Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.)

B.L. Sargeant, J. Mann, P. Berggren, and M. Krützen

Abstract: Foraging behaviors of bottlenose dolphins vary within and among populations, but few studies attempt to address the causes of individual variation in foraging behavior. We examined how ecological, social, and developmental factors relate to the use of a rare foraging tactic by wild bottlenose dolphins (*Tursiops* sp. Gervais, 1855) in Shark Bay, Western Australia. Beach hunting involves partial and nearly complete stranding on beach shores. Over 10 years of observation, only four adults and their calves were observed beach hunting in more than 1 year. Of two adult beach hunters observed in detail, one was more specialized in beach hunting than the other, indicating substantial flexibility in degree of use. Only calves born to beach hunters developed the tactic, although complete stranding was not observed at least up to 5 years of age. Beach hunters used shallow, inshore habitats significantly more than others and were more likely to hunt during incoming tide. Mitochondrial DNA haplotypes were not consistent with strict matrilineal transmission. Thus, beach hunting likely involves vertical social learning by calves, while individual, horizontal, and (or) oblique learning may occur among individuals who frequent coastal habitats.

Résumé : Les comportements alimentaires des grands dauphins varient à l'intérieur d'une population et d'une population à une autre, mais peu d'études s'intéressent aux causes de la variation individuelle du comportement alimentaire. Nous examinons comment les facteurs écologiques et sociaux et le développement influencent l'utilisation d'une tactique inusitée de recherche de nourriture chez les grands dauphins (*Tursiops* sp. Gervais, 1855) à Shark Bay, Australie Occidentale. La chasse sur la grève implique un échouement partiel ou presque total sur les plages de la côte. En 10 années d'observation, seuls quatre adultes et leurs petits ont été observés à chasser sur la grève plus d'une année. Des deux adultes observés en détail chassant sur la grève, un était plus spécialisé pour la chasse sur la grève que l'autre, faisant montre d'une grande flexibilité dans l'importance de l'utilisation qu'il en faisait. Seuls les petits nés de parents qui chassaient sur la grève développent cette tactique, bien que l'échouement total ne s'observe pas avant l'âge de 5 ans. Les chasseurs de grève utilisent les habitats peu profonds près des côtes significativement plus que les autres et ils sont plus susceptibles de chasser durant la marée montante. Les haplotypes d'ADN mitochondrial n'appuient pas une transmission matrilinéaire stricte. La chasse sur la grève implique donc vraisemblablement un apprentissage social vertical par les petits, alors qu'il peut se produire un apprentissage individuel, horizontal et(ou) oblique chez les individus qui fréquentent les habitats côtiers peu profonds.

[Traduit par la Rédaction]

Introduction

Foraging behaviors apparently unique to populations, research sites, and (or) individuals have steadily dotted the cetacean literature, with increasing attention being given to specialization (e.g., Nowacek 2002; Mann and Sargeant 2003) and social learning (e.g., Rendell and Whitehead 2001; Mann and Sargeant 2003). Despite descriptions of this foraging diversity in cetaceans, few studies directly address the mechanisms that promote such variation. To better understand this behavioral diversity, we examined social, ecological, and developmental factors involved in the development of an unusual foraging tactic used by wild bottlenose dolphins (*Tursiops* sp. Gervais, 1855) in Shark Bay, Western Australia.

Foraging behaviors have been documented as variable and adaptable for many cetaceans, and show both inter- and intrapopulation variability. Cetacean foraging techniques include, for example, lobtail and bubble net feeding in humpback

Received 5 April 2005. Accepted 9 September 2005. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 26 October 2005.

B.L. Sargeant.[1] Georgetown University, Department of Biology, Reiss Science Building, 37th and O Streets, N.W., Washington, DC 20057, USA.
J. Mann. Georgetown University, Department of Psychology, White Gravenor Building, 37th and O Streets, N.W., Washington, DC 20057, USA, and Georgetown University, Department of Biology, Reiss Science Building, 37th and O Streets, N.W., Washington, DC 20057, USA.
P. Berggren. Stockholm University, Department of Zoology, SE-106 91 Stockholm, Sweden.
M. Krützen. Anthropological Institute and Museum, University of Zurich, Winterhurerstr. 190, CH-8057 Zurich, Switzerland.

[1]Corresponding author (e-mail: BLS4@georgetown.edu).

 doi: 10.1139/Z05-136

whales (*Megaptera novaeangliae* (Borowski, 1781)) (Hain et al. 1982; Weinrich et al. 1992), cooperative hunting and strand feeding by killer whales (*Orcinus orca* (L., 1758)) (Guinet 1991; Hoelzel 1991; Guinet and Bouvier 1995; Baird and Dill 1995), and bird-associated foraging and lunge feeding by minke whales (*Balaenoptera acutorostrata* Lacépède, 1804) (Hoelzel et al. 1989). Bottlenose dolphins (*Tursiops* spp.) are particularly well known for their foraging diversity, which can be population or site specific. They forage both in groups and individually (Shane et al. 1986), and have also adapted to human activity by following fishing boats to obtain discarded fish (Leatherwood 1975; Chilvers and Corkeron 2001), visiting provisioning locations (Orams et al. 1996; Mann and Kemps 2003), and catching fish cooperatively with net fishers (Pryor et al. 1990; Simões-Lopes et al. 1998). Additional tactics include using their rostra to dig into the substrate (Rossbach and Herzing 1997; Nowacek 2002; Mann and Sargeant 2003), smacking their tails on the water surface over shallow seagrass beds to disturb prey (Connor et al. 2000; Nowacek 2002), whacking fish with their tails (Shane 1990; Nowacek 2002), foraging with the aid of marine sponges worn over their rostra (Smolker et al. 1997; Mann and Sargeant 2003), and stirring up sediment to trap fish (Lewis and Schroeder 2003), among other behaviors (e.g., Leatherwood 1975; Würsig 1986; Mann and Sargeant 2003; Gazda et al. 2005). Despite these reports, only a few studies attempt to quantify and explain individual variation.

In Shark Bay, our longitudinal study of wild bottlenose dolphin (*Tursiops* sp.) mothers and calves has documented 13 distinct foraging tactics that are not used equally among individuals (Mann and Sargeant 2003). At least two levels of differentiation are apparent: specialization and rarity. In some cases, individuals may specialize, by using a few tactics relative to those of the population (i.e., reduced niche or diet breadth; Levins 1968), differing from others in the population (e.g., Bolnick et al. 2003), consistently utilizing particular tactics (e.g., diet consistency; Schindler et al. 1997), and (or) by distributing their foraging effort unequally across tactics (e.g., evenness or dominance). At another level, tactics either are used widely in the population or are rare (used by a few individuals) regardless of the level of individual specialization. One such behavior, beach hunting, involves individual dolphins surging partially or fully out of the water and onto the beach to catch single fish (Berggren 1995; Mann and Sargeant 2003). The prevalence of this behavior in a handful of known individuals and relative ease of observation (compared with subsurface behaviors) offered the potential to observe details on its development, including the possibility of teaching and other learning mechanisms.

