



Interpreting short-term behavioural responses to disturbance within a longitudinal perspective

LARS BEJDER*, AMY SAMUELS†, HAL WHITEHEAD* & NICK GALES‡

*Biology Department, Dalhousie University

†Biology Department, Woods Hole Oceanographic Institution

‡Australian Antarctic Division, Tasmania

(Received 23 May 2005; initial acceptance 8 September 2005;
final acceptance 26 April 2006; published online 20 September 2006; MS. number: A10168R)

We documented immediate, behavioural responses of Indo-Pacific bottlenose dolphins (*Tursiops* sp.) to experimental vessel approaches in regions of high and low vessel traffic in Shark Bay, Western Australia. Experimental vessel approaches elicited significant changes in the behaviour of targeted dolphins when compared with their behaviour before and after approaches. During approaches, focal dolphin groups became more compact, had higher rates of change in membership and had more erratic speeds and directions of travel. Dolphins in the region of low vessel traffic (control site) had stronger and longer-lasting responses than did dolphins in the region of high vessel traffic (impact site). In the absence of additional information, the moderated behavioural responses of impact-site dolphins probably would be interpreted to mean that long-term vessel activity within a region of tourism had no detrimental effect on resident dolphins. However, another study showed that dolphin-watching tourism in Shark Bay has contributed to a long-term decline in dolphin abundance within the impact site (Bejder et al., in press, *Conservation Biology*). Those findings suggest that we documented moderated responses not because impact-site dolphins had become habituated to vessels but because those individuals that were sensitive to vessel disturbance left the region before our study began. This reinterpretation of our findings led us to question the traditional premise that short-term behavioural responses are sufficient indicators of impacts of anthropogenic disturbance on wildlife.

© 2006 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Investigations of anthropogenic disturbance often must generate time-sensitive information under crisis conditions. Owing to inadequate time, resources and background information, these studies typically rely on short-term, behavioural measures that can be readily recorded and related to the source of disturbance (e.g. Duchesne et al. 2000; de la Torre et al. 2000; Lacy & Martins 2003). Little is known, however, about the suitability of short-term behavioural measures as indicators of biologically significant impacts. It is seldom known how immediate responses are transformed into long-term changes in condition or habitat use, for example, or how those changes may influence

reproduction, survival or population size (e.g. Gill et al. 2001; Beale & Monaghan 2004a). For example, Miller et al. (2000) found that male humpback whales, *Megaptera novaeangliae*, sing longer songs during exposure to anthropogenic sound, and they suggested that alterations to this sexual display would be detrimental to whale reproduction; however, this hypothesis will be difficult to test.

The traditional interpretation of behavioural change in the face of disturbance has also been challenged (e.g. Nisbet 2000; Gill et al. 2001; Beale & Monaghan 2004b). It was formerly assumed that animals that move away from disturbance are more greatly affected than those that remain (e.g. Foster & Rahe 1983; Fowler 1999), but recent studies suggest that departing animals may be the ones with sufficient condition to do so (e.g. Stillman & Goss-Custard 2002; Beale & Monaghan 2004b). Moreover, where disturbance is concentrated in critical habitat, animals may have no other option but to stay (e.g. Creel et al. 2002; Dyck & Baydack 2004).

The same issues are relevant to interpreting impacts of wildlife tourism. Cetacean (whale, dolphin and porpoise)

Correspondence and present address: L. Bejder, Centre for Fish and Fisheries Research, Division of Science and Engineering, Murdoch University, Murdoch, Western Australia, 6150, Australia (email: l.bejder@murdoch.edu.au). A. Samuels, Biology Department, Woods Hole, Oceanographic Institution, Woods Hole, MA 02543, U.S.A. H. Whitehead, Biology Department, Dalhousie University, Halifax, Nova Scotia, B3P 4J1, Canada. N. Gales, Australian Antarctic Division, Kingston, Tasmania, 7001, Australia.

watching is an ever-increasing form of wildlife tourism, targeting more than 50 (including endangered and threatened) species and involving more than \$1 billion (U.S.) and 9 million people annually (Hoyt 2001; Samuels et al. 2003). Cetacean watching is often represented as a benign substitute for whaling (e.g. Hoyt 1993) that augments local revenues (e.g. Hoyt 2001) and environmental awareness (e.g. Orams 1997). However, this tourism emphasizes repeated, close-up encounters with specific cetacean communities, thereby presenting considerable potential for harm to targeted animals. Assessments of effects of cetacean-watching tourism typically focus on short-term responses (e.g. Bejder et al. 1999; Williams et al. 2002; Lusseau 2003; Constantine et al. 2004; Samuels & Bejder 2004), the biological significance of which is seldom known (Corkeron 2004).

In the present study, we documented immediate, behavioural responses of Indo-Pacific bottlenose dolphins (*Tursiops* sp.) to experimental vessel approaches in regions of high and low vessel traffic in Shark Bay, Western Australia. Interpretation of our findings in the context of long-term impacts of vessel-based dolphin-watching tourism in Shark Bay (Bejder et al., *in press*) led us to question the traditional premise that short-term behavioural responses are sufficient indicators of impacts of anthropogenic disturbance on wildlife.

METHODS

Field Site and Study Population

Shark Bay, Western Australia (25°45'S, 113°44'E; Fig. 1), is populated by approximately 2700 Indo-Pacific bottlenose dolphins (Preen et al. 1997). The habitat consists of sea grass beds (<4-m depth), embayment plains (5–13 m) and channels (<14 m). Dolphin tourism and

long-term dolphin research are based from the resort of Monkey Mia in the eastern gulf.

Two forms of dolphin tourism occur in Shark Bay. Since the 1960s, several dolphins have received fish handouts from humans at a beach in Monkey Mia (Connor & Smolker 1985). At present, four adult female dolphins are provisioned with strict supervision by wildlife rangers. Provisioning is the area's primary tourist attraction with more than 100 000 annual visitors, most of which come to see dolphins (Stoeckl et al. 2005).

Commercial, vessel-based, dolphin-watching tourism began in 1993. One tour operator has offered tours since May 1993, and a second operator began in August 1998. The two tour vessels are 17-m and 19-m sailing catamarans with turbo140-hp and 50-hp engines, respectively. The two operators offer a combined total of eight trips daily.

Dolphin behavioural research began in 1984. Approximately 800 individual dolphins are studied within a 300-km² area (Fig. 1a). Photo-identification and focal-follow methods are conducted from small vessels (4–6 m long, 6–40-hp outboard engines). A long-term database provided individually specific information for dolphin subjects of our experiments, including age and sex (e.g. Mann et al. 2000; Krützen et al. 2004).

