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Alejandro Acevedo-Gutiérrez

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AERIAL BEHAVIOR IS NOT A SOCIAL FACILITATOR IN BOTTLENOSE DOLPHINS HUNTING IN SMALL GROUPS

ALEJANDRO ACEVEDO-GUTIÉRREZ

Marine Mammal Research Program, 4700 Avenue U, Building 303, Texas A&M University at Galveston, Galveston, TX 77551-5923

Present address: Institute of Marine Sciences, A316 Earth and Marine Science Building, University of California, Santa Cruz, CA 95604

Two hypotheses that could explain the function of aerial behavior in dolphins feeding in large groups are: it is a social facilitator that establishes social bonds before or after a hunt, or it aids in capture of prey. To test which hypothesis best explains the function of aerial behavior in bottlenose dolphins (*Tursiops truncatus*) that hunt in small groups, I described the behavior of dolphins based on a set of predefined parameters, estimated occurrence of aerial behavior in groups, estimated frequency of aerial behavior per dolphin, described types of aerial behavior, and related these variables to size of group and behavioral contexts: before-feeding, feeding, after-feeding, and non-feeding. Data were collected from 111 groups. Behavioral parameters were significantly different during feeding, with dolphins moving faster and engaging in aerial behavior more often than in any other context. Aerial behavior per dolphin and occurrence of aerial behavior were highest during feeding. Results did not support the social-facilitation hypothesis. Although the aid-in-capture-of-prey hypothesis was favored, data showing a positive correlation between intake of food by individuals and aerial behavior per dolphin are required as conclusive evidence.

Key words: *Tursiops truncatus*, bottlenose dolphin, aerial behavior, feeding, Isla del Coco

In social carnivores, intragroup interactions before feeding are important to alert individuals and prepare the group for hunting activities (Creel and Creel, 1995; Estes and Goddard, 1967). In dolphins, this socializing activity includes aerial behaviors, such as leaps and slaps on the water's surface (Saayman and Tayler, 1979; Shane, 1990; Slooten, 1994). Two hypotheses have been proposed to explain the function of aerial behavior of dolphins in relation to feeding: it is a social facilitator that reaffirms social bonds (Norris and Dohl, 1980; Norris et al., 1994) and it aids in capture of prey (Würsig and Würsig, 1980). Although the two hypotheses are not mutually exclusive, they make different predictions. The social-facilitation hypothesis of Norris and Dohl (1980) predicts that aerial behavior should increase with size of group because there are more dolphins with which to establish bonds. Aerial behavior also should increase

before feeding, to establish bonds and prepare individuals before hunting, or after feeding, to strengthen bonds after a hunt. The aid-in-capture-of-prey hypothesis of Würsig and Würsig (1980) predicts increases in aerial behavior during feeding, and different types of aerial behavior during feeding than before or after feeding.

In Hawaiian spinner dolphins (*Stenella longirostris*), Norris et al. (1994) found peaks in aerial behavior before a hunt, thus, supporting the social-facilitation hypothesis. In bottlenose dolphins (*Tursiops truncatus*) in South Africa and in dusky dolphins (*Lagenorhynchus obscurus*) in Argentina, aerial behavior increased after a feeding episode ended, thus, also supporting the social-facilitation hypothesis (Saayman et al., 1973; Würsig and Würsig, 1980). However, the same population of dusky dolphins also increased aerial behavior during feeding (Würsig and Würsig,

1980), thus, supporting the aid-in-capture-of-prey hypothesis. Although the three species of dolphins differ in their hunting tactics (Saayman et al., 1973; Würsig et al., 1991), they regularly feed in groups of >50 individuals (Norris and Dohl, 1980; Saayman et al., 1973; Würsig and Würsig, 1980). To determine which hypothesis best explains the function of aerial behavior in a population that hunts in small groups, I studied aerial behavior of bottlenose dolphins around Isla del Coco, Costa Rica. At Isla del Coco, bottlenose dolphins hunt communally on epipelagic schooling fishes (Acevedo-Gutiérrez, 1997). Size of groups increases modestly at onset of feeding to an average of 9.3 dolphins (A. Acevedo-Gutiérrez and N. Parker, in litt.). Therefore, this is an ideal population in which to examine the function of aerial behavior as a social facilitator, or as an aid in capture of prey by dolphins that hunt in small groups.