Some characteristics of beach hunting are shared by delphinids at several other locations. Killer whales intentionally strand themselves on sand beaches to catch pinnipeds in the surf zone in Argentina (Lopez and Lopez 1985; Hoelzel 1991) and on the beaches of the Crozet Archipelago (Guinet and Bouvier 1995). Humpback dolphins (*Sousa plumbea* (G. Cuvier, 1829)) near the Bazaruto Archipelago in the Indian Ocean have been noted to push fish onto exposed sand banks at low tide and to surge partially onto the banks to catch them (Peddemors and Thompson 1994). Finally, common bottlenose dolphins (*Tursiops truncatus* (Montagu, 1821)) use estuarine mud flats in several areas of the southeastern United States (Hoese 1971; Rigley 1983; Petricig 1993), the Colorado River Delta (Silber and Fertl 1995), and Portugal (dos Santos and Lacerda 1987) to trap fish (reviewed by Silber and Fertl 1995). In all cases, substrates such as sandy beaches, estuarine mudflats, or exposed sand banks are used to isolate and catch prey. These behaviors also share some risk of becoming stranded on land, which has been documented in killer whales (Condy et al. 1978; Guinet and Bouvier 1995). However, motor patterns, social context, and prey type vary substantially. For example, "strand-feeding" bottlenose dolphins in the southeastern United States create a bow wave, often as a group, sending many fish onto the exposed bank (Hoese 1971; Rigley 1983). This can be contrasted with beach hunting by bottlenose dolphins in Shark Bay, as they forage individually, chasing singular prey for hundreds of metres parallel to and onto the beach.

Here we examined social, ecological, and developmental factors that are associated with the development and use of this rare and potentially dangerous foraging tactic. Our interest was two-fold. We sought to examine the interplay of factors that may contribute to the development of foraging skills, as well as how these factors could allow for individual variation where only a handful of animals engage in beach hunting. We used detailed observations of individuals to assess level of specialization, developmental timing, and possible modes of behavioral development, in tandem with habitat assessments to determine if the behavior was correlated with ecological variables. We also determined whether mitochondrial DNA (mtDNA) patterns were consistent with vertical transmission. Our findings provide insight into the behavioral diversity shown by bottlenose dolphins and suggest that multiple approaches are required to understand causes of individual variation.

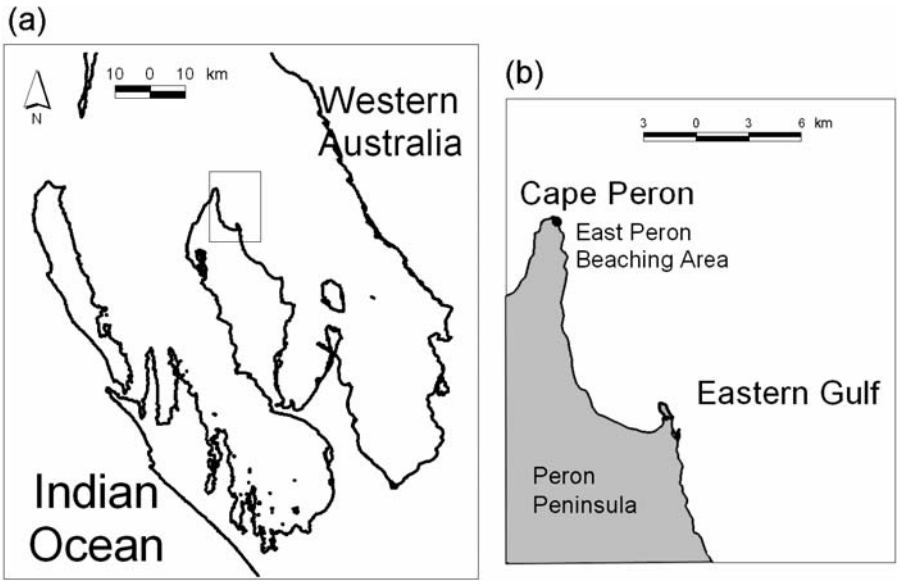
Materials and methods

Observations were conducted at Cape Peron, Peron Peninsula, Shark Bay, Western Australia (25°47′S, 113°43′E; Fig. 1) as part of the ongoing long-term dolphin research project. Individuals were identified by fin shape and markings, with the aid of photo-identification (Würsig and Würsig 1977). Sexes were determined by presence of a dependent calf and (or) views of the ventral area (Smolker et al. 1992), and DNA analyses (as described in Krützen et al. 2003). Adults were identified based on size, presence of a dependent calf, and (or) age estimates based on speckling (Smolker et al. 1992). Juveniles included animals weaned from their mothers (no longer in infant position) but younger than designated minimum adult ages. Calves were identified by being in infant position with their mothers (in contact, under the mother) (Mann et al. 2000). Calf age classes were defined by year of life (i.e., class 0 = 0–3 months, class 1 = 3–12 months, class 2 = 12–24 months, etc.).

Behavioral observations

Beach hunting is characterized by frequent fast swims in shallow water (less than 3 m from shore), creating a trail of water off the dorsal fin, as dolphins chase individual fish parallel to and then onto the beach surface. It frequently in-

Fig. 1. (*a*) Shark Bay, Western Australia. (*b*) Study area at Cape Peron, Western Australia (enlarged view of the inset in *a*).



volves surging out of the water onto the beach with the ventrum touching the substrate ("partial beaching"). Occasionally the dolphin emerges almost completely out onto the beach, which we refer to as "full beaching". The dolphin surges onto the beach, catches the fish in its mouth, and then returns to the water by means of a "u-turn" (Fig. 2). During beaching, the dolphin often has to wiggle side to side as it returns to the water. During field observations conducted in 1991–1997, 1999, and 2001–2004, four adult females that regularly engaged in beach hunting (at least once in >1 year) were identified (Table 1). Five of their offspring also engaged in beach hunting, and three other dolphins were observed engaging in it once (Table 1).

Initial data collected in 1991–1993 and 1996–1997 and data collected in 2004 include ad libitum sampling and photo-identification of dolphins in the area of Cape Peron, which were used to identify beach hunting dolphins and their associates. Additionally, film footage of foraging dolphins at Cape Peron recorded in 2004 was available courtesy of the BBC. Footage was used to determine only (*i*) prey types captured and (*ii*) beach hunting by a juvenile offspring of a beach hunting female.

Twenty-three focal animal follows (Altmann 1974; Mann 1999) were conducted on mother–calf pairs that engaged in beach hunting on a total of 19 days (1999–2004, except 2000), resulting in 51 h of focal data (Table 2). Point sampling was used to collect data on activities, group compositions, mother–calf distance, and other variables for focal mothers and calves every minute. Foraging bouts were defined as the duration of foraging, from onset to offset. This was identified by consistent point sample calls, starting with the first foraging point sample and ending with the first non-foraging point sample. Because beach hunting occurs in very shallow coastal waters, it can be viewed from both land and boats. Some observations were made from land (either a cliff overlooking a beach or the beach itself), during which beach hunting could be viewed in detail ("land-based observations"). Dolphins were generally close enough for visual and photo-identification from land, with the aid of binoculars if necessary. Other observations were made from a 4.5 m boat that could follow the dolphins when they headed to deeper water ("boat-based observations"). In all, we obtained 28 h of land-based observations and 23 h of boat-based observations. If dolphins moved too far from shore for recognition during land-based observations, the follow either ended or was continued by boat-based observers. Because beach hunting occurs only within metres of the shore and there was a natural break in the data (dolphins tended to be either well within or well beyond 20 m from shore), focal behavioral data were classified as inshore if the dolphin was less than or equal to 20 m of a beach shore and offshore if farther than 20 m. Foraging data were gathered on two beach hunting adult females and other frequent associates ad libitum. Group composition was determined using a 10 m chain rule, i.e., dolphins within 10 m of any group member were considered part of the group (Smolker et al. 1992). Other foraging behaviors (not beach hunting) were categorized according to Mann and Sargeant (2003).