Experimental Design

We studied effects of experimental vessel approaches on dolphin behaviour at two sites that had different histories of vessel activity: high vessel activity (impact site) and low vessel activity (control site). We evaluated group-level, nonvocal, behavioural responses of dolphins 15 min before (B), during (D) and after (A) approaches by an experimental vessel (e.g. BDA experimental design sensu Bejder & Samuels 2003).

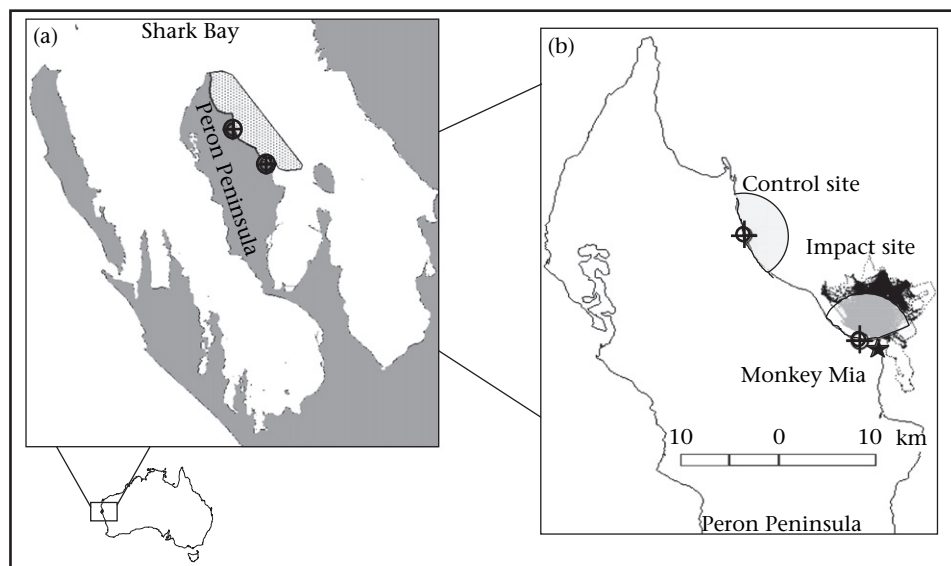


Figure 1. Study site. (a) Shark Bay, Western Australia, including the ~300-km² region of long-term research (hatched), and (b) control and impact sites with targets indicating shore stations. Impact site defined by GPS downloads of tour-vessel movements during 2000–2003 (dotted lines).

For each BDA experiment, shore-based observers selected a focal dolphin group based on the group's proximity to the shore station and the absence of any vessels within 300 m. A group was defined as one or more dolphins within proximity described by a 50-m chain rule (modified from Smolker et al. 1992). When several groups met these criteria (in 8 of 78 experiments), we alternated selecting larger and smaller groups. After selecting the focal group, shore observers recorded baseline behavioural data for 15 min (B period). At the end of the B period, shore observers contacted vessel-based observers via VHF radio to direct movement of the experimental vessel towards the focal group. The experimental vessel was a 4.3-m runabout with 25-hp, 4-stroke, outboard engine. We terminated experiments prematurely when the identity or behaviour of the focal group was uncertain (e.g. poor visibility, beyond range), or when another vessel came within 300 m of the focal group.

We defined the D period to begin once the experimental vessel was within 50 m of the nearest dolphin in the focal group. Throughout the 15-min D period, shore observers continued to record behavioural data while the vessel maintained a distance of approximately 10–50 m from the focal group and mimicked the behaviour of tour vessels as described in the operators' license conditions. Specifically, tour operators were limited to 15 min within 50 m of a dolphin group and were not permitted to restrict or impede the dolphins' behaviour (Western Australian Wildlife Conservation Notice 1998 (Close Season for Marine Mammals); Western Australian Wildlife Conservation Regulations 1970, Regulation 15 Marine Mammal Interaction License).

During the D period, observers aboard the experimental vessel identified individual dolphins in the focal group by taking dorsal fin photographs, which were later compared with a catalogue (Würsig & Jefferson 1990). Identities of dolphins that left or joined the focal group were also recorded. The shore team monitored movements of splinter subgroups that departed when the vessel was not nearby until those dolphins could be identified.

We defined the D period to end once the experimental vessel moved beyond 50 m of the nearest dolphin in the focal group. We defined the A period to begin when the experimental vessel was beyond 300 m of the focal group. Throughout the 15-min A period, the shore team continued to monitor the behaviour and movements of the focal group.

To delineate the impact site (Fig. 1b), we tracked tour-vessel movements at 75-s intervals via automatic GPS downloading during 188 tour-vessel trips monitored in 2000; additional trips were monitored in 2002–2003 to confirm that tour-vessel activity did not change during the study period ($N = 177$ and 195 total trips monitored per tour vessel). We defined the impact site as the portion of the region of tour-vessel activity that could be monitored reliably from the shore station. We selected a distant control site wherein dolphins were naïve to tourism and recreational vessels but had limited exposure to research-vessel activity (Fig. 1b). A distance of approximately 17 km between sites minimized overlap of individual dolphins between the two sites.

Data Collection

Shore-based observers at an elevated vantage point used focal-group sampling to monitor the dolphins continuously throughout each experiment. Behaviours and sampling schemes were selected to meet the rigorous requirements for a group-level focus (Altmann 1974). Concurrent theodolite tracking and behavioural sampling provided simultaneous information about the movements, behaviour and interindividual spacing of the focal dolphin group throughout the experiment. Theodolite tracking also documented the position of the experimental vessel throughout the D period. Shore observers consisted of a theodolite operator who recorded positions of targets, and a computer operator who downloaded positions. Both observers looked for dolphins and recorded behavioural data.

Response variables related to dolphin movements

We used a Leitz DT5 digital theodolite ($\times 30$ telescope) to record dolphin and vessel positions. A theodolite simultaneously measures horizontal and vertical angles to a target. The accuracy of a position acquired via theodolite is proportional to the instrument's elevation above sea level and inversely proportional to distance to the target. Shore-station elevations were 29.33 and 29.12 m above sea level at impact and control sites, respectively. On average, we observed dolphin groups at approximately 1500 m from the shore station. Thus, a 10-cm error in the instrument's height-above-sea-level measurement at an approximately 30-m elevation provided accuracy to within 9 m for targets at 2500 m, and to within 2 m for targets at 500 m (Würsig et al. 1991). Because shore stations at the two sites had nearly equal elevations, we assumed that between-site differences in accuracy of position calculations were negligible.

The theodolite was connected to a laptop computer that ran the data acquisition program, Pythagoras (Gailey & Ortega-Ortiz 2002). The software downloaded angles to targets (measured from a reference point of known latitude and longitude), associated each record with the exact time of acquisition and converted readings into rectangular (X, Y), latitude and longitude coordinates for the target ('fix'), taking into account the instrument's position and height above sea level (including tidal fluctuations). Two consecutive theodolite fixes of a dolphin group (taken at the group's estimated centre) defined one 'leg' of movement. On average, 15 fixes of the group, or 14 legs, were obtained for each 15-min BDA period.

