MARINE MAMMAL SCIENCE, **(*): ***–*** (*** 2010)

DOI: 10.1111/j.1748-7692.2010.00398.x

Risso's dolphins alter daily resting pattern in response to whale watching at the Azores

FLEUR VISSER
Institute for Biodiversity and Ecosystem Dynamics,
University of Amsterdam,
Nieuwe Achtergracht 127,
1018 WS Amsterdam, The Netherlands
and
Nova Atlantis Foundation,
Rua dr. A. Freitas Pimentel 11,
9930-309, Santa Cruz das Ribeiras,
Pico, Azores, Portugal
E-mail: f.visser@uva.nl

KARIN L. HARTMAN
Nova Atlantis Foundation,
Rua dr. A. Freitas Pimentel 11,
9930-309, Santa Cruz das Ribeiras,
Pico, Azores, Portugal

ENTE J. J. ROOD
Nova Atlantis Foundation,
Rua dr. A. Freitas Pimentel 11,
9930-309, Santa Cruz das Ribeiras,
Pico, Azores, Portugal
and
Zoological Museum,
University of Amsterdam,
Mauritskade 61,
1092 AD Amsterdam, The Netherlands

ARTHUR J. E. HENDRIKS
Nova Atlantis Foundation,
Rua dr. A. Freitas Pimentel 11,
9930-309, Santa Cruz das Ribeiras,
Pico, Azores, Portugal

DAAN B. ZULT
Department of Psychology,
University of Amsterdam,
Nieuwe Achtergracht 127,
1018 WS Amsterdam, The Netherlands

WIM J. WOLFF
Department of Marine Benthic Ecology and Evolution,
Groningen University,
P. O. Box 14, 9750 AA Haren, The Netherlands

JEF HUISMAN
Institute for Biodiversity and Ecosystem Dynamics,
University of Amsterdam,
Nieuwe Achtergracht 127,
1018 WS Amsterdam, The Netherlands

GRAHAM J. PIERCE
Oceanlab,
University of Aberdeen,
Main Street,
Newburgh, Aberdeenshire, AB41 6AA, United Kingdom
and
Instituto Español de Oceanografía,
Centro Oceanográfico de Vigo,
P. O. Box 1552, 36200 Vigo, Spain

ABSTRACT

Behavioral responses of Risso's dolphins (*Grampus griseus*) to whale watching vessels were studied off Pico Island, Azores. Dolphin behavior was studied from a land-based lookout, enabling observations of groups in the absence and presence of vessels. The number of whale watching vessels showed a clear seasonal pattern, dividing the whale watching period into a low season and a high season. During the low season, Risso's dolphins rested mainly in the morning and afternoon. During the high season, Risso's dolphins rested less and did so mainly at noon, when the number of active vessels was lowest. Data analysis using a generalized additive mixed model indicated that this change in resting behavior was associated with vessel abundance. When more than five vessels were present, Risso's dolphins spent significantly less time resting and socializing. During the high season, this vessel abundance was exceeded during 20% of observation days. While we cannot be sure that the observed changes in behavior have fitness consequences for Risso's dolphins, reduced resting and socializing rates can have negative impacts on the build-up of energy reserves and on reproductive success. We suggest the adoption of precautionary management measures to regulate the timing and intensity of whale watching activities.

Key words: Risso's dolphin, *Grampus griseus*, whale watching, Azores, behavioral budget, land observations, resting behavior.

Whale watching tourism has grown to a great extent over the last few decades, leading to a strong rise in the exposure of cetaceans to boat traffic and interactions with humans (Miller 1993, O'Connor *et al.* 2009). Although marine ecotourism can benefit the conservation of cetacean species through the increase of public awareness (Duffus and Dearden 1990), whale watching activities also may have harmful effects on the animals. Cetaceans have shown a range of short-term to long-term behavioral reactions to whale watching vessels, several of which seem comparable to predator-avoidance responses (*e.g.,* Williams *et al.* 2002). These responses include horizontal and vertical avoidance (Janik and Thompson 1996, Nowacek *et al.* 2001, Williams *et al.* 2002), changes in activity and energy budgets (Lusseau 2003*a*, *b*, 2004; Williams *et al.* 2006), changes in habitat use (Baker and Herman 1989, Allen and Read 2000), displacement (Kruse 1991, Lusseau 2005), and in some cases a decline in abundance in small resident populations (Bejder *et al.* 2006).

The nature and strength of cetacean responses to whale watching have been linked to the intensity, noise and conduct of the vessel traffic and to intrinsic factors such as the sex of individuals, habituation and behavior prior to exposure (Erbe 2002, Bejder *et al.* 2006, Stensland and Berggren 2007, Williams and Ashe 2007). It can be difficult to relate any observed short-term response to whale watching vessel presence to long-term biological effects on cetacean populations. However, changes in behavior often are related to the energy budget of individuals, and therefore can provide information on the biological significance of an impact at the population level (Bejder and Samuels 2003).

Whale watching tourism in the Azores has been growing rapidly since its start in 1992. In 2004 fifteen tour operators offered daily trips from seven islands of the Azores, the islands of Pico and Faial being the main centers of activity. Local legislation to regulate whale watching activities was implemented in 1999, including guidelines on approach distances, duration of interactions, angle of approach and maximum number of vessels allowed per cetacean group (Carlson 2008). However, Magalhães *et al.* (2002) found that only 54% of whale watching vessels fully complied with these regulations when targeting sperm whales. Due to the presence of cetaceans in inshore waters, whale watching vessels can be guided very efficiently by an observer from land, making it difficult for targeted cetaceans to avoid vessel encounters.

