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DIURNAL BEHAVIOR OF DUSKY DOLPHINS, *LAGENORHYNCHUS OBSCURUS*, IN GOLFO NUEVO, ARGENTINA

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Standardized measures of behavior can be powerful tools for predicting effects of human activities on natural populations of mammals. We quantified the diurnal activity budget of dusky dolphins (*Lagenorhynchus obscurus*) in Golfo Nuevo, Argentina, by examining variation in activity as a function of season and age composition of social groups. Observations were made from a research vessel during summer and autumn from 2001 to 2005. Focal group-follow methodology was used. The predominant activity in each social group was recorded using instantaneous sampling, with a 2-min interscan interval. The main daytime activity of dusky dolphins was traveling, followed by milling and feeding. Mother and calf pairs spent more time milling and resting, whereas larger groups of adults and juveniles as well as mixed–age-class groups spent more time traveling and feeding. Although a seasonal pattern of variation in group size and composition was found, little seasonal variation was found in activity budgets, which were almost constant during daylight hours. The activity budget generated by this study provides a baseline for detection of behavioral differences associated with tourism and other human activity in the region.

Key words: activity patterns, dusky dolphins, *Lagenorhynchus obscurus*, Patagonia

Baseline knowledge of behavior is critical to using activity patterns of animals as an indicator of environmental change. Activity patterns of animals result from a complex compromise between needs related to feeding, resting, reproduction, and socializing (Nielsen 1983). As this balance of needs changes, activity patterns also may change. As a result, activity patterns can be used as indicators of significant demographic or environmental alterations resulting from human activity (Parrish 2005).

Cetaceans are exposed to a variety of both targeted and incidental human activities in the marine environment. Although direct mortality (e.g., bycatch or whaling) is expected to have conspicuous population-level demographic consequences (Slooten et al. 2000), whale watching may represent a more subtle influence that alters normal patterns of behavior (Constantine et al. 2004; Lusseau 2003; Nowaceck et al. 2001; Samuels and Bejder 2004; Williams et al. 2002). Although relating short-term behavioral responses to long-term demographic changes is difficult (Bejder et al. 2006a, 2006b; Mann et al. 2000; Williams et al. 2006), documenting behavioral changes may provide compelling evidence of potential anthropogenic effects on threatened populations. Daily and seasonal patterns of activity represent a logical basis for characterizing baseline behavior as well as changes in behavior that may reflect anthropogenic disturbance.

Dusky dolphins (*Lagenorhynchus obscurus*) are small-bodied cetaceans that are found in temperate and cold-temperate waters in the Southern Hemisphere (Leatherwood and Reeves 1983). *L. obscurus* is probably the best-known species in the genus *Lagenorhynchus* (Au and Würsig 2004; Barr and Slooten 1998; Benoit-Bird et al. 2004; Cipriano 1992; Coscarella et al. 2003; Crespo et al. 1997; Markowitz et al. 2004; Van Waerebeek 1992; Würsig and Würsig 1980; Yin 1999) and is one of the most common species of small cetacean off the Patagonian coast in the southwestern Atlantic. Several aspects of the biology of this species have been studied previously, including its diet (Koen Alonso et al. 1998), reproductive biology (Dans et al. 1997), and parasitology (Dans 1999), as well as the sustainability of populations with high estimated levels of incidental mortality (Dans et al. 2003a, 2003b). A study of feeding behavior, group size, and movement patterns conducted during the 1970s in Golfo San José, Argentina (Würsig and Würsig 1980), suggested a daily pattern of activity, with greater swimming speeds and longer feeding bouts detected during the afternoon. However, this study did not quantify the amount of time spent in each of several other activities and, hence, more-detailed analyses of behavior are required to assess potential changes in activity resulting from changes in environmental conditions.