We recorded locations of dolphins at approximately 60-s intervals in B and A periods. We alternately located dolphins and the vessel at approximately 30-s intervals in D periods. Actual fixes were not taken at measured intervals, and we found that fix rates varied between BDA periods, with B and A periods typically having lower rates than D periods. This created a consistent positive bias in path resolution for the D period. The bias probably resulted from the operator's attempts to document in detail relative positions of the vessel and dolphin group, and the comparative ease in spotting dolphins with the vessel nearby. To eliminate this bias, we compared fix rates for all BDA

periods within each experiment to identify the period with the lowest rate. We then interpolated at the lowest fix rate the entire BDA track for that experiment, based on the assumptions that the dolphin group travelled in a straight line and at constant speed between consecutive fixes. We used interpolated fixes at evenly spaced intervals to compare movement variables between BDA periods.

We calculated four movement variables for each BDA period: average speed, standard deviation (SD) of speed (differences in speed between consecutive legs), distance travelled and average change in direction of movement (between consecutive legs, 0–180 degrees). Standard deviation of speed is a measure of consistency in travel speed, with low values indicating constant speed. Average change in direction is a measure of consistency in travel direction, with low values indicating constant direction.

Response variables related to dolphin sociality

In shore-based focal follows of dolphin groups, we recorded specified behavioural data, which were linked by time to theodolite tracks. We measured four social response variables for each BDA period: number of fission events (group splits), number of fusion events (group joins), interindividual spacing and group size. We used continuous, all-occurrence sampling of fission/fusion events, and scan sampling of interindividual spacing (Altmann 1974). Group size was estimated at the onset of each BDA period.

Fusions and fissions were defined to occur when one or more dolphins moved within or beyond the 50-m criterion that defined the group. When fissions occurred, we continued the follow by selecting the smaller or larger subgroup as our focal in alternate experiments. Interindividual spacing was assessed at 10-min intervals, typically producing one assessment per BDA period. Spacing was based on a relative scale of modal distances among dolphins in the group: ≤ 0.3 m, >0.3 –2 m, >2 –5 m, >5 –10 m, >10 –50 m. The elevated shore station was an excellent vantage for observing large-scale, group-level behaviour, therefore, the bias in path resolution among BDA periods was not likely to be a problem for recording social response variables.

Sample Size

We conducted a pilot study in 2000 to become familiar with theodolite operation, ensure tracking consistency and develop rigorous sampling protocols (34 days, 182 h). Pilot study data were not included in analyses. In 2001–2002, we conducted experiments at the impact site (80 days, 389 h) and the control site (20 days, 120 h).

We analysed 78 experiments in which dolphin behaviour and movements were recorded reliably through at least the B and D periods: 49 and 29 experiments at impact and control sites, respectively. In 37% of experiments, A-period data were not obtained because of interference or loss. We found no statistical difference between experiments composed of BD versus BDA periods (Student's *t* test: $t_{52} = 0.46$, $P = 0.65$); thus, both types of experiments were combined for analyses.

Statistical Methods

We calculated the mean and standard deviation for response variables per BDA period per site (Appendix, Table A1). Summary statistics were based upon 134 and 71 BDA periods at impact and control sites, respectively, with the exception of the response variable 'group spacing'. We eliminated group size of one dolphin from analyses, resulting in 99 and 64 BDA periods at impact and control sites, respectively.

We compared movement and behavioural variables among BDA periods and between control and impact sites. We used multivariate analyses (canonical variate analysis and multivariate analysis of variance tests) to summarize the data, identify patterns of response and reduce the number of hypothesis tests performed, thus minimizing the problem of multiple comparisons (Manly 1994). For the multivariate analysis of variance, we used a mixed-model approach because some experiments lacked A-period data. All response variables were normally distributed within BDA periods, with the exception of numbers of fissions and fusions. We normalized fission/fusion data with a square-root transformation.

We assumed that each focal group was an independent unit. An assumption of complete independence may not have been fulfilled because some individuals were present in more than one focal group (18 and 11 at impact and control sites, respectively). However, the composition of each focal group was different, so we assumed that each group could be considered reasonably independent of the others. In comparing response variables among periods within experiments, each focal dolphin group provided its own control, thereby minimizing environmental or site influences.

Characteristics of Study Subjects

We targeted no more than 118 dolphins in experiments. We identified 93 dolphins as individuals (41 and 52 at impact and control sites, respectively); however, 6–25 dolphins were not identified (4–11 and 2–14, respectively). We give the ranges for unidentified dolphins because we could not always establish whether these individuals had been observed more than once. Given the extensive identification catalogue for Shark Bay dolphins, unidentified animals were likely to be known individuals whose identities were unconfirmed.

None of the individual dolphins involved in experiments at the control site was involved in experiments at the impact site and vice versa. Complete segregation of dolphin subjects between sites validated our selection of experimental sites. There was no difference between sites in the sex (Fisher's exact test: $P = 0.647$) or age class (Fisher's exact test: $P = 0.462$) of subjects. We defined age classes as calf (dependent on mother), juvenile (weaning to adult) and adult (males aged >15 years; known reproductive females or females aged >13 years). There was also no difference between sites in focal group size per sampling period (Student's *t* tests: B: $t_{52} = -0.78$, $P = 0.43$; D: $t_{57} = -1.02$, $P = 0.32$; A: $t_{30} = -1.33$, $P = 0.20$). Average group size per

period was 3.9 versus 3.4 (B), 4.0 versus 3.3 (D) and 4.5 versus 3.4 (A) at control and impact sites, respectively.

The complete segregation of individuals between sites and the lack of differences in size and age/sex composition of focal groups between sites meant that any observed site-specific differences in dolphin responses to experimental vessel approaches in the present study were probably due to differences in the exposure to vessel activity by dolphins in each area.

RESULTS

We conducted a two-way, repeated measures, multivariate analysis of variance (R-MANOVA) to investigate how the two predictor variables, site (control, impact) and period (B, D, A), simultaneously related to the response variables (Appendix 1, Table A1). Considering all response variables for both sites combined, there was a significant difference between BDA periods ($F_{2,123} = 4.27$, $P = 0.01$). There was no significant difference between sites when sites were considered alone ($F_{1,76} = 1.92$, $P = 0.17$); however, the difference between sites was significant when the interaction term BDA*site was considered ($F_{2,123} = 3.64$, $P = 0.02$). Thus, there was an overall difference in response variables among BDA periods between the two sites.