MATERIALS AND METHODS

Isla del Coco (05°32'N, 87°04'W) is an isolated volcanic island ca. 500 km SW of Costa Rica. The island is small (23 km circumference, 46 km²) and rises 575 m above mean sea level (Castillo et al., 1988). The depth of Sechii disk, a measure of transparency of water, averages 15.9 m \pm 3.5 SD ($n = 164$) 400 m from shore, making underwater observations of dolphins feasible.

During February–August 1993 and November 1993–July 1994, non-random surveys were conducted from a 5-m, outboard-powered, skiff. Surveys were conducted an average of 5 days/week, with a minimum of 15 surveys/month. An effort was made to circumnavigate the island each day of the survey; however, research was concentrated on the north side of the island due to predominant winds from the southwest.

Each group of dolphins sighted was considered a focal group and followed for as long as possible while identifying individual dolphins (Würsig and Würsig, 1977) and recording location, size of group, and aerial behavior. Group-follows ended ad libitum (Altmann, 1974) when dolphins were lost or weather conditions prevented data collection. A group of dolphins was defined based on the 10-m chain-rule (Smolker

et al., 1992), any dolphin within 10 m (about two vessel lengths) of any other dolphin was considered part of the same group. Due to fluidity of dolphin groups, individual members of each focal group were continuously changing. When a focal group split, I alternated between staying with the group closest to the research vessel and following the group moving away from the area. Because most of the 765 individual dolphins identified thus far at Isla del Coco were sighted only once (A. Acevedo-Gutiérrez, in litt.), each focal group was considered an independent observation.

I scan-sampled (Altmann, 1974; Mann, 1999) six previously defined parameters when dolphins were at the surface (Table 1). This was possible because size of focal groups was typically <14 dolphins. I avoided re-sampling individuals within a surfacing period by keeping track of their positions while at the surface. A set of observations that included data for all six parameters was considered one behavioral bout; a change in any of the parameters initiated a new bout. Thus, duration and characteristics of each bout were variable and dependent on behavior at the surface. This departure from the standard definition of a bout (Martin and Bateson, 1986) was necessary because a standard sampling procedure would have missed recording behavior when dolphins were observable. The assumption of this protocol is that behavior at surface was an unbiased sample of below-water activities (Baird and Dill, 1996). Opportunistic underwater observations and observations of dolphins below the surface from the vessel confirmed the validity of this assumption.

I defined four behavioral contexts: pre-feeding, feeding, post-feeding, and non-feeding. I classified a behavioral bout as feeding as soon as fish were observed near dolphins (<100 m), and dolphins were either pursuing fish or holding them in their mouths (Acevedo-Gutiérrez, 1997). All bouts prior to a feeding bout were classified as pre-feeding. Bouts were classified as post-feeding when dolphins left the area where fish were located, when they remained in the area but no fish were observed, or when they did not continue pursuing fish. Bouts from groups of dolphins in which feeding was not observed were classified as non-feeding. They were included in the analysis to provide a baseline level of aerial activity in the population.

I included in the analysis 288 behavioral

TABLE 1.—Parameters recorded to describe behavior at the surface of bottlenose dolphins at Isla del Coco, Costa Rica.

