Characterizing the socially transmitted foraging tactic "sponging" by bottlenose dolphins (*Tursiops* sp.) in the western gulf of Shark Bay, Western Australia

Anna M. Kopps,[1] Evolution & Ecology Research Centre, School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia and Anthropological Institute & Museum, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland; **Michael Krützen**, Anthropological Institute & Museum, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland and Evolution & Ecology Research Centre, School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia and School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch, Western Australia 6150, Australia; **Simon J. Allen**, Murdoch University Cetacean Research Unit, Centre for Fish, Fisheries and Aquatic Ecosystems Research, School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch, Western Australia 6150, Australia; **Kathrin Bacher**, Anthropological Institute & Museum, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland; **William B. Sherwin**, Evolution & Ecology Research Centre, School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia and Murdoch University Cetacean Research Unit, Centre for Fish, Fisheries and Aquatic Ecosystems Research, School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch, Western Australia 6150, Australia.

Abstract

Individual foraging tactics are widespread in animals and have ecological and evolutionary implications. Indo-Pacific bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia, exhibit a foraging tactic involving tool use, called "sponging." Sponging is vertically, socially transmitted through the matriline and, to date, has been described in detail in the eastern gulf of Shark Bay (ESB). Here, we characterize sponging in the western gulf of Shark Bay (WSB), in which a different matriline engages in the behavior. We identified 40 individual "spongers" in 9 mo of boat-based surveys over three field seasons. As is the case in ESB, the majority of WSB spongers was female and engaged in sponging in deep channel habitats. In contrast to ESB, however, there was no difference in the number of associates between spongers and nonspongers in WSB, and activity budgets differed between spongers and deep-water nonspongers; spongers foraged more frequently and rested less than nonspongers. Group sizes in deep channel habitat, where sponging was prevalent, were typically larger than those in shallow habitat, except for foraging, perhaps indicative of higher predator abundance and/or scattered prey distribution in deep-water

[1]Corresponding author (e-mail: anna.kopps@gmx.com).

habitat. This research improves our understanding of within-population foraging variations in bottlenose dolphins.

Individual foraging tactics are widespread in vertebrate and invertebrate taxa. In populations with interindividual niche variation, an individual only feeds on a subset of resources in its population's niche breadth (Bolnick *et al.* 2003). This within-population foraging variation is thought to be driven by intraspecific resource competition (Svanbäck and Bolnick 2007). Segregation of individuals to different foraging tactics has been reported by sex, social status, or the opportunity to acquire skills (Durell 2000). At the population level, foraging tactics affect ecological and evolutionary dynamics. Within-population variation of foraging tactics can lead to a greater carrying capacity and might be triggered by an increase in population density (van Valen 1965, Tinker *et al.* 2008). At the individual level, foraging tactics can alter activity budgets (Chilvers *et al.* 2003) and influence diet-specific risk factors (*e.g.*, predation risk, parasites; Bolnick *et al.* 2003).

Some foraging tactics include the use of tools. Tool use has been described in many species (see Bentley-Condit and Smith 2010 for a review). Two, not mutually exclusive, hypotheses for benefits arising from tool use have been proposed, with contrasting predictions for foraging time. First, the "necessity" hypothesis predicts that high population densities increase resource competition and that tool use allows the exploitation of otherwise inaccessible resources (Fox *et al.* 1999). If the food accessed with tools is difficult to obtain, or low in some nutrient, there might be an increase in foraging time under the necessity hypothesis. The second "nutrition" hypothesis states that tool users benefit from the high nutritional value of extracted food items. For example, a substantial proportion of the diet of New Caledonian crows (*Corvus moneduloides*) consists of beetle larvae, which are only accessible through the use of stick tools. On average, only three larvae are needed to cover a crow's daily energy requirements, demonstrating the high energetic reward (Rutz *et al.* 2010). In contrast to the necessity hypothesis, the nutrition hypothesis may predict a decrease in foraging time once tool use has been learned.

Foraging tactics have been reported within many cetacean species. Two sympatric ecotypes of killer whales (*Orcinus orca*) off British Columbia, for example, have specialized on different prey (Ford *et al.* 1998). Individually identified minke whales (*Balaenoptera acutorostrata*) in Washington State waters were shown to engage in either lunge feeding or bird-associated feeding (Hoelzel *et al.* 1989). In Moreton Bay, Queensland, Australia, two sympatric social communities of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) differed in foraging tactics. One community engaged in feeding in association with trawlers and the other did not (Chilvers and Corkeron 2001).

In the eastern gulf of Shark Bay (ESB), Western Australia, 13 different foraging tactics have been described for the resident bottlenose dolphin population (*Tursiops* sp.; Connor *et al.* 2000, Mann and Sargeant 2003). Individual females used between one and seven of these tactics, one of which, exhibited primarily by females, is called "sponging" (Mann and Sargeant 2003, Mann *et al.* 2008).

Sponging is the only known tool use in cetaceans and a behavior whereby bottlenose dolphins carry conical, marine sponges on their rostra, which are thought to serve as protective tools when probing in the sea floor (Smolker *et al.* 1997, Krützen

et al. 2005, Mann *et al.* 2008). Individuals engaging in sponging, or spongers, can be identified because they carry the sponges up to the surface during breathing bouts. Sponging appears to be a foraging tactic for two reasons. First, the stereotypic dive pattern displayed during sponging resembles other deep foraging dives, and second, the time spongers devote to the behavior is similar to that devoted to foraging by nonspongers (Smolker *et al.* 1997, Mann *et al.* 2008). Patterson and Mann (2011) suggested that spongers may target benthic fish without swim bladders, which would be less detectable by dolphins' echolocation than potential prey swimming in the water column.

Since its discovery in the 1980s (Smolker *et al.* 1997), sponging has been described in some detail as part of long-term studies in ESB (Monkey Mia; Smolker *et al.* 1997, Krützen *et al.* 2005, Mann *et al.* 2008). More recently, dolphins off Useless Loop in the western gulf of Shark Bay (WSB) have also been found to use sponges as foraging tools (Bacher *et al.* 2010, Tyne *et al.* 2012).