Focal data (1999, 2001–2004) were used to calculate activity budgets, developmental patterns, and foraging rates. Additionally, to examine rates of beach hunting and minimum capture success rates, only land-based observations conducted in 2002 were used (18 h). Because land-based observers were in closer proximity to foraging dolphins, stages of beach hunting and presence of fish could be recorded more consistently. During boat-based observations, observers generally maintained larger distances (>300 m) to avoid disturbing the dolphins.

With so few individuals engaging in beach hunting, hypothesis testing is limited owing to small sample sizes. However, the small sample is unlikely a result of sampling bias, but rather because of the rarity of the behavior. Within individual beach hunters, we tested whether the foraging budgets, group sizes, and association patterns differed between being inshore and being offshore using nonparametric statistics. For the Wilcoxon matched-pairs signed-ranks tests, sample sizes vary because this method excludes cases in which paired values are equal (difference to be ranked is zero).

Fig. 2. A bottlenose dolphin (*Tursiops* sp.) beaches during beach hunting (from Mann and Sargeant 2003, reproduced with permission of Cambridge University Press, © 2003).

Tidal data

Tidal data for a site nearby (Monkey Mia) were used to estimate times of high and low waters, as well as tidal height. Each beach hunting bout was categorized as occurring during incoming or outgoing tide and during high or low tidal heights. We determined the corresponding tidal height in Australian chart datum (height above lowest astronomical tide) for each bout. To control for variation in the strength of tides, tidal heights were then categorized according to the range of all tidal heights for the years with focal observations (1999, 2001–2004). The minimum, maximum, and mean predicted tidal heights were 0.18, 2.48, and 1.40 m, respectively. We then categorized tidal heights during foraging as high (above mean tidal height) and low (below mean tidal height). Within each focal individual, we tested whether the frequency of beach hunting was higher than expected (based on observation effort) during incoming and high tides using χ^2 tests. To account for variable observation times in each tide category, we adjusted the expected frequency according to time observed in each category. One individual (RUM) was not used in the analysis of incoming and outgoing tide since s/he was not observed in both categories.

Associates

A highly conservative minimum number of associates in the area was estimated from focal, scan, and ad libitum data. Because many individuals in this area have not been individually identified, we included only identified dolphins to ensure individuals were not counted twice, so the true number of associates is likely to be much greater. Because it was clear which dolphins had engaged in beach hunting, we will refer those who have ever used beach hunting as "beach hunters" and all others as "non-beach hunters". To determine whether beach hunters preferentially associate, we compared the number of days each focal beach hunter associated with at least one other beach hunter (except her current calf) to the number of days with at least one non-beach hunter. We tested for differences in association inshore and offshore because we anticipated that there may be fewer dolphins using the shallow inshore areas. We used Fisher's exact tests to examine these differences for each focal female.

Genetic analyses

As part of a larger study, genetic data were obtained from biopsy samples (Krützen et al. 2002) of 4 beach hunters, 1 non-beach hunter associate, and 31 other individuals near Cape Peron. Sample processing and DNA extractions were carried out as described in Krützen et al. (2004). mtDNA haplotypes were determined by sequencing the first hypervariable region of the mitochondrial control region, using primers dlp 1.5 and dlp 3R (Krützen et al. 2004). The resulting polymerase chain reaction product of 355 base pairs was automatically sequenced on an ABI 377 Genetic Analyzer (Applied Biosystems, Foster City, California).

Habitat use

To examine whether use of coastal areas is associated with use of beach hunting, we used scans to determine the presence of dolphins within a designated 1 km long coastal area where beach hunting typically occurred. Scans were conducted from cliffs at East Peron Beach for 96 h on 19 days in June and July 2002. Presence or absence of dolphins in a defined inshore area (East Peron beaching area; Figs. 1, 3) was determined every 15 min, as well as the number and identities of animals when possible. Our high vantage point and the shallow, sandy nature of the area enabled us to easily

Table 1. All bottlenose dolphins (*Tursiops* sp.) observed beach hunting, years in which they were observed beach hunting, and whether they engaged in full beaching.

Dolphin ID	Calf ID	Years observed beach hunting	Age when beach hunting	Sex	Full beaching
REG		1991–1993, 1996, 1997, 1999–2004	Adult	♀	Yes
	CF2	1993	Calf		No
	CF4	1996, 1997	Calf		No
	RUM	2001, 2004	Calf, juvenile		No
	MEY	2002	Calf		No
RHY		2001–2004	Adult	♀	Yes
	BES	2002–2003	Calf		No
TBA		1997, 2001–2004	Adult	♀	Yes
CHC		1997, 2002–2004	Adult	♀	Yes
TD5		1997	Adult		No
HUM		1996	Adult	♀	No
	1BD1	1992	Calf		No

Table 2. Summary of focal follow hours on two mothers (REG, RHY) and their three calves (RUM, MEY, BES) from 1999 to 2004.

ID	No. of land-based observations (hours)	No. of boat-based observations (hours)	Total no. of observations (hours)	No. of beach hunting bouts	No. of full beaching events
REG	17.7	15.0	32.7	34	16
RUM	6.1	0	6.1	2	0
MEY	11.2	15.0	26.2	3	0
RHY	9.7	8.8	18.5	16	2
BES	9.4	8.9	18.3	8	0

determine the presence of dolphins, and the majority of scans were conducted in fair conditions (beaufort state <3). The East Peron Beach area is very shallow, typically less than 2 m deep compared with depths of 6–9 m outside the area, with a sloping sandy beach. Additionally, a sudden drop-off to deeper water (roughly 500 m from the shore) creates a distinctive visual and physical border enabling us to easily categorize dolphins as within the East Peron Beach area (Fig. 3). Although beach hunting has been observed occurring along many kilometres of coastline, the East Peron Beach is used frequently by beach hunters and is conducive to observation of foraging dolphins because of road and beach access. Using scans, we tested whether beach hunters were present in the East Peron beaching area on more days than non-beach hunters. We tested only days with scans in which the identities of all dolphins present were known, which should not be biased towards either group.

Results

Description of beach hunting

We observed the occurrence of beach hunting at Peron 98 times (distinct foraging bouts) for seven individuals (four adults: REG, RHY, TBA, CHC; three of their calves: RUM, MEY, BES) during focal follows and ad libitum data collection from 1999 to 2004. At least 28 of these bouts involved full beaching, which was performed at least once by each adult. Although calves and juveniles were observed beach hunting and partial beaching, none were ever observed using full beaching. When ad libitum data on the two non-mother females (TBA and CHC) were excluded and only mother–calf focal data were examined, 63 beach hunting bouts were observed, 18 of which involved full beaching events (Table 2). Identified prey include mullets (*Mugil cephalus* L., 1758 and *Liza argentea* (Quoy and Gaimard, 1825)) and longtoms (*Tylosurus gavialoides* (Castelnau, 1873)), and in all cases individuals pursued only one fish at a time. Cooperative and coordinated foraging was not observed, even though several individuals occasionally engaged in beach hunting simultaneously within metres of each other while pursuing different fish.