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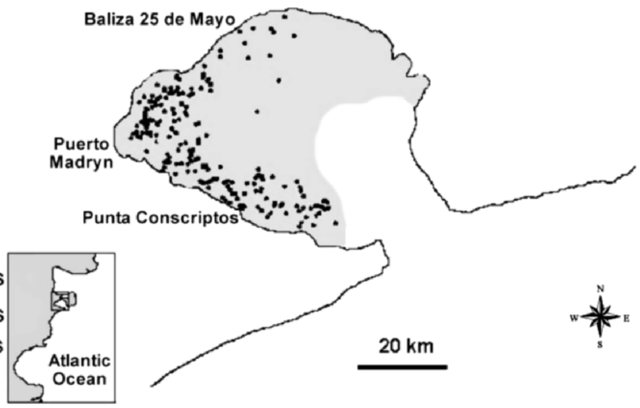

FIG. 1.—Map of the study area in Golfo Nuevo, Argentina. The gray area represents the region surveyed; the black dots represent locations at which dolphin groups were encountered.

During the past 3 decades, whale watching has become an important tourist activity in Golfo Nuevo, Península Valdés, Argentina. During the 1990s, an estimated 50,000 visitors per year took whale-watching trips in the gulf. The primary focus of this industry is the southern right whale (*Eubalaena australis*) but, with the steady increase in tourist demand, some tour operators have begun searching for alternative targets. As a result, dusky dolphins and other small cetaceans are now included in tours as an additional attraction, particularly outside of the whale-watching season (June–December).

To assess the potential impact of tourism on the population of dusky dolphins in Golfo Nuevo, an investigation of the behavioral patterns, group dynamics, movements, habitat use, and abundance of these animals was initiated in 2000. Preliminary findings indicated that dolphins interrupt their feeding efforts when a boat approaches too closely or swiftly (Coscarrella et al. 2003). The change from feeding to traveling occurs more frequently when the animals are approached by commercial as opposed to research vessels, suggesting that this response is influenced by the distance and manner of approach (Coscarella et al. 2003). The objectives of our study are to characterize daily and seasonal patterns of activity in this population in greater detail. Specifically, temporal variation in activity is examined in relation to group size and composition provide a baseline for detection of behavioral differences associated with tourism and other human activity in the region.

MATERIALS AND METHODS

Study area.—The study area consisted of a roughly 1,600-km^2 region in the western portion of Golfo Nuevo, Argentina (42°30′S, 64°40′W; Fig. 1). The total size of Golfo Nuevo is approximately 2,500-km^2; the maximum depth of the gulf is 184 m (Mouzo et al. 1978). Together, Golfo Nuevo and Golfo San José surround Península Valdés. In the 1980s, this region was declared a protected area by the Province of Chubut; in 1999, it was designated as a World Heritage Site by the United Nations Educational, Scientific and Cultural Organization.

Behavioral surveys.—Surveys of dolphin behavior were conducted from January to June 2001, 2003, 2004, and 2005. Surveys were carried out from either a 6-m fiberglass boat powered with a 50-hp outboard engine or a 7.2-m fiberglass boat powered with a 105-hp outboard engine. Although this data collection procedure may have affected the behavior of the study animals (Coscarella et al. 2003), the benefits of boat-based research were thought to outweigh this potential cost, because use of research vessels allowed dolphins to be observed at greater distances from the shore, allowed collection of more-detailed behavioral data, and allowed coverage of a larger study area than would have been possible using land-based monitoring.

One survey was completed each day between 0800 to 2000 h. The mean duration of trips was 5 h $\pm$ 1 *SD* (range = 2–8 h), with the duration of a given survey determined by sea and weather conditions (Beaufort Sea state $\leq$4). A nonsystematic search method was used to locate dolphins, with a search speed of 10–12 knots. To minimize the potential impact of this procedure on the behavior of the study animals, each group of dolphins encountered was approached slowly, from the side and rear, with the vessel moving in the same direction as the animals. The study subjects were followed at a constant distance of about 100 m, with minimal changes in vessel heading and speed. The procedures performed during this study comply with the current laws of Argentina and with the guidelines for animal research approved by the American Society of Mammalogists (Gannon et al. 2007).