Genetic and behavioral evidence suggest that the sponging behavior is socially transmitted from mother to offspring (Mann and Sargeant 2003, Krützen *et al.* 2005, Mann *et al.* 2008). Only offspring born to spongers have been observed sponging, while offspring born to nonspongers have not (Mann and Sargeant 2003, Mann *et al.* 2008). All but one of the 15 biopsy sampled spongers in ESB share the same maternally inherited mitochondrial DNA haplotype (H, Krützen *et al.* 2005, Ackermann 2008), whereas all 26 biopsy sampled spongers in WSB share a different haplotype (E, Ackermann 2008, Kopps 2012). This suggests that sponging in ESB and WSB arose through separate innovations, although occasional transmission between matrilines cannot be ruled out (Ackermann 2008).

Sponging is restricted to channels deeper than 6 m in ESB (Sargeant *et al.* 2007, Mann *et al.* 2008), and similar channels deeper than 10 m in WSB (Tyne *et al.* 2012). Ecological factors have been shown to play an important role in the occurrence of the sponging behavior, because sponges only grow in deep water with sufficient water flow (Sargeant *et al.* 2007, Tyne *et al.* 2012). However, not all individuals inhabiting these deep channel habitats use sponges to forage and the home ranges of some spongers and nonspongers overlap (Mann and Sargeant 2003, Krützen *et al.* 2005, Mann *et al.* 2012). Therefore, an ecological explanation alone cannot account for the heterogeneity of foraging strategies observed in channel habitats.

In ESB, spongers and nonspongers differ in their social strategies. Female spongers have fewer associates than nonsponging females and spend less time in groups than nonsponging females (Mann *et al.* 2008, 2012). Differences in group size between spongers and nonspongers might be attributed to several factors, such as predator avoidance and food distribution (Alexander 1974). Because sponging occurs primarily in deep water (Sargeant *et al.* 2007, Tyne *et al.* 2012), it is important to investigate how these factors differ between habitats and between spongers and nonspongers. Group size is expected to increase with increasing predation pressure and increasing prey density (Heithaus and Dill 2002). Tiger sharks (*Galeocerdo cuvier*) are known to prey upon dolphins, with almost three quarters of adult bottlenose dolphins in ESB bearing shark bite scars (Heithaus 2001). In ESB, fish biomass and tiger shark abundance are higher in shallow (less than 4 m deep) than in deep water where sponging occurs (deeper than 6 m, Heithaus and Dill 2002). Both factors, predator abundance and prey availability, would predict larger dolphin group sizes in the shallows than in the deeper water. However, no relation has been found between dolphin group size and water depth in ESB (Mann *et al.* 2000).

Group sizes can differ depending on behavioral activity and relative time spent in different activities (*e.g.*, Caraco 1979, Boesch 1996). Resting, for example, is probably more dangerous than foraging, socializing, or traveling, due to reduced vigilance. It might, therefore, be safer to rest in larger groups. In contrast, foraging in small groups or alone might be more beneficial when food items are scattered. Indeed, Heithaus and Dill (2002) found that resting groups of ESB bottlenose dolphins were significantly larger than foraging groups.

Here, we characterize sponging off Useless Loop in WSB. We compare habitat preference, group size, number of associates, and activity budgets between spongers and nonspongers. Where possible, we drew comparisons to previous findings from similar research in ESB. These comparisons are important because WSB spongers belong to a different matriline from those in ESB (Ackermann 2008), and habitat characteristics differ markedly between the two gulfs (Tyne *et al.* 2012).

Specifically, we address the following questions: (1) How many spongers occur in the WSB study site and, therefore, (2) what proportion of the population are spongers? (3) Is there a sex bias in sponging? (4) Is sponging restricted to a particular habitat? (5) Do numbers of associates differ between spongers and nonspongers? (6) Do activity budgets differ between spongers and nonspongers? We use the answers to these questions to evaluate two nonexclusive hypotheses, "necessity"—that sponging is a suboptimal behavior, which some individuals are compelled to do, and "nutrition"—that sponging fulfills specific nutritional needs for certain individuals. Our results provide improved understanding of within-population foraging variation in bottlenose dolphins.

MATERIAL AND METHODS

Study Site

Shark Bay, Western Australia, is a subtropical embayment located about 850 km north of Perth (Fig. 1). The Malgana Aboriginal people call Shark Bay Gathaagudu ("two waters") because it is partly divided into two gulfs, the eastern and the western gulf, separated by Peron Peninsula (Fig. 1). A long term field study of bottlenose dolphins (*Tursiops* sp.) commenced in ESB in 1982 (Connor and Smolker 1985), taking advantage of the accessibility of habituated dolphins provisioned at the beach of Monkey Mia. In 2007 a second study site was established off Useless Loop in WSB. The WSB and ESB study sites are separated by *ca.* 110 km (by water; Fig. 1). This study focused on dolphins off Useless Loop in WSB and we will refer to our study site as WSB hereafter. Dolphins also engage in sponging outside this area, indicated by exploratory trips to Useless Inlet and South Passage (UI and SP, Fig. 1). We identified one sponger in Useless Inlet and four in South Passage, but these were not included in our analyses.

The WSB study site provided an ideal opportunity to study within-population foraging tactics because it consists of two distinct habitats: seagrass meadows and sand flats characterize the substrate of the shallows (<10 m water depth); these areas are bisected by deep channels (10–17 m water depth), where sand, shell, and rocky rubble dominate the substrate. Channels in WSB cover a larger proportion of the study site than in ESB, and the conical sponges used by dolphins for sponging are found only in these channels (Tyne *et al.* 2012).
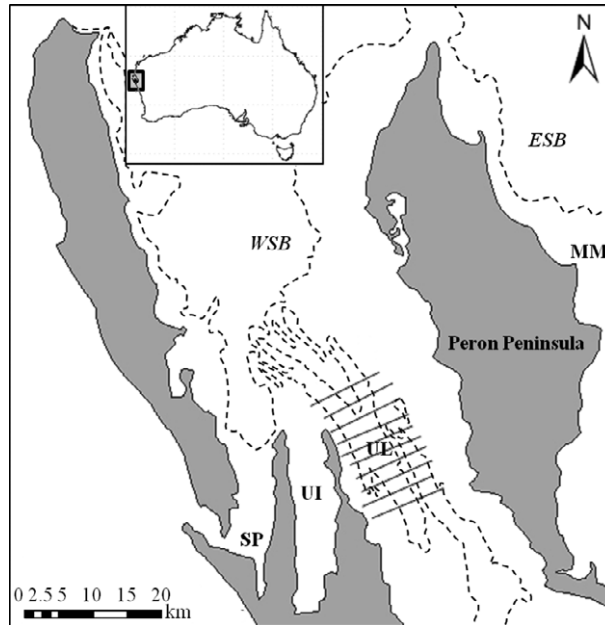
Figure 1. Map of Shark Bay. The western gulf of Shark Bay (WSB) is subdivided into the main study area Useless Loop (UL), Useless Inlet (UI), and South Passage (SP). The continuous lines in UL represent the 10 transects and the dashed outline the 10 m depth contour. East Shark Bay (ESB) and Monkey Mia (MM), the focus of earlier studies are also shown. Insert indicates location of Shark Bay in Australia.

