Bottlenose Dolphins (*Tursiops truncatus*) Increase Number of Whistles When Feeding

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Abstract

We examined the hypothesis that dolphins increase their rate of sound production during feeding events to recruit new individuals. We recorded 135.5 min of underwater sounds from bottlenose dolphins (*Tursiops truncatus*) near Isla del Coco, Costa Rica. Data were collected from eight feeding groups and three nonfeeding groups. We classified sounds as whistles, click trains, or pulse bursts. The number of whistles per min per dolphin was higher in feeding groups than in nonfeeding groups. More whistles than click trains or pulse bursts were produced when dolphins were feeding. On the other hand, there was no difference in the proportion of each sound type produced when dolphins were not feeding. New dolphins joined the feeding events for which we recorded dolphin sounds. Results supported the hypothesis that dolphin group size increases in response to an increase in the number of whistles by conspecifics; however, confounding factors, such as the use of specific feeding calls, need to be accounted for to support the increased sound-rate hypothesis.

Key Words: feeding, sounds, *Tursiops truncatus*, bottlenose dolphin, Isla del Coco

Introduction

Group size increases during feeding events in several dolphin species (reviews by Norris & Dohl, 1980; Würsig, 1986). In Argentina, small groups of bottlenose dolphins (*Tursiops truncatus*) form larger groups to feed cooperatively (Würsig, 1979), a behavior in which dusky dolphins (*Lagenorhynchus obscurus*) also engage in the same area (Würsig & Würsig, 1980). In the Gulf of Mexico, Atlantic spotted dolphins (*Stenella frontalis*) have been observed to rapidly converge at a feeding site (Fertl & Würsig, 1995). Hypotheses to explain the adaptive value of increases in group size include enhancement of feeding efficiency and/or defense of food against other species (Acevedo-Gutiérrez, 2002; Norris & Dohl, 1980; Würsig & Würsig, 1980). The first hypothesis predicts that individual food intake will be higher with the addition of new individuals to the group. The second hypothesis predicts that the amount of food lost to other competing species will be lower with the addition of new individuals.

Hypotheses to explain the mechanism increasing group size include variations in the types or number of calls and number of leaps (Würsig & Würsig, 1980). Each of these hypotheses predicts that an increase in the variable in question will result in the arrival of new individuals to the feeding event. Most of the predictions deriving from these hypotheses remain untested, in part because prolonged observations of dolphins are difficult when they feed in murky waters or at night. At Isla del Coco, Costa Rica, however, bottlenose dolphins feed during the day in the clear waters that surround the island (Acevedo-Gutiérrez, 2002). We took advantage of this good opportunity to examine the hypothesis that new dolphins arrive to feeding events when the sound rate of the group increases.

Acoustics play an important role in the feeding behavior of cetaceans. Würsig & Würsig (1980) and Würsig (1986) hypothesized that an increase in either characteristic calls or the total number of calls is employed by dusky dolphins to recruit individuals to feeding events. Most cetacean studies have examined the relationship between specific calls and the onset of feeding events. Killer whales (*Orcinus orca*) and humpback whales (*Megaptera novaeangliae*) produce sounds associated with the initiation of coordinated feeding behaviors (D'Vincent et al., 1985; Steiner et al., 1979). Bottlenose dolphins in Scotland produce a unique feeding signal during certain times of the year that appears to recruit more dolphins to aid in the hunting effort (Janik, 2000); however, the potential role of an increased number of sounds to recruit dolphins to feeding events has not been examined. Norris et al. (1994) reported variations

in the number of calls per individual relative to behavioral context in spinner dolphins (*Stenella longirostris*); however, because spinner dolphins are nocturnal feeders, the authors were unable to establish when the dolphins were feeding. At Isla del Coco, we recorded the underwater signals of bottlenose dolphins and established whether or not they were feeding.

Isla del Coco harbors many marine predators besides bottlenose dolphins, one of which is the silky shark (*Carcharhinus falciformis*). Bottlenose dolphins and silky sharks regularly feed on the same school of fish, and dolphin food intake diminishes as the number of feeding sharks increases. Apparently in relation to this contest over food, dolphin group size increases when sharks are present (Acevedo-Gutiérrez, 2002). Hence, according to our hypothesis, the number of sounds produced by dolphins should be higher when sharks are present than when they are absent.

Materials and Methods

Data Collection
Isla del Coco (05° 32' N, 87° 04' W) is a 46-km^2 island in the eastern tropical Pacific Ocean 550 km from mainland Costa Rica. Underwater observations are possible in the area because subsurface visibility averages $16 \pm$ SD 3.5 m ($n = 164$), as measured with a Sechii disk. Bottlenose dolphins are sighted regularly around the island throughout the year and feed on epipelagic schooling fish (Acevedo, 1996; Acevedo-Gutiérrez & Parker, 2000). It is possible that dolphins also feed on buried prey as reported in other areas (e.g., Rossbach & Herzing 1997); however, we were unable to ascertain this because at Isla del Coco the water depth increases rapidly from shore. Hence, we concentrated our analysis to dolphins feeding near the surface on clumped shoals of fish (Acevedo-Gutiérrez, 2002).