Risso's dolphin (*Grampus griseus*) is one of the target species of the whale watching activities in the Azores (Gomes Pereira 2008). They are relatively shy cetaceans and do not readily approach boats (Tinker 1988). Off Pico Island, more than 1,000 individuals have been identified, many of which are present in the inshore waters on a regular basis. Risso's dolphin individuals show high site fidelity in the area, as well as a complex social organization involving stable, long-term bonds and age- and sex-specific social segregation (Hartman *et al.* 2008). A considerable part of the identified population is composed of mother-calf pairs, suggesting that the area may serve as a nursery ground. These factors make Risso's dolphins in the Azores potentially vulnerable to disturbance.

In this article, we investigate the effects of whale watching vessel presence and abundance on the behavior of Risso's dolphins around the Azores. Since Risso's dolphins can be observed readily in Azorean inshore waters, we were able to use land-based observations, which have the advantage of eliminating possible confounding effects of a research vessel (Williams *et al.* 2006).

Methods

Research Area

From 1 May to 28 October 2004, daily land-based observations were made from a fixed look-out 30 m above sea level on the south coast of Pico island, Azores (38°24′N, 28°11′W). The observations were conducted using Steiner Observer binoculars (Steiner Binoculars, Bayreuth, Germany), with 25× magnification and 80 mm objective lenses. The sighting range from our land-based look-out was determined empirically by recording the GPS locations of our research vessel at the limits

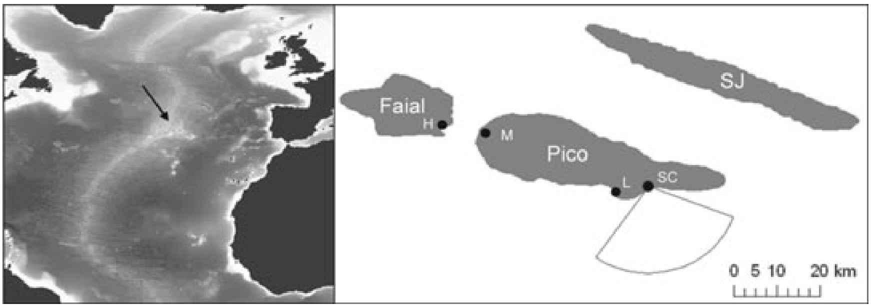

Figure 1. Location of the Azores in the North Atlantic Ocean (left panel). Location of the lookout in Santa Cruz (SC), and the harbors of Madalena (M), Lajes do Pico (L), and Horta (H) from which the whale watching vessels depart (right panel). The outline indicates the research area off Pico Island covered by our land-based observations from the lookout in Santa Cruz. Bathymetry map of the North Atlantic Ocean was reproduced from the GEBCO Digital Atlas (IOC, IHO, and BODC 2003).

of the sighting range. Results indicate that the sighting range from the look-out was 20 km offshore, encompassing a research area of 367 km^2 (Fig. 1). Risso's dolphin presence could be determined reliably up to 15 km offshore. Whale watching companies operating in the research area generally organize two trips per day. Trips usually last 3–4 h, starting at 930/1000 and at 1400/1430, with occasional evening or whole-day trips. Most vessels observed in the research area depart from the harbor of Lajes do Pico (Pico Island); the remainder departs from Madalena (Pico Island), or Horta (Faial Island).

Data Collection

Observations were conducted daily, at regular intervals between sunrise and dawn. Two types of sampling were used: surveys and focal follows. Sea state on the Beaufort scale (Bft), visibility and weather conditions were recorded at the start of each observation. Standardized surveys, conducted at the start of all observations, consisted of a scan of the research area, recording the number of Risso's dolphin groups and individuals and the number of whale watching vessels present. The presence of fishing vessels and recreational vessels was also recorded. The area was scanned twice to account for individuals submerged or missed during the first scan. Surveys had a duration of 15–30 min and were spaced at least 2 h apart to obtain independent samples.

Behavioral observations recorded during focal follows consisted of sampling of group size, group composition, location, direction and speed of travel, group spacing, display events and behavior of Risso's dolphin groups, using a standardized ethogram (Mann 1999). Behavioral parameters were recorded once every minute. The relatively small average group size of Risso's dolphin largely rules out the vulnerability to sampling bias of focal group sampling (Bejder and Samuels 2003, Hartman *et al.* 2008). Focal groups were followed for at least 15 min, unless the group moved too far offshore for reliable observation or sighting conditions deteriorated. We recorded the number of whale watching vessels present at the start of each observation, and the timing of vessels entering and leaving the research area during the observations.

Behavior of Risso's Dolphin

A group of Risso's dolphins was defined as a set of individuals that interacted socially and/or showed coordinated activity in their behavior (Whitehead 2003). In general, Risso's dolphins in the area formed tight groups with inter-animal distances <4 body lengths. The largest group spacings, up to 15 body lengths, were usually observed during foraging. We distinguished four mutually exclusive behavioral types: resting, traveling, socializing, and foraging (Altmann 1974, Shane 1990). Resting was defined as individuals organized in cohesive group formation characterized by calm, regular surface behavior, moving at low speed, with events of logging individuals (floating at or just below the water surface). Traveling was defined as individuals moving steadily in a directional path, at normal to high speed. Socializing behavior was defined as individuals showing interanimal interaction (contact) and regular surface display events in cohesive group formation, with larger socializing groups generally organized in dynamically interacting subgroups. Foraging behavior was defined as loosely spaced individuals or pairs, with individuals displaying regular, long, non-synchronized dives.

