



Notes

MARINE MAMMAL SCIENCE, 32(3): 1152–1160 (July 2016)
© 2016 Society for Marine Mammalogy
DOI: 10.1111/mms.12314

Driver-barrier feeding behavior in bottlenose dolphins (*Tursiops truncatus*): New insights from a longitudinal study

STEFANIE K. GAZDA,¹ Biology Department, University of Massachusetts Boston, 100 Morrissey Boulevard, Boston, Massachusetts 02125, U.S.A.

Anderson and Franks (2001) defined a “division of labor” as occurring when individuals, working as a team to complete a task, perform different subtasks. A division of labor with role specialization, where individuals regularly assume different subtasks in a team task, is rare in noneusocial mammals. A possible case was described in wild dogs: the same individual selects and chases the prey, one or two dogs maintain a distance behind the leader to head off any prey that may escape, and others lag behind (Estes and Goddard 1967). The first definitive case of a division of labor with role specialization in noneusocial mammals was reported in the African lion (*Panthera leo*) (Stander 1992). Females in “center” roles waited for prey to move towards them while those in “wing” positions initiated an attack on the prey (Stander 1992). Hunting success was higher when lionesses occupied preferred stalking positions. Recently, Hurtado *et al.* (2013) described role specialization in mound-building mice: within a group of six mice, two individuals carried most of the materials for building. Additionally, these carrier mice specialized in the type of materials they carried and did not switch. Gazda *et al.* (2005) described an example of a division of labor with role specialization in a population of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida. Two groups (the A group and B group) were part of this study. In each group, one dolphin herded or drove fish toward other dolphins that appeared to line up and form a barrier. The trapped fish leapt into the air where they were captured by “driver” and “barrier” dolphins. Individuals in each group were consistent in their roles as driver and barrier. Nondriving dolphins were defined as all group members within the 10 m chain rule (all individuals in the group must be within 10 m of another individual, Smolker *et al.* 1992) that did not drive. This included the barrier dolphins that were tightly bunched and raised their heads out of the water attempting to catch leaping fish, as well as any other dolphins in the group that did not drive or form the barrier. In the A, but not the B group, the driver captured more fish than

¹Corresponding author (e-mail: sgazda@umassd.edu).

the barrier dolphins caught, a difference Gazda *et al.* (2005) attributed to the greater stability of the A group.

In the Cedar Keys, bottlenose dolphins display a variety of feeding behaviors including kerplunking (Connor *et al.* 2000, Wells 2001), snacking, tail up/peduncle up dives, “fish whacking” (Shane 1990, Nowacek 1999), and fish chasing onto shore (Quintana-Rizzo 1998, Gazda 2002). In other populations, there are multiple cases of foraging tactics exhibited by a limited subset of dolphins (such as sponge carrying, Smolker *et al.* 1997, Krützen 2005, Mann *et al.* 2008, Kopps *et al.* 2014; and kerplunking, Connor *et al.* 2000, Wells 2001, Nowacek 2002). For example, in Shark Bay, Australia, a small percentage of mostly female dolphins specialize in deep-water foraging by carrying sponges, a probable tool worn to protect the forager’s rostrum during benthic feeding (Krützen 2005; Mann *et al.* 2008, 2012; Patterson and Mann 2011; Kopps *et al.* 2014).

The driver-barrier behavior in the Cedar Keys is another example of a behavior used by a limited subset of individuals. Only a small portion (approximately 6.7%) of the approximately 325 dolphins identified in the Cedar Keys have been observed to engage in driver-barrier feeding. At least four groups have been identified: the A and B groups from the Gazda *et al.* (2005) study and two other groups for which there are only a few sightings. The B group has not been seen in the study area since 2001.

During the initial study in 2001, the A group consisted of the same three individuals. Over time, its group membership has changed from three to two to just one individual dolphin, the original driver “TLFN”; 2001: 56 driver-identified driver-barrier bouts, 52 with three dolphins (one driver, two barriers), 4 with two dolphins (one driver, one barrier); 2008: 101 driver-identified bouts, 93 with two dolphins (one driver, one barrier), 8 with one driver (no barriers); 2010: 110 driver-identified bouts, all with one driver dolphin (no barriers). Since the A group barrier dolphins were last seen in the group, they have not been sighted in the study area.

