Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*)

Rob Williams[a,b,], David Lusseau[c,1], Philip S. Hammond[a]*

[a]*Sea Mammal Research Unit, Gatty Marine Laboratory, University of St. Andrews, St. Andrews, Fife KY16 8LB, Scotland, UK*
[b]*Pearse Island, Box 193, Alert Bay BC, Canada V0N 1A0*
[c]*Lighthouse Field Station, University of Aberdeen, George Street, Cromarty, Ross-shire IV11 8YJ, Scotland, UK*

A B S T R A C T

This study examined the activities of "northern resident" killer whales (*Orcinus orca*) in Johnstone Strait, British Columbia, Canada, in July and August, from 1995 to 2002. Disturbance from boat traffic has been identified as a conservation concern for this population. The primary aims of the study were to test whether boat presence altered whales' activities, and if so, to estimate whether behavioural responses were likely to have carried energetic costs. A land-based observation site near a vessel-exclusion marine protected area allowed us to conduct a natural experiment to monitor whale activities in the presence and absence of boats. Using Time-Discrete Markov Chain models, boat presence was linked to significant changes in the probability that focal whales would switch from one activity state to another, which led to significantly different activity budgets in the presence and absence of boats. We estimated that the energetic cost of meeting these budgets differed by only 3–4%. In the presence of boats, however, whales reduced their time spent feeding and the time spent rubbing their bodies on smooth pebble beaches. These lost feeding opportunities could have resulted in a substantial (18%) estimated decrease in energy intake. Our sensitivity analysis provides preliminary evidence that disturbance could carry higher costs to killer whales in terms of reducing energy acquisition than increasing energetic demand, and future research should address this directly. Meanwhile, our observations suggest that protected areas would confer greatest conservation benefit to endangered killer whale populations if they were designed to protect important foraging areas.

© 2006 Elsevier Ltd. All rights reserved.

1.   Introduction

Some predators are valued by humans, either for their ecological or aesthetic attributes, whereas others are viewed as pests. Increasingly, applied ecologists are asked to consider effects of anthropogenic activities on valued predators (Ormerod, 2002). For reasons of tractability, animals' behavioural responses are often used to indicate their vulnerability to disturbance, although the relationship between the strength of these responses and the underlying sensitivity of wildlife is unlikely to be straightforward (Gill et al., 2001; Beale and Monaghan, 2004a,b). Certainly, equating lack of response with indifference is incorrect – those animals least likely to exhibit avoidance responses may simply be those that can least afford to demonstrate their sensitivity, namely those in poorest body condition (Beale and Monaghan, 2004b).

This complexity becomes especially apparent when dealing with conservation and management of cetaceans (whales, dolphins and porpoises), which are long-lived and elusive study animals. Cetaceans are also exposed to a variety of both targeted and incidental human activities in the marine environment. While the effects of direct mortality impacts, such as by-catch or whaling, can be unambiguously related to population-level consequences (Slooten et al., 2000), it is very challenging to assess the potential long-term effects of anthropogenic activities, such as whalewatching, which elicit subtle, short-term reactions (Bejder et al., 1999; Williams et al., 2002a,b; Lusseau, 2003a). Clearly, linking short-term behavioural responses to long-term population-level impacts presents difficulties, a fact that can lead to the false, or at least premature conclusion that human activities have no biologically significant effects on the targeted animals. In 1993, the International Whaling Commission (IWC) adopted a resolution that declared its desire "to encourage the further development of whale watching as a sustainable use of cetacean resources" (IWC, 1994). Recent studies, however, have raised concerns about the consequences of anthropogenic activities in the marine environment on cetacean populations generally, and an unchecked development of the whalewatching industry more specifically. There are indications that repeated short-term avoidance tactics can lead to long-term impacts at the population level, either through habitat displacement (Morton and Symonds, 2002; Lusseau, 2005; Bejder et al., in press), which can reduce the fitness of targeted populations, or via physiological constraints at the individual level (Lusseau, 2003b), which may lead to decreased reproductive output (Lusseau, 2003b). For a food-limited population, energetics can provide the missing causal link between demonstrable short-term behavioural responses and difficult-to-detect population-level impacts. This study presents the results of a sensitivity analysis to assess whether short-term behavioural responses were likely to carry energetic consequences for killer whales (*Orcinus orca*) in the northeast Pacific.

Three killer whale ecotypes are found in the coastal waters of British Columbia (BC), Canada (Ford et al., 2000): mammal-hunting *transients*; recently identified and poorly studied *offshores*; and northern and southern communities of fish-eating *resident* killer whales. A core area for "northern residents" is found in Johnstone and Queen Charlotte Straits (Fig. 1;

Zone	Area (ha)
2a	493
2b	1089
2c	552
x	357
3	307
4	420
5	342
6	176

Fig. 1 – The study area bounded by lines drawn from the cliff-top observation site (•). Shaded area of zones 3–6 marks the boundaries of RBMBER, and zones X and 2a–c indicate the boundaries of the study area outside the Reserve.