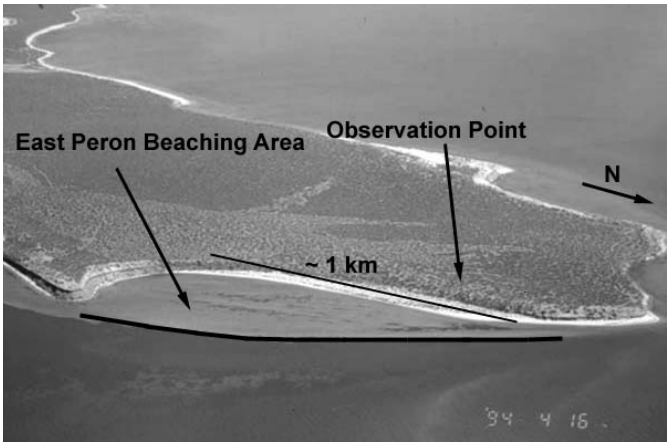
During land-based observations in 2002 (18 focal h), 45 beach hunting bouts for two focal mother–calf pairs were recorded. Twenty (44%) of these bouts involved dolphins coming partially out onto the beach. Full beaching was less common, occurring 13 times (29%). Successful captures by focal dolphins were identified for 12 of the 45 observed beach hunting bouts. Ten of these 12 occasions involved partial or full beaching. These behaviors (high speed swims near the shoreline and surging onto the beach) were only used in foraging contexts, typically with prey seen.

Beach hunting was originally believed to be limited to one beach, but boat-based focal follow data have shown that this behavior occurs on many beaches around Cape Peron, and that one female (REG) forages and beaches along at least 10 km of coastline.

Foraging specializations

To determine the diversity and degree of specialization of foraging tactics used by beach hunters, we examined whether focal adult female beach hunters foraged differently inshore versus offshore, how they distributed their foraging

Fig. 3. East Peron beaching area (photograph by Janet Mann).



time among foraging tactics, and how many foraging tactics they used. Treating observation days as independent, we found no significant differences in percent time foraging inshore versus offshore for either female (Wilcoxon matched-pairs signed-ranks tests; REG: inshore — n = 12, median = 9.0, minimum = 0.0, maximum = 23.8; offshore — n = 13, median = 0.0, minimum = 0.0, maximum = 50.0; Z = –1.02, p = 0.308, n = 12; RHY: inshore — n = 8, median = 2.2, minimum = 0.0, maximum = 22.2; offshore — n = 8, median = 0.2, minimum = 0.0, maximum = 77.5, Z = –0.67, p = 0.500, n = 5), indicating that their overall foraging budgets are similar in both areas. However, REG was inshore 55% of her observation time, while RHY was inshore 39% of her observation time. Therefore, to determine the degree of specialization, we calculated the proportion of foraging time that they engaged in various foraging tactics, which also better reflects foraging given habitat use. REG predominately (57%) used beach hunting, whereas RHY predominately (66%) used mill foraging (characterized by direction changes on each surface and irregular surfacings). Therefore, both used the rare tactic of beach hunting, but they predominantly used different tactics. Additionally, REG used five identified foraging tactics, while RHY used three. RHY's foraging tactics (aside from beach hunting) were moderate and deep water (≥4 m) behaviors, while REG frequently engaged in other tactics associated with shallow water (<4 m). Despite using more tactics, REG may be considered more specialized in beach hunting in terms of niche evenness, since it was her predominant tactic.

Of the 45 systematic land-based observations of beach hunting from 2002 in which stages of beaching and success could be determined more consistently, the two focal mothers (REG, RHY) engaged in beach hunting a combined total of 35 times during focal follows. REG and RHY had beach hunting rates of 2.1 bouts per h of observation (7.7 h observation) and 1.7 bouts per h of observation (10.4 h observation), respectively. Their minimum success rates (percentage of bouts in which fish captures were observed) were 36% and 31%, respectively. In some cases dolphins failed to capture fish during a beach hunting bout. After consideration of observation time per female, REG uses beach hunting more frequently than RHY and may also have slightly higher success.

Calf development

To determine the time-course of beach hunting development by calves, we examined whether and how much calves of different ages engaged in beach hunting using calves observed frequently (born 1998–2002). All but one calf born to beach hunters were observed beach hunting themselves, although that calf was only observed on 4 days. Calves used beach hunting and occasionally partially beached, placing their ventral surfaces on the sand. However, no calves were ever observed full beaching or definitely catching fish while beach hunting. The number of beach hunting bouts observed in the calves by age class is shown in Table 3, along with the beach hunting rates (bouts per h of observation) for two calves observed in 2002. To address exposure of calves to maternal beach hunting, we determined the average percentage of maternal beach hunting bouts that calves were in the same group as their mothers (Fig. 4). Younger calves appeared to wait separately from their mothers when mothers were beach hunting, but then seemed to stay closer to mothers at older ages. We also attempted to record any behaviors consistent with teaching (sensu Caro and Hauser 1992). However, mothers were never observed attending to their calves or altering their foraging behavior in response to calf presence during beach hunting, presenting no evidence for teaching. Full beaching is a late-developing behavior compared with the majority of foraging behaviors used in Shark Bay (Mann and Sargeant 2003).

After weaning, RUM was observed during 2002 scans and as an associate of focal dolphins during 2002 and 2003, at which time she was never observed beach hunting. Film footage from 2004 showed RUM, then a 5 year old juvenile, beach hunting and partially beaching while tightly associating with her mother REG and younger sibling MEY.

Effects of tide and stranding risk

We hypothesized that beach hunting would be more likely to occur in incoming tides and high tides, as we predicted stranding risk would be lower during this time. It is also possible that access to shallows is restricted during low tides, or that beach hunting could be related to tidal movements of prey. Three of four individuals tested engaged in beach hunting during incoming tide significantly more than expected (Fig. 5). The fourth individual (MEY) showed a similar pattern, although it was not significant ($\chi^2_{[1]}$ = 3.64, p = 0.056, n = 2). High tide, however, did not appear to be a factor for the occurrence of beach hunting. One of the five dolphins (RHY) used beach hunting significantly more in low tide than expected ($\chi^2_{[1]}$ = 6.63, p = 0.01, n = 16). Tests should be interpreted with caution because expected values were often <5 for calves because of low behavioral rates.

Cape Peron dolphins: beach hunters and their associates

To examine the possibility of horizontal or oblique social learning, patterns of association between beach hunters and non-beach hunters were determined. Based on photo-identification methodology, we identified a minimum of 25 individuals in association with the two beach hunting focal females (1999–2004), excluding their offspring and other beach hunters (CHC, TBA). Two frequent associates (TAI, WEL) have been observed regularly in groups with beach hunters since 1993. Thus, despite consistent association with

Table 3. Number of beach hunting bouts for three calves, over all years of observation.