We followed dolphins from a 5-m inflatable boat during 1993 and 1994. Each dolphin group sighted was considered a focal group and was followed for as long as possible to identify individual dolphins by taking photographs of their dorsal fins (Würsig & Würsig, 1977). Group-follows ended when dolphins were lost or weather conditions prevented data collection. We defined a dolphin group in two manners: (1) 10-m definition—any dolphin within 10 m (about two vessel lengths) of any other dolphin, regardless of behavior (Acevedo-Gutiérrez, 2002; Smolker et al., 1992); and (2) inclusive definition—any number of dolphins behaving in a similar manner or moving in the same direction, regardless of distance among dolphins (Shane, 1990).

We recorded sounds of both nonfeeding and feeding groups. We considered a dolphin as feeding when it pursued fish or held fish in the mouth. We considered that dolphins stopped feeding when they left the area where fish were located, remained in the area but no fish were observed, or stopped pursuing fish. The amount of time that a focal group spent feeding comprised a feeding event. Observations of groups of dolphins in which feeding was never observed were classified as nonfeeding (Acevedo-Gutiérrez, 1999, 2002).

To record dolphin sounds, we stationed the vessel within 10 m of the periphery of the group with the engine off and lowered a hydrophone to a depth that varied between 5-10 m. We used an omni-directional hydrophone with a frequency response of 0.140-14.000 kHz and sensitivity of -162 dB re 1 μPa, and a Sony TCD-15 recorder with a linear frequency response up to 20.000 kHz. Equipment settings were consistent throughout all recordings, and the upper frequencies of echolocation clicks were cut off due to the system's limited frequency response. Although several feeding and nonfeeding groups were observed, we made recordings only after we followed dolphins for at least 15 min and no other cetacean species or dolphin group (inclusive definition) were observed in the vicinity. Since there were many occasions when more than one dolphin group was simultaneously sighted, the restriction limited the amount of dolphin groups that we recorded but ensured that we could relate sounds with group size. We obtained a total of 135.5 min of recordings: feeding groups were recorded an average of $15.8 \pm$ SD 12.44 min ($n = 8$), and nonfeeding groups were recorded an average of $3.0 \pm$ SD 2.58 min ($n = 3$).

Data Analysis
Sounds Produced—Sounds from dolphins were analyzed on a PC computer with RTS, the real-time sonogram analysis program of *SIGNAL*TM (Beeman, 1990). Analysis bandwidth was 174 Hz, the display frame duration was 2.902 ms, and the dynamic range was -80 dB.

We employed *SIGNAL*TM to visually examine the dolphin sounds as real-time spectrograms while the recordings were played through a speaker. This simultaneous visual and aural monitoring allowed for a more complete analysis of the recordings; faint sounds could be categorized with spectrographic images and faint images with aural inputs (Stienessen, 1998). Based on the visual and aural outputs, the number of whistles, click trains, and burst pulses were recorded and compared between feeding and nonfeeding samples. A tonal, narrow-band signal was tallied as a whistle.

A single click consisted of a broadband signal with a rapid onset and a rapid decay. A click train was defined as a series of distinct and rapid clicks with an interclick interval of < 1 sec. A burst pulse was defined as many clicks in such rapid succession that to the human ear it was perceived as a single buzz (Caldwell & Caldwell, 1966).

We compared the number of each sound per min per dolphin relative to behavior (feeding, nonfeeding) and sound type (whistles, click trains, burst pulses) with a fixed-factors ANOVA (Zar, 1984). We were unable to ascertain which dolphin produced a sound; thus, for this analysis, we employed the inclusive definition of a dolphin group to account for all individuals producing sounds.

We compared the change in dolphin group size before and during feeding with a paired *t*-test (Zar, 1984). For this analysis, we employed the 10-m definition of a dolphin group because it was consistent with the number of dolphins feeding around the prey. We recorded feeding events on underwater video to determine the number of dolphins and shark occurrence (Acevedo-Gutiérrez, 2002). We then analyzed the number of whistles and the number of new dolphins arriving to feeding events relative to shark occurrence with a Hotelling's two-sample T^2 test (Hintze, 2001).

All sound and group size data were logarithmically transformed because they were not normally distributed and had unequal variances (Zar, 1984). Each group was considered an independent observation because all recordings were made with different individuals present (the median number of individuals identified was 53%, with an interquartile range of 14-100%) and because there was a long time between recordings (M = 25.5 days, interquartile range = 6-48 days).