The behavioral budget and group size of Risso's dolphin were determined from focal follow data. Activity rates were calculated on hourly and monthly time scales from the cumulative time over which a behavioral state was observed divided by the total effort of focal follow observations during that period. Relative abundance of Risso's dolphins was calculated as the average number of individuals present per survey. Surveys at Beaufort sea states >3 or at limited visibility and focal follows <15 min were excluded from analysis.

Intensity of Whale Watching

The intensity of whale watching was determined by calculating vessel abundance on hourly, daily, and monthly time scales. Whale watching intensity was monitored during the entire research period, including days of rough sea state conditions (>3). Seasonal patterns were quantified by calculating the total number of vessels frequenting the research area per observation day. Based on seasonal variation in whale watching intensity, the research period was divided into a high season (July and August) and low season (May, June, September, and October). Daily patterns were quantified by calculating average vessel abundance at 1 h intervals.

Statistical Analysis

We used generalized additive mixed models (GAMMs; Wood 2006, Zuur *et al.* 2009) to analyze effects of vessel abundance in the research area on the behavior of Risso's dolphins. In addition to vessel abundance, we included effects of time of day (h) and time of year (mo). Dolphin behavior is likely to vary on different temporal scales and may, for example, show daily and seasonal variation irrespective of vessel abundance.

GAMMs were used because (1) initial data exploration showed non-linear relationships between dolphin behavior and vessel abundance, and (2) observation records within focal follows were correlated. As the data are binary (presence or absence of behavioral type), we used a binomial distribution with a logistic link function. The full GAMM predictor function is given by

$$Y_{ij} \sim B(\pi_{ij}, 1)$$
$$\text{logit}(\pi_{ij}) = \alpha + f(\text{Vessels}_{ij}) + \text{Month}_{ij} + \text{Hour}_{ij} + a_i + \varepsilon_{ij}$$

where Y_{ij} is the presence/absence of a given behavior in the jth observation record of focal-follow number i. The presence of a given behavior is assumed to be characterized by a binomial distribution $B(\pi_{ij}, 1)$ with probability π_{ij} for each observation record. A GAMM was applied separately to each of the four behavioral types. The logit function contains an intercept α and a smoothing function, $f(\text{Vessels}_{ij})$, describing non-linear effects of vessel abundance on dolphin behavior. The smoothing function was estimated by thin plate splines, and the optimal amount of smoothing was estimated using cross-validation (Wood 2006). The factors Hour_{ij} and Month_{ij} were fitted as categorical variables. The random effect a_i takes into account the fact that observation records within the same focal follow are correlated; it is assumed to be normally distributed with mean 0 and variance σ_a^2. We allowed for additional temporal autocorrelation between observation records by imposing an auto-regressive correlation structure of order 1 (AR1 model) on the residuals ε_{ij} (Pinheiro and Bates 2000, Zuur *et al.* 2009). Various models were fitted using different subsets of the explanatory variables, and the optimal model was selected using the Akaike Information Criterion (AIC; Akaike 1973). If the optimal models showed significant effects of the categorical variables Hour or Month, *post hoc* testing was conducted to investigate the contrasts between different hours and months. *Post hoc* testing involved rerunning the optimal model, each time selecting a different hour or month as the new baseline value. A Bonferroni correction was applied to the P values obtained in *post hoc* testing (Dalgaard 2008).

GAMM analysis was carried out using the mgcv package in R, version 2.9.0 (Wood 2006, R Development Core Team 2009). All other statistical tests were performed in SPSS, version 12.0. A significance level of 0.05 was used for all analyses.

Results

Research Effort

During 172 observation days, we conducted 448 focal follows and 87 surveys during suitable environmental conditions. The focal follow observations yielded 8,238 observation records (of 1 min each) in total, with 4,156 observation records in the low season and 4,082 observation records in the high season.

Intensity of Whale Watching

A total of 487 vessel visits was recorded in the research area, including 460 visits of whale watching vessels and 27 visits of fishing vessels and pleasure boats. Thus, whale watching vessels constituted almost 95% of all vessels visiting the research area. Whale watching vessels were present during 42% of the observation days. The whale watching season started in spring, with one observation of vessel presence in May and daily activities starting in mid-June. Vessel abundance strongly fluctuated over the research period, showing significant differences between months (Kruskal-Wallis test, $H = 93.1$, df $= 5$, $P < 0.001$) (Fig. 2). During the high season months (July and August), we recorded 6.0 ± 4.7 (mean $\pm$ SD) vessels per day, while

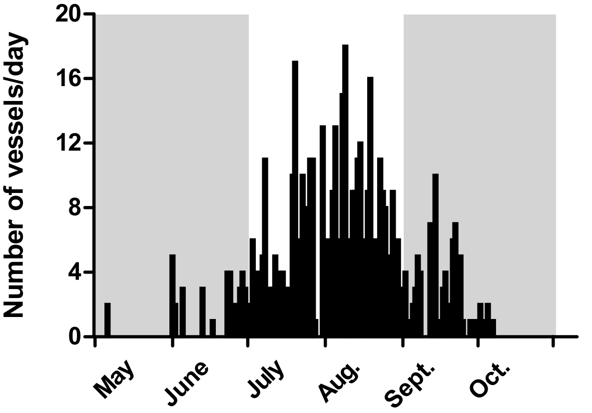

Figure 2. Number of whale watching vessels per day observed during May–October 2004. Shaded area indicates the low season, while the non-shaded area indicates the high season.

we recorded 1.0 ± 1.8 vessels per day during the low season months (May, June, September, October).