Parameter	Description
Size of subgroups	Maximum number of dolphins in the largest subgroup. A subgroup was the number of individuals surfacing together within one body length of each other.
Orientation	Yes, all or most subgroups were heading in the same general direction; no, otherwise.
Speed	Based on surfacing patterns of each subgroup: slow, subgroups did not create a wake while surfacing; regular, subgroups produced a wake while surfacing; fast, subgroups leaped clear of the water while moving.
Diving	A dive was defined as a period of time underwater (>90 s), noticeably longer than the pattern immediately before: yes, subgroups dived as a group; no, subgroups did not dive as a group or did not dive at all.
Synchrony of diving	Synchronous, subgroups dived at same time; asynchronous, subgroups did not dive at the same time.
Aerial behavior	Any leaps, slaps at the water, splashes, or head completely above the water (nose-outs): yes, present; no, not present.
Size of group	Any dolphin within 10 m of another dolphin was considered part of the same group. This variable was not employed to describe dolphin behavior but to correlate with number of leaps, slaps, and nose-outs.

bouts from 76 feeding groups and 89 bouts from 35 randomly selected non-feeding groups that included more than one individual. No more than five bouts from each focal group were employed to avoid over representing any group. Groups were observed an average of 56.0 ± 46.4 min ($n = 111$ groups), with a minimum observation time of 7 min. Behavioral bouts lasted an average of 8.7 ± 11.6 min ($n = 377$ bouts). Calculations were performed with the software Statistica, Version 4.1 (Statsoft, Inc., 1994).

I employed principal components analysis (PCA) with varimax rotation (Jackson, 1983; Manly, 1986) to reduce number of behavioral parameters (Table 1) from each bout to a smaller number of components. Categorical behavioral parameters (i.e., orientation, diving, synchrony and aerial behavior) were treated as dummy variables. Kolmogorov-Smirnov tests (Zar, 1984) indicated that the distribution of principal components obtained after PCA was not normal. Therefore, each component was compared among the four behavioral contexts with Kruskal-Wallis analysis of variance (ANOVA—Zar, 1984), with median and interquartile range (M , IQ) reported as descriptors of central tendency. Because I was interested in differences between all four contexts, post-hoc, non-parametric, multiple comparisons were conducted for these ANOVA-fixed-effects models (Zar, 1984).

I used a Spearman's coefficient of rank cor-

relation (Zar, 1984) to estimate for each context the relationship between size of group and principal component indicative of the occurrence of aerial behavior in a bout. Due to a few bouts for which size of group was not assessed, size of samples in this section was slightly smaller than the one employed in previous analyses.

I employed a log-likelihood ratio test (Zar, 1984) to compare the proportion of bouts with and without aerial behavior between the four behavioral contexts. To estimate frequency of aerial behavior per dolphin, I recorded number of slaps, leaps, and nose-outs per bout and divided it by number of dolphins in the group. Aerial events that were difficult to quantify, such as splashes and roll-overs, were not included in this analysis. Because I was able to estimate number of slaps, leaps, and nose-outs in a small number of bouts, size of samples were small and varied among behavioral contexts. Bouts analyzed belonged to different focal groups. Duration of bouts in which I recorded aerial behavior per dolphin was not different among the four behavioral contexts (Kruskal-Wallis ANOVA, $H = 1.13$, $d.f. = 3, 41$, $P = 0.771$). Median duration of a bout was 7 min ($IQ = 4-12$ min, $n = 41$ bouts). I also correlated size of group with aerial behavior per dolphin for each behavioral context with a Spearman's coefficient of rank correlation (Zar, 1984), and reported the power of the test for $\alpha = 0.05$ if the null hypothesis was not rejected and size of sample was small.

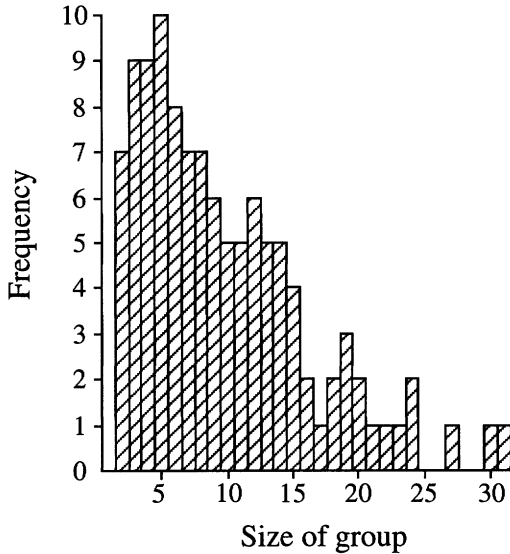


FIG. 1.—Frequency distribution of number of bottlenose dolphins per group at Isla del Coco, Costa Rica.