For the purpose of our analyses, we used different definitions for "deep" and "shallow" water habitats between ESB and WSB, because sponges are found at different absolute depths in the two gulfs (Sargeant *et al.* 2007, Tyne *et al.* 2012). This is likely driven by differences in channel bathymetry. In order to compare the two sites, we based deep and shallow on whether the water was deep enough to allow sponges to grow rather than absolute water depth.

Transects and Surveys

We conducted boat-based surveys of dolphins along 10 predefined transects of 6 nautical miles (*ca.* 11.1 km) in length in WSB (Tyne *et al.* 2012). Transects were loosely parallel and separated by a mean of 2.5 km, resulting in a study area of *ca.* 260 km^2 (Fig. 1). The transect lines were placed roughly perpendicular to depth contours and covered approximately equal proportions of deep and shallow water. Transects were navigated aboard a 5.5 m research vessel at a speed of 7–8 knots (13–15 km/h). When dolphin(s) were sighted within 300 m of a transect line, we interrupted the transect and approached the dolphin(s) to conduct a transect survey. A behavioral survey was defined by a minimum 5 min encounter, during which we recorded group composition (number of adults, juveniles, and calves), predominant group activity (rest, travel, forage, socialize, or unknown) and whether any individuals were carrying a sponge. On encounter, we also recorded the location (GPS position) and water depth. One or more dolphins were considered a group as defined by the

10 m chain-rule (Smolker *et al.* 1992). Individuals were identified by the shape of their dorsal fin and characteristic nicks and scars using photo-identification (Würsig and Würsig 1977). When weather conditions or time constraints did not favor running transects, we conducted *ad hoc* surveys within the study area, classifying these surveys as nontransect surveys. Both survey types were included in our analyses.

We included only adults in our analyses, with age being determined by relative size and, sometimes, by the presence of a dependent calf for adult females. The size criterion was applied uniformly to spongers and nonspongers.

Definition of Spongers and Nonspongers

We adopted the same definition for a sponger as that detailed in Mann *et al.* (2008), *i.e.*, individuals that were observed carrying a sponge on at least two separate days were classified as spongers. However, for the purposes of comparing spongers and nonspongers, we set a threshold of five or more sightings per dolphin to define nonspongers. This was because our analyses showed that most spongers were identified after only two sightings (see below, Fig. 2), suggesting that five sightings should be sufficient to reliably differentiate between spongers and nonspongers.

Sex Determination

Sex was determined visually in the field or *via* genetic analyses. Females were identified in the field by the presence of a dependent calf in infant position (calf swims close to, just behind, and below the mother's abdomen) (Connor and Smolker 1985). Biopsy samples were taken for genetic analyses on an opportunistic basis (Krützen *et al.* 2002). We only darted animals after completing the standard behavioral survey, so that any responses to biopsy sampling would not influence behavioral data. Genetic sex was determined as previously applied to this population (Krützen *et al.* 2004*b*).

Foraging and Water Depth

We investigated whether sponging in WSB occurred primarily in deep water channels as in ESB (Sargeant *et al.* 2007, Mann *et al.* 2008). Based on genetic data, dolphins off Useless Loop show natal habitat preferences, *i.e.*, both adolescent and
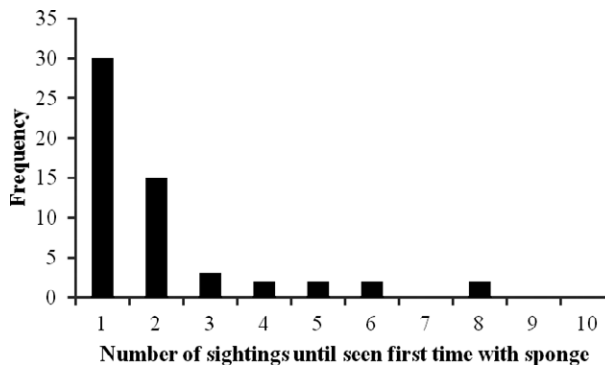

Figure 2. Number of times until spongers were seen for the first time carrying a sponge.

adult dolphins prefer either deep or shallow habitat for different behavioral categories and are only rarely seen in the other habitat (Kopps 2012). Females seen at least five times in the respective habitats were categorized as "deep water" (>10 m) or "shallow water" (<10 m) dolphins. These habitat categories were chosen based on sponge occurrence in the study site (Tyne *et al.* 2012). The five dolphins observed in both habitats were excluded from this analysis.

We also classified dolphins according to sponge use. Surveys of dolphins observed at least five times with the predominant activity "forage" were split into four categories: sponger with sponge, sponger without sponge, nonsponger deep, and nonsponger shallow. The discrimination between nonsponger deep and nonsponger shallow aided in disentangling differences in potential foraging tactics based on habitat, because dolphins of both categories forage without sponges, but might differ in how they obtain prey or they might forage for different prey.

Proportions of Spongers in the Population

First, we examined the proportion of spongers in the WSB study population that were sighted at least five times. Because sponging is only observed in deep water, we also calculated the proportion of spongers among all dolphins observed predominantly in this habitat type. Dolphins that were seen in deep and shallow water were considered deep water dolphins for this analysis. Third, we estimated the proportion of spongers observed in deep water that were females.

