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SURFACE BEHAVIOR OF BOTTLENOSE DOLPHINS IS RELATED TO SPATIAL ARRANGEMENT OF PREY

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ABSTRACT

We tested the hypothesis that spatial arrangement and movements of bottlenose dolphins (*Tursiops truncatus*) are related to the spatial arrangement of their prey. From 65 groups we: (1) classified feeding behavior of dolphins according to spatial arrangement and movements of individuals; (2) assessed spatial arrangement and location of prey from direct observations, numbers of associated seabirds, and echosounder recordings; and (3) related feeding behavior of dolphins to spatial arrangement and location of prey. Four feeding categories were defined from cluster and principal component analyses: (1) moving rapidly with no diving, (2) milling with no diving, (3) diving in several locations, and (4) diving in one location. These feeding categories were related to spatial arrangement and location of prey.

Key words: feeding, prey location, *Tursiops truncatus*, bottlenose dolphins, behavior.

The feeding behavior of delphinids has been predominantly described in relation to bottom topography, water depth, and other environmental variables (*e.g.*, Evans 1974, Hanson and Defran 1993, Hoelzel 1993, reviews by Würsig 1986, Shane 1990). However, the accessibility and behavior of prey largely explain feeding activity in aquatic predators (*e.g.*, Savino and Stein 1982, Croxall *et al.* 1985, Rahel and Stein 1988). Observations of feeding dolphins suggest that direction of movement, distance between individuals, and frequency of diving, among other variables, are influenced by the type, spatial arrangement, and location of prey (Thomas and Felleman 1988, Similä 1997, reviews by Würsig 1986, Shane 1990). In Argentina, bottlenose dolphins (*Tursiops truncatus*) feed individually in a single-line formation near shore and

move in a line-abreast formation far from shore apparently to feed on shoaling fish (Würsig and Würsig 1979). Similarly, populations of killer whales (*Orcinus orca*) that prey on fish have different feeding behavior than populations that prey on marine mammals (Hoelzel 1993, Baird and Dill 1995). However, the relationship between dolphin feeding behavior, and spatial arrangement and location of prey has not been quantified. In part, this is because prolonged observations are difficult when the predator moves constantly, hunts at depth in murky waters, or feeds at night. At Isla del Coco, Costa Rica, bottlenose dolphins feed during the day in the clear, nearshore waters which surround the island (Acevedo-Gutiérrez 1997). We took advantage of this unique opportunity to test the hypothesis that spatial arrangement and movements of bottlenose dolphins are related to spatial arrangement and location of prey. We classify feeding behavior of dolphins based on spatial arrangement and movements of individuals, assess spatial arrangement and location of prey during feeding events, and relate feeding behavior of dolphins to spatial arrangement and location of prey.

Methods

Isla del Coco (05°32′N, 87°04′W) is a 46-km^2 oceanic island in the eastern tropical Pacific Ocean 550 km from mainland Costa Rica. Underwater observations are possible around the island because subsurface visibility averages 16 ± 3.5 m (n = 164). Bottlenose dolphins are regularly sighted around the island throughout the year (Acevedo 1996). They hunt as a group on epipelagic shoaling fish and have not been observed feeding on nearshore prey (Acevedo-Gutiérrez 1997).

Sampling Procedures

We conducted 296 boat surveys during 1993 and 1994 from a 5-m inflatable boat. Each dolphin group sighted was considered a focal group and followed for as long as possible to describe behavior. Group-follows ended when dolphins were lost or weather conditions prevented data collection. A dolphin group was defined based on the 10-m chain-rule, which states that any dolphin within 10 m (about two vessel lengths) of any other dolphin is considered part of the same group (Smolker *et al.* 1992). When a focal group split, we alternated between staying with the group closest to the research vessel and following the group moving away from the area. Focal groups were considered independent observations because the majority of the 765 individual dolphins identified were sighted only once.

Sampling and recording of behavior closely followed the methods described in Acevedo-Gutiérrez (1999). One observer (AA) scan-sampled (Altmann 1974, Mann 1999) five previously defined parameters when dolphins were at the surface (Table 1). At the same time, another observer recorded data on location and spatial arrangement of prey (see below). A set of observations

Table 1. Parameters recorded to describe behavior at surface of bottlenose dolphins at Isla del Coco.