Researchers have recorded type of leap (Würsig and Würsig, 1980) or frequency of leaps (Saayman et al., 1973) when studying aerial behavior of dolphins. I classified leaps based on their re-entry into the water as clean and noisy and recorded the proportion of bouts with clean-entry leaps to those with noisy-entry leaps. Due to small samples, I combined the two types of leaps into one class and employed a log-likelihood test (Zar, 1984) to compare number of bouts with leaps and number of bouts with any other form of aerial behavior between the four contexts.

RESULTS

Bottlenose dolphins typically were observed in groups numbering <14 individuals. Size of group averaged 9.8 ± 6.5 dolphins, median size of group was eight individuals ($IQ = 5\text{--}13$ dolphins), and maximum size of group was 31 individuals ($n = 111$ groups; Fig. 1).

Two PCs accounted for 54.9% of variability in behavioral parameters, with PC1 measuring occurrence of aerial behavior. PC1 included, along the positive region, bouts in which speed of movements and

TABLE 2.—Loadings of principal components for the parameters describing behavior at the surface of the bottlenose dolphins at Isla del Coco, Costa Rica.

Parameter	Component 1	Component 2
Size of subgroups	0.135	-0.511
Orientation	0.046	0.564
Speed	-0.417	0.138
Synchrony	0.273	0.253
Diving	0.407	-0.205
Aerial behavior	-0.281	-0.227
Variability explained	33.15%	21.77%

frequency of aerial behavior decreased as frequency and synchrony of diving increased. Along the negative region, it included bouts in which speed of movements and frequency of aerial behavior increased as frequency and synchrony of diving decreased (Table 2). PC2 characterized, along the positive region, bouts in which number of dolphins in subgroups decreased as orientation between subgroups increased. Along the negative region, it characterized bouts in which number of dolphins in subgroups increased as orientation between subgroups decreased (Table 2).

There was no significant difference in behavioral parameters during the three behavioral contexts: before, after, and non-feeding. However, during feeding, behavioral parameters were significantly different (PC1, $H = 66.57$, $d.f. = 3$, 377 , $P < 0.001$; PC2, $H = 11.41$, $d.f. = 3$, 377 , $P = 0.001$; Fig. 2). When feeding, dolphins moved faster, headed in different directions more frequently, engaged in aerial behavior more often, and dived less frequently than in any other context (Fig. 2). During before, after, and non-feeding, dolphins were more oriented, swam at regular speed, dived more often, and displayed fewer aerial behavior than when feeding (Fig. 2). Non-parametric multiple comparisons indicated that feeding bouts were significantly different for PC1 (before feeding, $Q = 5.32$, $d.f. = 4$, $P < 0.001$; after feeding, $Q = 7.13$, $d.f. = 4$, $P < 0.001$; non-feeding, $Q = 6.29$, $d.f. = 4$,

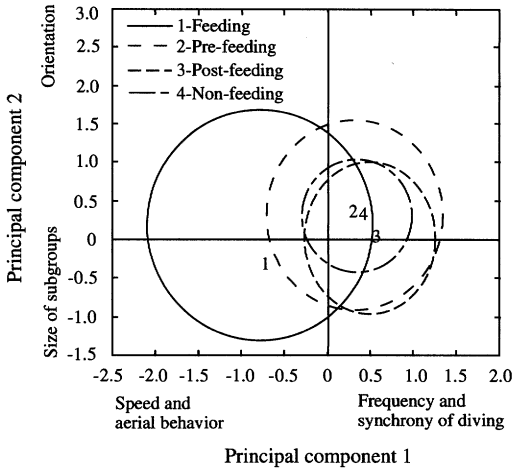


FIG. 2.—Principal components representing different linear combinations of behavioral parameters in bottlenose dolphins at Isla del Coco, Costa Rica. Boundary of ellipse indicates interquartile range, and number inside ellipse indicates location of median.