JSKWC, 1991). The northern resident community comprises 34 matrilines, the basic killer whale social unit (Ford et al., 2000). The so-called resident matrilines are, in fact, resident to the area only during summer months. Many matrilines return to this area each summer to mate, feed on salmon, and rub their bodies on smooth pebble beaches (Ford et al., 1998, 2000; Ford and Ellis, 2006). One of the area's benefits to killer whales is the tendency for narrow Johnstone Strait to concentrate migratory salmon (Nichol and Shackleton, 1996). Commercial fishing vessels, freighters, cruise liners and commercial and recreational whalewatching boats also use the area heavily. Part of this area has been set aside in 1982 as a killer whale sanctuary (Robson Bight-Michael Bigg Ecological Reserve, RBMBER) to prevent boaters from approaching the gravel beaches on which the whales rub (Ford et al., 2000). The functional role of this activity is unknown, but beach-rubbing behaviour is rarely seen in other cetaceans.

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) currently lists northern resident killer whales as *Threatened* (Baird, 2001). Their listing was made partly in response to lack of population growth; and more recently, a population decline observed in annual censuses (Ford et al., 2000). While the cause(s) of the decline remains unknown, it is generally agreed that both northern and southern resident communities face a variety of threats (Baird, 2001) in the form of reduced prey availability (Allendorf et al., 1997), high toxin loads (Ross et al., 2000), and anthropogenic disturbance (Williams et al., 2002a,b). The most contentious example of human disturbance may be commercial whalewatch operators, however these represent only a small fraction of the vessels that use the same waters as northern resident killer whales in Johnstone Strait, and their compliance with the Reserve boundaries was highest of the 10 vessel types in the area (Ashe and Williams, 2003).

The decision to create a reserve proved prescient when, subsequently, studies began reporting correlations between vessel traffic and whale behaviour (Kruse, 1991). Even non-whale-oriented vessel traffic, such as fishing boats, altered the behaviour of killer whales (Williams et al., 2002a). It is unclear whether these subtle avoidance responses observed in experimental studies carried energetic costs to whales and it is unknown whether animals were equally vulnerable to disturbance in all activity states. Previous experimental studies targeted only whales engaged in typical "travel/forage" activity, in order to avoid confounding effects of activity state and vessel traffic on whale behaviour (Williams et al., 2002a,b). No quantitative attempt has been made to assess whether these animals respond differently to disturbance depending on the whales' activity state. Consequently, it is unclear whether the focal animals sampled in impact assessments conducted to date were representative of population-level responses. An impact assessment should include subjects from all age–sex classes and span the entire repertoire of activity states.

The primary goal of this study was to test whether whale activity budgets differed when boats were present from activity budgets when boats were absent. The fact that time-activity budgets can be linked to energetic demands in this species (Kriete, 1995) set a secondary goal: to estimate whether the energetic demand of killer whales in the presence of boats

was greater than in their absence. This framework, using killer whales as an example, can serve as a model linking field observations of short-term responses to human activities to longer-term energetic effects at individual and population levels. This study illustrates the utility of integrating behavioural studies and physiology into conservation strategies for large mammals (Sutherland, 1998).

2. Methods

2.1. Data collection

Data were collected from a cliff on West Cracroft Island (Fig. 1) approximately 50 m above mean water level, which offered an expansive view across Johnstone Strait. Field seasons varied in length among years (1995–2002), but the longest period common to all years was 1 July to 31 August. A minimum of three observers recorded boat and whale activity from 08h00 to 20h00 daily. The study area was divided into eight zones, four inside the Reserve and four in the waters immediately adjacent to the Reserve. These zones were readily identifiable from the cliff based on sightlines drawn to prominent landmarks. Every 15 min, these observers scanned the area with 7×50 binoculars and a 25×50 spotting scope to record the number of boats in each zone of the study area.

Whale activity was recorded on the same 15-minute schedule by scanning the main activity of whales in focal groups (Altmann, 1974). Whales were recorded as being in a group if they were within approximately 10 body lengths of one another, and displaying the same behaviour at the surface. Once whales entered the study area, observers used both visual and acoustic cues to identify matrilines and individuals within matrilines using photo-identification catalogues (Ford et al., 2000). The exact identification of individuals was not always necessary to follow groups because of the ease of tracking separate schools across sampling periods. Focal groups were defined post-hoc from the subset of the data in which group composition remained constant across a sequence of samples.