Parameter	Description
Packing of individuals	Maximum number of individuals surfacing together within one body length of each other.
Orientation	Yes: The focal group was heading in the same general direction. No: Otherwise.
Speed	Based on surfacing patterns of the focal group. Slow: The focal group did not create a wake while surfacing. Regular: The focal group produced a wake while surfacing. Fast: The focal group leapt clear of the water while moving, termed porpoising.
Diving	A dive was defined as a period of time underwater (>90 sec), noticeably longer than the pattern immediately before. Yes: The focal group dived as a group. No: The focal group did not dive as a group or did not dive at all.
Aerial behavior	Any leaps, slaps at the water, splashes, or heads completely above the water: Yes: Present. No: Not present.

that included data for all five parameters and the prey was considered one behavioral bout; a change in any of the parameters initiated a new bout.

Feeding Behavior of Dolphins

We classified dolphin behavior as feeding when dolphins were pursuing fish or holding fish in their mouths. We considered that dolphins stopped feeding when they left the area where fish were located, when they remained in the area but no fish were observed, or when they did not pursue fish anymore. The amount of time that a focal group spent feeding comprised a feeding event.

We recorded 126 feeding bouts by 65 focal groups. To ensure statistical independence of observations we randomly selected one bout for each group for analysis. Cluster analysis (Ward's method and percent disagreement distances: Jackson 1983, Manly 1986, Statsoft 1994) allowed us to categorize the spatial arrangement and movement of feeding dolphins based on the five parameters recorded (Table 1). Prior to clustering, all parameters were standardized to a mean of zero and a standard deviation of one. Categorical parameters were treated as dummy variables (Jackson 1983). The most inclusive clusters, separated by distances of 40 or more, were considered different categories.

Each category was then described based on the five parameters, complemented with field notes. The five parameters were reduced to a smaller number of variables with principal components analysis (PCA) (Jackson 1983, Manly 1986). Kolmogorov-Smirnov tests (Zar 1984) indicated that the distribution of the components obtained after PCA was not normal. Therefore, each component was compared among dolphin feeding categories with Kruskal-Wallis analysis of variance (Zar 1984). We used the median and interquartile range (Med, IQ) as descriptors of central tendency.

Location and Spatial Arrangement of Prey

Location of prey was described as near the surface (= 10 m) or at depth (>10 m). The spatial arrangement of fish was defined as scattered or clumped. Prey was clumped if found in a tight, immobile shoal and scattered if found in a loose, mobile shoal. We utilized three different indices to estimate spatial arrangement and location of prey during feeding events (Table 2). (1) One person observed prey from the boat or while snorkelling underwater to record its spatial arrangement and location. (2) Seabirds were utilized as indirect indicators of prey location in the water column. Number of feeding birds associated with dolphins was estimated for each bout. Seabirds were considered to be feeding in association with the dolphins when seen plunging or pecking for prey within 10 m (about four dolphin lengths) of any surfacing dolphin. This definition excluded bouts in which birds were seen either following dolphins, sitting in the water next to dolphins, or feeding at distance from the dolphins. The number of seabirds feeding per bout was compared among feeding activities with fixed-effects ANOVA (Zar 1984). (3) Recordings were taken during feeding events with a Lowrance X-16 echosounder (20° long-stem through-hull transducer, 200 kHz frequency, and 200–1,000-msec pulse length). The vessel moved at idle speed along a straight line for 1 min through what was considered the center of activity. Echosounder transects were not taken when dolphins were feeding near the surface, to avoid disrupting their behavior.

RESULTS

Feeding Behavior of Dolphins

Four feeding categories were defined based on spatial arrangement and movement of dolphins: (1) moving rapidly with no diving, (2) milling with no diving, (3) diving in scattered locations, and (4) diving in one location (Table 3). Two PC's were obtained from the PCA and accounted for 61.9% of the variability in the 65 bouts. PC1 included, along the positive region, bouts in which frequency of diving increased and speed of movements decreased. Along the negative region, it included bouts in which frequency of diving decreased and speed of movements increased (Table 4). PC2 characterized, along the positive region, bouts in which frequency of aerial behavior and

Table 2. Information used to infer spatial arrangement and location of prey at Isla del Coco.