$P < 0.001$). However, feeding bouts were only significantly different from non-feeding bouts for PC2 (non-feeding, $Q = 3.03$, $d.f. = 4$, $P < 0.02$). There was no significant difference between before, after, and non-feeding for either of the two components (PC1, $Q < 1.34$, $d.f. = 4$, $P > 0.50$; PC2, $Q < 2.27$, $d.f. = 4$, $P > 0.10$).

During feeding and non-feeding, dolphins moved faster and displayed aerial behavior more frequently as size of group increased. There was a significant correlation between size of group and PC1 during feeding and non-feeding (feeding, $r_s = -0.26$, $P = 0.004$, $n = 120$ bouts; non-feeding, $r_s = -0.37$, $P < 0.001$, $n = 89$ bouts). However, no relationship between these two variables was observed before or after feeding (before feeding, $r_s = -0.01$, $P = 0.990$, $n = 75$ bouts; after feeding, $r_s = -0.16$, $P = 0.140$, $n = 90$ bouts).

Occurrence of aerial behavior was highest when dolphins were feeding. Proportion of bouts with and without aerial behavior was significantly different between the four contexts (log-likelihood ratio, $G = 15.79$,

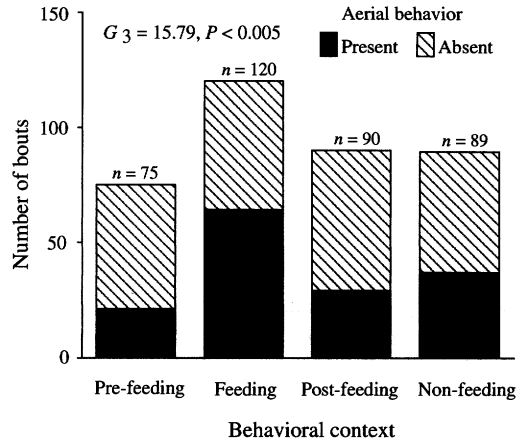


FIG. 3.—Number of bouts with aerial behavior present and absent per behavioral context in bottlenose dolphins at Isla del Coco, Costa Rica.

$d.f. = 3$, $P < 0.005$, $n = 374$ bouts; Fig. 3). This difference became non-significant when excluding feeding bouts from the analysis ($G = 3.57$, $d.f. = 2$, $P > 0.10$, $n = 254$ bouts). The percentage of bouts with aerial behavior was 53.3% during feeding, 28.0% during before-feeding, 32.2% during after-feeding, and 41.6% during non-feeding (Fig. 3).

Dolphins typically leaped less than five times in each bout (Table 3). Aerial behavior per dolphin was greatest when dolphins were feeding (Fig. 4). Frequencies of slaps, leaps, or nose-outs per dolphin were different between the four contexts ($H = 11.01$, $d.f. = 3$, 41 , $P = 0.012$; Fig. 4). A median

TABLE 3.—Size of groups and number of leaps, slaps, and nose-outs by bottlenose dolphins at Isla del Coco, Costa Rica.

Context	Size of group ^a	Number of leaps, slaps, and nose-outs ^a	Number of bouts
Pre-feeding	6.0, 6.0–9.0	1, 1–3	5
Feeding	8.0, 5.0–11.0	4, 3–8	15
Post-feeding	7.5, 6.5–12.5	1, 1–3	12
Non-feeding	9.0, 7.0–13.0	3, 2–3	9

^a Values are M and IQ .