Description of Dolphin Whistles—Whistles that had a good signal-to-noise ratio and that were not concurrent were examined using *Canary*™ software on a Macintosh computer (Charif et al., 1995). We described the following measurements of whistles: (1) beginning frequency, (2) end frequency, (3) minimum frequency, (4) maximum frequency, (5) duration, (6) peak time, and (7) peak frequency (Stienessen, 1998). From these data, we also described the difference between the start and end frequency, and between the minimum and maximum frequency. For this analysis, we characterized 88 whistles from three of the eight feeding groups and 26 whistles from three nonfeeding groups. We were unable to analyze more whistles because they did not have a good signal-to-noise ratio or, most commonly, because they were concurrent with one another and we were unable to differentiate among them. Because each dolphin

group was considered an independent observation and because the number of groups for which we had recordings was very small, we did not statistically compare feeding and nonfeeding whistles. To describe the whistles, we calculated the mean values for whistle parameters per group and then averaged these means across groups to produce mean values for whistles from feeding and nonfeeding dolphins.

Results

Dolphins produced more sounds during feeding than during nonfeeding events (two-way ANOVA: $F_{2, 27} = 4.35$, $p = 0.023$; Figure 1). In the units of the original data, dolphins produced 2.7 ± SD 0.70 whistles, 0.2 ± SD 0.20 click trains, and 0.8 ± SD 0.52 pulse bursts per min per dolphin during feeding events; whereas, they produced 0.4 ± SD 0.08 whistles, 0.4 ± SD 0.32 click trains, and 0.4 ± SD 0.32 pulse bursts per min per dolphin during nonfeeding events. There was also a significant interaction between the type of sound and the
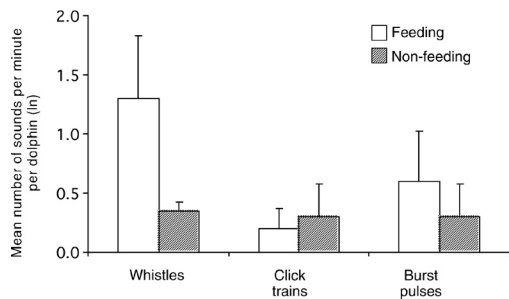

Figure 1. Number of whistles, click trains, and burst pulses produced by bottlenose dolphins relative to a behavioral feeding context at Isla del Coco, Costa Rica (mean + SD); data were transformed to natural logarithms.

behavioral context (two-way ANOVA: $F_{2, 27} = 4.38$, $p = 0.022$; Figure 1). Whistles were predominant during feeding events; however, no single type of sound predominated during nonfeeding events.

New dolphins joined the feeding events for which we recorded sounds (paired Student's *t*-test: $t_7 = 3.31$, $p = 0.013$). In the original units, the number of dolphins within 10 m of a feeding event averaged 4.0 ± SD 0.46 dolphins at the start of the feeding event and 6.7 ± SD 0.61 dolphins when the event ended.

Sharks did not have a significant effect on the number of dolphins that joined a feeding event or the number of whistles per minute per dolphin during feeding events; however, the power of the test was very low (Hotelling's two-sample T^2 test:

$T^2_{2, 6} = 13.0$, $p = 0.056$, $n = 8$; Figure 2). In the units of the original data, dolphins produced 3.5 ± SD 0.60 whistles per min per dolphin when sharks were present and 1.5 ± SD 0.55 whistles per min per dolphin when sharks were absent. The number
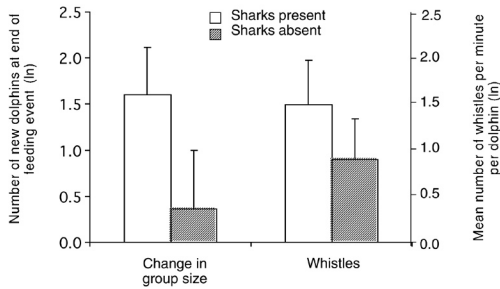

Figure 2. Changes in dolphin group size and number of whistles produced by bottlenose dolphins during feeding relative to shark occurrence at Isla del Coco, Costa Rica (mean ± SD); data were transformed and values are natural logarithms.

of new dolphins joining a feeding event averaged 3.9 ± SD 0.69 dolphins when sharks were present ($n = 5$) and 0.4 ± SD 0.89 dolphins when sharks were absent ($n = 3$).

Whistles by feeding and nonfeeding dolphins were very similar; typically < 1 sec and had start and end frequencies close to 10,000 Hz (Table 1).