The intensity of whale watching showed a bimodal distribution over the day, resulting from the timing of the whale watching trips (Fig. 3). During the high season, two peaks of high activity, from 1000 to 1300 and 1400 to 1700, were separated by a period of less activity from 1300 to 1400. During the low season, activities were centered primarily in the morning hours (1000–1300). On average, we recorded 1.5–3 vessels at the same time during the high season, and 0.5–1.5 vessels during the low season.

Risso's dolphin Presence and Abundance

The presence of Risso's dolphin in the research area was largely continuous, with records during 90% of the observation days and during 74% of the surveys. On

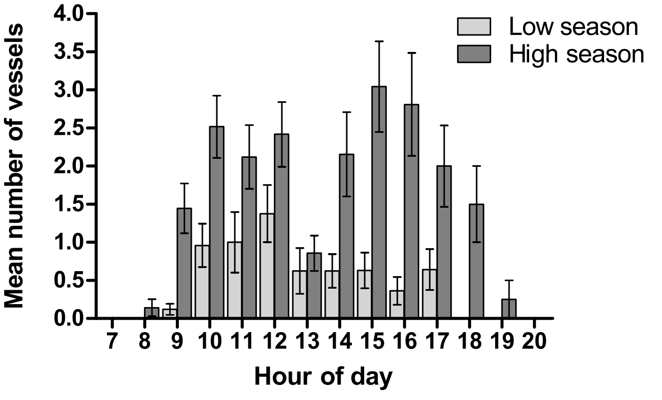

Figure 3. Daily distribution of whale watching vessels (mean ± SE), during the low season and high season. Data are binned in 1-h intervals (*i.e.*, 8 = interval 0800–0859).

average (mean ± SD), we recorded 2.6 ± 2.5 Risso's dolphin groups per survey (range: 0–14). Mean group size (±SD) was 11.1 ± 7.5 individuals with a median group size of 10 individuals (range: 1–50). Risso's dolphin relative abundance did not show significant differences between months over the study period (Kruskal-Wallis test, $H = 10.2$, df = 5, $P = 0.07$).

Behavioral Budget

Based on focal follow data, Risso's dolphins spent a substantial portion of their time during the low season traveling (38%), resting (31%), and socializing (22%), and spent relatively little time foraging (7%). For the remaining 2%, behavioral type could not be determined. They spent significantly less time resting (20%, $\chi^2 = 124.2$, df = 1, $P < 0.0001$) and more time socializing (33%, $\chi^2 = 155.8$, df = 1, $P < 0.0001$) during the high season than during the low season.

Dolphin behavior varied during the day (Fig. 4). Foraging behavior was observed mainly during the early morning and the latter half of the afternoon (Fig. 4E, F). A similar but less pronounced pattern was observed for socializing (Fig. 4C, D). The time allocated to traveling remained fairly constant over the day (Fig. 4G, H). There was a clear difference in the timing of resting between the low season and high season (Fig. 4A, B). The low season was characterized by a double-peaked resting pattern, with highest resting rates from 0900 to 1200 and from 1400 to 1600. During the high season, the morning peak of resting activity was absent, while the main resting period was from 1300 to 1400 (Fig. 4B) when vessel abundance was lowest (Fig. 3).

Statistical Analysis

The GAMM analysis revealed a high degree of temporal autocorrelation between consecutive observation records (autocorrelation coefficients ranged from 0.8 to 0.9). That is, the behavior observed in 1 min was very similar to the behavior in the next minute. In addition, the GAMM analysis also pointed to seasonal variation in dolphin behavior and to effects of vessel abundance.

The optimal model for each of the four behavioral types was selected using AIC-values (Table 1). For resting behavior, the optimal model included the covariates "Vessels" as a smoothing function and "Hour" as categorical variable (model 5). For socializing behavior, the optimal model included the covariates "Vessels" and "Month" (model 6). For traveling and foraging behavior, the optimal model included the covariate "Month" only (model 2).

The GAMM analysis showed a significant negative effect of vessel abundance on resting behavior (Table 2). The probability of observing resting behavior decreased when more than five whale watching vessels were present in the research area (Fig. 5A). During the high season, this threshold value of more than five vessels was exceeded in 317 observation records (*i.e.*, 7.8% of the observation records) spread over 10 observation days (20% of the observation days). During the low season, the threshold vessel abundance of five vessels was never exceeded. In addition, the analysis indicated hourly variation in resting rates (Table 2). However, no significant differences between hours were found in *post hoc* testing.

Similar results were found for socializing behavior, which was also negatively affected by vessel abundance (Table 2, Fig. 5B). In addition, significant differences in socializing behavior were observed between months (Table 2). *Post hoc* testing