Behavioral and group categories.—For data collection and analysis, a group was defined as any collection of individuals located in close proximity ($<$10 m) from one another (Smolker et al. 1992). The predominant activity of the focal group (Mann 1999), or "behavioral state," was defined as the activity in which $\geq$50% of group members were engaged; for our study population, typically $>$90% of the animals in a group were engaged in the same activity, indicating that this form of sampling provided a robust measure of the behavior of group members. During behavioral sampling, group members were observed continuously and the predominant activity was recorded at 2-min intervals using an instantaneous sampling protocol (Altmann 1974).

Five predominant activities were identified. During feeding, group members swam in circles or in a zigzag pattern to enclose a school of fish. The presence of birds foraging with or following the group also was indicative of feeding behavior. Traveling consisted of persistent movement, with all group members swimming in the same direction. Socializing was characterized by frequent interactions between individuals, usually in the form of body contact accompanied by high-speed movements, frequent changes in direction, and aerial displays such as leaps, tail-over-head leaps, backslaps, headslaps, and tailslaps (described by Norris and Dohl [1980]). Resting consisted of a low level of activity, with individuals remaining stationary, apparently floating motionless on the surface, with some occasional slow forward movement. Milling consisted of low-speed movements with frequent changes in direction, resulting in little apparent overall directional of movement by the group. These activities were defined to be mutually exclusive and, collectively, they described effectively the entire behavioral repertoire of the study animals.

Each group of dolphins observed was placed into 1 of the following 3 categories based on the apparent age classes of group members: adults and juveniles, mothers with calves, and mixed (all age class) groups. In general, age was assessed based on the body length of an individual, as outlined below. Dusky dolphins reach sexual maturity at the age of 6–7 years (Dans et al. 1997), although 3-year-old animals have almost the same length as adults (approximately 1.70 m—Dans 1999). Smaller animals were presumed to be juveniles; individuals that were less than two-thirds of adult length (and that were consistently accompanied by an adult) were considered calves (<1 year of age—Dans 1999). Groups of adults and juveniles consisted of animals of different lengths, all of which were larger than calves. Groups of mothers and calves were composed of >80% mother–calf pairs. Mixed groups were a combination of adults, juveniles, and calves, all of which formed a single unit. Groups were classified into the following arbitrary size categories: <10, 10–20, 21–50, 51–70, and >70 individuals.

Independence of behavioral observations.—Dusky dolphins are characterized by a fluid, fission–fusion society and their associations are not static over time (Markowitz et al. 2004; Würsig et al. 1997). As a result, groups sighted on different days were considered distinct. No group was sampled more than once per day. When more than 1 group was found during the same trip, each was considered an independent sample. When new dolphins joined the focal group or the group split, the resulting collection of individuals was considered a new group. Thus, although we attempted to minimize the nonindependence of our behavioral data, it is possible that some individuals were observed more than once in the same day.

Bejder and Samuels (2003) indicated that the group-follow protocol may result in over- or underestimation of the frequency of specific states or events. Bias could occur because observers are more likely to start or to continue following groups engaging in certain kinds of behavior (Whitehead 2004). At the same time, bias may result if, after group composition changes (e.g., a group fissions), there is a tendency to follow the more active subgroup (Mann 1999). To minimize these biases, we began group-follows after a collection of individuals was encountered, regardless of their current behavior; all group-follows continued until weather conditions became prohibitive or the animals were no longer visible. When a group split, the new group to be followed was selected randomly.

Data analysis.—To analyze seasonal effects, groups were classified as having occurred during the summer (January–March, average surface temperature 18°C) or autumn (April–June, average surface temperature 15°C). To analyze daily patterns, groups also were classified into 3 time blocks: morning (0900–1159 h), noon (1200–1459 h), and afternoon (1500–1759 h). To avoid problems of nonindependence of data, groups that were followed during >1 time block were included only within the block for which they were followed for the longest period of time. Frequencies were arranged in 3-way contingency tables (group size × season × time and group composition × season × time). These tables were analyzed by log-linear models to determine whether there was significant daily or seasonal variation in group size or composition. A 4-way contingency table was not possible because of the large number of cells with a value of 0 (Caswell 2001).