Variable	Estimate	Index		
		Echosounder	Sea birds	Observations above and below water
Location				
	Prey near the surface	Not utilized	Feeding (0–10 m)	Prey observed (0–10 m)
	Prey at depth	Actual depth	Not feeding (>10 m)	Prey observed deeper than 10 m or dolphins seen coming from below that depth with prey in mouth
Spatial arrangement				
	Prey scattered	Continuous fish recordings during transect	Moving in various directions Feeding in several locations	Fish swimming in small aggregations or as individuals
	Prey clumped	Fish recordings constrained to one location	Feeding only in one location	Fish aggregated into a tight ball

Table 3. Feeding categories based on spatial arrangement and movement of bottlenose dolphins at Isla del Coco.

Context/category	Description
Feeding	Dolphins pursuing a holding prey in their mouths.
Moving rapidly with no diving.	Group moving at regular or fast speeds, porpoising present, with no diving. Usually heading in the same direction. Leaps or slaps on the water. Individuals rarely surfacing close together.
Milling with no diving.	Group surfacing in one location (<20 m wide). Heading in different directions without diving. Leaps or slaps on the water. Moving at regular speed but sometimes porpoising. Individuals typically surfacing close together in trios.
Diving in scattered locations.	Group surfacing in various locations within a large area (>50 m wide). Diving at the same time with no leaps or slaps on the water. At times heading in the same direction. Individuals seldom surfacing close together.
Diving in one location.	Group surfacing in one location (<20 m wide). Heading in different directions and diving at different times. Moving at regular speed. Leaps or slaps on the water. Three to six individuals surfacing close together.

Table 4. Loadings of principal components for parameters describing the behavior at surface of bottlenose dolphins at Isla del Coco.

Parameter	Component 1	Component 2
Packing of individuals	0.028	0.485
Orientation	−0.231	−0.403
Speed	−0.460	0.100
Diving	0.416	0.054
Aerial behavior	−0.256	0.731
Variability explained	39.97%	29.77%
Main parameter explaining component	Positive values: Diving	Positive values: Aerial behavior Packing
	Negative values: Speed	Negative values: Orientation

packing of individuals increased as orientation between individuals decreased. Along the negative region, it characterized bouts in which frequency of aerial behavior and packing of individuals decreased as orientation between individuals increased (Table 4). There were significant differences in behavioral parameters between the four feeding categories (Kruskal-Wallis ANOVA, PC1: $H_{3,65} = 52.62$, $P < 0.001$; PC2: $H_{3,65} = 45.44$, $P < 0.001$; Fig. 1).

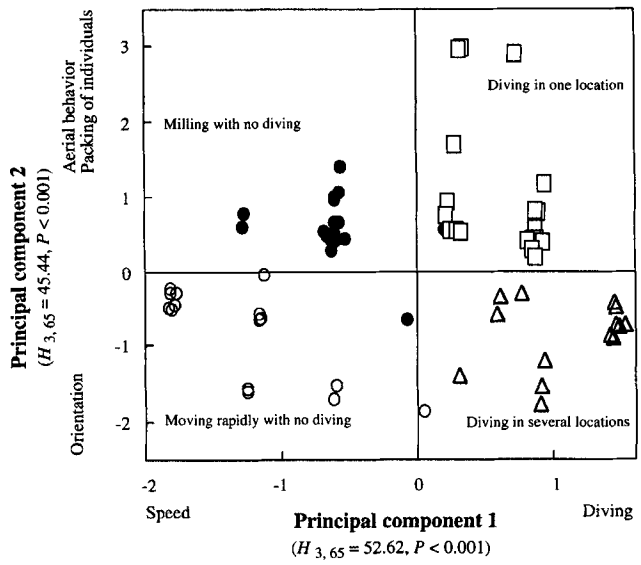

Figure 1. Principal components representing different linear combinations of behavioral parameters in bottlenose dolphins at Isla del Coco.