The A group driver TLFN has only been observed to drive fish and has not been seen using any other feeding method (28 total sightings: 2001, ten sightings, six driver foraging, and four socializing; 2008, nine sightings, five driver foraging, one traveling, and three socializing; 2010, nine sightings, seven driver foraging, and two traveling). While the proportion of individuals that use this behavior is small, it is clear that the A group driver TLFN specializes in this method of feeding.

This change in group size provides a unique opportunity to examine questions about the feeding success of the driver dolphin and the role of the barrier dolphins. In the initial study, one of the barrier dolphins from the B group was observed to drive fish alone, and significantly fewer fish jumped per bout. Accordingly, Gazda *et al.* (2005) suggested that the barrier role may not be essential but nonetheless important for trapping fish. An alternative hypothesis for this behavior was that the barrier dolphins were scroungers in a producer-scrounger system (P-S model; Barnard and Sibly 1981, Hamilton and Dill 2002).

Therefore, the objective of this Note is to determine if the decrease in the number of barrier dolphins in Group A was associated with a change in feeding success for the A group driver and with respect to barrier dolphin success. Measures of feeding success examined are (1) number of fish caught, (2) the number of fish leaping per bout, (3) bout duration, and (4) the proportion of completed bouts.

Methods followed closely those described in Gazda *et al.* (2005). The study area encompassed most of the Cedar Keys (29°05'49"N, 83°03'58"W), which comprise five major islands, numerous smaller islands, and wetland areas connected to the

mainland off the northwest coast of Florida. Briefly, observations were made from a 4.3 m boat from June through August 2001, July through December 2008, and March through August 2010. In 2001, individuals were photographed using a Nikkormat camera fitted with an 80–250 zoom lens. In 2008 and 2010, a Nikon D300 camera with a 400 mm Nikkormat zoom lens was used. Once a dolphin was encountered, the dorsal fin was photographed for individual identification (Caldwell 1955) using the methods described by Defran *et al.* (1990). Individuals were included in the group if they were within 10 m of any other group member (Smolker *et al.* 1992).

Feeding behaviors were recorded with a camcorder (2001: a Panasonic digital zoom S-VHS; 2008 and 2010: SONY HDR-HC1 HDV Handycam 1080i digital camcorder), and the dorsal fin of the driver was photographed during each bout. Blank photographs were taken between bouts to demarcate sequential feeding bouts. In addition, observers on board identified the driver verbally for the video camera. A feeding bout began when the driving dolphin began swimming rapidly in tight circles—either with or without fluke slaps—and was considered to be *complete* when the participating dolphins put their heads back under water and rolled upright. An *incomplete* bout was defined as a bout where the driver began swimming in tight circles—with or without fluke slaps—but stopped before fish started jumping out of the water and no participating dolphins put their heads above water. No fish jumped during incomplete bouts.

Only aerial fish capture was recorded, and only dolphins that had their heads up (*i.e.*, drivers and barrier dolphins) were used to calculate capture success. Fish-capture success was determined by counting the number of fish each dolphin caught in air, indicated by either observing the fish in the dolphin's mouth or observing the dolphin's lunge followed by repeated biting motions. A lunge that was not followed by biting motions was not counted because dolphins sometimes missed fish at which they lunged. Recording the capture rates of individual barrier dolphins was not possible because the dolphins frequently changed positions and their dorsal fins were often submerged. Therefore, for each bout, an average number of fish captured by the barriers was calculated from the number of barriers and the total number of fish that they captured (Gazda *et al.* 2005). Fish that jumped were identified by eye as mullet (*Mugil cephalus*).

Fish-capture success might relate to the number of leaping fish; therefore, the number of fish leaping per feeding bout was counted from the videotape. Some leaps occurred after a leaping fish fell back into the water and thus could have been a fish leaping for a second time. These cases were not included in the total of fish leaping per bout (Gazda *et al.* 2005). Bout duration and the proportion of completed bouts may have a relationship to group size and foraging efficiency; complete bouts were timed in seconds, and incomplete bouts were noted when they occurred.