Calf ID	Calf year of life	Total no. of beach hunting bouts	Percentage of foraging time	2002 beach hunting rate
RUM	1	0	No foraging	
	3	2	21	
MEY	1	3	15	0.3
	2	0	0	
	3	0	0	
BES	1	0	No foraging	
	2	5	21	0.9
	3	1	100	

Fig. 4. Percentage of maternal beach hunting bouts in which the dependent calf was in the same group as the mother, averaged for three calves (RUM, MEY, BES). Standard error bars are shown.

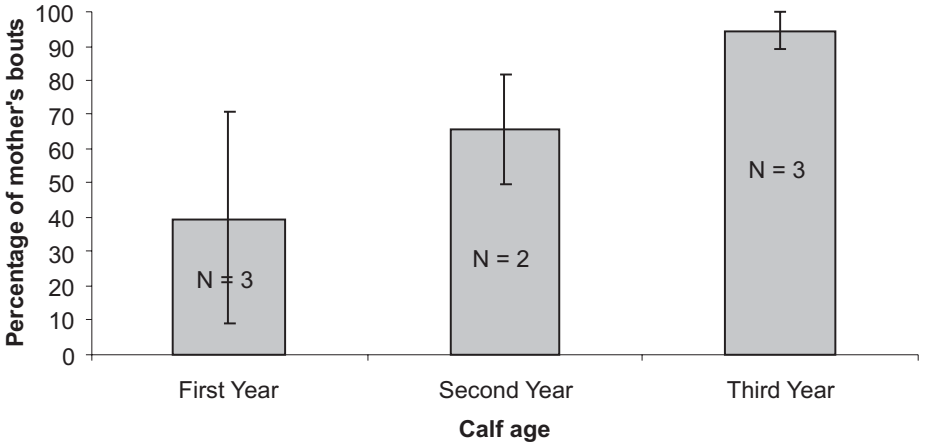
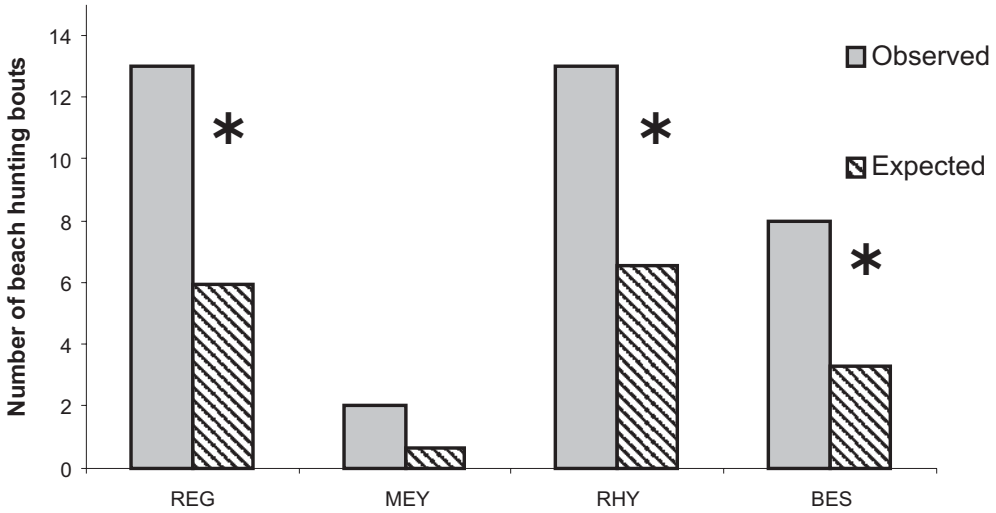


Fig. 5. Observed number of beach hunting bouts during incoming tide, and expected number based on time observed during incoming tide for four individuals. Asterisks indicate that observed frequencies are significantly different from expected frequencies (χ^2 tests, $p < 0.001$).



many other dolphins, regular use of beach hunting in the Cape Peron area currently appears restricted to just four adult females and their offspring.

Average daily group size was significantly larger offshore (>20 m from shore) than inshore (≤20 m from shore) for both focal females (Wilcoxon matched-pairs signed-ranks test; REG: inshore — n = 12, median = 1.9, minimum = 2.0, maximum = 6.0; offshore — n = 13, median = 3.1, minimum = 1.1, maximum = 6.9; Z = –2.35, p = 0.019, n = 12; RHY: inshore — n = 8, median = 3.0, minimum = 1.0, maximum = 4.0; offshore — n = 9, median = 4.8, minimum = 2.7, maximum = 8.2; Z = –2.38, p = 0.017, n = 8). REG spent 44% of her time with other dolphins (not including her current calf) compared with 77% for RHY. There was no significant difference in association with beach hunters versus non-beach hunters across days for RHY or REG (Table 4). However, the top three associates (by percentage of time with other dolphins, excluding offspring) for both REG

Table 4. Patterns of association for two focal females (REG, RHY) that engage in beach hunting.

ID	Inshore or offshore	No. of days observed	No. of days with other beach hunters	No. of days with non-beach hunters	Pearson's $\chi^2_{[1]}$	*P*
REG	Inshore	12	5	3	0.15	1.00
	Offshore	13	7	6		
RHY	Inshore	8	6	4	0.046	1.00
	Offshore	9	9	5		

and RHY were exclusively adult female beach hunters. Degree of sociality may differ between the two females, with RHY tending to be in larger groups and tending to spend more time with non-beach hunters than REG, but this was not tested directly.

Mitochondrial haplotypes

Similarity in mitochondrial haplotypes among beach hunting dolphins was examined to determine if matrilineal transmission was the primary mechanism of transmission, as has been found for another foraging tactic in Shark Bay (Krützen et al. 2005). We obtained genetic samples for four adult female beach hunters (REG, RHY, TBA, and CHC), as well as one frequent non-beach hunting associate and several others in the Cape Peron area (total of 36 individuals with known haplotypes). RHY, TBA, and CHC have the same haplotype (*D*), while REG has a different haplotype (*H*). TAI, who frequently associated with beach hunters for at least 11 years, has yet another haplotype (*E*). The *D* and *E* haplotypes appear to be fairly common for dolphins sampled in the area near Cape Peron (42% and 14% of 36 sampled, respectively). Interestingly, REG is the only dolphin with the *H* haplotype sampled near Cape Peron.

Habitat use

To address whether habitat use contributes to the variation in use of beach hunting, we used scans to determine if beach hunters were present in shallow inshore areas more often than non-beach hunters. Of 19 scanning days and 400 scans, at least one dolphin was observed in the East Peron Beach Area on 18 days and 45% of scans. REG was present in the East Peron Beach Area on 10 days (53% of days) and for 95 scans (24% of scans). RHY was present on 9 days (47% of days) and for 69 scans (17% of scans). The identities of all individuals in the East Peron Beach Area could be determined on 106 of 181 scans and on 13 of 18 days when dolphins were present. Of the 13 days in which there was at least one scan with all identities known, at least one adult or juvenile beach hunter was present all 13 days. At least one non-beach hunter was present on 4 days. Beach hunters were present on significantly more days than non-beach hunters ($\chi^2_{[1]} = 4.8$, $p = 0.029$, $n = 17$). This is a conservative analysis, given that there were only four adult and one juvenile beach hunters in 2002 and they have associated with a minimum of 25 non-beach hunters.