Location and Spatial Arrangement of Prey

Dolphin feeding categories were related to spatial arrangement and location of prey. Dolphins fed on clumped prey while milling with no diving or while diving in one location. They fed on scattered prey while moving rapidly with no diving or while diving in several locations (Table 5). Based on direct observations and frequency of occurrence of associated seabirds, prey were scattered when dolphins were moving rapidly with no diving and clumped when dolphins were milling with no diving (Chi-square test: $\chi^2_1 = 28.11$, $n = 32$, $P < 0.001$, direct observations; $\chi^2_1 = 28.11$, $n = 32$, $P < 0.001$, seabirds; Table 5).

Dolphins were always observed feeding within 10 m of the surface while moving rapidly with no diving or while milling with no diving. They fed at depth while diving in one or several locations (Table 6). Results were significantly different for both direct observations and frequency of occurrence of feeding seabirds associated with dolphins ($\chi^2_3 = 65.00$, $n = 65$, $P < 0.001$, direct observations; $\chi^2_3 = 18.15$, $n = 65$, $P < 0.001$, seabirds; Table 6).

The largest numbers of feeding seabirds were associated with dolphins moving rapidly with no diving or milling with no diving (Table 6). The smallest numbers were recorded while the dolphins were diving in one or several locations (Table 6). The number of associated seabirds per bout differed significantly among the four feeding activities (Kruskal-Wallis ANOVA: $H_{3,65} = 18.43$, $P < 0.001$). Seabird species associated with dolphins always included red-footed (*Sula sula*) and brown (*S. leucogaster*) boobies, and great frigatebirds (*Fregata minor*).

Discussion

The correlations between dolphin feeding and movements and the spatial arrangement of their prey match one's intuitive expectations. When dolphins were moving rapidly without diving, prey were scattered near the surface; when dolphins were milling without diving, prey were clumped near the surface; when dolphins were diving in scattered locations, prey were scattered at depth; and when dolphins were diving in one location, prey were clumped at depth.

Qualitative descriptions had previously indicated that dolphins that fed on schooling fish would search for prey while moving in the same direction, in a line-abreast formation at a variable pace (Tomilin 1957, Evans 1974, Würsig and Würsig 1980, Norris and Dohl 1980). The surface behavior of feeding delphinids also varies according to type and distribution of prey (reviews by Würsig 1986, Shane 1990); however, no study had demonstrated such a link. This study demonstrates that there is such a link and that the behavior at the surface of feeding bottlenose dolphins can potentially serve as an indicator of the spatial arrangement of their prey. However, it is unclear if there is a link between surface and underwater behavior of dolphins outside of the feeding

Table 5. Frequency of bouts cross-classified by dolphin feeding category and spatial arrangement of prey at Isla del Coco.

Feeding category	Number of bouts	Index	Prey spatial arrangement (bouts)	
			Scattered	Clumped
Moving rapidly with no diving	16	Echosounder	—	—
		Sea birds	16	0
		Observations	16	0
Milling with no diving	17	Echosounder	—	—
		Sea birds	0	17
		Observations	0	17
Diving in several locations	14	Echosounder	3	0
		Sea birds	—	—
		Observations	12	0
Diving in one location	18	Echosounder	0	6
		Sea birds	—	—
		Observations	0	14

Table 6. Frequency of bouts cross-classified by dolphin feeding category and location of prey at Isla del Coco.

Feeding category	Number of bouts	Index	Prey location (bouts)		Feeding sea birds (Med, IQ)
			Surface (0–10 m)	Depth (>10 m)	
Moving rapidly with no diving	15	Echosounder	—	0	
		Sea birds	12	3	100, 10–250
		Observations	15	0	
Milling with no diving	17	Echosounder	—	0	
		Sea birds	15	2	100, 20–200
		Observations	17	0	
Diving in several locations	14	Echosounder	0	3 (20–60 m)	
		Sea birds	3	11	0, 0–6
		Observations	0	14	
Diving in one location	18	Echosounder	0	6 (15–45 m)	
		Sea birds	7	11	0, 0–100
		Observations	0	18	

context. It is also unclear whether our results are applicable to other dolphin populations.

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