Seventy driver-barrier bouts of the A group were seen in 2001 (56 bouts with an identified driver; 80% identification rate), 116 in 2008 (101 bouts with an identified driver; 92% identification rate), and 110 in 2010 (110 with an identified driver; 100% identification rate). All data were analyzed using SPSS Statistics (Version 19). Differences in catch success between driver and barrier dolphins (overall and by number of dolphins per group) were analyzed *via* paired samples *t*-tests. Welch's *t*-tests were used to determine catch success of barriers compared to group size, catch success of TLFN compared to group size (complete bouts only), the number of fish leaping per bout, and bout duration; it does not assume equal variance or sample size between

the two samples being tested (Ruxton 2006) and is robust to violations of normality (Zar 2009). Two-by-two contingency tables were used to analyze the proportion of expected *vs.* observed for complete and incomplete bouts. Each table lists the number of bouts that were used for a given analysis.

TLFN was the driver in every identified bout. This finding of a consistent driver is significantly different from a distribution derived from a hypothesis that the driving individual is randomly selected for each bout (binomial test, $n = 163$, $P < 0.001$). Bouts where a driver was not identified were due to poor video or photo quality. Any bouts where fish could not be counted due to poor video quality were removed from the analysis.

When analyzing complete bouts only, the driver did better than the barrier dolphins regardless of group size (Fig. 1). There was no indication that group size was related to driver fish-capture success (Table 1, complete bouts only, no significant differences in TLFN catch rates between group sizes). There was no significant difference in barrier catch rates in complete bouts across group sizes (Fig. 1). Based on these results, it seems that the driver dolphin does not benefit from an increased catch success with differing numbers of barrier dolphins participating, nor do the barrier dolphins benefit.

The number of barrier dolphins did not have a significant relationship with fish jumping per bout (Table 2) or bout duration (Table 3). It should be noted that the decrease in driver-barrier group size is very closely correlated with change in year ($n = 267$, Pearson correlation -0.912 , $P > 0.001$). This means that any change in success could be a measurement of time and of group size or that one may mask the other. It is possible that TLFN improved with time, which may be why number of fish per bout and bout duration did not change with group size.

There is a significant difference (two-by-two contingency table, Table 4) in the proportion of incomplete bouts between group sizes of one (one driver, no barriers) and three (one driver, two barriers; $P < 0.05$), as well as marginal significance between groups of two (one driver, one barrier) and three ($P = 0.07$). There is no significant difference in the proportion of incomplete bouts between group sizes of one and two ($P = 0.11$).

Of the four measures considered here (number of fish captured, leaping, bout duration, and proportion of completed bouts), the number of barrier dolphins was associated with only the proportion of completed bouts. The number of completed bouts had not been considered in the original study. The increase in incomplete bouts as group size decreases may mean that the driver catches less fish across all attempts. I estimated the reduced feeding success of the driver in small groups by running a general linear model (Poisson loglinear) using all of the bouts: incomplete (no fish jumped therefore no captures) and complete (fish jumped therefore captures were possible) and tested for catch success of the driver by group size. There was a significant decrease in the number of fish caught by the driver from a group size of three (one driver, two barriers) to a group size of one (only the driver; $B = -0.448$, $P = 0.039$). There was also a significant decrease in the number of fish caught by the driver from a group size of three to two (one driver, one barrier; $B = -0.454$, $P = 0.046$). I tested for barrier success in the same fashion, and found a significant decrease in barrier catch from a group size of three to two ($B = -0.25$, $P = 0.037$).

Having a group size of three means that there are fewer incomplete bouts, which increases the foraging efficiency for both driver and barriers. In incomplete bouts, there are no fish captures, though the driver does start driving and the barriers start