Whale activity recorded during each 15-minute scan sample was assigned to one of five mutually exclusive and cumulatively inclusive activity states (Table 1). The definitions of these states were adapted from those used in other killer whale behaviour and bioenergetics studies (Felleman et al., 1991; Hoelzel, 1993; Kriete, 1995; Barrett-Lennard et al., 1996; Ford et al., 2000; Lusseau et al., 2004; Ford and Ellis, 2006). At each scan, the whales were recorded as being either inside or outside the reserve, based on zone boundaries. This allowed subsequent accounting for known effect of location on whale behaviour (e.g., beach-rubbing). They are presented roughly in order of increasing energetic cost of the activity, as estimated from captive and field experiments on killer whales by Kriete (1995) (Table 1).

2.2. Data analyses

Adjacent 15-minute observations were unlikely to be statistically independent, so the scan sample data were analysed as a series of time-discrete Markov chains (TDMC) (Lusseau, 2003a, 2004). This technique allowed us to model

Table 1 – List of activity state codes (A–E) used in this study with their equivalent energetic cost categories defined by Kriete (1995)

Activity state (this study)	Energetic cost (Kriete, 1995)	Definition	Probable function
A	1	Whales were swimming at slow speed with highly predictable sequences of several short (30 s) dives followed by a long dive of 3–5 min. This activity state was characterised by the absence of surface-active behaviour (e.g., breaching or tail-slapping)	Resting
B	1	Whale presence within 50 m of a gravel beach; independent surfacing and diving of individuals; long periods spent stationary at the surface, followed by slow swim speeds toward a beach; at which point, bubbles or splashing could be observed in the vicinity of the beach	Beach-rubbing
C	Mean(2 + 3)	Whales surfaced and dove independently but all whales in the group were heading in the same general (east–west) direction. The dive sequences of individuals showed regular patterns of several short dives followed by a long one, and whales swam at moderate speeds	Travelling /Foraging
D	Mean(2 + 3)	Individuals were spread out across the Strait; individuals were surfacing and diving independently in irregular sequences of long and short dives; and individuals displayed fast, non-directional surfacings in the form of frequent directional changes	Feeding
E	3	Animals surfaced in tight groups with individuals engaged in tactile behaviour; whales showed irregular surfacing and diving sequences and swim speeds; irregular direction of movement; and high rates of surface-active behaviour	Socialising

Activity State B, beach rubbing, is considered equal to rest in terms of energetic cost, but probably plays a social role (Ford et al., 2000). Probable functional roles for the other activity states are inferred from earlier studies of behaviour and feeding ecology in northern and southern resident killer whales (Felleman et al., 1991; Hoelzel, 1993; Ford et al., 1998).

the probability of a focal group switching from one activity state to another as a function of a given factor (in this case, boat presence in the same zone as the whale), and therefore to quantify the effect of this factor.

Two binary grouping variables were created. First, each scan sample of whale activity was given a value for location, either inside or outside the Reserve. The dataset was further categorised depending on the presence of boats. If no boats were present in the same zone as a focal group of animals, then that scan was identified as a control (i.e., no-boat) observation, regardless of whether boats were present in other parts of the study area. Similarly, observations were scored as treatment (i.e., boat-present) observations only when boats were present in the same zone as the focal animal. Focal follows were separated into four data files: those in the presence versus absence of boats, and those inside versus outside the Reserve.

Program UNCERT (available from http://uncert.mines.edu) was used to tally the number of times one state was observed following another from these series of samples, conditional on location of the focal group and boat presence in the same zone as the whales. Four-way contingency tables were constructed with the following categories: preceding activity (five possible states, factor labeled P in the model in Table 3), succeeding activity (five possible states, labeled S in the model), boat traffic (present or absent, labeled B) and location (inside or outside the Reserve, labeled L).

Dependence of transitions in activity states on location and boat traffic variables was tested for in SPSS 10.0 (SPSS Inc.) using General Log-Linear Analysis. The candidate independent covariates in this case were boat traffic and location, and the response variable was the number of times one state was observed following another. The G-statistic for goodness-of-fit was computed for each model and the difference between the G-values was used to test the significance of the term being left out (Caswell, 2001; Lusseau, 2003a). To test for the effects of location and boat presence, these terms were added sequentially to the null model assuming that succeeding state was dependent on preceding state and taking into consideration data sampling structure (included terms **PS** and **PBL**, Table 3) (Lusseau, 2003a). The effect of both boat and location were then tested by adding the dependence of **S** on each of these factors (by adding the terms **BS** and **BPS**, and the terms **LS**, **LPS**, respectively) (Lusseau, 2004). The best fitting model was selected using Akaike's Information Criterion (Burnham and Anderson, 1998) (Fig. 2). This analysis therefore provided not only a way of identifying the best fitting model, but also a way of quantifying the significance of the contribution of each factor to explaining the variance observed in the dataset.