To further explore those differences, we conducted a canonical-variate (CV) analysis to identify which response variables were most useful for discriminating between BDA periods. We calculated CV scores for each response variable and BDA period with data from both sites combined. Eigenvalues indicated that the first canonical variate (CV1) described the greatest variability among the means of all variables for the three periods, and the second canonical variate (CV2) contributed little towards this separation (eigenvalue = 0.259 and 0.061 for CV1 and CV2, respectively). Therefore, CV1 was the best discriminator of BDA periods and is the sole summary measure of further interest. All of the following analyses are based upon these CV1 values.

Numeric canonical loadings indicated the strength (divergence from zero) and direction (positive or negative) of the relationship between CV1 and each of the response variables (Table 1). High canonical loadings indicated that there were five variables with substantial influence on CV1: these variables were related to sociality (group spacing, numbers of fission and fusion events) and movement consistency (SD of speed, average change in direction), with group spacing having the greatest influence.

To examine responses among periods, we compared CV1 values per BDA period with both sites combined. The mean CV1 value for the D period was significantly lower than the means calculated for B and A periods (Student's t test: D–B: $t_{120} = 5.85$, $P < 0.000$; D–A: $t_{97} = -4.71$, $P < 0.000$; Fig. 2). Thus, significant behavioural changes occurred during approaches (D) when compared with before (B) and after (A) periods. A positive canonical loading for group spacing indicated that groups were least dispersed when CV1 was smallest (i.e. during approaches compared to before and after). Negative canonical loadings for the four other influential variables indicated that, during approaches, there were

Table 1. Canonical loadings for the first canonical variate (CV1) with substantial influences indicated in bold

Response variable	CV1
Distance travelled	0.051
Average speed	-0.064
SD of speed	-0.372
Average change in direction	-0.342
Number of fission events	-0.365
Number of fusion events	-0.398
Group spacing	0.725

more fissions and fusions, and swimming speeds and directions were more erratic.

To compare duration of response between sites, we calculated differences in the CV1 scores (Δ CV1) before and during the approach (B–D) and before and after approach (B–A) for each experiment. Under the null hypothesis of no difference between two periods within an experiment, the percentage of experiments in which Δ CV1 was less than zero for B–D was significantly greater than expected at both sites (chi-square test: control site: 95.6%, $\chi^2_{11} = 19.17$, $N = 23$, $P < 0.0000$; impact site: 74.2%, $\chi^2_3 = 7.26$, $N = 31$, $P < 0.0070$). Negative Δ CV1 values represented a shift from B to D towards more fission and fusion events, more compact group spacing and more erratic swim speeds and directions. The percentage of experiments with Δ CV1 < 0 from B to A was significantly greater than expected at the control site but not at the impact site (chi-square test: control site: 81.8%, $\chi^2_1 = 4.45$, $N = 11$, $P = 0.0348$; impact site: 48.0%, $\chi^2_1 = 0.044$,

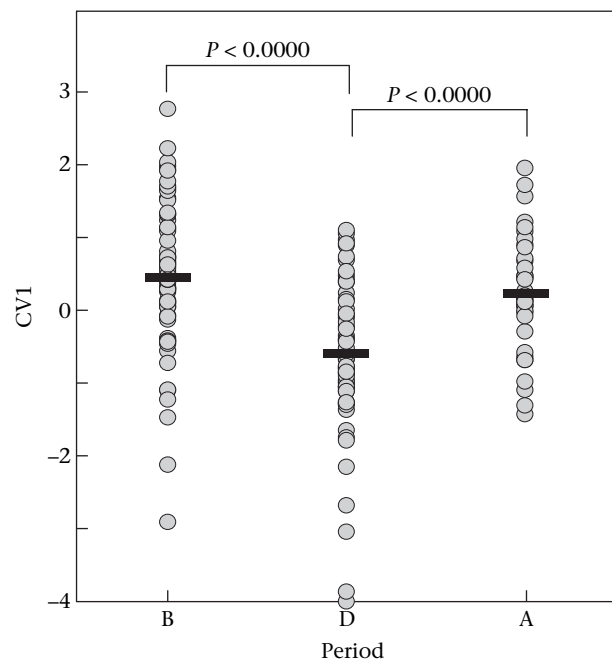


Figure 2. First canonical variate scores (CV1) for focal groups of bottlenose dolphins before (B), during (D) and after (A) experimental vessel approach at both sites combined. Student's t test was used to compare mean CV1 values among BDA periods. Solid black bars indicate mean values.

$N = 23$, $P = 0.83483$). Thus, responses of dolphins at the control site remained altered and did not resume pre-approach levels for up to 15 min after the experimental vessel departed; whereas, impact-site dolphins did resume pre-approach levels during the A period.

To further compare duration of response between sites, we calculated differences between mean Δ CV1 values for B–A periods. Mean Δ CV1 values for experiments at the control site were significantly lower (-0.896) than those at the impact site (0.089) (Student's t test: $t_{17} = 2.36$, $P = 0.029$; Fig. 3). This result is similar to the finding presented above, both showing that responses of dolphins at the control site were longer lasting than those at the impact site.

To compare the strength of response between sites, we calculated differences between mean Δ CV1 values for B–D periods. Mean Δ CV1 values for experiments at the control site were significantly lower (-1.50) than those at the impact site (-0.65) (Student's t test: $t_{48} = 2.65$, $P = 0.011$; Fig. 4). Thus, responses of dolphins at the control site were stronger than those at the impact site.

In conclusion, experimental vessel approaches elicited changes in behavioural responses related to sociality and movement consistency at both the impact and control sites. However, behavioural changes were stronger and longer lasting at the control site where dolphins seldom experienced vessel activity.

DISCUSSION

Experimental vessel approaches elicited significant changes in the behaviour of targeted dolphins when

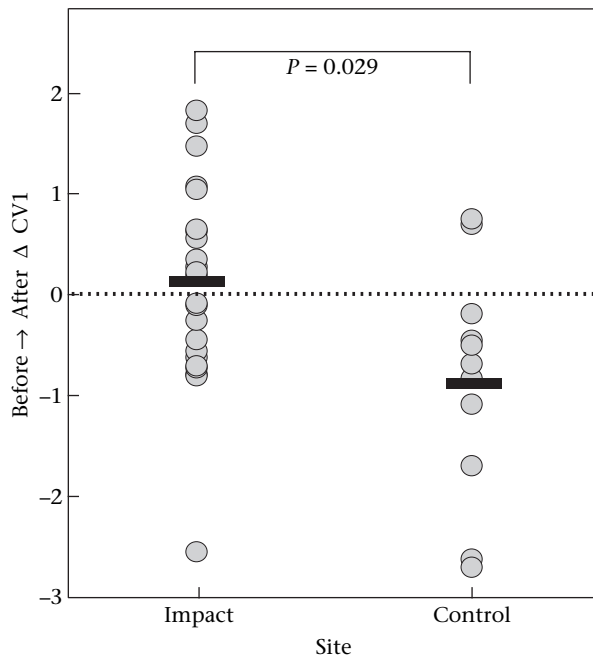


Figure 3. Between-site comparison of differences in Δ CV1 values for focal groups of bottlenose dolphins before (B) and after (A) experimental vessel approach. Student's t test was used to compare mean differences in Δ CV1 values between sites. Solid black bars indicate mean values.

