle dive in the sponge channel, but never pick up sponges. There might be some inhibition to development of foraging tactics that are not exhibited by one's mother or such tactics may require some threshold of exposure, perhaps during a sensitive period.

Other foraging techniques observed in our study population but not in our focal animals (e.g., kerplunking, see Connor *et al.*, 2000b) indicate that there may be other foraging and prey specializations of which we are yet unaware. For example, Square, one of the focal mothers in this study, forages for an average of only 10% of her time during daylight hours, yet during one night-time follow, she foraged for approximately 55% of the time. Therefore, we suspect that some females may be "nocturnal" specialists. Further, we know little about the diversity of prey consumed, and there may be specializations in this domain as well. Although Wedges' consumption of golden trevally is obvious, smaller prey are difficult to identify. We have observed only one female in our sample catching and eating stingrays (blue spotted fantail, *Taeniura lymma*). Another female

frequently catches flathead (possibly *Sorsogono tuberculata*); only her daughter has been observed catching the same type of fish.

9.4.2 Vertical transmission and developmental mechanisms

We suggest that social learning, especially between mothers and calves (vertical transmission), plays an important role in the calf's foraging development. Laland and Kendal (Ch. 2) suggest that predominantly vertical transmission is adaptive when environmental change occurs relatively slowly. They make two predictions for conditions favorable to social learning that are relevant for Shark Bay dolphins (see Ch. 2). First, social learning is favored when the observer and demonstrator experience the same environment. It would be expected that specialized foraging types in dolphins would be passed on from generation to generation only when the environmental conditions were similar. This is also relevant to the discussion of sex differences in the adoption of the mother's foraging strategy; females are more likely to associate with their mothers and, therefore, experience the same environmental conditions. We predict that daughters are more likely to adopt foraging strategies similar to their mothers than are sons, especially when the strategies are highly habitat specific. This appears to be the case for sponge carrying, but we have insufficient data to test this hypothesis more broadly.

The second prediction from Laland and Kendal relevant to dolphins in Shark Bay is that information regarding resources that are relatively static is more likely to be socially learned than information regarding resources that are rapidly changing. At Shark Bay, specialized foragers do not shift foraging techniques seasonally, suggesting that prey are static or specialists can exploit multiple prey types with one technique.

Laland and Kendal's third prediction is that costly skills are more likely to be socially learned. Our findings relevant to this prediction concern the restriction of sponge carrying to mothers and female calves, coupled with its delayed appearance in the calves. Given the length of time apparently necessary for the development of sponge foraging, it appears to be a difficult strategy to learn.

Why do female calves, but not male calves, readily adopt and appear to maintain foraging traditions within matriline? It seems clear that daughters, who maintain strong ties with their mothers after weaning, would clearly benefit by developing similar foraging tactics so long as the mother's foraging tactics are adequate. Peglet, Square's fully grown daughter, appears, like her mother, to forage little during the daytime

(< 10%, J. Watson, unpublished data), although night-time follows have not been conducted. After weaning, sons may be less prone to maintain the same tactics as their mothers. Although their ranging overlaps extensively with that of their mothers after weaning, the development of strong bonds with males is likely to take precedence over feeding sites. Consequently, we would expect males to become more opportunistic and eclectic in foraging with age. By the time they reach adulthood, a male's foraging tactics may depend more upon who his alliance partner is than who his mother is.

We still know little about precisely how the calves learn to forage. Although calves are often close to their mothers while she is foraging and they can obviously see and perhaps hear what she is doing, they also are more likely separate from their mothers (> 10 m) during foraging than during other activities (J. Mann and J. J. Watson, unpublished data) and at these times would not be able to see what prey items she chases or catches. However, calves may not only hear the patterning of the mother's sonar but might also hear some of the feedback from those pulses. During the first year, when most foraging techniques appear, the calf could have significant opportunities to link acoustic and visual phenomena with foraging activity when it is close to the mother. Most foraging techniques were initiated in the first year. Data from captivity suggest that adult and immature dolphins are excellent mimics, both in gestural/motor and vocal domains (e.g., Bauer and Harley, 2001). Field data offer additional support for acoustic matching (Janik, 2000) and mother-calf swimming and breathing synchrony (Mann and Smuts, 1999). Such abilities could clearly predispose calves to learn foraging tactics from their mothers, even outside of close visual proximity.

In addition to observing or hearing maternal chase and capture methods, calves may need to learn which prey are desirable. Some fish are toxic or have spines that are difficult to process. As described in Section 9.1.2, when sizeable prey are caught (> 20 cm inches), calves frequently approach and closely inspect the fish. The "owner" can even allow the fish to float at the surface and no one will attempt to steal it. In the absence of food sharing, this behavior suggests that calves learn about prey types by inspecting what others catch.

9.4.3 Future directions

Individual differences in foraging among Shark Bay dolphins are robust, consistent, and acquired by offspring. We suggest that social learning is

likely to play a part in the development of most foraging tactics in young dolphins, but only two of the eleven tactics we observed meet the more stringent definitions of tradition. Most of the literature on cetacean social learning to-date has demonstrated acoustic traditions, such as killer whale dialects (Deecke *et al.*, 2000). Our data suggest that elaborate motor skills can also be socially learned and maintained across generations. This is not surprising given the importance of social living for most cetaceans. The parallels between primates and cetaceans are striking, and such comparisons will continue to provoke us. In an environment so alien to our own, dolphins have evolved flexible learning strategies that challenge our primate-centric perspectives.

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