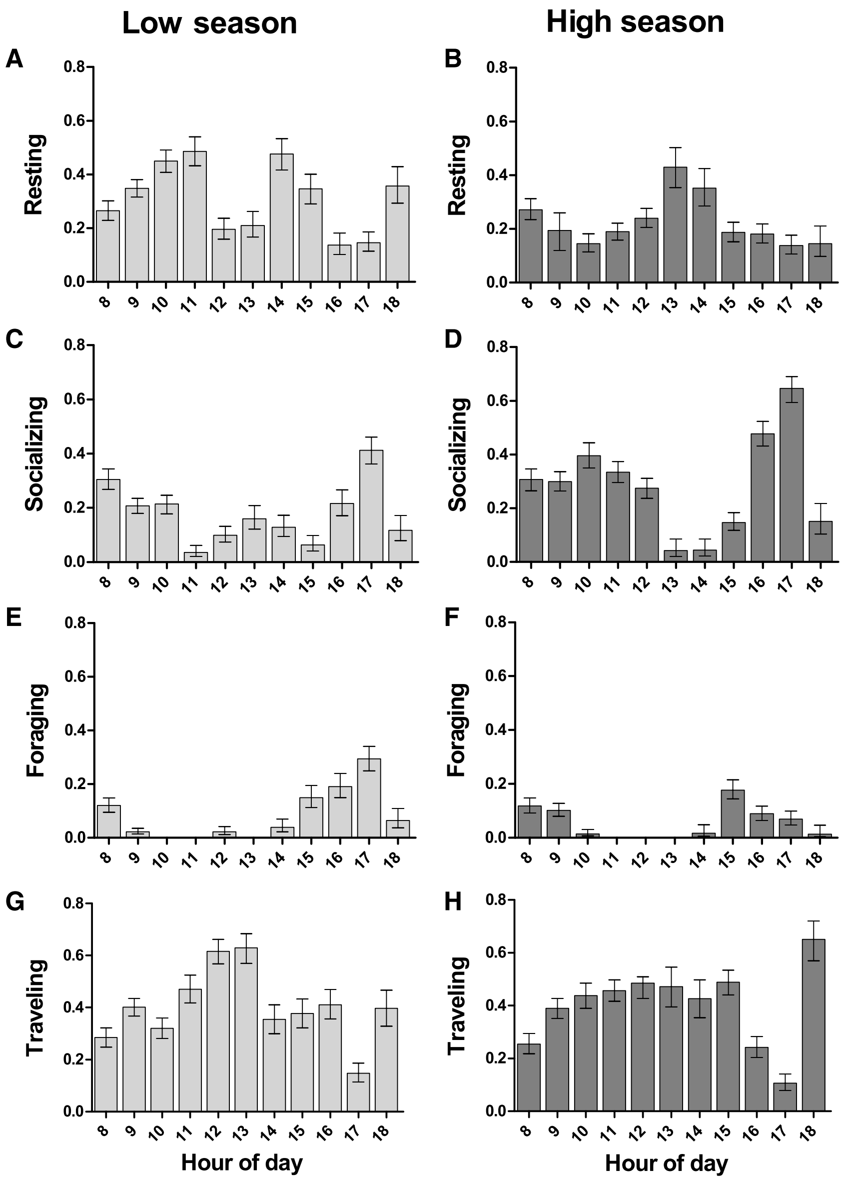

Figure 4. Daily patterns of resting, socializing, foraging, and traveling (mean ± 95% CI), during the low season (left panels) and high season (right panels). The behavioral budget is expressed as the average activity rate per 1-h interval (*i.e.*, 8 = interval 0800–0859).

confirmed that dolphins allocated significantly more time to socializing in July than in August and September ($P = 0.001$ and $P = 0.027$, respectively). The time allocated to foraging showed weakly significant monthly variation (Table 2), but no significant differences between months were found in *post hoc* testing. Monthly variation in traveling behavior was not significant.

Table 1. AIC-values of the seven models included in model selection for the GAMM analysis. For each behavioral type, the optimal model (lowest AIC-value) is indicated by a superscript*. Models for which no AIC-value is given did not converge.

Model	Selected covariates	Resting	Socializing	Foraging	Traveling
1	Hour	27,467	62,052	574,219	20,930
2	Month	27,189	27,329	43,843*	20,797*
3	Vessels	26,957	–	46,345	20,840
4	Hour + Month	27,869	23,013	574,916	23,561
5	Hour + Vessels	23,159*	–	–	86,949
6	Month + Vessels	27,999	15,590*	48,020	33,680
7	Hour + Vessels + Month	–	–	–	–

Overall, the GAMM analysis showed that Risso's dolphins (1) displayed seasonal patterns for socializing, and (2) spent less time resting and socializing during periods of high vessel abundance.

Discussion

Behavioral Shifts Induced by Vessel Presence

The number of whale watching vessels in the research area showed a clear seasonal pattern, dividing the whale watching period in a low and a high season. Risso's

Table 2. Statistical results from the GAMM models, investigating the dependence of the four behavioral types on vessel abundance and temporal variables. Only variables significant at the 0.05 level are given.

Behavioral type	Factor	Coefficient	SE	t	P
Resting	Intercept	−0.96	0.29	−3.26	0.001
	Hour(8)	−0.48	0.24	−2.03	0.04
	Hour(9)	−0.60	0.26	−2.27	0.02
	Hour(13)	−1.19	0.37	−3.26	0.001
	Hour(14)	−1.22	0.38	−3.20	0.001
	Hour(15)	−0.92	0.37	−2.46	0.014
	Hour(17)	−0.81	0.39	−2.09	0.036
	Hour(18)	−0.92	0.41	−2.27	0.023
	Smoother term	edf[a]	df	$F_{edf,df}$	P
	Vessels	3.92	7,880	3.47	0.008
Socializing	Intercept	−1.39	0.31	−4.50	<0.0001
	Month (July)	0.91	0.35	−0.46	0.009
	Smoother term	edf[a]	df	$F_{edf,df}$	P
	Vessels	4.9	7,893	5.3	<0.0001
Foraging	Intercept	−6.79	1.20	−5.59	<0.0001
	Month (September)	2.70	1.31	2.08	0.03
Traveling	Intercept	−0.76	0.36	−2.13	0.034
	Month				n.s.