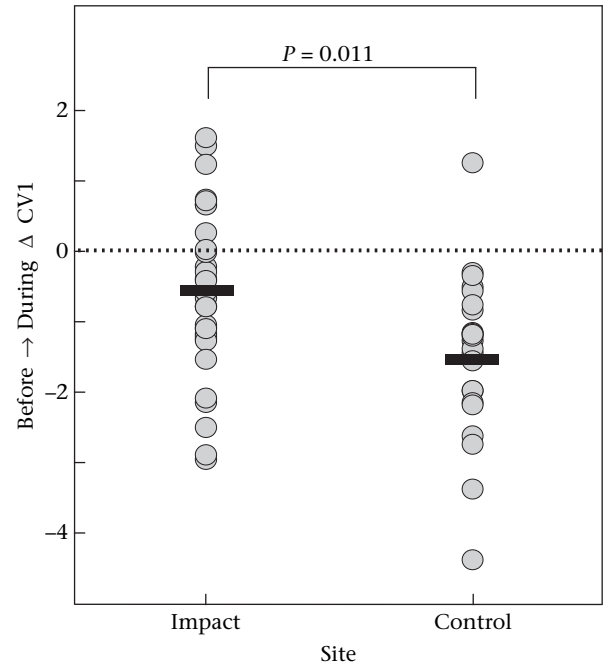


Figure 4. Between-site comparison of differences in Δ CV1 values for focal groups of bottlenose dolphins before (B) and during (D) experimental vessel approach. Student's t test was used to compare mean differences in Δ CV1 values between sites. Solid black bars indicate mean values.

compared with their behaviour before and after approaches. During approaches, focal groups at both sites became more compact and had higher rates of change in membership, reflecting changes in social measures, and they had more erratic speeds and directions of travel, reflecting changes in movement patterns. However, dolphins at the control site had stronger and longer-lasting responses than those at the impact site. Elsewhere, variability in disturbance response has been linked to various characteristics of targeted dolphins (e.g. sex: Williams et al. 2002; Lusseau 2003; age: Constantine 2001; group size: Constantine et al. 2004); however, we found no differences between sites in the age/sex composition or size of focal dolphin groups. Thus, site-specific differences in behavioural response were probably due to differences in exposure to vessels by dolphins residing in each area.

Effects of Disturbance on Sociality

For cetaceans, increased group cohesion has been suggested as a means for group members to better track each other's movements, thereby accelerating reactions to danger (e.g. Johnson & Norris 1986; Norris & Schilt 1988). Cetaceans reportedly increase cohesion in the presence of vessels (e.g. Denardo 1998; Bejder et al. 1999; Nowacek et al. 2001; this study), and in contexts of presumed surprise or threat (e.g. Whitehead & Glass 1985; Norris et al. 1994). Increased cohesion has also been documented as a response by terrestrial mammals to disturbance (e.g. mountain goats, *Oreamnos americanus*: Foster & Rahe 1983; pronghorns, *Antilocapra americana*: Berger et al.

1983), and by schooling fish to predation threats (e.g. Pitcher & Parrish 1993).

Effects of disturbance on group membership have not been described previously for cetaceans. Unstable group membership has been reported as a disturbance response by terrestrial mammals (e.g. mountain goats: Foster & Rajs 1983, Côté 1996; Sulawesi black macaques, *Macaca nigra*: Kinnaird & O'Brien 1996). In some cases, separations enabled predators to prey upon unprotected offspring (e.g. Dall sheep, *Ovis dalli dalli*: Nette et al. 1984; mountain goats: Côté & Beaudoin 1997; numerous species of water birds: Carney & Sydeman 1999).

One benefit of group life is reduced risk of predation by enhancing, for example, predator detection, individual survival via dilution and confusion effects, and/or cooperative defence (e.g. Hamilton 1971; Krebs & Davies 1993). In the context of the fluid, fission–fusion society of coastal bottlenose dolphins (e.g. Wells et al. 1987; Smolker et al. 1992), changes to grouping behaviour in response to vessels might be considered unimportant. We suggest that disruption of grouping behaviour, no matter how short term, may have far-reaching repercussions for species such as bottlenose dolphins that rely on long-term, individually specific bonds (e.g. Connor et al. 1992; Smolker et al. 1992). For these species, social interdependence may be important in reducing vulnerability to shark predation, which has been suggested as a primary determinant in the evolution of cetacean grouping behaviour (e.g. Norris & Dohl 1980; Wells et al. 1980; Norris et al. 1994). For Shark Bay dolphins, whose risk of shark predation is high (Heithaus 2001), frequent group changes in response to vessels may result in smaller subgroups or split up mutually reliant associates, thereby escalating their predation risk.

Interpreting Short-term Behavioural Responses to Disturbance within a Longitudinal Perspective

Dolphins responded to experimental vessel approaches at both sites but responses at the control site were more dramatic. The moderated responses of impact-site dolphins might be interpreted to indicate that those dolphins had become habituated to vessels in a region of long-term vessel traffic. Behavioural habituation, defined as a reduction in response over time as individuals learn that there are neither adverse nor beneficial consequences to a stimulus (Thorpe 1963), is often considered a positive outcome when people want to observe natural behaviour at close range (e.g. Tutin & Fernandez 1991; Johns 1996). Thus, concluding that impact-site dolphins had become habituated to vessel traffic would probably be taken to mean that vessel-based, dolphin-watching tourism has had no adverse effects on targeted dolphins.

There are, however, multiple mechanisms that can result in moderated response to disturbance (Bejder 2005). For example, individual animals can learn that there are no adverse effects from disturbance stimuli; animals can be injured or deafened by exposure to disturbance; animals can respond to ecological factors other

than the disturbance; or the more responsive individuals of a community may not be present at the time of assessment, for example, through displacement (Griffiths & van Schaik 1993; Fowler 1999). These mechanisms all produce habituation-like responses but only learning results in true behavioural habituation (Bejder 2005).