The transition probability matrices obtained from the contingency tables were eigen decomposed using the PopTools add-in for Excel, to estimate the stationary distribution of each matrix, which corresponded to the eigenvector of the dominant eigenvalue (Caswell, 2001). This eigenvector corresponds to the time-activity budget of the population (Caswell, 2001; Lusseau, 2004). Activity budgets were calculated in the presence and absence of boats.

2.3.   Estimating energetic requirements from time-activity budgets

The time-activity budgets observed with respect to boat presence were converted to rough estimates of the energetic demand of free-ranging killer whales (Kriete, 1995). Only
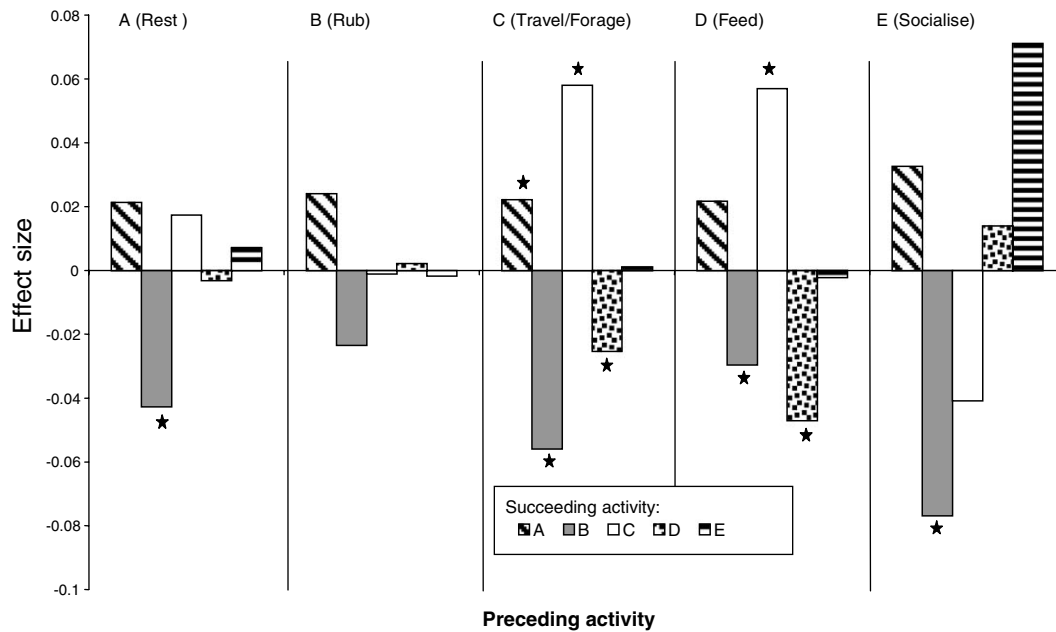
Fig. 2 – Difference between the transition probability of the no-boat chains and the boat chains. A negative value on the y-axis means that the transition probability of the impact chain was lower than the control one. The significance of the difference between two transition probabilities was assessed using a Z-proportion test. Stars mark significant differences (P < 0.05).

Kriete's data from *Hyak* (a 4733 kg adult male) and *Yaka* (a 2800 kg adult female) were used, rather than values for both adult and sub-adult subjects, because data on the sub-adult female were thought to be unreliable (Kriete, 1995). For comparative purposes, we also calculated the theoretical field metabolic rates for individuals of known weights to estimate energetic demand (Kleiber, 1975). The estimates presented thus illustrate the energetic demand for two hypothetical adults of the same mass as the captive adult subjects. Caloric demand was presented using the category-specific (Table 2) estimates of the energetic cost of each activity state (Kriete, 1995). Time-activity budgets were converted to rough estimates of the energetic requirements of a free-ranging 4733 kg adult male and a 2800 kg adult female, which represent the average masses of mature male and female killer whales for which metabolic rate data were available (Williams

et al., 2004). Male and female energy budgets were estimated using the average activity budget described above, rather than using sex-specific activity budgets, because the animals were generally in mixed-sex schools.

3. Results

This study synthesises observations from eight seasons, during 496 days (5952 h) of effort, including 2000 h observing killer whales. After censoring, 7517 transitions of focal groups from one activity state to another were observed. All 34 matrilines appeared more than once in the dataset.

3.1. Log-linear analyses

Both variables affected the behaviour of the whales (Table 3: testing components BS, BPS for the effect of boat presence and components LS, LPS for the effect of location). When starting with a null model in the log-linear analyses (i.e., that adjacent scans are dependent, and that location and boats have no effect on succeeding whale activity), the best model considered both location and boat factors (AIC = −32.8, Table 3). The effect of location was much stronger than the effect of boats, but adding the boat effect explained a significant portion of the variance (Table 3). There was no significant interaction between the boat and location terms (Table 3), which meant that whale response to boats was similar inside and outside the Reserve.