Group Size and Number of Associates

We investigated whether spongers were more solitary and whether they had fewer associates than nonspongers, as had been documented for ESB spongers (Mann *et al.* 2008, 2012). In WSB, we compared group sizes between deep water and shallow water dolphins, subdivided by different predominant group activities (*i.e.*, forage, rest, travel, socialize). Only surveys with known actual group size and with all dolphins identified were included in this analysis; we excluded cases in which the group size was only an estimate. Group size was ln-transformed in order to normalize the data distribution. The analysis was carried out twice: once including all dolphins and once excluding dependent calves.

In order to estimate an individual's number of associates, we counted the total number of dolphins with which an individual was seen throughout the study. We categorized the associates by sex, age class, and whether they were seen carrying a sponge. The number of associates was only determined for dolphins seen at least five times. We discriminated between numbers of male and female associates because males herd females (Connor *et al.* 1992) and, hence, the association may not be voluntary. Even though calves sometimes separate from their mothers and associate with other dolphins (Stanton *et al.* 2011), they spend prolonged periods with their mothers and their associates. Therefore, we compared number of associates in WSB both including and excluding calves. Mann Whitney U-tests were performed to determine whether spongers and nonspongers differed in their number of associates.

Activity Budgets

We compared the activity budgets of females that were encountered in at least five surveys engaged in one of the following activities: forage, rest, socialize, and travel. A

multivariate analysis of variance (MANOVA) was performed to determine whether spongers and nonspongers differed in the frequency they were observed engaging in different activities. Pillai's Trace was chosen due to its robustness to deviation from normality. We performed univariate ANOVAs to determine which behaviors were contributing to the significant MANOVA. Statistical analyses were carried out in PASW Statistics 18.0.1.

Results

Sample Sizes and Number of Spongers

During 9 mo of fieldwork over three field seasons in the austral autumn and winters of 2007–2009, 1,036 behavioral and photo-identification surveys were conducted. Twenty runs through the ten transects were completed, resulting in 481 transect surveys. We also conducted 555 nontransect surveys. In total, we identified 498 bottlenose dolphins, including 77 calves, in the study area off Useless Loop and in Useless Inlet. Individual dolphins were seen between one and 33 times. At least one individual was documented sponging in 99 (21%) of all 481 transect surveys.

In WSB, 39 adult dolphins and one calf met the sponger definition (Table 1). Additionally, 14 individually identified bottlenose dolphins were observed carrying a sponge only once. Of the 53 adult and juvenile dolphins carrying sponges in WSB, 49 (92.5%) were observed carrying sponges within the first five sightings (Fig. 2). Of the 53 adult and juvenile dolphins and one calf observed sponging, 34 were seen five times or more. All but one of the sponging females observed more than five times were sponging in at least two sightings (Table 1).

Sex Bias

Sex was determined for 91 individuals seen at least five times. However, there was a bias in the sex ratio (0.63 males/females), which likely arose from the ease of determining the sex of females compared to males in the field. To account for this bias, we conducted the sex ratio analysis including only animals for which sex was determined

Table 1. Sample sizes used for analyses with different cut off values of the number of sightings (5× indicates five times, 2× twice, and 1× once). Numbers in parentheses refer to genetically sexed individuals whereas numbers outside parentheses refer to genetically and/or behaviorally sexed individuals.

	No. of dolphins seen			
Sex	≥5× including ≥2× sponging (= spongers)[a]	≥2× sponging (= spongers)	sponging 1× (= nonspongers)	≥5× and ≤1× sponging (= nonspongers)[a]
F	21 (15)	27	3	33 (21)
M	1 (1)	1	1	34 (34)
Unknown	8	12	10	82
Total	29	40	14	149

[a]The individuals in the first and last data columns qualified for further analyses comparing spongers and nonspongers.

genetically (n_{males} = 35, $n_{females}$ = 36, Table 1). There were significantly more female than male spongers ($n_{sponger}$ = 16, χ^2 = 15.312, df = 1, P < 0.001).

The study was not of sufficient duration to quantify how many offspring of spongers developed sponging behavior. We did, however, observe one offspring of a sponger engaging in sponging in proximity to her mother. The offspring was at least three years of age when first seen sponging.

Sponging and Water Depth

In WSB, sponging females were encountered almost exclusively in deep channel habitat in which conical sponges grow. Sponging females were encountered in shallow water in only six out of 93 surveys (6.5%, Fig. 3). Spongers foraging without a sponge were seen exclusively in deep water (n = 20 surveys). Nonsponging dolphins (mean ± SE = 9.53 ± 0.45 sightings/individual) foraged both in deep (n = 20 surveys) and shallow water (n = 73 surveys).

Proportions of Spongers

Of the 149 individuals surveyed five times or more, 19.5% were spongers. Of the dolphins encountered only in deep water (n = 112), 25.9% were spongers. Of the females encountered only in deep water (n = 36), 58.3% were spongers.

Group Size

We investigated whether group size differed between habitats and among activities. For this analysis, we also included data from the 2010 field season, because three field seasons did not yield enough data to arrive at robust conclusions. Group size
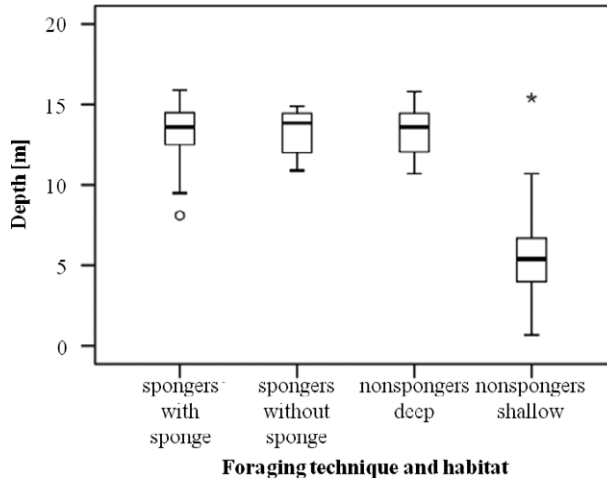

Figure 3. Boxplot showing the depth spectra (m) of foraging female dolphins with and without sponge. Boxes contain 50% of data points. Medians are indicated by black horizontal lines within boxes. Whiskers delimit the lower and upper quartile respectively. The circle and the asterisk represent outliers which are more than 1.5 and 3 times the box length away from either end of the box, respectively.