Habituation has come into recent usage to refer to all instances of moderated response without differentiating among potential mechanisms; however, many claims to habituation are actually based on measuring tolerance, which is the intensity of disturbance that animals tolerate at one point in time (Nisbet 2000). Confirmation that habituation has occurred requires longitudinal, sequential measurements of individual responses to controlled stimuli (Nisbet 2000; Bejder 2005), a rigorous assessment that is rarely used (but see, e.g. Tutin & Fernandez 1991; Johns 1996). In the present study, we did not measure a gradual waning of response by individuals over time; therefore, we cannot assume that impact-site dolphins were habituated to vessels. Dolphins residing in the impact site showed greater tolerance to vessels than control-site dolphins at the time of this study, but our study design did not allow us to distinguish among alternative mechanisms for their moderated responses.

We were able, however, to evaluate the short-term behavioural responses to experimental disturbance within the context of long-term impacts of vessel activity on dolphin abundance in Shark Bay (Bejder et al., *in press*). Based on longitudinal, individually specific data, Bejder et al. (*in press*) compared dolphin abundance in two adjacent sites during three consecutive 4.5-year periods wherein vessel-based research was relatively constant but vessel-based tourism increased from zero, to one, to two dolphin-watching operators. In the Bejder et al. (*in press*) study, the tourism site was equivalent in location but larger than the impact site of the present study; an adjacent nontourism site was a region of low vessel traffic but distinct from the control site of the present study; and the long-term study period (1988–2003) encompassed the period of the present study (2001–2002).

In the Bejder et al. (*in press*) study, a nonlinear logistic model demonstrated that when comparing periods with no tourism and with one tour operator, there was no change in dolphin abundance within the tourism site. However, when the number of tour operators increased to two, there was a significant average decline in dolphin abundance within the tourism site (14.9%; 95% CI = –20.8 to –8.23), equivalent to a decline of one per seven individuals. Concurrently within the adjacent nontourism site, there was a nonsignificant increase in dolphin abundance (8.5%; 95% CI = –4.0 to +16.7). Tour-vessel activity was identified as the main cause of declining dolphin abundance. The local decline was not part of an overall population decline because an opposite trend occurred in the adjacent nontourism site, and the local decline was not explained by ecological factors, which would have had equivalent effects in the adjacent site. Possible between-site differences in immigration or mortality could not be discounted, and differential recruitment via reproduction is under investigation (Bejder 2005). However, the findings indicated that the decline

in dolphin abundance in the tourism site was partly due to the displacement of more sensitive animals away from the area of disturbance. During the period of greatest tour-vessel activity (1998–2003), dolphin abundance declined in the tourism site and slightly increased in the adjacent nontourism site, suggesting a long-term shift from an area of higher to lower vessel traffic.

We can better interpret the short-term behavioural responses to experimental vessel approaches in the context of the long-term decline in dolphin abundance (Bejder et al., in press). We suggest that the moderated response of impact-site dolphins was not the result of habituation to vessel activity. Instead, we propose that individuals sensitive to vessel-based dolphin-watching tourism had departed the region prior to our study; thus, the moderate response to disturbance probably resulted from a biased sample in which one subset of the study population was absent from the assessment (see also: Griffiths & van Schaik 1993; Fowler 1999).

Implications for Wildlife Management

Wrongful application of the term habituation can mislead wildlife managers to conclude that anthropogenic activity has neutral, or even benign, consequences for wildlife, and thus, can seriously undermine management plans and conservation efforts. Moderation in the behavioural response of wildlife to anthropogenic disturbance, which is often taken to signify that behavioural habituation has occurred, may instead indicate that the more sensitive individuals left the region of disturbance before the onset of assessment. In the present study, in the absence of a longitudinal perspective, the moderated behavioural responses of impact-site dolphins to vessel activity probably would be misconstrued to mean that long-term vessel activity within a tourism region had no detrimental effect on resident dolphins. Reversal of this interpretation in light of supplementary, long-term information leads us to challenge the traditional assumption that short-term behavioural responses are sufficient indicators of the impacts of human disturbance on wildlife (see also: e.g. Beale & Monaghan 2004b).

This does not mean that short-term behavioural assessments have no value, only that behavioural responses to disturbance must be interpreted with caution. Short-term assessments conducted at specified intervals over periods of years can be useful in detecting, for example, behavioural change over time, and thereby, distinguishing among mechanisms for responses resembling habituation (or sensitization) (e.g. Constantine 2001; this study).

In the case of Shark Bay dolphins, we conclude that we narrowly avoided the mistake of providing incorrect information to wildlife managers. This narrow escape is cause for concern with respect to cetacean-watching tourism worldwide. Cetacean-watching tourism is a growth industry (Hoyt 2001), and there are many locales where tourist demands are considerably greater than in Shark Bay (e.g. British Columbia, Canada: Williams et al. 2002; Foote et al. 2004; Bay of Islands and Fjordland, New Zealand: Lusseau 2003; Constantine et al. 2004; Port Stephens, Australia:

Allen 2005; Hawaii, U.S.A.: Forest 2001). In contrast, there are few locations other than Shark Bay where behavioural responses to tourism can be evaluated within a longitudinal perspective. Typically, studies of impacts of cetacean-watching tourism are constrained to brief, one-time assessments in which individual animals are not known. As shown in the present study, these limited assessments may result in incomplete or inaccurate conclusions as to how tourism affects targeted animals. For cetaceans targeted by tourism at locations where no longitudinal or before/after data sets are available, we suggest that management planning draw strong inference from the best-studied sites, such as Shark Bay, where long-term, individually specific information can be taken into account. Given the complexities of assessing impacts of human activity on wildlife, we advocate an adaptive management approach, which eschews the one-final-solution strategy, and instead enables managers to move forward in the face of uncertainty, multiple variables, and/or incomplete information about cause-and-effect relationships (e.g. Holling 1978; Walters 1986). A tactical mix of brief, focused assessments, in coordination with longitudinal observation at the best-supported sites, seems a prudent way forward to devise long-range, adaptive management plans to mitigate impacts of tourism on targeted animals.

Acknowledgments

We are grateful to our colleagues in Shark Bay who contributed data to this research: L. Barre, P. Berggren, A. Coakes, R. Connor, C. Flaherty, Q. Gibson, M. Heithaus, V. Janik, M. Krützen, J. Mann, B. Sargeant, J. Watson-Capps and A. Wirsing. We thank the research assistants who helped collect data during this study: S. Allen, K. Burnett, A. Coakes, R. Constantine, M. Davies, S. Gero, D. Heimeier, A. MacArthur, A. MacKay, L. Marshall, J. Munifumbo, F. O'Neill, A. Ottensmeyer, S. Rimella, E. Robinson, H. Smith and R. Wrangham. G. Gailey graciously repeatedly modified the software program, Pythagoras, to meet our ever-changing needs. We especially thank G. Ridgley, H. Raven and the crews of *Aristocat 2* and *Shotover* for a good and productive working relationship. We are grateful for the financial, logistic and moral support provided by the Western Australian Department of Conservation and Land Management, with special thanks to D. Charles, D. Rose and the Denham staff. We are also grateful for logistical support provided by the Monkey Mia Dolphin Resort, especially D. Massie. Two anonymous referees, S. Allen, P. Corkeron, M. Leonard, J. Mitani and B. Scheibling made insightful comments on earlier versions of this manuscript. L.B. was funded by the Danish Research Agency, the Western Australian Department of Conservation and Land Management, the PADI Foundation, the Dalhousie University Faculty of Graduate Studies and the Patrick Lett Fund. A.S. received support from the Western Australian Department of Conservation and Land Management and the Chicago Zoological Society. This research was conducted under Western Australian Conservation and Land Management License No. SF003052.