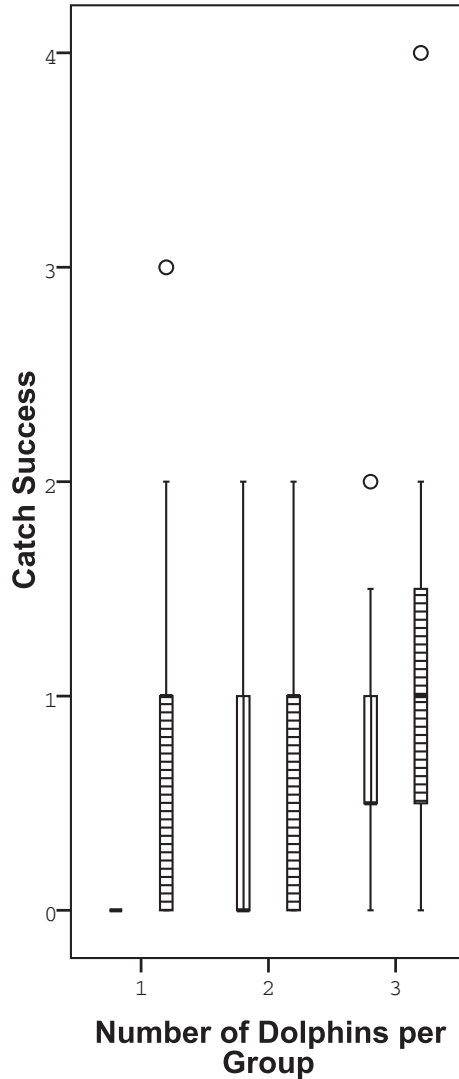


Figure 1. Boxplots of catch success of the driver (horizontal hatch marks) and average catch success of barrier dolphins (vertical hatch marks) by the number of dolphins per group. Complete bouts only; there is no potential for catch during incomplete bouts. Group size of one (one driver, no barriers) mean driver catch per bout $0.78 (\pm 0.65 \text{ SD})$, $n = 92$. Group size of two (one driver, one barrier) mean driver catch per bout $0.70 (\pm 0.62 \text{ SD})$, mean barrier catch per bout $0.50 (\pm 0.53 \text{ SD})$, $n = 70$. Group size of three (one driver, two barriers), mean driver catch per bout $1.07 (\pm 0.69 \text{ SD})$, mean average barrier catch per bout $0.70 (\pm 0.56 \text{ SD})$, $n = 28$. The driver did better than the barrier dolphins regardless of group size (paired samples t -tests: group size of two, $t = 2.572$, $P = 0.012$; group size of three, $t = 2.469$, $P = 0.02$, with a Bonferroni correction). There was no significant difference in barrier catch rates in complete bouts across group sizes (Welch's t -test average barrier catch in group size of three *vs.* barrier catch in group size of two: $t = -1.079$, $P = 0.20$).

Table 1. Welch's *t*-tests of catch success of TLFN compared to group size. Only completed bouts were used in this analysis. Group size is number of dolphins per group: three dolphins (one driver, two barrier dolphins), two dolphins (one driver, one barrier dolphin), or one dolphin (one driver, no barrier dolphins). There are no significant differences between groups ($P > 0.05$).

Group size	n^a	Mean \pm SD	<i>t</i>	<i>P</i>
1	104	0.78 \pm 0.64	0.488	0.63
2	79	0.73 \pm 0.59		
2	79	0.73 \pm 0.59	-1.802	0.08
3	27	1.07 \pm 0.92		
1	104	0.78 \pm 0.64	-1.577	0.12
3	27	1.07 \pm 0.92		

^aNumber of bouts used for each analysis.

Table 2. Welch's *t*-test of number of fish leaping per bout. Only completed bouts were used in this analysis (incomplete bouts end before fish leap). Group size is number of dolphins per group: three dolphins (one driver, two barrier dolphins), two dolphins (one driver, one barrier dolphin), or one dolphin (one driver, no barrier dolphins). There are no significant differences between groups ($P > 0.05$).

Group size	n^a	Number fish jumping per bout \pm SD	<i>t</i>	<i>P</i>
1	67	17.95 \pm 15.71	0.419	0.68
2	75	16.75 \pm 18.41		
2	75	16.75 \pm 18.41	0.329	0.743
3	32	15.63 \pm 15.09		
1	67	17.95 \pm 15.71	0.706	0.48
3	32	15.63 \pm 15.09		

^aNumber of bouts used for each analysis.

Table 3. Welch's *t*-tests of bout duration. Only completed bouts were used in this analysis. Group size is number of dolphins per group: three dolphins (one driver, two barrier dolphins), two dolphins (one driver, one barrier dolphin), or one dolphin (one driver, no barrier dolphins). There are no significant differences between groups ($P > 0.05$).

Group size	n^a	Mean bout duration, seconds \pm SD	<i>t</i>	<i>P</i>
1	94	21.16 \pm 12.71	0.928	0.35
2	90	22.47 \pm 11.37		
2	90	19.76 \pm 8.45	-1.180	0.25
3	22	21.96 \pm 7.67		
1	97	21.16 \pm 12.71	0.392	0.7
3	22	21.96 \pm 7.67		

^aNumber of bouts used for each analysis.

to line up. It is possible that the driver or barriers catch fish below the surface, which would make it a different feeding technique, but there is no evidence (such as jerking motions from dolphins as they bite and chew their prey) that this is the case.