Discussion

In summary, we have shown that beach hunting corresponds with tidal state and habitat use, develops later than other foraging behaviors, does not occur strictly within matrilines, and may involve social learning (but not teaching, sensu Caro and Hauser 1992; see below). Additionally, we document that some dolphins are more specialized in beach hunting than other dolphins.

Individual and subgroup variations in foraging behaviors among cetaceans have been gaining increasing attention (e.g., Rendell and Whitehead 2001; Nowacek 2002; Mann and Sargeant 2003). In some cases, this variability may represent individual foraging specializations. Although exact definitions in the literature vary and depend on the resource in question, individual foraging specializations are generally viewed in terms of narrower use of foraging behaviors, feeding technique, or prey species by an individual relative to the population at large (Partridge and Green 1985; Kohda 1994; Bolnick et al. 2003). To our knowledge, this study is the first to explicitly quantify foraging specializations for individual wild bottlenose dolphins by calculating foraging time budgets. Although bottlenose dolphins as species are well known for their diet breadth and versatile foraging behaviors, individuals use different tactics and can specialize (Mann and Sargeant 2003; this study). Interestingly, we found that two adult females which use this rare foraging tactic — beach hunting — are otherwise quite different. One female spends more time in shallow beach habitats, specializes in beach hunting (in terms of predominant tactics), has a higher success rate while beach hunting, and appears to be more solitary. The other female spends less time in shallow beach habitats, specializes in another foraging tactic used in deeper water, has a lower success rate while beach hunting, and appears to be more social. This indicates that dolphins overlapping in range can partition niche use, and may also show that once a dolphin learns one tactic it is not limited to that tactic alone. A rare and particularly challenging behavior need not limit the individual's foraging repertoire. Our findings suggest the need for further research on intraspecific competition and niche partitioning in this species.

Beach hunting and full beaching in particular seem to develop later than many other foraging tactics studied in Shark Bay. Previous findings showed that most foraging tactics are used by calves within the first year of life (Mann and Sargeant 2003). Although beach hunting has been observed in one calf in the first year, full beaching was not observed for at least the first 5 years. These data suggest that complete development of beach hunting takes longer than other tactics, possibly because its complexity requires lengthy learning periods (Johnston 1982) and (or) because calves are continuing to develop physically (e.g., Noren et al. 2001, 2002). Limited experience and (or) physical abilities of calves may even increase the risk of stranding during beach hunting. The challenge or even danger of becoming stuck on the beach (e.g., Condy et al. 1978; Guinet and Bouvier 1995) is consistent with the fact that beach hunting occurs more during incoming tide, which could lower stranding

risk. Prey behavior may also explain this pattern, however, as many fishes are known to migrate tidally (Gibson 2003). Complex foraging in Shark Bay bottlenose dolphins may help explain their unusually long dependency periods (3–6 years) (Mann et al. 2000) and the sizable overlap between independent foraging and nursing (Mann and Sargeant 2003). By addressing factors involved in calf foraging development and examining foraging abilities over time, this study provides supporting evidence that foraging complexity and learning correspond to longer periods of dependency.

Why is this behavior limited to so few individuals? We propose that it is likely a result of both habitat use and social learning. Individual foraging specializations can result from numerous proximate and ultimate factors, including patchy resource distribution and social learning (Partridge and Green 1985). Here, social learning, broadly defined, refers to "learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products" (Heyes 1994). Social learning in nonhuman animals has been gaining increasing attention (Heyes and Galef 1996; Rendell and Whitehead 2001; Fragaszy and Perry 2003; Laland and Hoppitt 2003) and is a potential mode of transmission of foraging behaviors (e.g., Wrangham et al. 1994; Terkel 1996; Laland and Williams 1997; Galef and Giraldeau 2001; Estes et al. 2003). Social learning in cetaceans has been suggested as the mode of transmission of acoustic behaviors (Janik and Slater 1997; Tyack and Sayigh 1997; Deecke et al. 2000; Noad et al. 2000; Rendell and Whitehead 2003) and foraging skills (Lopez and Lopez 1985; Hoelzel et al. 1989; Weinrich et al. 1992; Guinet and Bouvier 1995; Baird 2000; Mann and Sargeant 2003). In fact, most reports of similar foraging behaviors involving beaches or sand/mud flats mention social learning as the mechanism for transmission of the behavior (Lopez and Lopez 1985; Guinet 1991; Hoelzel 1991; Hoese 1971; Guinet and Bouvier 1995), although few studies attempt to examine this directly (but see Guinet and Bouvier 1995). Beach hunters preferentially associate and may have learned the behavior socially, and this appears especially likely for calves of beach hunters. The only calves ever observed beach hunting were born to beach hunters. Calves have extensive exposure to the beach hunting bouts of mothers and associates, and may increase involvement with age. Older calves stay close to their mothers during beach hunting, occasionally even chasing the same fish as the mother. Calf habitat use is essentially determined by that of the mother, and exposure to the area that would result in foraging development qualifies as social learning (e.g., local enhancement; Heyes 1994). All beach hunting adults are females, similar to other female-biased foraging behaviors in this population (Mann and Sargeant 2003) and is also consistent with matrilineal transmission of the behavior. Several factors may promote development and (or) continued use of maternal foraging tactics in females as opposed to males, including the fact that female offspring may be more likely to have habitat-use patterns similar to their mothers'. In terms of evolutionary pressures, selection to learn socially or to develop foraging skills may be stronger for females than for males because food resources generally limit female reproduction in this species.

Do dolphins actively "teach" foraging tactics to others? Caro and Hauser (1992) defined teaching as behaviors that are modified only in the presence of a naïve observer, are costly to the actor, and result in increased learning by the observer compared to if it had not been exposed to the actor's actions. Although the notion of teaching in animals has been popularly entertained, unequivocal evidence for teaching in nonhuman animals has not been shown. Possible cases have been found in birds, carnivores, primates, and cetaceans (Caro and Hauser 1992), with a few studies indicating that teaching may occur in killer whales. Killer whale adults may teach juveniles how to intentionally strand on the beach while hunting pinnipeds, by aiding in practice attempts and providing prey rewards (Lopez and Lopez 1985; Guinet 1991; Guinet and Bouvier 1995). Beach hunters in Shark Bay never assisted calves or juveniles or modified their behavior in the presence of naïve observers. With ample opportunity to observe such behaviors if they occurred, we suggest that this behavior does not involve teaching.