[a]edf = effective degrees of freedom.

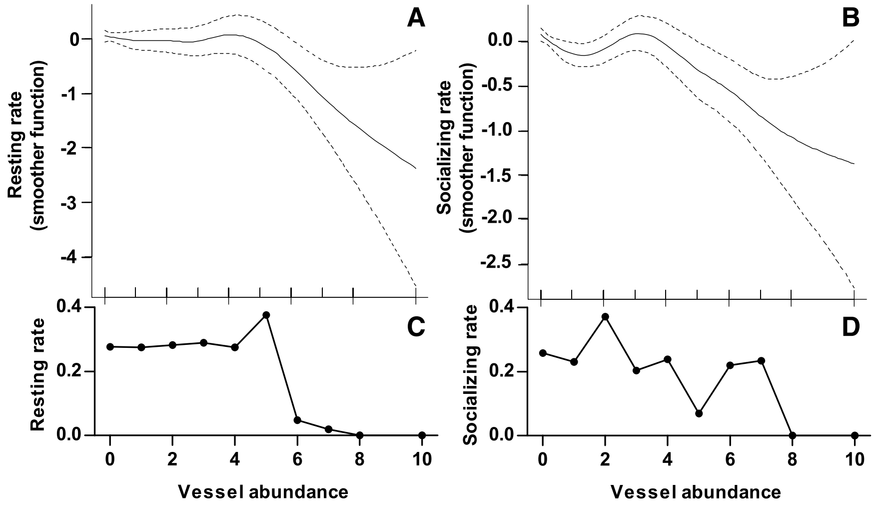

Figure 5. GAMM smoothing functions of (A) resting behavior and (B) socializing behavior as a function of vessel abundance. Dashed lines represent 95% confidence intervals. For comparison, the observed resting (C) and socializing (D) rates as a function of vessel abundance are also shown.

dolphin displayed changes in behavioral patterns in concordance with these two seasons. During the low season, Risso's dolphin displayed a bimodal resting pattern; their resting rate peaked at around 1100 and 1500. During the high season, this pattern changed into a single peak, with highest resting rates at around 1300. Whale watching vessels usually went out on two daily trips, one in the morning and one in the afternoon. As such, the peak resting activity of Risso's dolphin during the high season was shifted to the hours of lowest whale watching intensity, at lunch-break. In addition, resting rates were significantly lower during the high season.

This was not merely a seasonal behavioral pattern. The GAMM results suggest that, once vessel abundance was taken into account, there was no significant seasonal variation in the probability of observing resting behavior. The analysis did reveal some variation in resting behavior on an hourly time scale, although *post hoc* testing did not reveal significant differences between specific hours of the day. However, resting rate showed a significant negative relationship with vessel abundance. The probability of observing resting behavior decreased when more than five whale watching vessels were present in the research area. Events with more than five whale watching vessels were recorded only during the high season, indicating that effects of vessel abundance on resting behavior were concentrated in this period. While models including an effect of vessels, but no effect of month, performed better than models including an effect of month, but no effect of vessels, it is evident that the high collinearity between these two variables makes it difficult to reliably distinguish between their effects.

The time allocated to socializing behavior showed a significant negative relation with vessel abundance when more than five vessels were present in the area. Again, this effect was restricted to the high season, the only time this many vessels were recorded in the area. During the high season, socializing rates were significantly higher in July than in August and September. Increased social interactions between individuals are likely to indicate the timing of the breeding or the calving season.

Foraging

The incidence of foraging behavior did not show a pattern related to whale watching vessels present, which may indicate that this behavioral type is less sensitive to disturbance by whale watching vessels. However, foraging occurred primarily outside the high-intensity hours of whale watching. Foraging activities were concentrated during the early morning and late afternoon, while very little foraging activity was recorded between 1000 and 1500. Low foraging rates observed during daytime might be explained by nighttime foraging on deep-sea squid, as has been observed for Risso's dolphin and short-finned pilot whales (*Globicephala macrorhynchus*) off California (Shane 1995). Spinner dolphins (*Stenella longirostris*) living in the somewhat comparable habitat of the Hawaiian archipelago show a similar diurnal behavioral pattern of high daytime resting rates in inshore waters and foraging activity during the late afternoon and night (*e.g.*, Lammers 2004, Danil *et al.* 2005). The spinner dolphins enter sheltered bays during daytime, probably to reduce the chances of deepwater shark predation (Norris and Dohl 1980). Nighttime foraging and daytime sheltering in inshore areas may explain the relatively high resting rate of Risso's dolphin observed during the day (25%), compared to other cetaceans (Moberg 2000, Constantine *et al.* 2003, Lusseau 2003*a*).

Ecological Significance

Risso's dolphins were present almost continuously in the study area and previous research in the area has shown high site-fidelity of individuals and the presence of calves (Hartman *et al.* 2008). According to the behavioral budget recorded in our study, the dolphins displayed a variety of behaviors with considerable time dedicated to social behavior and resting during the day.