depended on activity (Fig. 4A, $n = 682$ surveys with known group size and identifications, ANOVA, $F_{7, 682} = 40.127$, $P < 0.001$) and habitat ($F_{1, 682} = 4.182$, $P = 0.041$). There was a significant interaction between group size and habitat when calves were excluded ($F_{3, 682} = 9.072$, $P < 0.001$). When calves were included, activity (Fig. 4B, $n = 682$, ANOVA, $F_{7, 682} = 35.735$, $P < 0.001$), but not habitat ($F_{1, 682} = 2.959$, $P = 0.086$) predicted group size; however, the interaction between habitat and activity was statistically significant ($F_{3, 682} = 3.731$, $P = 0.011$). Group sizes in deep water were larger than those in shallow water for all activities, except foraging. Group sizes differed significantly among all behavioral activities (*post hoc* Tukey HSD, $P < 0.001$ for all activity pairs, including and excluding calves; except rest-social (including calves): $P = 0.041$). Foraging groups were the smallest, resting and traveling groups were of intermediate size, and social groups were the largest (Table 2).

Number of Associates for Spongers and Nonspongers

For independent females seen at least five times, spongers ($n = 21$) had fewer female associates (mean $\pm$ SE = 5.95 $\pm$ 0.65, range 0–12) than nonspongers ($n = 33$, 8.12 $\pm$
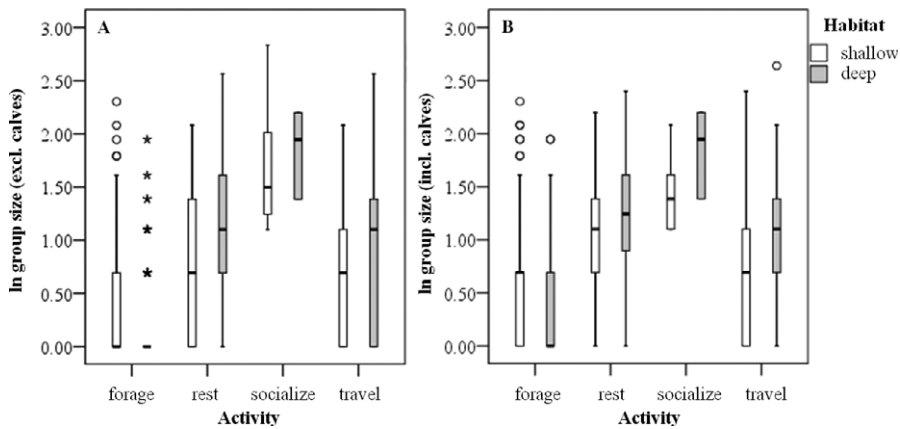

Figure 4. Group sizes of bottlenose dolphins (A) without calves and (B) including calves in shallow and deep water for four activities. Boxes contain 50% of data points. Medians are indicated by black horizontal lines within boxes. Whiskers delimit the lower and upper quartiles, respectively. Circles and asterisks represent outliers, which are more than 1.5 and 3 times the box length away from either end of the box respectively.

Table 2. Group size by activity. Actual means (not ln transformed) $\pm$ SE are shown.

Activity	n	Mean group size	
		Excluding calves	Including calves
Forage	473	1.47 ± 0.05	1.78 ± 0.05
Travel	111	2.46 ± 0.17	2.95 ± 0.20
Rest	88	3.25 ± 0.22	3.89 ± 0.23
Socialize	10	5.70 ± 0.73	5.70 ± 0.73

0.86, range 1–21; Mann Whitney-U test, $P = 0.049$). However, the total number of noncalf associates for female spongers (16.67 $\pm$ 2.16, range 2-33) and nonspongers (17.27 $\pm$ 1.66, range 0–36) did not differ significantly (Mann Whitney-U test, $P > 0.817$). The number of sightings of spongers and nonspongers did not differ (Mann Whitney-U test, $P = 0.972$). The number of associates of the one male sponger (25 associates) was in the second quartile of the number of associates for males. Males ($n = 35$) had more independent associates (25.34 $\pm$ 1.59, range 4–51) than females ($n = 54$, 17.04 $\pm$ 1.31, range 0–36; Mann Whitney-U test, $P < 0.001$).

Activity Budgets

We compared behavioral activity frequencies based on surveys of 43 females sighted between five and 22 times, engaged in one of the four activities: forage, rest, travel, and socialize. The data set included 18 spongers and 25 nonspongers. Multivariate analysis indicated that activity budgets differed significantly between spongers and nonspongers (Pillai's Trace = 0.259, $F_{4, 38} = 3.328$, $P = 0.020$, Fig. 5, Table 3). Spongers were seen foraging significantly more often than nonspongers, although there could be a bias in our data as sponging is a conspicuous behavior. In contrast, nonspongers rested and traveled more frequently. The proportion of surveys in which dolphins were observed socializing did not differ between female spongers and female nonspongers. The comparison of spongers and deep water nonspongers ($n = 9$) yielded the same result: spongers foraged more frequently, and traveled less than nonspongers. There was no difference between the average frequency of socializing and resting behaviors. Spongers carried sponges in a mean of 85.6% of the surveys in which they were recorded foraging. The activity budgets did not differ between deep ($n = 9$) and shallow water nonspongers ($n = 13$) (Pillai's Trace = 0.322, $F_{4, 17} = 2.020$, $P = 0.137$). The number of sightings of spongers and nonspongers did not differ (Mann Whitney-U test, $P = 0.142$).
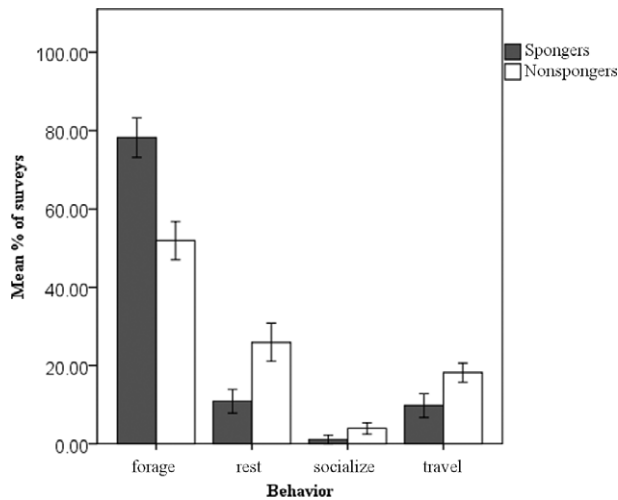

Figure 5. Average activity budgets of sponging and nonsponging females in WSB based on surveys. Error bars represent ± 1 standard error.