3.2. Relationship between boat presence and whale activity state transition probabilities

Boat presence showed strong effects on the probability of whales switching from one activity state to another for most

Table 2 – Approximate energetic cost of five activity states on equivalent categories used by Kriete (1995), and proportion of time spent in each state in the presence and absence of boats

Activity	Cost of activity (kcal/kg/h)[a]		Proportion of time in activity	
	Male	Female	No-boat	Boat
A	1.17	0.91	0.152	0.230
B	1.17	0.91	0.168	0.029
C	1.935	1.79	0.533	0.598
D	1.935	1.79	0.125	0.102
E	2.19	2.28	0.023	0.040
Transitions observed			3500	4017

a After Kriete (1995).

Table 3 – Results of the log-linear analyses

Model	Component added	ΔG^2, df, P-value	AIC	ΔAIC
Null (PS, PBL)			348.3	381.1
	BS, BPS	164, 20, <0.0001		
Boat effect (BPS, PBL)			224.3	257.1
	LS, LPS	297.1, 20, <0.0001		
Boat + Location (BPS, LPS, PBL)			−32.8	0
	BLS, BLPS	7.2, 20, 0.996		
Boat × Location (PSBL)			0	32.8

P: preceding behavior; S: succeeding behaviour; B: boat presence; and L: location. The null model assumed that succeeding behaviour was independent of boat and location effects, given preceding behaviour, as defined by a first-order Markov chain. However, there was strong support from the data for a model that included effects of vessel traffic and location on succeeding behaviour.

initial activity states (Fig. 2). The strongest effect of boat presence on transition probabilities was observed in Activity State B. Animals were less likely to enter Activity State B from any other state when boats were present.

Whales were less likely to switch from Activity States C to D when boats were present than in their absence (Fig. 2). In addition, whales observed in Activity State D were less likely to remain in that state (and more likely to switch to lower-energy Activity States C or A) when boats were present than when boats were absent. Whales engaged in Activity State C were more likely to remain in that state when boats were present.

3.3. Effect of boat presence on activity budget

Whales spent significantly less time in Activity States B and D when boats were present (Fig. 3). The proportion of time spent in Activity States A, C and E was significantly greater when boats were present.

3.4. Effect of boat presence on energetic requirements

While activity budgets were significantly different in the presence and absence of boats, the effect of boat presence on energetic demand was relatively small after converting the time spent in each activity state (Table 2) to estimates of 12 h energetic demand in the presence and absence of boats (Table 4). Our estimates fell well within the range of other estimates of killer whale's energetic demand calculated in various ways (Table 4). Williams et al. (2004) obtained estimates using the scaling relationship between mass and both basal and field metabolic rate (Kleiber, 1975). The estimates of Barrett-Lennard et al. (1995) were also based on Kriete's measures (1995); while Baird (1994) derived estimates for mammal-eating killer whales from observed prey ingestion rate. Overall, estimated energetic demand over 12 h for a free-ranging 4733 kg male and a 2800 kg female represented approximately 3% greater demand in the presence of boats
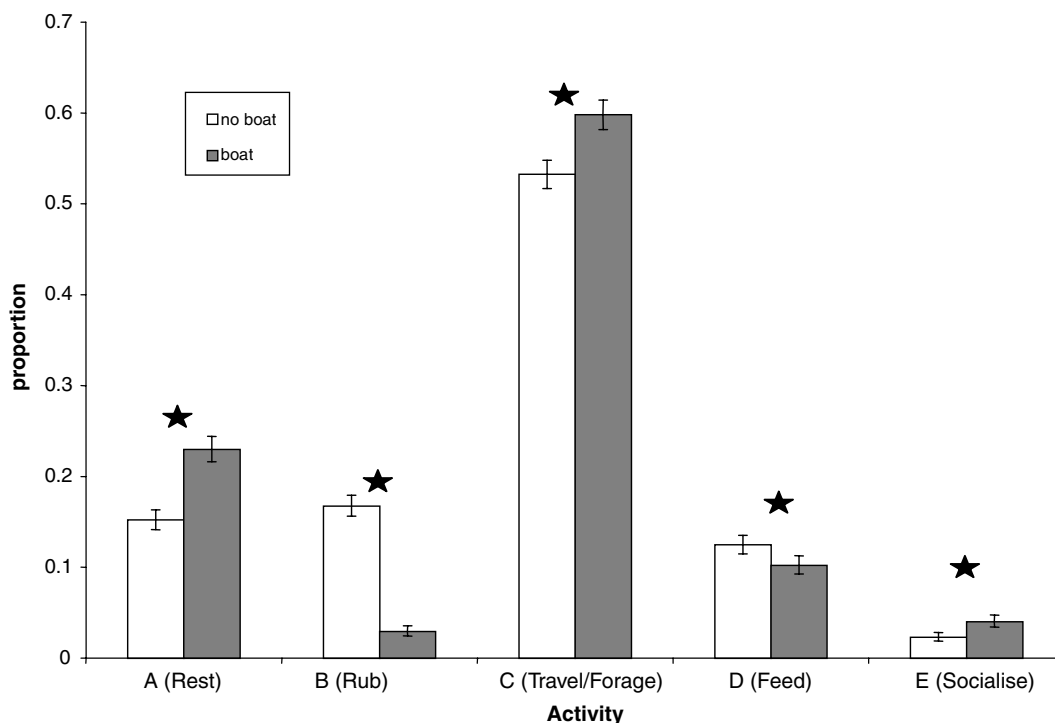