These results suggest that the waters off Pico Island function as a resting, foraging, and nursery area for the population of Risso's dolphins, and do so on a daily basis for at least part of the population inhabiting the inshore waters. Areas used for nursing, resting, foraging, and socializing form important habitats for cetaceans (Hoyt 2005*a*). We observed an overall reduction in resting rates and a shift in the daily resting pattern during periods of high whale watching vessel abundance. Socializing rates also decreased when many whale watching vessels were present. This is consistent with previous work on bottlenose dolphins, which spent less time on resting and socializing and more time on traveling following interactions with boats (Lusseau 2003*a*, 2004; Stensland and Berggren 2007) and avoided areas with intense boat traffic (Lusseau 2005). A reduction in resting and socializing rates can result in reduced energy reserves and can negatively affect foraging and reproductive success, an effect that has been found throughout the animal kingdom including fish, birds, and marine mammals (*e.g.*, Ricklefs *et al.* 1996, Grantner and Taborsky 1998, Frid and Dill 2002, Williams *et al.* 2006). Nursing females and their calves form an especially vulnerable group, for which disturbances by vessels can suppress the build-up of energy reserves. In small resident populations, this may directly affect reproductive success (Bejder 2005).

Management Implications

Tourism is growing rapidly at the Azorean islands, including a further increase in whale watching activities. Although, at present, whale watching pressure in the

Azores is still relatively low compared to other regions such as the Canary Islands (Hoyt 2005*b*) or British Columbia (*e.g.*, Erbe 2002), our results show that the presence of more than five vessels in a relatively small area can have a statistically significant effect on the behavioral pattern of Risso's dolphins. Some caution is nevertheless required in interpretation. In particular, the 95% confidence intervals obtained from our statistical analysis widen at high vessel abundance (Fig. 5). This reflects the relatively low number of observations with high vessel abundances. Hence, although the analysis indicates significant effects of vessel abundance on dolphin behavior, any estimation of the magnitudes of these effects based on currently available data would have a high degree of uncertainty. Furthermore, we cannot be sure to what extent the observed changes in behavior reflect important changes in daily energy budgets or stress levels and, therefore, whether they have negative consequences for individual condition or reproductive fitness. Also, our study was limited to a single year and the seasonal variation in vessel abundance during our study period makes it intrinsically difficult to distinguish between natural seasonal variation in behavior and the effects of vessel abundance on behavior. Continued data collection over several years would be desirable to evaluate the impact of boats on cetacean behavior in this area with higher precision.

Nevertheless, based on our results, we suggest that a precautionary approach is taken to current and future whale watching activities in the Azores, through management of the number of whale watching vessels per area. Low-intensity vessel presence did not decrease the probability of resting or socializing behavior, providing a reference from which threshold measures of vessel abundance could be determined (see also Williams and Ashe 2007). Additionally, it would be beneficial to introduce a time period with no whale watching activity for several hours per day, to create sufficient resting opportunities for the Risso's dolphin population. Other target species in the Azores may benefit as well, in particular the bottlenose dolphin, a species that also makes extensive use of the area (Silva 2007) and has shown sensitivity to vessel traffic in other areas (*e.g.*, Lusseau 2005, Bejder *et al.* 2006).

Acknowledgments

We gratefully thank WWF the Netherlands and Greenpeace Netherlands, the Prins Bernhard Cultuurfonds, the Schure-Beijerinck-Popping Fund, the Dr. Catharina van Tussenbroek Foundation, the Foundation Vrijvrouwe van Renswoude for supporting our research. This article and its contents would not have been possible without the dedication of our M.Sc. students and volunteer team members, especially Machiel Oudejans, Kees den Hollander, and Else Nuyten. Special thanks go out to Dr. Alain F. Zuur for his help with the GAMM analysis and to Dr. Colin MacLeod and three anonymous reviewers for their constructive comments that greatly improved the manuscript. This project was carried out under scientific license nr. 4/CN/2004, issued to Nova Atlantis Foundation by the Azorean Department of the Environment, *Direçcao de Regional do Ambiente*, island of Faial. G. J. Pierce was supported by the ANIMATE project (MEXC-CT-2006-042337).

Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, eds. Proceedings of the 2nd International Symposium on Information Theory. Akademia Kiado, Budapest, Hungary.

Allen, M. C., and A. J. Read. 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. Marine Mammal Science 16:815–824.

Altmann, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49:227–267.

Baker, C. S., and L. M. Herman. 1989. Behavioral responses of summering humpback whales to vessel traffic: Experimental and opportunistic observations. U.S. Department of the Interior. National Park Service, Technical Report NPS-NR-TRS-89-01. 50 pp.

Bejder, L. 2005. Linking short and long-term effects of nature-based tourism on cetaceans. Ph.D. thesis, Dalhousie University, Halifax, Canada. 158 pp.

Bejder, L., and A. Samuels. 2003. Evaluating the effects of nature-based tourism on cetaceans. Pages 229–256 *in* N. M. Gales, M. Hindell and R. Kirkwood, eds. Marine mammals and Humans: Towards a sustainable balance. CSIRO Publishing, Collingwood, Australia.

Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. Connor, M. Heithaus, J. Watson-Capps, C. Flaherty and M. Krützen. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20:1791–1798.

Carlson, C. 2008. A review of whale watch guidelines and regulations around the world, version 2008. Available at http://www.iwcoffice.org/conservation/whalewatching.htm#regulations. Accessed October 2009.

Constantine, R., D. H. Brunton and C. S. Baker. 2003. Effects of tourism on behavioral ecology of bottlenose dolphins of northeastern New Zealand. DOC Science Internal Series 153. Department of Conservation, Wellington, New Zealand. 26 pp.

Dalgaard, P. 2008. Introductory statistics with R. Springer, New York, NY.

Danil, K., D. Maldini and K. Marten. 2005. Patterns of use of Maku'a Beach, O'ahu, Hawai'i, by spinner dolphins (*Stenella longirostris*) and potential effects of swimmers on their behavior. Aquatic Mammals 31:403–412.