References

- Allen, S. J. 2005. Management of bottlenose dolphins (*Tursiops aduncus*) exposed to tourism in Port Stephens, N.S.W., Australia. M.Sc. thesis, Macquarie University.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–266.
- Beale, C. M. & Monaghan, P. 2004a. Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, **41**, 335–343.
- Beale, C. M. & Monaghan, P. 2004b. Behavioural responses to human disturbance: a matter of choice. *Animal Behaviour*, **68**, 1065–1069.
- Bejder, L. 2005. Linking short and long term effects of nature-based tourism on cetaceans. Ph.D. thesis, Dalhousie University.
- Bejder, L. & Samuels, A. 2003. Evaluating impacts of nature-based tourism on cetaceans. In: *Marine Mammals: Fisheries, Tourism and Management Issues* (Ed. by N. Gales, M. Hindell & R. Kirkwood), pp. 229–256. Collingwood: CSIRO.
- Bejder, L., Dawson, S. M. & Harraway, J. A. 1999. Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science*, **15**, 738–750.
- Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R. C., Heithaus, M., Watson-Capps, J., Flaherty, C. & Krützen, M. In press. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology*. doi:10.1111/j.1523-1739.2006.00540.x
- Berger, J., Daneke, D., Johnson, J. & Berwick, S. H. 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. *Biological Conservation*, **25**, 193–208.
- Carney, K. M. & Sydeman, W. J. 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds*, **22**, 68–79.
- Connor, R. C. & Smolker, R. A. 1985. Habituated dolphins (*Tursiops* sp.) in Western Australia. *Journal of Mammalogy*, **66**, 398–400.
- Connor, R. C., Smolker, R. A. & Richards, A. F. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences, U.S.A.*, **89**, 987–990.
- Constantine, R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science*, **17**, 689–702.
- Constantine, R., Brunton, D. H. & Dennis, T. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biological Conservation*, **117**, 299–307.
- Corkeron, P. 2004. Whale watching, iconography and marine conservation. *Conservation Biology*, **18**, 847–849.
- Côté, S. D. 1996. Mountain goat responses to helicopter disturbance. *Wildlife Society Bulletin*, **24**, 681–685.
- Côté, S. D. & Beaudoin, C. 1997. Grizzly bear (*Ursus arctos*) attacks and nanny–kid separation on mountain goats (*Oreamnos americanus*). *Mammalia*, **61**, 614–617.
- Creel, S., Fox, J. E., Hardy, A., Sands, J., Garrott, B. & Peterson, R. O. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. *Conservation Biology*, **16**, 809–814.
- Denardo, C. 1998. Investigating the role of spatial structure in killer whale (*Orcinus orca*) behaviour. MSc. thesis, University of Aberdeen.
- Duchesne, M., Côté, S. D. & Barrette, C. 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. *Biological Conservation*, **96**, 311–317.
- Dyck, M. G. & Baydack, R. K. 2004. Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. *Biological Conservation*, **116**, 343–350.
- Footo, A. D., Osborne, R. W. & Hoelzel, A. R. 2004. Whale-call response to masking boat noise. *Nature*, **428**, 910.
- Forest, A. 2001. The Hawai'ian spinner dolphin, *Stenella longirostris*: effects of tourism. MSc. thesis, Texas A&M University.
- Foster, B. R. & Rahe, E. Y. 1983. Mountain goat response to hydroelectric exploration in northwestern British Columbia. *Environmental Management*, **7**, 189–197.
- Fowler, G. S. 1999. Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. *Biological Conservation*, **90**, 143–149.
- Gailey, G. & Ortega-Ortiz, J. G. 2002. A note on a computer-based system for theodolite tracking of cetaceans. *Journal of Cetacean Research and Management*, **4**, 213–218.
- Gill, J. A., Norris, K. & Sutherland, W. J. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, **97**, 265–268.
- Griffiths, M. & van Schaik, C. P. 1993. The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. *Conservation Biology*, **7**, 623–626.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology*, **31**, 295–311.
- Heithaus, M. R. 2001. Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: attack rate, bite scar frequencies and attack seasonality. *Marine Mammal Science*, **17**, 526–539.
- Holling, C. S. 1978. *Adaptive Environmental Assessment and Management*. New York: J. Wiley.
- Hoyt, E. 1993. Saving whales by watching them. *New Scientist*, **138**, 45–46.
- Hoyt, E. 2001. *Whale Watching 2001: Worldwide Tourism Numbers, Expenditures and Expanding Socioeconomic Benefits*. Yarmouth Port, Massachusetts: International Fund for Animal Welfare.
- Johns, B. G. 1996. Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. *Biological Conservation*, **78**, 257–262.
- Johnson, C. M. & Norris, K. S. 1986. Delphinid social organisation and social behavior. In: *Dolphin Cognition and Behavior: a Comparative Approach* (Ed. by R. J. Schusterman, J. A. Thomas & F. G. Wood), pp. 335–346. Hillsdale, New Jersey: L. Erlbaum.
- Kinnaird, M. F. & O'Brien, T. G. 1996. Ecotourism in the Tangkoko DuaSudara Nature Reserve: opening Pandora's box? *Oryx*, **30**, 65–73.
- Krebs, J. R. & Davies, N. B. 1993. *An Introduction to Behavioural Ecology*. Oxford: Blackwell Scientific.
- Krützen, M., Barre, L. M., Connor, R. C., Mann, J. & Sherwin, W. B. 2004. 'O father: where art thou?' Paternity assessment in an open fission–fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Molecular Ecology*, **13**, 1975–1990.
- Lacy, K. E. & Martins, E. P. 2003. The effect of anthropogenic habitat usage on the social behaviour of a vulnerable species, *Cyclura nubila*. *Animal Conservation*, **6**, 3–9.
- Lusseau, D. 2003. 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.
- Manly, B. F. 1994. *Multivariate Statistical Methods: a Primer*. Dune-din: Chapman & Hall.
- Mann, J., Connor, R. C., Barre, L. M. & Heithaus, M. R. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group size effects. *Behavioral Ecology*, **11**, 210–219.