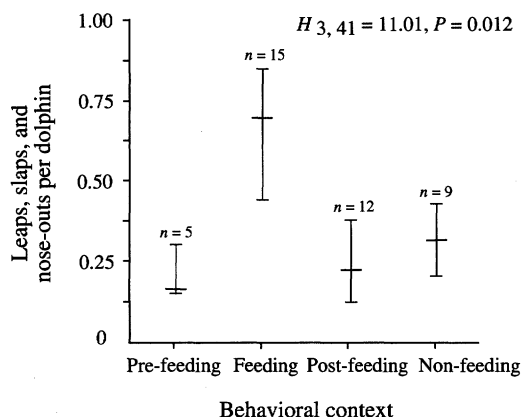


FIG. 4.—Frequency of aerial behavior per dolphin according to behavioral context in bottlenose dolphins at Isla del Coco, Costa Rica. Values are $M \pm 1Q$.

of 0.67 slaps, leaps, or nose-outs/dolphin was recorded during feeding ($1Q = 0.43$ – 0.83 slaps, leaps, or nose-outs/dolphin, $n = 15$ bouts). A median of 0.24 slaps, leaps, or nose-outs/dolphin was recorded during the remaining three contexts (before feeding, $1Q = 0.15$ – 0.33 slaps, leaps, or nose-outs/dolphin, $n = 5$ bouts; after feeding, $1Q = 0.13$ – 0.38 slaps, leaps, or nose-outs/dolphin, $n = 12$ bouts; non-feeding, $1Q = 0.23$ – 0.43 slaps, leaps, or nose-outs/dolphin, $n = 9$ bouts).

Aerial behavior per dolphin diminished with increasing size of group when not feeding. There was a negative correlation between number of leaps, slaps, or nose-outs per dolphin and number of dolphins during non-feeding contexts ($r_s = -0.79$, $P = 0.011$, $n = 9$ bouts). There was no correlation before and after feeding between aerial behavior per dolphin per minute and size of group (before feeding, $r_s = -0.72$, $P = 0.172$, $n = 5$ bouts; after feeding, $r_s = -0.44$, $P = 0.153$, $n = 12$ bouts). However, apparently these last two results were not significant because of their small sample size (Power for $\alpha_{0.05} = <0.63$). When dolphins were feeding, there was no correlation between aerial behavior per dolphin and size of group (feeding, $r_s = -0.22$, P

$= 0.599$, $n = 15$ bouts). The power of the test suggested that the lack of correlation was not an artifact of size of sample (Power for $\alpha_{0.05} = 0.84$).

Leaps were observed with the same relative frequency in all contexts, except that clean-entry leaps were more common when not feeding. There was no significant difference in relative number of bouts with leaps and number of bouts with other forms of aerial behavior between the four contexts ($G = 5.81$, $d.f. = 3$, $P > 0.10$, $n = 207$ bouts). The ratio of bouts with clean-entry leaps to bouts with noisy-entry leaps was highest during non-feeding contexts (non-feeding, 1.25:1, $n = 13$ bouts; pre-feeding, 1:3, $n = 7$ bouts; feeding, 1:1.45, $n = 37$ bouts; post-feeding, 1:4, $n = 10$ bouts). However, due to the small number of bouts in which dolphins leaped (<30% of the total number of bouts), I was unable to test the significance of those results.

DISCUSSION

Behavioral parameters were significantly different during feeding. Dolphins moved faster and engaged in aerial behavior more often during feeding than in any other context (Fig. 2). Frequency of occurrence of aerial behavior was correlated positively with size of group when feeding and non-feeding, but not before or after feeding. Aerial behavior per dolphin and occurrence of aerial behavior per bout were highest during feeding (Figs. 3 and 4). No increase in aerial behavior per dolphin with increasing size of group was detected during any context. Clean-entry leaps were more common when not feeding; noisy-entry leaps were more common before, after, and during feeding.

My data did not support the hypothesis that aerial behavior is an important social facilitator in bottlenose dolphins at Isla del Coco. Dolphin behavior during feeding was different from any other context, which agrees with observations from other studies (Baird and Dill, 1995; Shane, 1990; Slooten, 1994; Würsig and Würsig, 1980). If ae-

rial behavior is important in dolphins at Isla del Coco as a socializing activity, overall behavior of dolphins before or after feeding should be different from any other context. This is because social activity in dolphins involves interactive movements between individuals and aerial behavior in the group that are not associated with capture of prey (Baird and Dill, 1995; Johnson and Norris, 1986; Saayman et al., 1973). However, before-feeding and after-feeding behaviors of dolphins were essentially the same as that observed when dolphins were not feeding (Fig. 2).