Table 4. Two-by-two contingency tables analysis of the proportion of expected *vs.* observed for complete and incomplete bouts. Incomplete bouts do not have any aerial fish catch (no fish jumped). Group size of one has only TLFN the driver; group size of two has one driver, one barrier; and group size of three has one driver, two barriers.

Group size	Complete bouts	Incomplete bouts	<i>P</i>
1	118	16	0.11
2	97	6	
2	97	6	0.07
3	52	0	
1	118	16	0.009 ^a
3	52	0	

^aSignificant *P*-value after a Bonferroni correction.

Evidence suggests that specialists in a foraging task outperform those that do not have a specialization in the same task (reviewed in Vickery *et al.* 1991, Tinker *et al.* 2008). This study has shown that a driver dolphin does have greater catch success than the barrier dolphins regardless of group size. This is different than what was initially predicted (Gazda *et al.* 2005). Because the barrier dolphins disappeared from the study site, it is difficult to determine whether they were barrier specialists. Focal follows of barrier dolphins to clarify this are needed.

This study does not provide convincing evidence that the driver-barrier behavior fits a producer-scrounger model. The driver does not have a significant difference in catch success related to the number of barrier dolphins when only accounting for complete bouts, but when accounting for both types, success significantly decreases from a group size of three to two or one. Further, barrier dolphins do better when there are more of them, when accounting for both types of bouts. In all scenarios of the P-S model the increase in numbers of scroungers leads to a decrease in payoff to each scrounger (Giraldeau and Dubois 2008). Cooperation with role specialization still remains the best explanation for this behavior. Connor (2010) defines cooperative behavior as “that which provides a benefit to another individual (recipient), and which is selected for because the actor’s behavior yields a direct benefit from the receiver.” There are two cooperative interactions occurring: one between the barriers and one between barriers and the driver.

The first cooperative interaction is between the barrier dolphins themselves. There is a significant difference in barrier catch rates across group sizes when accounting for incomplete bouts, and two barriers were more successful at fish capture than one barrier. The barriers increase foraging benefits by coordinating their behavior with the other group members (by-product, by-product mutualism, Connor 1995). The second cooperative interaction is between the barriers and the driver. Barriers in groups of three provided a benefit to the driver by reducing the number of incomplete bouts. When accounting for incomplete bouts when testing for driver fish-capture success, there is a significant decrease in success rate as the group size decreases. Group size does not significantly relate to the number of fish leaping per bout, which when combined with the increased catch success in a larger group, means that barriers and the driver catch a higher percentage of available fish leaping per bout. Fish may jump away from one individual but towards another.

The variable of the proportion of incomplete bouts was ignored in the initial study (Gazda *et al.* 2005). If this was not accounted for here, it would lead to a conclusion

that this behavior was not necessarily cooperative, but one where barrier dolphins were opportunists. A similar shift in interpretation with the inclusion of a previously ignored variable was found in a study of African wild dogs. Hunting was not found to favor group formation until the cost of locomotion was taken into account (Creel and Creel 1995). Larger packs had more successful and shorter hunts. It is widely assumed that mullet (*Mugil cephalus*) jump to avoid predation. Larger driver-barrier groups may be able to corral fish more efficiently, and there may be some sort of "threshold" of fish school size that has to be reached before a bout can be completed. Determining how barrier dolphins relate to foraging efficiency in different sized groups (and what an appropriate measure of efficiency is) is critical to understanding the role of barriers within this behavior, as well as the impact of their removal from the system. Studies on a larger number of groups that vary in the number of barrier dolphins and where time effects can be removed are needed to clarify these issues.

ACKNOWLEDGMENTS

All work was performed under MMPA Permit no. 779-1633-02 and approved by the University of Massachusetts Boston Institutional Animal Care and Use Committee (UMB IACUC no. 2009.115). I thank field research assistants K. Davis, S. Hosford, O. Harries, E. Griffiths, I. Paynter, C. Ciarella, and C. Soden for their contributions. This research was supported by the National Geographic Society, International Fund for Animal Welfare, the American Society of Mammalogists, The Explorer's Club, the Goranson Endowment, and a grant from the School for Marine Sciences. I also thank the two anonymous reviewers that improved the quality of this Note.