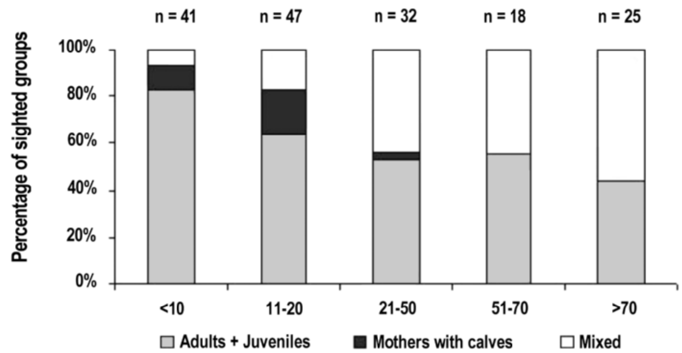

FIG. 2.—Size and composition of groups of dusky dolphins (*Lagenorhynchus obscurus*; $n = 164$) in Golfo Nuevo, Argentina, during summer and autumn 2001–2005.

Each dolphin group-follow was considered an independent observation for analyses of activity patterns. Because behavior at consecutive 2-min intervals was not independent, the proportion of time spent in each of the 5 designated activities was calculated for each group-follow. Based on exploratory analyses indicating that all designated activities could occur within a 10-min period, only group-follows with a minimum duration of 10-min were included in subsequent analyses of activity patterns. Initially, the nonparametric Kruskal–Wallis test was used to assess differences in activity among daily time blocks and the nonparametric Mann–Whitney *U*-test was used to assess differences in activity among seasons. Nonparametric tests were selected because assumptions regarding normality and homogeneity of variance between samples were not met and because the existence of outliers made the median more representative than the mean for these samples (Lehner 1998). In all cases, a significance level of $\alpha = 0.05$ was used (Conover 1999; Siegel and Castellan 1995).

RESULTS

Group size and composition.—A total of 168 groups of dolphins were encountered during this study, with encounters occurring during 57 (71.3%) of 80 sampling trips. More than one-half (54%) of the groups observed during the study consisted of <20 dolphins. Groups of <10 and 10–20 dolphins occurred most frequently and at similar frequencies; groups of 21–50 animals were the next most commonly encountered. With regard to age structure, groups of adults and juveniles were most frequently sighted, whereas mother and calf groups were least frequently sighted. Group size was significantly associated with group age composition ($\chi^2 = 34.9$, $d.f. = 8$, $P < 0.001$; Fig. 2). The largest groups were typically mixed groups, whereas the smallest groups were composed primarily of adults and juveniles. All but 1 of the mother and calf groups encountered contained <20 individuals.

Group composition varied significantly between seasons but not with time of day (seasons: $\Delta G^2 = 7.64$, $d.f. = 2$, $P < 0.03$; time of day: $\Delta G^2 = 0.69$, $d.f. = 4$, $P > 0.8$). Mother and calf groups were observed only during the summer. Groups of

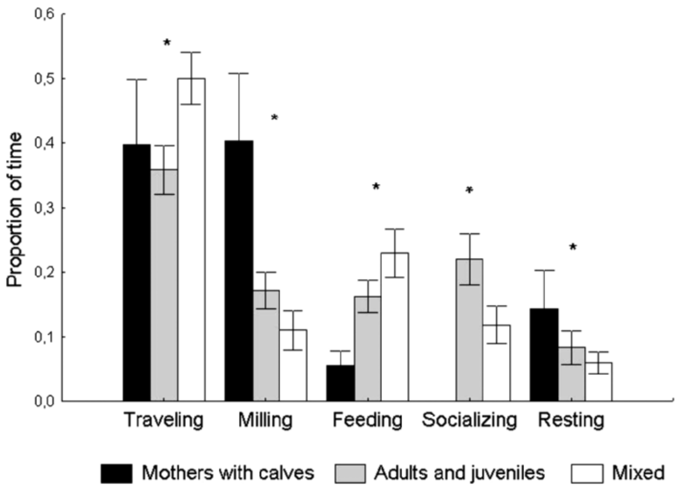

Fig. 3.—Proportion of time dusky dolphins (*Lagenorhynchus obscurus*) spent in the 5 focal behaviors as a function of group composition ($n_{\text{mothers with calves}} = 13$, $n_{\text{adult+juveniles}} = 73$, $n_{\text{mixed}} = 42$). Bars represent mean values; lines represent standard errors for these means. Significant differences are indicated by asterisks.