Discussion

Bottlenose dolphins at Isla del Coco increased their sound rate when they were feeding, and whistles were the sounds most frequently produced. In addition, new dolphins arrived at the onset of feeding events. Whistles are employed by dolphins to communicate with one another (reviews by Herman & Tavolga, 1980; Richardson et al., 1995). Dolphins apparently employ the

characteristics of individual whistles to convey information (e.g., to function as cohesion calls) (Janik & Slater, 1998; Smolker et al., 1993). Although conclusive data are needed to show that the rate of sound production also serves a similar function, circumstantial evidence suggests that this is the case. Terrestrial social carnivores increase the number of calls to attract more individuals. For instance, female spotted hyenas (*Crocuta crocuta*) vocalize more often to rally group members and to defend communal resources (East & Hofer, 1991). In marine systems, the number of sounds produced by spinner dolphins was positively correlated with the distance between group members (Norris et al., 1994), and dusky dolphins apparently whistled more often when they were feeding than when they were searching for prey (Würsig, 1986).

Confounding factors need to be addressed to support the hypothesis conclusively that rate of sound production influences dolphin group size. Würsig & Würsig (1980) indicated that the number of leaps of feeding dusky dolphins or the large number of birds associated with feeding might be used as cues by other dolphins to join these events. Although the number of seabirds associated with dolphins in our study site was very small during some feeding events, new dolphins still joined those events (Acevedo-Gutiérrez, 2002). Thus, it is unlikely that seabirds were a cue informing dolphins about the occurrence of prey. The aerial behavior of dolphins at the study site, however, increased when dolphins began to feed (Acevedo-Gutiérrez, 1999). Thus, further observations are necessary to discriminate between number of leaps and number of whistles as cues informing dolphins of a feeding event.

Silky sharks feed on a variety of fish and squid (Branstetter, 1987; Compagno, 1984) and are not considered a predator of dolphins (Heithaus, 2001); however, they are comparable in size to bottlenose dolphins: adult silky sharks range from 2.1 to 3.3 m in length and from 64 to 274 kg in

Table 1. Descriptors of whistles from bottlenose dolphins at Isla del Coco relative to behavioral context

Behavioral context	Duration (s)	Peak time (s)	Start freq. (Hz)	End freq. (Hz)	Bandwidth start-end	Minimum freq. (Hz)	Maximum freq. (Hz)	Bandwidth high-low	Peak freq. (Hz)
Nonfeeding	n = 3 groups, 26 whistles								
μ =	0.380	0.530	10,176	8,911	1,265	7,506	12,409	4,903	8,440
SD =	0.294	0.414	4,821	3,721	4,790	3,015	4,071	3,288	3,062
Feeding	n = 3 groups*, 88 whistles								
μ =	0.660	1.770	12,819	9,390	3,429	8,511	13,975	5,464	9,350
SD =	0.407	1.544	2,815	2,546	3,765	1,808	2,632	3,011	2,016

*We were able to record whistles matching the criteria for numerical description (see "Materials and Methods") for three of eight groups.

weight (Branstetter, 1987; Garrick et al., 1964), while adult bottlenose dolphins range from 2.0 to 3.8 m in length and from 110 to 282 kg in weight (Wells & Scott, 1999). Silky sharks thus appear to represent a formidable adversary of dolphins when trying to gain access to food. At Isla del Coco, dolphin food intake diminished as the number of feeding sharks increased, and the number of dolphins was negatively correlated with the number of sharks during feeding events (Acevedo-Gutiérrez, 2002).

If our hypothesis is correct, feeding dolphins should remain silent when there are no sharks in the area and whistle more frequently when there are sharks around. The results provide evidence consistent with such a hypothesis. Dolphins produced more whistles and new dolphins arrived when sharks were present, while whistle production and changes in group size remained constant when sharks were absent. Hence, they could be interpreted as indicative of feeding dolphins increasing the production of whistles to recruit more dolphins and limit the number of sharks feeding on the same prey patch. Unfortunately, sample size was not large enough, and it is unclear if new dolphins joined a feeding event because they were actively recruited or passively cued by soniferous dolphins.

It is unknown if dolphins at Isla del Coco produce unique feeding calls because our limited data prevented testing if feeding and nonfeeding whistles were different. Delphinids produce different sounds relative to behavioral context (Herzing, 1996; McCowan & Reiss, 1995; Norris et al., 1994; Weilgart & Whitehead, 1990). In Scotland, bottlenose dolphins produce a characteristic feeding call (Janik, 2000). Consequently, additional data are necessary to rule out the possibility that new dolphins at the island were cued by specific feeding calls.

In conclusion, our results provide evidence that the rate of whistling may represent an important causative mechanism by which group size is increased during feeding events; however, other mechanisms, such as number of leaps or a specific feeding call, may also be at work, thus, the question of whether the increase in group size is intentional or unintended remains unresolved.

Acknowledgments

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