- Miller, P. J. O., Biassoni, N., Samuels, A. & Tyack, P. L. 2000. Whale songs lengthen in response to sonar. *Nature*, **405**, 903.
- Nette, T., Burles, D. & Hoefs, M. 1984. Observations of golden eagle, *Aquila chrysaetos*, predation on Dall sheep, *Ovis dalli dalli*, lambs. *Canadian Field-Naturalist*, **98**, 252–255.
- Nisbet, I. C. T. 2000. Disturbance, habituation and management of waterbird colonies. *Waterbirds*, **23**, 312–332.
- Norris, K. & Dohl, T. P. 1980. The structure and functions of cetacean schools. In: *Cetacean Behavior: Mechanisms and Functions* (Ed. by L. M. Herman), pp. 211–261. New York: J. Wiley.
- Norris, K. S. & Schilt, C. R. 1988. Cooperative societies in three-dimensional space: on the origins of aggregation, flocks, and schools with special reference to dolphins and fish. *Ethology and Sociobiology*, **9**, 148–179.
- Norris, K. S., Würsig, B., Wells, R. S. & Würsig, M. 1994. *The Hawaiian Spinner Dolphin*. Berkeley: University of California Press.
- Nowacek, S. N., Wells, R. S. & Solow, A. R. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, **17**, 673–688.
- Orams, M. B. 1997. The effectiveness of environmental education: can we turn tourists into 'Greenies'? *Progress in Tourism and Hospitality Research*, **3**, 295–306.
- Pitcher, T. J. & Parrish, J. K. 1993. Functions of shoaling behaviour in teleosts. In: *Behaviour of Teleost Fishes* (Ed. by T. J. Pitcher), pp. 365–439. London: Chapman & Hall.
- Preen, A. R., Marsh, H., Lawler, I. R., Prince, R. I. T. & Shepherd, R. 1997. Distribution and abundance of dugongs, turtles, dolphins and other megafauna in Shark Bay, Ningaloo Reef and Exmouth Gulf, Western Australia. *Wildlife Research*, **24**, 185–208.
- Samuels, A. & Bejder, L. 2004. Chronic interactions between humans and wild bottlenose dolphins (*Tursiops truncatus*) near Panama City Beach, Florida. *Journal of Cetacean Research and Management*, **6**, 69–77.
- Samuels, A., Bejder, L., Constantine, R. & Heinrich, S. 2003. A review of swimming with wild cetaceans with a specific focus on the Southern Hemisphere. In: *Marine Mammals: Fisheries, Tourism and Management Issues* (Ed. by N. Gales, M. Hindell & R. Kirkwood), pp. 277–303. Collingwood: CSIRO.
- Smolker, R. A., Richards, A. F., Connor, R. C. & Pepper, J. W. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, **123**, 38–69.
- Stillman, R. A. & Goss-Custard, J. D. 2002. Seasonal changes in the response of oystercatchers *Haematopus ostralegus* to human disturbance. *Journal of Avian Biology*, **33**, 358–365.
- Stoeckl, N., Smith, A., Newsome, D. & Lee, D. 2005. Regional economic dependence on iconic wildlife tourism: case studies for Monkey Mia and Hervey Bay. *Journal of Tourism Studies*, **16**, 69–81.
- Thorpe, W. H. 1963. *Learning and Instinct in Animals*. London: Methuen.
- de la Torre, S., Snowdon, C. T. & Bejarano, M. 2000. Effects of human activities on wild pygmy marmosets in Ecuadorian Amazonia. *Biological Conservation*, **94**, 153–163.
- Tutin, C. E. G. & Fernandez, M. 1991. Responses of wild chimpanzees and gorillas to the arrival of primatologists: behaviour observed during habituation. In: *Primate Responses to Environmental Change* (Ed. by H. O. Box), pp. 187–197. London: Chapman & Hall.
- Walters, C. 1986. *Adaptive Management of Renewable Resources*. New York: McGraw Hill.
- Wells, R. S., Irvine, A. B. & Scott, M. D. 1980. The social ecology of inshore Odontocetes. In: *Cetacean Behavior: Mechanisms and Functions* (Ed. by L. M. Herman), pp. 263–318. New York: J. Wiley.
- Wells, R. S., Scott, M. D. & Irvine, A. B. 1987. The social structure of free-ranging bottlenose dolphins. In: *Current Mammalogy* (Ed. by H. H. Genoways), pp. 247–305. New York: Plenum.
- Whitehead, H. & Glass, C. 1985. Orcas (killer whales) attack humpback whales. *Journal of Mammalogy*, **66**, 183–185.
- Williams, R. M., Trites, A. W. & Bain, D. E. 2002. Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. *Journal of Zoology*, **256**, 255–270.
- Würsig, B. & Jefferson, T. A. 1990. Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission*, **12**, 43–55.
- Würsig, B., Cipriano, F. & Würsig, M. 1991. Dolphin movement patterns. Information from radio and theodolite tracking studies. In: *Dolphin Societies: Discoveries and Puzzles* (Ed. by K. Pryor & K. Norris), pp. 78–111. Los Angeles: University of California Press.

Appendix

Table A1. Mean (\pm SD) responses of bottlenose dolphins before (B), during (D) and after (A) experimental vessel approach at sites with high ('impact') and low ('control') vessel traffic

Response variable	Impact			Control		
	B	D	A	B	D	A
Average speed (km/h)*	2.70 (0.90)	2.64 (1.0)	2.76 (1.03)	2.91 (0.88)	2.92 (0.98)	3.12 (0.91)
SD of speed*	1.21 (0.63)	1.77 (2.17)	1.38 (0.71)	1.15 (0.57)	1.62 (1.47)	1.64 (1.12)
Distance travelled (km)*	0.68 (0.23)	0.70 (0.30)	0.71 (0.26)	0.67 (0.26)	0.74 (0.26)	0.80 (0.26)
Average change in direction (0–180°)*	34.20 (19.43)	42.46 (23.32)	37.76 (19.55)	29.74 (23.70)	39.02 (22.23)	36.65 (16.69)
Number of fission events*	0.41 (0.57)	0.45 (0.58)	0.25 (0.44)	0.10 (0.31)	0.69 (0.71)	0.31 (0.59)
Number of fusion events*	0.43 (0.61)	0.57 (0.68)	0.17 (0.38)	0.28 (0.46)	0.55 (0.74)	0.31 (0.62)
Group spacing†	1.82 (1.21)	1.21 (0.59)	1.63 (1.18)	2.40 (1.08)	1.58 (0.86)	1.92 (0.98)
*Number of periods	49	49	36	29	29	13
†Number of periods	38	34	27	25	26	13