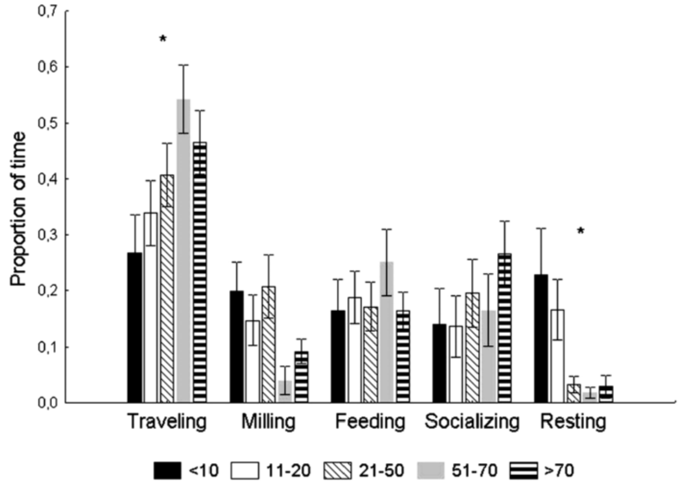

Fig. 4.—Proportion of time dusky dolphins (*Lagenorhynchus obscurus*) spent in the 5 focal behaviors as a function of group sizes ($n_{<10} = 22$, $n_{10–20} = 27$, $n_{21–50} = 27$, $n_{51–70} = 16$, $n_{>70} = 22$). Bars represent mean values; lines represent standard errors for these means. Significant differences are indicated by asterisks.

adults and juveniles were observed in both seasons, whereas mixed groups were most frequent during the autumn. Because of their typically small size (<20 individuals) and tendency to occur only during the summer, mother and calf groups were not included in analyses of temporal variation in group size. With mother and calf groups excluded, group size varied significantly with time of day, with group sizes being larger in the afternoon ($\Delta G^2 = 15.71$, *d.f.* = 8, $P < 0.05$); this tendency was observed in both seasons ($\Delta G^2 = 7.31$, *d.f.* = 4, $P > 0.1$).

Activity patterns.—Activity was recorded for 128 of the 168 groups sighted; the rest of the groups were not followed long enough to allow focal-group sampling. Activity was recorded during 111 h of observation, which represents 26% of the total survey effort. Mean observation time was 52 min ± 42 *SD* per group. The longest sampling session exceeded 4.5 h; the shortest session was 4 min. As indicated above, only group-follows that lasted ≥10 min were analyzed.

When data from both seasons were combined, traveling was the primary daytime activity of animals in the study population, comprising 40% of their behavioral budget. Milling was the 2nd most frequent activity (18% of budget), followed by feeding and socializing (16% of budget each). Resting was the least frequent activity (10% of budget). Members of the study population displayed significant seasonal variation in the proportion of time spent traveling (Mann–Whitney *U*-test, $U = 728$, $P < 0.01$), with this activity being more common during autumn (56% of activity budget) than during summer (35% of activity budget). Comparing data for summer and autumn revealed that although the animals appeared to spend less time feeding (autumn versus summer: 11% versus 18%), socializing (14% versus 16%), milling (13% versus 19%), and resting (8% versus 9%) during the autumn, no significant seasonal variation was detected for these behaviors (all $U > 1,065$, all $P > 0.05$). Because the frequency of traveling (the most common activity in the study population) differed significantly between seasons, variation in activity over the course of a day was analyzed separately for summer and autumn for all behaviors considered. No significant differences in activity were found as a function of time of day (Kruskal–Wallis tests, all $H < 4.1$, all $P > 0.15$).