Table 3. Activity budgets (in %) of spongers and nonspongers based on surveys. Statistics refer to the comparisons of nonspongers and spongers. *F* indicates the test statistic and *P* the significance of *post hoc* ANOVAs.

Activity	Spongers (18) mean ± SE	Nonspongers all (25)			Nonspongers deep (9)		
		mean ± SE	*F*	*P*	mean ± SE	*F*	*P*
Forage	78.2 ± 5.0	51.9 ± 4.8	13.565	0.001	50.3 ± 5.4	11.814	0.002
Rest	10.9 ± 3.1	26.0 ± 4.9	5.665	0.022	17.7 ± 5.4	1.387	0.250
Travel	9.8 ± 3.0	18.2 ± 2.4	4.779	0.035	26.1 ± 4.0	10.147	0.004
Socialize	1.1 ± 1.1	3.9 ± 1.5	2.068	0.158	5.9 ± 3.0	3.313	0.081

Discussion

Sponging is a common foraging tactic in the deep channel habitats in WSB: we identified 40 spongers in just three field seasons, as well as 14 potential spongers seen carrying a sponge once, 41.2% of all surveyed and independent female dolphins (seen at least five times) were spongers, representing 58.3% of females identified in the deep water (Table 4). Thus, sponging appears to be more prevalent in WSB than in ESB, where 54 spongers have been identified in 27 field seasons (Patterson and Mann 2011). In ESB, only 11% of all observed female dolphins are regularly seen sponging but, at more than 50%, the percentage of spongers in the channels is similar to the percentage seen in WSB channels (Sargeant *et al.* 2007, Mann *et al.* 2008). See Table 4 for a summary of our results and a comparison with ESB findings. Deep water channels cover a larger area in WSB and this might explain the difference in the abundance of spongers between the two study sites (Tyne *et al.* 2012).

Group size is expected to correlate positively with predator and prey abundance (Shane *et al.* 1986). Furthermore, larger groups are expected to form during activities that restrict opportunities for vigilance. As expected, we found that resting, traveling, and socializing dolphin groups are larger than foraging groups in WSB. In ESB, tiger sharks are more abundant in the warmer months and in shallow water (Heithaus and Dill 2002). Accordingly, larger group sizes were predicted in shallow water. However, this was not borne out by our finding that dolphins in deep water (spongers and nonspongers) form larger groups than dolphins in shallow water, except when foraging. We conducted field work predominantly in colder months and occasionally encountered tiger sharks in both deep and shallow water, as well as documenting fresh shark bite wounds on dolphins (data not shown). Thus, in contrast to ESB, there may be a higher risk of predation in deep water. However, even if there was higher predation pressure in deep habitat, sponging may not be a high risk foraging tactic. Sponging dolphins tend to swim just above the substrate (Mann *et al.* 2008), thereby protecting their ventral body parts, which are most vulnerable and most often the target of shark attacks on cetaceans (Long and Jones 1996, Heithaus 2001).

In WSB, the number of associates did not differ between spongers and nonspongers, but spongers had significantly fewer female associates. Spongers primarily foraged alone (or with a dependent calf only, 71.2% of observations) and, to a lesser extent, with another sponger or with nonspongers (17.6% and 11.2% of observations, respectively). The latter observation, coupled with the single maternal mitochondrial haplotype found in WSB spongers (Ackermann 2008), suggests that calves of nonspongers do not adopt sponging, despite some exposure to sponging. This is also the case in ESB (Mann and Sargeant 2003). In WSB, sponging appears to be

Table 4. Summary table showing the differences between spongers and nonspongers in WSB compared to spongers in ESB. Size of study sites are similar between WSB (257 km^2) and ESB (286 km^2).

	WSB	WSB nonspongers	ESB
Number of spongers	40 (3 field seasons)[a]	n/a	54 (27 field seasons)[1]
Proportion of spongers	All ♀: 41.2% (27.6%–55.8%)[a] 58.3% (40.8%–74.5%) of ♀ in deep water[a] 19.5% (13.4%–26.7%) of all ♂ and ♀[a] 25.9% (18.1%–35.0%) of ♂ and ♀ in deep water[a]	n/a	All ♀: 11.0%[2] >50.0% of ♀ in channels[3]
Sex	♀-biased[a]	n/a	♀-biased[3,4,5]
Habitat	Channels (>10 m deep)[a,6]	Channels and shallows[a]	Channels (>6 m deep)[7]
Group size	No difference[a]		Spongers more solitary[3,5]
Number of associates	No difference[a]		Spongers fewer associates[3]
	16.7 ± 2.2 (range 2–33)[b]	17.3 ± 1.7[b] (range 0–36)	15.0 ± 4.8[b] (range 0–55)
Activity budget	Forage ↑ (survey based)[a] Foraged 78.2% ± 5.0%[b] of surveys	Rest/travel ↑ (survey based)[a] Foraged 51.9% ± 4.8%[b] of surveys	No difference except for ♀ with dependent calves (follow based)[3] Spongers foraged 47.2% ± 4.77%[b] of time (follows)
mtDNA haplotype	22 haplotype E[8,9]	Haplotypes D, E, F, H, I[8,9]	14 haplotype H 1 haplotype E[4,8]

References: [1]Patterson and Mann 2011, [2]Mann and Sargeant 2003, [3]Mann *et al.* 2008, [4]Krützen *et al.* 2005, [5]Smolker *et al.* 1997, [6]Tyne *et al.* 2012, [7]Sargeant *et al.* 2007, [8]Ackermann 2008, [9]Kopps 2012.
[a]This study.
[b]Mean ± SE, 95% confidence levels.

biased towards females as it is in ESB (Mann and Sargeant 2003, Krützen *et al.* 2005, Mann *et al.* 2008), raising the question of why sponging confers an advantage for females. Some proximate explanations include that sponging may simply be more compatible with other aspects of female behavior than male behavior. For example, male reproductive success depends on alliance partners (Krützen *et al.* 2004*a*), hence the solitary lifestyle described for spongers in ESB may not be competitive for gaining access to females (Smolker *et al.* 1997, Krützen *et al.* 2005, Mann *et al.* 2008). Another possible explanation for the lack of male spongers could be that males range further than females and, thus, tend to forage in a variety of habitats (Randic 2008), conflicting with a sponger's need to stay in deep channel habitat where sponges grow. However, this seems an unlikely explanation for our study area in WSB, because the

deep channel habitat covers a large, continuous area (Tyne *et al.* 2012). A third plausible explanation for the occurrence of more female than male spongers may be due to differences in time spent sponging. If male spongers spend less time sponging than females, they are less likely to be observed sponging during surveys. Alternatively, a general female bias in frequency and learning acquisition of tool use may explain the observed sex bias (Lonsdorf *et al.* 2004, Gruber *et al.* 2010). Female dolphin foraging tactics are certainly diverse in Shark Bay, suggesting high learning ability (Mann and Sargeant 2003).