Aerial behavior per dolphin and occurrence of aerial behavior per bout at Isla del Coco were highest during feeding (Figs. 3 and 4). These two variables were not different during before, after, and non-feeding. In the only other study that has attempted to measure levels of aerial behavior at different stages of a feeding episode, Würsig and Würsig (1980) found that dusky dolphins in Argentina increased number of acrobatic leaps, equivalent to noisy leaps, immediately after feeding. They hypothesized that those leaps were indicators of social activity in that population.

There was a negative trend in aerial behavior per dolphin with size of group before and after feeding. This result further supports the argument that aerial behavior is not an important social facilitator in populations of dolphins that hunt in small groups. It has been hypothesized that dusky dolphins increase aerial behavior after feeding to reaffirm social bonds (Würsig and Würsig, 1980; Würsig et al., 1991). In spinner dolphins, increases in aerial behavior before heading out to feed may enhance efficient and safer nighttime feeding, including avoidance of predators (Norris and Dohl, 1980; Norris et al., 1994; Würsig et al., 1991). These two species move in groups that regularly number >50 individuals (Norris and Dohl, 1980; Norris et al., 1994; Würsig and Würsig, 1980), while dolphins at Isla del Coco typically moved in groups numbering <14 dolphins (Fig. 1).

As such, communal efforts of dusky and spinner dolphins involve larger numbers of individuals and coordination of movements than those observed in bottlenose dolphins around the island. Therefore, reaffirmation of social bonds and coordination of activities before a hunt appear less necessary in bottlenose dolphins at Isla del Coco than in the other two populations.

Lack of correlation between size of group and aerial behavior per dolphin indicates that the increasing occurrence of aerial behavior per bout (correlation between size of group and PC1) was a reflection of the number of dolphins available. That is, during feeding and non-feeding, there were more bouts with aerial behavior because there were more dolphins in the group.

The hypothesis that aerial behavior facilitates capture of prey predicts variations in type of leap according to behavioral context because each leap has a different function (Würsig and Würsig, 1980). However, noisy leaps in bottlenose dolphins at Isla del Coco were more frequently performed before, during, and after feeding than clean-entry leaps, suggesting no variations in their use. One explanation for this result is that there are several types of noisy leaps, each having a different function. Noisy leaps performed by dusky dolphins when feeding are different from those performed in other contexts (Würsig and Würsig, 1980). Another explanation is that the same type of noisy leap could have different functions under different contexts.

Data support the aid-in-capture-of-prey hypothesis; leaps may allow dolphins to control movements of prey or to reduce time to return to prey after breathing. However, two alternative explanations also may account for my results. First, although bottlenose dolphins at Isla del Coco feed in groups, they do not herd fish and interference by sharks feeding on the same prey diminishes as size of dolphin group increases (Acevedo-Gutiérrez, 1997). Because number of dolphins at Isla del Coco increase at the onset of feeding (Acevedo-Gu-

tiérrez, 1997), aerial behavior may function to recruit new dolphins to defend food resources. Second, aerial behavior could have been a by-product of the high level of activity associated with feeding (Fig. 2). Unfortunately, data on intake at feeding in relation to aerial behavior, necessary to discriminate between these two explanations and the aid-in-capture-of-prey hypothesis, are unavailable.

In conclusion, my results did not support the hypothesis that aerial behavior prepares individuals before hunting, or strengthens social bonds after a hunt. However, evidence is inconclusive regarding the hypothesis that aerial behavior aids in capture of prey by bottlenose dolphins at Isla del Coco. Support for this hypothesis will be provided by data showing a positive correlation between intake of food by individuals and aerial behavior per dolphin.

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