Fig. 3 – Effect of boat presence on activity budget. Bars represent 95% confidence intervals, and all differences are significant at the conventional level (P < 0.05).

Table 4 – Estimated 12 h energetic demand of a free-ranging male and female killer whale in activity budgets observed in the absence and presence of boats				
	Male (4733 kg)		Female (2800 kg)	
	No-boat	Boat	No-boat	Boat
Energetic demand (kcal/12 h) (this study)	96,356	99,216	51,080	53,138
Theoretical field metabolic rate[a]	121,750		81,750	
Reported range (kcal/12 h)[b]	71,000–146,723		42,000–86,800	
Increase in energetic demand		2.9%		3.2%
Energetic gain (kcal/h spent feeding)	64,237	46,507	34,054	24,655
Decrease in energetic gain		27.6%		27.6%

Energetic requirement is presented in terms of both caloric demand and lost energetic gain opportunities. Both these requirements are presented in kcal/12 h. Energetic gain represents the amount of energy whales need to acquire while feeding to meet their total energetic demand. When boats are present, the energetic gain is the amount of energy they can acquire (related to the amount of time they can spend feeding) assuming the same acquisition rate as during control (no-boat) situations. Other published values of killer whale's energetic demand are provided for comparison.
a (Williams et al., 2004).
b (Baird, 1994; Barrett-Lennard et al., 1995; Williams et al., 2004).

than in the absence of boats. However, the lost opportunities to gain energy translating from the decrease in time spent feeding (Activity State D) had the potential to carry a heavier burden. A decrease from 12.5% of time spent feeding to 10.2% when in the presence of boats corresponds to an 18% decrease in the amount of time spent feeding. No attempt was made to test for statistical significance of these differences, because variance estimates have not been presented for the estimates of energetic costs of the different activity states (Kriete, 1995).

4. Discussion

This study has provided evidence that the way in which whales used the study area changed when boats were present, and presented a point estimate of the extent to which these changes in activity may have carried energetic costs to whales. These objectives were met using a non-invasive, inexpensive behavioural study while addressing two shortcomings of previous studies: this study included observations of all age–sex classes of whales in the population, and sampled across the entire repertoire of killer whale activity in Johnstone Strait. Most importantly, the striking difference in potential relative costs between energetic expenditure and acquisition provides a clear mandate to prioritise future research.

4.1. Effects of boats on killer whale activity budgets

Commercial salmon catches and whale activity in the Reserve indicate that Robson Bight offers good fishing opportunities. The ability of the Reserve to provide good feeding habitat to resident killer whales, however, may be compromised when boats enter it. Overall, whales reduced their time spent feeding from 13% to 10% when boats were present. Focal whales not only showed a lower probability of continuing feeding, but also a lower probability of initiating a feeding bout (i.e., switching from travel/forage to feeding activity) when boats entered the Reserve (Fig. 2). Recall that the vast majority of boats in the study area were not engaged in whalewatching, but rather were commercial fishing vessels (Ashe and Wil-

liams, 2003). While the exponential increase in commercial whalewatching activity has caused some to question the benign nature of that industry (Corkeron, 2004), it is important to note that the disturbance (primarily commercial fishing traffic) driving the trend we report was largely tangential to the whales. In addition, whales spent nearly 17% of their time in the study area rubbing when boats were absent, compared with 3% when boats were present in the same zone as the whales (Fig. 3). The whales increased their travel budget by 12.5% (Fig. 3). This echoes a previous finding that whales' avoidance reactions to an experimental boat would result in their having to travel 13% farther along a circuitous route to cover the same effective distance that they were covering prior to the arrival of the boat (Williams et al., 2002a).