Another possible explanation for the observed sex bias might be that the dominant sex is forcing the other into suboptimal foraging. For instance, male downy woodpeckers (*Picoides pubescens*) appear to control resources by dominance over females. After male removal, female foraging behavior changed to resemble that of males, but after female removal, males did not change their foraging behavior (Peters and Grubb 1983). In captivity, male bottlenose dolphins are dominant over females (Samuels and Gifford 1997) and, in the wild, males sometimes threaten consorted females (Connor and Smolker 1996). If male dolphins are dominant this raises the question of whether sponging (and other female-biased foraging tactics) is a suboptimal foraging tactic. For dolphins, monopolizing mobile prey may be difficult without defending territories, but females could elude competition by sponging to access other foraging niches. Similarly, Corkeron *et al.* (1990) showed that males occupy the prime foraging positions around trawlers and suggested that females might be forced to take greater risks in order to benefit from trawl-associated foraging.

If sponging is a suboptimal foraging tactic in WSB, additional costs to pursuing sponging could be found in altered activity budgets. Compared to nonspongers, spongers showed an increased foraging frequency and reduced resting frequency. Foraging tactics have previously been linked to foraging frequency: trawler-associated dolphins were also observed to forage more frequently than dolphins which did not engage in trawl foraging (Chilvers *et al.* 2003). It should be noted here that there could be a bias in our data as sponging is conspicuous, and the behavior of most sponge carrying dolphins was recorded as foraging. However, even the foraging effort of nonspongers in WSB seems to be higher than in any other studied dolphin population, which typically ranges from 15% to 22% (summarized in Chilvers *et al.* 2003). The increased foraging rate may result in proximate costs for spongers, suggesting that there could be less prey available in the channels. Indeed, ESB channel habitat was categorized as inferior, based on finding the lowest density of female dolphins over all major habitat types (Mann *et al.* 2008), supporting the necessity hypothesis. However, activity budgets of spongers and nonspongers could be different during the night. Anecdotal data of an ESB female nonsponger showed that she only spent 10% of the day foraging, but foraged 55% of the time during a night follow (Mann and Sargeant 2003).

On the other hand, there are indications that sponging is not an inferior foraging tactic: in ESB, spongers have an elevated, albeit nonsignificantly so, calving success compared to nonspongers (Mann *et al.* 2008). Moreover, simulations suggest that fitness benefits are likely to be required for a behavior that is socially, vertically transmitted to be stable over generations (Whitehead 1998, Kopps and Sherwin 2012). Therefore, sex differences in foraging strategies might reflect different nutritional needs between sexes, rather than the direct resource competition implied by the necessity hypothesis.

Here, we showed that sponging behavior is a widespread foraging tactic throughout Shark Bay. Similar to ESB, in which few males are known to be spongers,

sponging is highly sex-biased in WSB and is restricted to deep channel habitats. In contrast to ESB, however, there are larger overall numbers of spongers in WSB, spongers have as many associates as do nonspongers, and activity budgets differed between spongers and deep-water nonspongers. This research broadens our understanding of within-population foraging tactics, including tool use, in delphinids.

Literature Cited

Ackermann, C. 2008. Contrasting vertical skill transmission patterns of a tool use behaviour in two groups of wild bottlenose dolphins (*Tursiops* sp.), as revealed by molecular genetic analyses. M.Sc. thesis, University of Zurich, Zurich, Switzerland. 93 pp.

Alexander, R. D. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics 5:325–383.

Bacher, K., S. Allen, A. Lindholm, L. Bejder and M. Krützen. 2010. Genes or culture: Are mitochondrial genes associated with tool use in bottlenose dolphins (*Tursiops* sp.)? Behavior Genetics 40:706–714.

Bentley-Condit, V. K., and E. O. Smith. 2010. Animal tool use: Current definitions and an updated comprehensive catalog. Behaviour 147:185–221.

Boesch, C. 1996. Social grouping in Taï chimpanzees. Pages 101–113 *in* W. C. Mcgrew, L. F. Marchant and T. Nishida, eds. Great ape societies. Cambridge University Press, Cambridge, U.K.

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

Caraco, T. 1979. Time budgeting and group size: A test of theory. Ecology 60:618–627.

Chilvers, L. B., and P. J. Corkeron. 2001. Trawling and bottlenose dolphins' social structure. Proceedings of the Royal Society of London Series B: Biological Sciences 268:1901–1905.

Chilvers, B. L., P. J. Corkeron and M. L. Puotinen. 2003. Influence of trawling on the behaviour and spatial distribution of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Moreton Bay, Australia. Canadian Journal of Zoology 81:1947–1955.

Connor, R. C., and R. S. Smolker. 1985. Habituated dolphins (*Tursiops* sp.) in Western Australia. Journal of Mammalogy 66:398–400.

Connor, R. C., and R. A. Smolker. 1996. 'Pop' goes the dolphin: A vocalization male bottlenose dolphins produce during consortships. Behaviour 133:643–662.

Connor, R. C., R. A. Smolker and A. F. Richards. 1992. Two levels of alliance formation among male bottle-nosed dolphins (*Tursiops* sp.). Proceedings of the National Academy of Sciences of the United States of America 89:987–990.

Connor, R. C., M. R. Heithaus, P. Berggren and J. L. Miksis. 2000. "Kerplunking": Surface fluke-splashes during shallow-water bottom foraging by bottlenose dolphins. Marine Mammal Science 16:646–653.