When data from both seasons were combined, the frequencies of all activities varied significantly among group types (Kruskal–Wallis tests, traveling: $H = 8.7$, $P < 0.05$; milling: $H = 8$, $P < 0.05$; feeding: $H = 7.1$, $P < 0.05$; socializing: $H = 9.6$, $P < 0.05$; resting: $H = 6.1$, $P < 0.05$). Mothers and calves spent more time milling and resting than did other group types (Fig. 3). Mixed groups spent a greater proportion of time feeding and traveling, whereas adults and juveniles were more often engaged in socializing than other group types (Fig. 3). Two of the activities monitored also varied with group size, with smaller groups spending more time resting than larger groups (Kruskal–Wallis test, $H = 10.7$, $P < 0.05$), and larger groups spending more time traveling than smaller groups (Kruskal–Wallis test, $H = 10.6$, $P < 0.05$). In contrast, milling, socializing, and feeding did not vary significantly with group size (Kruskal–Wallis test, $H = 6.9$, $H = 6.3$, and $H = 4.1$, not significant, respectively; Fig. 4).

Discussion

Dusky dolphins were present in Golfo Nuevo during the entire sampling period. The main daytime activity of dusky dolphins was traveling, followed by milling and feeding. However, activity budgets vary markedly both within and among dolphin species. For example, in New Zealand, groups of dusky dolphins in Admiralty Bay spent roughly equal amounts of time feeding, resting, traveling, and milling (approximately 25% each), whereas those in Kaikoura fed mainly at night, with only 1% of daylight hours spent feeding (Markowitz et al. 2004). Commerson's dolphins (*Cephalorhynchus commersonii*) in Bahía Engaño, an open-water area near Golfo Nuevo, spent

37% of their time traveling, 30% resting, and approximately 23% feeding (Coscarella 2005). Humpback dolphins (*Sousa chinensis*) in Algoa Bay, South Africa, also fed during daytime and spent more than 50% of their time feeding (Barros and Cockroft 1991). A population of the same species from Plettenberg Bay, South Africa, spent 50% of its time traveling and 26% feeding (Karczmarski and Cockroft 1999). Finally, bottlenose dolphins (*Tursiops truncatus*), from an enclosed bay at Sanibel Island, Florida, spent nearly 60% of their time traveling and less than 10% feeding; these values changed to 40% and 20%, respectively, when the animals were followed in open waters (Shane 1990), suggesting that activity may vary with habitat.

Temporal variation in behavior.—In our study, activity budgets of dusky dolphins did not vary significantly with time of day. Diurnal variation in activity budgets is expected if prey behavior or availability change during the course of the day. It has been suggested that dusky dolphins in northern Patagonia feed during the daytime on pelagic fish such as Argentine anchovies (*Engraulis anchoita*). Although some pelagic prey species form compact shoals at depth during the daytime but are widely scattered and closer to the surface at night (Hansen and Madirolas 1996; Hansen et al. 2001), no such diurnal variation in activity has been reported for the anchovies on which the study population is believed to feed (Hansen et al. 2001). The observed absence of daily variation in dolphin activity in Golfo Nuevo is consistent with this apparent lack of variation in prey behavior.

Seasonal variation in activity budgets is expected if energy requirements differ throughout the year, as would be the case if reproduction is temporally concentrated or food resource availability changes over time. The greater proportion of time dolphins spent traveling in autumn may be related to a change in feeding strategy; traveling is necessary to locate prey and, hence, at least some proportion of time that dusky dolphins spent traveling could be directly related to foraging. A decrease in prey abundance or decrease in patchiness of prey distribution in the autumn could account for the observed pattern. Although the movements and distribution of anchovies in Golfo Nuevo are not currently known, recent studies of the spatial distribution of these fish along the adjacent continental shelf revealed a seasonal pattern, with anchovies being more spatially dispersed in late summer and early autumn (Hansen et al. 2001). Thus, changes in prey distribution and associated patterns of foraging may contribute to the observed seasonal changes in traveling behavior.