LITERATURE CITED

- Anderson, C., and N. R. Franks. 2001. Teams in animal societies. *Behavioral Ecology* 12:534–540.
- Barnard, C. J., and R. Sibly. 1981. Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29:543–550.
- Caldwell, D. K. 1955. Evidence of home range of an Atlantic bottlenose dolphin. *Journal of Mammalogy* 36:304–305.
- Connor, R. C. 2010. Cooperation beyond the dyad: On simple models and a complex society. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365:2687–2697.
- 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.
- Creel, S., and N. M. Creel. 1995. Communal hunting and pack size in African wild dogs, *Lycan pictus*. *Animal Behaviour* 50:1325–1339.
- Defran, R., G. M. Shultz and D. W. Weller. 1990. A technique for the photographic identification and cataloging of dorsal fins of the bottlenose dolphin (*Tursiops truncatus*). Report of the International Whaling Commission 12:53–55.
- Estes, R. D., and J. Goddard. 1967. Prey selection and hunting behavior of the African wild dog. *The Journal of Wildlife Management* 31:52–70.
- Gazda, S. K. 2002. Evidence of role specialization among foraging bottlenose dolphins (*Tursiops truncatus*) of Cedar Key, Florida. M.S. thesis, University of Massachusetts Dartmouth, Dartmouth, MA. 49 pp.
- Gazda, S. K., R. C. Connor, R. K. Edgar and F. Cox. 2005. A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society B: Biological Sciences* 272:135–140.

- Giraldeau, L. A., and F. Dubois. 2008. Social foraging and the study of exploitative behavior. *Advances in the Study of Behavior* 38:5–1104.
- Hamilton, I. M., and L. M. Dill. 2002. Three player social parasitism games: Implications for resource defense and group formation. *The American Naturalist* 159:670–686.
- Hurtado, M. J., R. Fénelon and P. Guat. 2013. Specialization in building tasks in the mound-building mouse, *Mus spicilegus*. *Animal Behaviour* 85:1153–1160.
- Kopps, A. M., C. Y. Ackermann, W. B. Sherwin, S. J. Allen, L. Bejder and M. Krützen. 2014. Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences* 281:20133245.
- Krützen, M. 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.
- Mann, J., B. L. Sargeant, J. J. Watson-Capps, Q. A. Gibson, M. R. Heithaus, R. C. Connor and E. Patterson. 2008. Why do dolphins carry sponges? *PLOS ONE* 3: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.
- Nowacek, D. P. 1999. Sound use, sequential behavior and ecology of foraging bottlenose dolphins, *Tursiops truncatus*. Ph.D. dissertation, Massachusetts Institute of Technology/Woods Hole Oceanographic Institution. 196 pp.
- Nowacek, D. P. 2002. Sequential foraging behaviour of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, FL. *Behaviour* 139:1125–1145.
- 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.
- Quintana-Rizzo, E. 1998. Habitat use of resident and non-resident bottlenose dolphins (*Tursiops truncatus*) in the open estuarine system of the Cedar Keys, Florida. M.S. thesis, University of Florida, Gainesville, FL. 170 pp.
- Ruxton, G. D. 2006. The unequal variance *t*-test is an underused alternative to Student's *t*-test and the Mann-Whitney *U* test. *Behavioral Ecology* 17:688–690.
- Shane, S. H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. Pages 245–266 in S. Leatherwood and R. R. Reeves, eds. *The bottlenose dolphin*. Academic Press, San Diego, CA.
- Smolker, R., A. Richards, R. Connor and J. Pepper. 1992. Association patterns among bottlenose dolphins in Shark Bay, Western Australia. *Behaviour* 123:38–69.
- 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.
- Stander, P. 1992. Cooperative hunting in lions: The role of the individual. *Behavioral Ecology and Sociobiology* 29:445–454.
- 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.
- Vickery, W. L., L. A. Giraldeau, J. J. Templeton, D. L. Kramer and C. A. Chapman. 1991. Producers, scroungers, and group foraging. *American Naturalist* 137:847–863.
- Wells, R. S. 2001. Dolphin social complexity: Lessons from a long-term study and life history. Pages 32–56 in F. B. M. de Waal and P. L. Tyack, eds. *Animal social complexity: Intelligence, culture, and individualized societies*. Harvard University Press, Cambridge, MA.
- Zar, J. H. 2009. *Biostatistical analysis*. 5th Edition. Pearson, New York, NY.

Received: 29 June 2015

Accepted: 17 February 2016