Corkeron, P. J., M. M. Bryden and K. E. Hedstrom. 1990. Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. Pages 329–336 in S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.

Durell, S. E. A. L. D. 2000. Individual feeding specialisation in shorebirds: Population consequences and conservation implications. Biological Reviews 75:503–518.

Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm and K. C. Balcomb. 1998. Dietary specialization in two sympatric populations of killer whales (Orcinus orca) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76:1456–1471.

Fox, E. A., A. F. Sitompul and C. P. Van Schaik. 1999. Intelligent tool use in wild Sumatran orangutans. Pages 99–116 in S. T. Parker, R. W. Mitchell and H. L. Miles, eds. Intelligent tool use in wild Sumatran orangutans. Cambridge University Press, Cambridge, U.K.

Gruber, T., Z. Clay and K. Zuberbühler. 2010. A comparison of bonobo and chimpanzee tool use: Evidence for a female bias in the Pan lineage. Animal Behaviour 80:1023–1033.

Heithaus, M. R. 2001. Shark attacks on bottlenose dolphins (Tursiops aduncus) in Shark Bay, Western Australia: Attack rate, bite scar frequencies, and attack seasonality. Marine Mammal Science 17:526–539.

Heithaus, M. R., and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491.

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

Kopps, A. M. 2012. Ecological, social and genetic forces shaping behavioural variation in bottlenose dolphins. Ph.D. thesis, University of New South Wales, Sydney, Australia. 196 pp.

Kopps, A. M., and W. B. Sherwin. 2012. Modelling the emergence and stability of a vertically transmitted cultural trait in bottlenose dolphins. Animal Behaviour 84:1347–1362.

Krützen, M., L. M. Barre, L. M. Möller, M. R. Heithaus, C. Simms and W. B. Sherwin. 2002. A biopsy system for small cetaceans: Darting success and wound healing in Tursiops SPP. Marine Mammal Science 18:863–878.

Krützen, M., L. M. Barre, R. C. Connor, J. Mann and W. B. Sherwin. 2004a. 'O father: where art thou?'—Paternity assessment in an open fission-fusion society of wild bottlenose dolphins (Tursiops sp.) in Shark Bay. Western Australia. Molecular Ecology 13:1975–1990.

Krützen, M., W. B. Sherwin, P. Berggren and N. Gales. 2004b. Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: Bottlenose dolphins (Tursiops sp.) in Shark Bay. Western Australia. Marine Mammal Science 20:28–47.

Krützen, M., J. Mann, M. R. Heithaus, R. C. Connor, L. Bejder and W. B. Sherwin. 2005. Cultural transmission of tool use in bottlenose dolphins. Proceedings of the National Academy of Sciences of the United States of America 102:8939–8943.

Long, D. J., and R. E. Jones. 1996. White shark predation and scavenging on cetaceans in the eastern North Pacific Ocean. Pages 293–307 in A. P. Klimley and D. G. Ainley, eds. Great white sharks: The biology of Carcharodon carcharias. Academic Press, New York, NY.

Lonsdorf, E. V., L. E. Eberly and A. E. Pusey. 2004. Sex differences in learning in chimpanzees. Nature 428:715–716.

Mann, J., and B. L. Sargeant. 2003. Like mother, like calf: The ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (Tursiops sp.). Pages 236–266 in D. Fragaszy

and S. Perry, eds. The biology of traditions: Models and evidence. Cambridge University Press, Cambridge, U.K.

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

Mann, J., B. L. Sargeant, J. Watson-Capps, Q. A. Gibson, M. R. Heithaus, R. C. Connor and E. Patterson. 2008. Why do dolphins carry sponges? PLoS ONE 3(12):e3868.

Mann, J., M. A. Stanton, E. M. Patterson, E. J. Bienenstock and L. O. Singh. 2012. Social networks reveal cultural behaviour in tool-using dolphins. Nature Communications 3:980.

Patterson, E. M., and J. Mann. 2011. The ecological conditions that favor tool use and innovation in wild bottlenose dolphins (*Tursiops* sp.). PLoS ONE 6:e22243.

Peters, W. D., and T. C. Grubb, Jr. 1983. An experimental analysis of sex-specific foraging in the downy woodpecker, *Picoides pubescens*. Ecology 64:1437–1443.

Randic, S. 2008. Spatial analysis of the distribution and home ranges of male bottlenose dolphins in Shark Bay, Australia. M.S. thesis, University of Massachusetts, Dartmouth, MA. 67 pp.

Rutz, C., L. A. Bluff, N. Reid, *et al.* 2010. The ecological significance of tool use in New Caledonian crows. Science 329:1523–1526.

Samuels, A., and T. Gifford. 1997. A quantitative assessment of dominance relations among bottlenose dolphins. Marine Mammal Science 13:70–99.

Sargeant, B. L., A. J. Wirsing, M. R. Heithaus and J. Mann. 2007. Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (*Tursiops* sp.)? Behavioral Ecology and Sociobiology 61:679–688.

Shane, S. H., R. S. Wells and B. Würsig. 1986. Ecology, behavior and social organization of the bottlenose dolphin: A review. Marine Mammal Science 2:34–63.

Smolker, R. A., A. F. Richards, R. C. Connor and J. W. Pepper. 1992. Sex-differences in patterns of association among Indian-Ocean bottle-nosed dolphins. Behaviour 103:38–69.

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

Stanton, M. A., Q. A. Gibson and J. Mann. 2011. When mum's away: A study of mother and calf ego networks during separations in wild bottlenose dolphins (*Tursiops* sp.). Animal Behaviour 82:405–412.

Svanbäck, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society Series B: Biological Sciences 274:839–844.

Tinker, M. T., G. Bentall and J. A. Estes. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proceedings of the National Academy of Sciences 105:560–565.

Tyne, J., N. Loneragan, A. M. Kopps, S. J. Allen, M. Krützen and L. Bejder. 2012. Ecological characteristics contribute to sponge distribution and tool use in bottlenose dolphins (*Tursiops* sp.). Marine Ecology Progress Series 444:143–153.

van Valen, L. 1965. Morphological variation and width of ecological niche. The American Naturalist 99:377–390.

Whitehead, H. 1998. Cultural selection and genetic diversity in matrilineal whales. Science 282:1708–1711.

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