Because beach hunters use shallow beach areas significantly more than others, habitat use is highly related to the behavior. Although the importance of habitat use does not exclude social learning as a factor, without a comparison group that uses the shallow beach habitat as much as beach hunters, we cannot definitively conclude whether individual learning combined with habitat use is sufficient for beach hunting development, or if social learning is involved. It should be noted that beach hunting has also been used by four other females in our main study area near Monkey Mia, where mother–calf observations have been conducted since 1988 (observations on 46 mothers and their 83 calves, total ~1600 focal h). These dolphins, however, have never been observed full beaching while hunting. Similarly, these dolphins are frequent associates and also appear to use shallow waters with sand beaches frequently. Three of them are provisioned at Monkey Mia (Mann and Kemps 2003) and tend to range closely to that coastal site. Monkey Mia is roughly 40 km from Cape Peron, and these dolphins do not overlap in range with Cape Peron dolphins. In summary, these data suggest that beach hunting may develop from vertical transmission from mothers to calves but also from individual learning by those who frequent coastal areas. Horizontal or oblique transmission may also occur in adults. Genetic comparisons were consistent with either individual learning or horizontal or oblique transmission, but not with strict matrilineal transmission.

Multiple factors are likely to be involved in the development of foraging behaviors in cetaceans, and maternal influence appears to be particularly important in *Tursiops* spp. Both ecological and social patterns must be examined carefully to determine their relative importance. We encourage future studies of foraging variation at the individual level that can better address roles of specialization, niche partitioning and habitat use, life history, and social influences. Such studies are critical to understanding the importance of foraging areas to dolphins, species often heavily influenced by coastal development and habitat loss.

Acknowlegdements

We thank the Western Australia Department of Conservation and Land Management and D. Charles for logistical support, the Western Australia Department for Planning and Infrastructure for providing tidal data, and the BBC for

providing film footage. Special thanks go to K. Bracke, C. Bump, K. Burmon, L. Durbin, Q. Gibson, A. Hough, R. Lam, N. Marcel, K. McAuliffe, M. McNamara, J. Skelton, and J. Watson-Capps for assistance in data collection and management. The Monkey Mia Dolphin Resort provided valuable assistance during fieldwork. We thank R. Barr, H. Whitehead, A. Wirsing, and one anonymous reviewer for helpful comments on earlier drafts of the manuscript. Funding was provided by Georgetown University, National Science Foundation grants #9753044 and #0316800, The Eppley Foundation for Research, and The Brach Foundation, a National Science Foundation Graduate Research Fellowship, the Animal Behavior Society, and the Dolphins of Monkey Mia Research Foundation. Research was conducted under permits from the Western Australia Department of Conservation and Land Management and the Georgetown University Animal Care and Use Committee.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour, **49**: 227–267.

Baird, R.W. 2000. The killer whale: foraging specializations and group hunting. *In* Cetacean societies: field studies of dolphins and whales. *Edited by* J. Mann, R.C. Connor, P.L. Tyack, and H. Whitehead. University of Chicago Press, Chicago. pp. 127–153.

Baird, R.W., and Dill, L.M. 1995. Occurrence and behaviour of transient killer whales: seasonal and pod-specific variability, foraging behaviour, and prey handling. Can. J. Zool. **73**: 1300–1311.

Berggren, P. 1995. Foraging behaviour by bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia: beaching for a meal. Proceedings of the 11th Biennial Conference on the Biology of Marine Mammals, Orlando, Florida, 14–18 December 1995. The Society for Marine Mammalogy, Lawrence, Kans. p. 11.

Bolnick, D.I., Svanbäck R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., and Forister, M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. Am. Nat. **161**: 1–28.

Caro, T.M., and Hauser, M.D. 1992. Is there teaching in nonhuman animals? Q. Rev. Biol. **67**: 151–174.

Chilvers, B.L., and Corkeron, P.J. 2001. Trawling and bottlenose dolphins' social structure. Proc. R. Soc. Lond. B Biol. Sci. **268**: 1901–1905.

Condy, P.R., van Aarde, R.J., and Bester, M.N. 1978. The seasonal occurrence and behaviour of Killer whales *Orcinus orca*, at Marion Island. J. Zool. (1965–1984), **184**: 449–464.

Connor, R.C., Heithaus, M.R., Berggren, P., and Miksis, J.L. 2000. "Kerplunking": surface fluke-splashes during shallow-water bottom foraging by bottlenose dolphins. Mar. Mamm. Sci. **16**: 646–653.

Deecke, V.B., Ford, J.K.B., and Spong, P. 2000. Dialect change in resident killer whales: implications for vocal learning and cultural transmission. Anim. Behav. **60**: 629–638.

dos Santos, M.E., and Lacerda, M. 1987. Preliminary observations of the bottlenose dolphin (*Tursiops truncatus*) in the Sado estuary (Portugal). Aquat. Mamm. **13**: 65–80.

Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., and Lyon, B.E. 2003. Individual variation in prey selection by sea otters: patterns, causes, and implications. J. Anim. Ecol. **72**: 144–155.

Fragaszy, D.M., and Perry, S. (*Editors*). 2003. The biology of traditions: models and evidence. Cambridge University Press, Cambridge, UK.

Galef, B.J., Jr., and Giraldeau, L.-A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim. Behav. **61**: 3–15.

Gazda, S.K., Connor, R.C., Edgar, R.K., and Cox, F. 2005. A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. Proc. R. Soc. Lond. B Biol. Sci. **272**: 135–140.

Gibson, R.N. 2003. Go with the flow: tidal migration in marine animals. Hydrobiologia, **503**: 153–161.

Guinet, C. 1991. Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). Can. J. Zool. **69**: 2712–2716.

Guinet, C., and Bouvier, J. 1995. Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. Can. J. Zool. **73**: 27–33.

Hain, J.H.W., Carter, G.R., Kraus, S.D., Mayo, C.A., and Winn, H.E. 1982. Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the Western North Atlantic. Fish. Bull. (Wash., D.C.), **80**: 259–268.

Heyes, C.M. 1994. Social learning in animals: categories and mechanisms. Biol. Rev. **69**: 207–231.

Heyes, C.M., and Galef, B.G., Jr. (*Editors*). 1996. Social learning in animals: the roots of culture. Academic Press, San Diego, Calif.

Hoelzel, A.R. 1991. Killer whale predation on marine mammals at Punta Norte, Argentina: food sharing, provisioning, and foraging strategy. Behav. Ecol. Sociobiol. **29**: 197–204.

Hoelzel, A.R., Dorsey, E.M., and Stern, S.J. 1989. The foraging specializations of individual minke whales. Anim. Behav. **38**: 786–794.

Hoese, H.D. 1971. Dolphin feeding out of water in a salt marsh. J. Mammal. **52**: 222–223.

Janik, V.M., and Slater, P.J.B. 1997. Vocal learning in mammals. Adv. Stud. Behav. **26**: 59–99.

Johnston, T.D. 1982. Selective costs and benefits in the evolution of learning. Adv. Stud. Behav. **12**: 65–106.

Kohda, M. 1994. Individual specialized foraging repertoires in the piscivorous cichlid fish *Lepidiolamprologus profundicola*. Anim. Behav. **48**: 1123–1131.

Krützen, M., Barrè, L.M., Möller, L.M., Heithaus, M.R., Simms, C., and Sherwin, W.B. 2002. A biopsy system for small cetaceans: darting success and wound healing in *Tursiops* spp. Mar. Mamm. Sci. **18**: 863–878.

Krützen, M., Sherwin, W.B., Connor, R.C., Barre, L.M., Van de Casteele, T., Mann, J., and Brooks, R. 2003. Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. Proc. R. Soc. Lond. B Biol. Sci. **270**: 497–502.