Noise, rather than simple presence of the boats, seems the likeliest mechanism for boats to disturb whale behaviour. Evidence exists for killer whales evading annoying noise on fine temporal and spatial scales (Williams et al., 2002b) and harmful noise on annual and regional spatial scales (Morton and Symonds, 2002). Empirical evidence exists that boat noise can impair killer whales' ability to detect pure tones (Bain and Dahlheim, 1994) and low-frequency omni-directional components of calls (Miller, 2002) thereby reducing these calls' active space, the volume of water within which a call is detectable by a whale. This masking of low frequency components would also reduce the effectiveness of any directionality cues for coordinating movement (Bain and Dahlheim, 1994; Miller, 2002), and could disrupt any coordinated foraging activity (Foote et al., 2004). Whalewatching vessels can increase anthropogenic noise in substantial fractions of killer whale foraging habitat (Erbe, 2002). However, our analyses are the first to suggest that vessel traffic did alter feeding activity of free-ranging northern resident killer whales.

4.2. Potential effects of boat traffic on killer whale energetic demand and acquisition

Overall, killer whale activity budgets varied markedly between absence and presence of boats, but the net energetic effect was relatively small (Table 4). This reflects the tendency

for whales to replace one low-energy activity (e.g., beach-rubbing) with another (e.g., resting) in the presence of boats. As a result, the point estimates of the total energetic demand spent in the two different activity budgets are quite similar, suggesting that at low traffic levels, northern resident killer whales may be able to balance the energetic cost of avoiding boats.

This exercise was presented to illustrate the point that short-term behavioural responses can carry energetic costs that could have long-term population effects if the population were food-limited. The point estimates of the energetic cost of each activity state (Kriete, 1995) reflect categorisation of a continuum of energetic costs, and carry uncertainty that has not been quantified, and therefore could not be included in this exercise.

However, this is the third study to suggest that, while responding to boats may carry some energetic cost to northern resident killer whales, the upper limit of that cost is currently likely to be low (Williams et al., 2002a,b). The question therefore becomes whether whales are able to satisfy their energetic demands either under disturbed or undisturbed conditions. In the context of a conservation strategy for northern resident killer whales where prey availability is already a concern (Baird, 2001), the real issue may not be increased energy expenditure in the presence of boats so much as the potential for boats to cause a reduction in overall energy acquisition, via masking effects of boat noise, interruption of feeding bouts or replacement of feeding activity with boat-avoidance activities.

This study provides indirect evidence that feeding activity is disrupted by the presence of boats, which could lead to a substantial decrease in energy gain opportunities in the presence of boats. Several studies have associated the fast, non-directional swimming typical of activity state D (Feeding, Table 1) with successful fish captures as evidenced by finding scales or bits of fish floating near the surface (Felleman et al., 1991; Hoelzel, 1993; Ford et al., 1998; Ford and Ellis, 2006), thus its functional role appears to be related to feeding – prey detection, if not prey capture. Killer whale populations will respond numerically in the same way to reduced prey abundance as they will to an equivalent reduction in prey detection due to masking effects of boat noise. In a food-limited population, this is one mechanism that could link short-term consequences of vessel traffic to long-term, population-level consequences. Prey availability has been cited as a concern for both the Threatened northern resident and Endangered southern resident killer whales (Baird, 2001). The difficulties inherent in assessing prey preference, prey availability and quantity of prey acquisition in free-ranging killer whales are obvious. Indirect impact assessments such as this one may represent a practical first step while methods are developed to assess impact of boat traffic on feeding activity directly in free-ranging cetaceans. The need to rely on indirect methods of assessing environmental impact of human activity is a recurring problem in marine research (Inglis and Gust, 2003).

Assuming that the fast, non-directional swimming behaviour observed in Activity State D was associated with prey capture attempts (as reported by Felleman et al. (1991), Hoelzel (1993), Ford et al. (1998) and Ford and Ellis (2006)), it is per-

haps unsurprising that killer whales near boats shortened their feeding bouts and initiated fewer of them than in the absence of boats. It has been demonstrated that many bird species respond to tourism presence by shortening feeding bouts (Burger et al., 1997; Galicia and Baldassarre, 1997; Ronconi and St Clair, 2002). This has been found also in numerous studies of terrestrial mammals, where feeding activity is easier to observe than in free-ranging cetaceans. Bighorn sheep (*Ovis canadensis nelsoni*) reduced food intake dramatically when approached by helicopters near the Grand Canyon (Stockwell, 1991), and woodland caribou (*Rangifer tarandus*) exposed to tourists reduced their time spent feeding in the Charlevoix Biosphere Reserve (Duchesne et al., 2000). Terrestrial carnivores, as well as herbivores, have been shown to reduce food intake as a consequence of increased vigilance in the presence of humans. Grizzly bears (*Ursus arctos*) spent 53% less time feeding on army cutworm moths (*Euxoa auxiliaris*) in Glacier National Park, Montana, USA after detecting the presence of climbers in the area (White et al., 1999). This represented a substantial reduction in the caloric value of estimated food intake. Similarly, Amur tigers (*Panthera tigris altaica*) in Krai, Russia showed strong vulnerability to human disturbance in the form of roads (Kerley et al., 2002). Tigers at undisturbed sites spent more time at kills and consumed more of the kill than tigers disturbed by humans. Ultimately, disturbance to tigers was linked to lower reproductive success and higher adult mortality than tigers that occupied sites far from roads (Kerley et al., 2002). Thus, a range of disparate studies has found that feeding activity of large mammals was disrupted by human activity.