Variation in group composition.—Along with variation in activity budgets, dusky dolphins showed marked seasonal changes in group size and composition. The occurrence of mother–calf pairs during the summer only suggests a seasonal pattern of births. This observation is consistent with the findings of Würsig and Würsig (1980) as well as data regarding fetus lengths measured from pregnant female dusky dolphins caught in fishing nets (Dans et al. 1997). The subsequent increase in the occurrence of mixed groups in late summer and autumn may reflect the incorporation of calves into larger groups containing multiple age and sex classes of individuals.

Multiple factors may affect group size, making it challenging to interpret changes in group composition (Gygax 2002a, 2002b). For example, during the spring and summer breeding season, females may segregate newborn calves to reduce the risk of predation (Heithaus 2001; Heithaus and Dill 2002; Norris 1994; Wells et al. 1980) or to avoid hostile interactions with conspecifics (Patterson et al. 1998). At the same time, aggregations of smaller groups—sometimes into collections of hundreds of dolphins—may reflect the spatial distribution of prey (Wilson and Richards 2000) as well as behavioral adaptations for herding and capturing prey (Würsig and Würsig 1980). During our study, we frequently observed multiple large feeding groups in the same general vicinity, perhaps feeding on different portions of the same school of fish. This observation, in conjunction with the observed seasonal variation in group size, suggests that dolphin group sizes vary in response to reproductive cycle and distribution of prey.

Conservation implications.—With regard to the potential impact of tourist activities during summer in Golfo Nuevo, dusky dolphins showed a short-term response to dolphin-watching boats. The most frequently observed response was a change from feeding to traveling (Coscarella et al. 2003), which could mean that tourist trips interfere with foraging by dolphins. This effect may be particularly damaging to mother–calf pairs because of the extreme energetic needs of nursing mothers. The resulting changes in behavior of dolphins also could lead to long-term impacts at the population level (Williams et al. 2006). Specifically, displacement to lower-quality habitats may lead to changes in the demographic structure of the population, including decreased reproduction and recruitment of new individuals (Lusseau 2003; Mann et al. 2000).

There is evidence that, among years, the locations of dolphins within the gulf varied (Garaffo et al. 2007). During the 1st years of the study, dusky dolphins primarily used the areas nearest to Puerto Madryn; since 2004, however, the animals have been farther away from the city. This may have been due to the dolphins' normal pattern of movement in the area, or to the displacement of dolphins away from areas of high human activity, including commercial vessel traffic as well as whale- and dolphin-watching; further studies are required to understand this change in the dolphins' movements. Garaffo et al. (2007) suggest that, because of displacement of dolphins within the gulf, it will not be possible to identify areas in Golfo Nuevo for protection and thus management tools that do not rely on restricting access to specific regions must be employed. The results of our study suggest that one possible management strategy would be to keep whale and dolphin watchers away from resting animals and mother–calf pairs. However, continued monitoring of the study population is critical to allowing resource managers to devise and implement effective regulations for sustainable tourist activity in Golfo Nuevo.

Resumen

Las medidas estandardizadas del comportamiento pueden ser una poderosa herramienta para predecir los efectos de las actividades humanas sobre poblaciones naturales de mamíferos.

Cuantificamos el presupuesto diario de la actividad de los delfines oscuros (*Lagenorhynchus obscurus*) en el Golfo Nuevo, Argentina, examinando los cambios de actividad en función de la estación y de los tipos de grupos. Las observaciones fueron hechas desde una embarcación de investigación durante el verano y el otoño desde 2001 hasta 2005. Se utilizó una metodología de seguimiento de grupo focal. La actividad predominante de cada grupo fue registrada usando un muestreo instantáneo, con intervalos de 2 minutos. La actividad mas frecuentemente observada fue el traslado, seguido por nado errático y alimentación. Las madres con cría invirtieron más tiempo en nado errático y descanso, mientras que grupos grandes de adultos y juveniles y los grupos mixtos invirtieron más tiempo en traslado y alimentación. Aunque se encontró un patrón estacional en cuanto al tamaño y la composición de los grupos, poca variación estacional fue encontrada en los presupuestos de la actividad, que fueron casi constantes durante las horas del día. Los resultados generados en este estudio proporcionan información de base para poder detectar diferencias en el comportamiento asociadas al turismo y otras actividades humanas en la región.

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