Krützen, M., Sherwin, W.B., Berggren, P., and Gales, N. 2004. Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. Mar. Mamm. Sci. **20**: 28–47.

Krützen, M., Mann, J., Heithaus, M.R., Connor, R.C., Bejder, L., and Sherwin, W.B. 2005. Cultural transmission of tool use in bottlenose dolphins. Proc. Natl. Acad. Sci. U.S.A. **102**: 8939–8943.

Laland, K.N., and Hoppitt, W. 2003. Do animals have culture? Evol. Anthropol. **12**: 150–159.

Laland, K.N., and Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. Anim. Behav. **53**: 1161–1169.

Leatherwood, S. 1975. Some observations of feeding behavior of bottlenose dolphins (*Tursiops truncatus*) in the Northern Gulf of Mexico and (*Tursiops* cf. *T. gilli*) off Southern California, Baja California, and Nayarit, Mexico. Mar. Fish. Rev. **37**: 10–16.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, N.J.

Lewis, J., and Schroeder, W.W. 2003. Mud plume feeding, a unique foraging behavior of the bottlenose dolphin (*Tursiops truncatus*) in the Florida Keys. Gulf Mex. Sci. **1**: 92–97.

Lopez, J.C., and Lopez, D. 1985. Killer whales (*Orcinus orca*) of Patagonia, and their behavior of intentional stranding while hunting nearshore. J. Mammal. **66**: 181–183.

Mann, J. 1999. Behavioral sampling methods for cetaceans: a review and critique. Mar. Mamm. Sci. **15**: 102–122.

Mann, J., and Kemps, C. 2003. The effects of provisioning on maternal care in wild bottlenose dolphins, Shark Bay, Western Australia. *In* Marine mammals: fisheries, tourism, and management issues. *Edited by* N. Gales, M. Hindell, and R. Kirkwood. CSIRO Publishing, Collingwood, Victoria, Australia. pp. 304–317.

Mann, J., and Sargeant, B. 2003. Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). *In* The biology of traditions: models and evidence. *Edited by* D.M. Fragaszy and S. Perry. Cambridge University Press, Cambridge, UK. pp. 236–266.

Mann, J., Connor, R.C., Barre, L.M., and Heithaus, M.R. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. Behav. Ecol. **11**: 210–219.

Noad, M.J., Cato, D.H., Bryden, M.M., Jenner M.-N., and Jenner, K.C.S. 2000. Cultural revolution in whale songs. Nature (London), **408**: 537.

Noren, S.R., Williams, T.M., Pabst, D.A., McLellan, W.A., and Dearolf, J.L. 2001. The development of diving in marine endotherms: preparing the skeletal muscles of dolphins, penguins, and seals for activity during submergence. J. Comp. Physiol. B, **171**: 127–134.

Noren, S.R., Lacave, G., Wells, R.S., and Williams, T.M. 2002. The development of blood oxygen stores in bottlenose dolphins (*Tursiops truncatus*): implications for diving capacity. J. Zool. (Lond.), **258**: 105–113.

Nowacek, D.P. 2002. Sequential foraging behaviour of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Fla. Behaviour, **139**: 1125–1145.

Orams, M.B., Hill, G.J.E., and Baglioni, A.J., Jr. 1996. "Pushy" behavior in a wild dolphin feeding program at Tangalooma, Australia. Mar. Mamm. Sci. **12**: 107–117.

Partridge, L., and Green, P. 1985. Intraspecific feeding specializations and population dynamics. *In* Behavioural ecology: ecological consequences of adaptive behaviour. *Edited by* R.M. Sibly and R.H. Smith. Blackwell Scientific Publications, Oxford. pp. 207–226.

Peddemors, V.M., and Thompson, G. 1994. Beaching behaviour during shallow water feeding by humpback dolphins *Sousa plumbea*. Aquat. Mamm. **20**: 65–67.

Petricig, R.O. 1993. Diel patterns of "strand feeding" behavior by bottlenose dolphins in South Carolina salt marshes. *In* Proceedings of the 10th Biennial Conference on the Biology of Marine Mammals, Galveston, Texas, 11–15 November 1993. The Society for Marine Mammalogy, Lawrence, Kans. p. 86.

Pryor, K., Lindbergh, J., Lindbergh, S., and Milano, R. 1990. A dolphin–human fishing cooperative in Brazil. Mar. Mamm. Sci. **6**: 77–82.

Rendell, L., and Whitehead, H. 2001. Culture in whales and dolphins. Behav. Brain Sci. **24**: 309–382.

Rendell, L.E., and Whitehead, H. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). Proc. R. Soc. Lond. B Biol. Sci. **270**: 225–231.

Rigley, L. 1983. Dolphins feeding in a South Carolina salt marsh. Whalewatcher, **17**(2): 3–5.

Rossbach, K.A., and Herzing, D.L. 1997. Underwater observations of benthic-feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahama Island, Bahamas. Mar. Mamm. Sci. **13**: 498–504.

Schindler, D.E., Hodgson, J.R., and Kitchell, J.F. 1997. Density-dependent changes in individual foraging specialization of largemouth bass. Oecologia (Berl.), **110**: 592–600.

Shane, S.H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. *In* The bottlenose dolphin. *Edited by* S. Leatherwood and R.R. Reeves. Academic Press, Inc., San Diego, Calif. pp. 245–265.

Shane, S.H., Wells, R.S., and Würsig, B. 1986. Ecology, behavior and social organization of the bottlenose dolphin: a review. Mar. Mamm. Sci. **2**: 34–63.

Silber, G.K., and Fertl, D. 1995. Intentional beaching by bottlenose dolphins (*Tursiops truncatus*) in the Colorado River Delta, Mexico. Aquat. Mamm. **21**: 183–186.

Simões-Lopes, P.C., Fabian, M.E., and Menegheti, J.O. 1998. Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. Rev. Bras. Zool. **15**: 709–726.

Smolker, R.A., Richards, A.F., Connor, R.C., and Pepper, J.W. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour, **123**: 38–69.

Smolker, R.A., Richards, A., Connor, R., Mann, J., and Berggren, P. 1997. Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.): a foraging specialization involving tool use? Ethology, **103**: 454–465.

Terkel, J. 1996. Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). *In* Social learning in animals: the roots of culture. *Edited by* C.M. Heyes and B.G. Galef, Jr. Academic Press, San Diego, Calif. pp. 17–47.

Tyack, P.L., and Sayigh, L.S. 1997. Vocal learning in cetaceans. *In* Social influences on vocal development. *Edited by* C. T. Snowdon and M. Hausberger. Cambridge University Press, Cambridge, UK. pp. 208–233.

Weinrich, M.T., Schilling, M.R., and Belt, C.R. 1992. Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. Anim. Behav. **44**: 1059–1072.

Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., and Heltne, P.G. (*Editors*). 1994. Chimpanzee cultures. Harvard University Press, Cambridge, Mass.

Würsig, B. 1986. Delphinid foraging strategies. *In* Dolphin cognition and behavior: a comparative approach. *Edited by* R.J. Schusterman, J.A. Thomas, and F.G. Wood. Lawrence Erlbaum, Associates, Hillsdale, N.J. pp. 347–359.

Würsig, B., and Würsig, M. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science (Washington, D.C.), **198**: 755–756.