Duffus, D. A., and P. Dearden. 1990. Non-consumptive wildlife-oriented recreation: A conceptual framework. Biological Conservation 53:213–231.

Erbe, C. 2002. Underwater noise of whale watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. Marine Mammal Science 18:394–418.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11. Available at http://www.ecologyandsociety.org/vol6/iss1/art11/inline.html

Gomes Pereira, J. N. D. S. 2008. Daily species checklist from whale watching—studying the research potential with an Azorean case study. Journal of the Marine Biological Association of the United Kingdom 88:1283–1288.

Grantner, A., and M. Taborsky. 1998. The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: *Cichlidae*). Journal of Comparative Physiology B 168:427–433.

Hartman, K. L., F. Visser and A. J. E. Hendriks. 2008. Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: A stratified community based on highly associated social units. Canadian Journal of Zoology 86:294–306.

Hoyt, E. 2005*a*. Marine protected areas for whales, dolphins and porpoises. Earthscan, London, UK.

Hoyt, E. 2005*b*. Sustainable ecotourism on Atlantic islands, with special reference to whale watching, marine protected areas and sanctuaries for cetaceans. Biology and Environment: Proceedings of the Royal Irish Academy 105B:141–154.

IOC, IHO and BODC. 2003. Centenary Edition of the GEBCO Digital Atlas. Published on CD-ROM on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans. British Oceanographic Data Centre, Liverpool, UK.

Janik, V. M., and P. M. Thompson. 1996. Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. Marine Mammal Science 12:597–602.

Kruse, S. 1991. The interactions between boats and killer whales in Johnson strait, B.C. Pages 149–160 *in* K. S. Norris and K. Pryor, eds. Dolphin societies discoveries and puzzles. University of California press, Berkeley, CA.

Lammers, M. O. 2004. Occurrence and behavior of Hawaiian spinner dolphins (*Stenella longirostris*) along Oahu's leeward and south shores. Aquatic Mammals 30:237–250.

Lusseau, D. 2003*a*. Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. Conservation Biology 17:1785–1793.

Lusseau, D. 2003*b*. Male and female bottlenose dolphins *Tursiops spp*. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. Marine Ecology Progress Series 257:267–274.

Lusseau, D. 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. Ecology and Society 9:2. Available at http://www.ecologyandsociety.org/vol9/iss1/art2/inline.html

Lusseau, D. 2005. The residency pattern of bottlenose dolphins (*Tursiops spp*.) in Milford Sound, New Zealand, is related to boat traffic. Marine Ecology Progress Series 295:265–272.

Magalhães, S., R. Prieto, M. A. Silva, J. Gonçalves, M. Afonso-Dias and R. S. Santos. 2002. Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale watching vessels in the Azores. Aquatic Mammals 28:267–274.

Mann, J. 1999. Behavioral sampling methods for cetaceans: A review and critique. Marine Mammal Science 15:102–122.

Miller, M. L. 1993. The rise of coastal and marine tourism. Ocean and Coastal Management 20:181–199.

Moberg, G. P. 2000. Biological response to stress: Implications for animal welfare. CAB International, Cambridge, UK.

Norris, K. S., and T. P. Dohl. 1980. Behavior of the Hawai'ian spinner dolphin, *Stenella longirostris*. Fishery Bulletin 77:821–849.

Nowacek, S. M., R. S. Wells and A. R. Solow. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota bay, Florida. Marine Mammal Science 17:673–688.

O'Connor, S., R. Campbell, H. Cortez and T. Knowles. 2009. Whale watching worldwide: Tourism numbers, expenditures and expanding economic benefits, a special report from the International Fund for Animal Welfare, Yarmouth, MA, prepared by Economists at Large.

Pinheiro, J., and D. Bates. 2000. Mixed effects models in S and S-Plus. Springer-Verlag, New York, NY.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricklefs, R. E., M. Konarzewski and S. Daan. 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. American Naturalist 147:1047–1071.

Shane, S. H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island Florida. Pages 245–265 *in* S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, New York, NY.

Shane, S. H. 1995. Behavior patterns of pilot whales and Risso's dolphins off Santa Catalina Island, California. Aquatic Mammals 21:195–197.

Silva, M. A. E. 2007. Population ecology of bottlenose dolphins in the Azores Archipelago. Ph.D. thesis, University of St. Andrews, St. Andrews, UK. 254 pp.

Stensland, E., and P. Berggren. 2007. Behavioral changes in female Indo-Pacific bottlenose dolphins in response to boat-based tourism. Marine Ecology Progress Series 332:225–234.

Tinker, S. W. 1988. Whales of the world. Bess Press Inc., Honolulu, HI.

Whitehead, H. 2003. Sperm whales: Social evolution in the ocean. University of Chicago Press, Chicago, IL.

Williams, R., and E. Ashe. 2007. Killer whale evasive tactics vary with boat number. Journal of Zoology 272:390–397.

Williams, R., A. W. Trites and D. E. Bain. 2002. Behavioral responses of killer whales (*Orcinus orca*) to whale watching boats: Opportunistic observations and experimental approaches. Journal of Zoology 256:255–270.

Williams, R., D. Lusseau and P. S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biological Conservation 133:301–311.

Wood, S. N. 2006. Generalized additive models: An introduction with R. Chapman and Hall/CRC Press, Boca Raton, FL.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

Received: 16 July 2009
Accepted: 1 April 2010