Although this study has provided evidence that boat traffic disrupted feeding activity, the case for boat traffic reducing energy acquisition in resident killer whales is equivocal. Fast, non-directional swimming does not always indicate prey location and capture (Wilson and Dill, 2002), and conversely, observed prey capture events were not always preceded by bouts of fast, non-directional swimming (Baird and Hanson, 2004). Neither is the relationship between time spent searching for food and energy acquisition a straightforward one. Increasing the cost of transport to foraging fur seals caused adult females to stay away from their pups longer than the control group, but animals appeared to be able to alter their diving behaviour to compensate for this cost (Boyd et al., 1997). Mothers must have been able to compensate for the cost of longer foraging trips and higher swimming costs, since pup growth in treatment and control groups was similar (Boyd et al., 1997). In our study, longer travelling/foraging bouts and shorter feeding bouts for killer whales when boats were present could mean that whales near boats had to search for food longer, but not find it. Alternatively, it could mean that boats improved the whales' foraging efficiency. Perhaps the location of fishing boats and their nets helped whales to find fish quickly, enabling whales to return to other activities. However, the masking effects of boat noise on killer whale echolocation ability (Bain and Dahlheim, 1994) are well established. The energetic cost of avoiding boats is likely to be small, and it may be that it could be compensated for by adjusting the proportion of time spent foraging at night or whenever boats are absent. The energetic consequences of reducing energy acquisition

are unknown, but we demonstrate that they have the potential to be four to six times as great as the cost of avoidance behaviour. Overall, we conclude that research that investigates the feeding ecology of resident killer whales (and the impacts of anthropogenic activities on feeding behaviour) should be a higher priority than studies that investigate energetic cost of avoiding boats.

4.3. Implications for endangered southern resident killer whales

It is useful to examine these findings in the context of the Endangered southern resident killer whale community, which is not only in a more vulnerable conservation status than the Threatened northern resident community, but also experiences far greater levels of boat traffic (Baird, 2001). One major implication for ongoing studies of the impact of vessels on southern resident killer whales is apparent immediately from the results of this study. These studies should target the most vulnerable activities and individuals to be most informative and precautionary. Therefore, southern resident vessel-impact studies should incorporate scan-sampling to record activity of all individuals in a study area to avoid unintentionally excluding the most challenging (but perhaps the most informative) scenarios from behavioural studies. Similarly, experiments that unintentionally exclude females and calves (e.g., Williams et al., 2002b), due to the difficulty in discriminating them reliably from conspecifics on each surfacing, may inaccurately reflect the average response of whales to disturbance.

If southern residents were influenced by boat traffic in a similar way to their northern counterparts, then our study has implications for the use of small, but well-chosen marine protected areas to mitigate impact of anthropogenic activities on whales. The southern residents' Depleted status under the US Marine Mammal Protection Act requires a management plan that reduces 'take', including harassment, of whales. Marine protected areas could play a role in reducing 'take' of southern resident killer whales, as long as no-entry zones were placed in areas where whales feed, rather than along travel corridors, or in areas used primarily by whales for resting or socialising. Killer whales do indeed have preferred habitats, some of which are strikingly obvious in nature. Some populations of killer whales intentionally strand themselves to capture prey off beaches with unique topographic features that lend themselves to allowing this to take place (Lopez and Lopez, 1985; Guinet et al., 2000). The data presented here were collected in a similarly blatant example of preferred habitat – the ecological reserve was set aside to protect the unusual smooth gravel beaches on which these killer whales rub their bodies – although the reserve parenthetically has turned out to be protecting important feeding habitat as well (Williams, 2003). It would be useful to identify whether preferred feeding habitat exists for southern resident killer whales, and if so, to protect it. Protecting seemingly trivial fractions of the range of cetaceans may at first appear futile, but ultimately, small marine protected areas may offer utility both for measuring and mitigating impact of human activity on cetaceans.

4.4. Wider implications

Studies of animal behaviour have an important role to play in conservation biology, but linking the two fields have been slow (Sutherland, 1998; Blumstein and Fernàndez-Juricic, 2004). Partly, conservation biologists may be skeptical of equating animal disturbance (a function of human activity that is confounded by the animal's sensitivity, tolerance, habituation and tradeoffs) with conservation risk (Gill et al., 2001). One way that behavioural studies can be integrated into biological conservation is to help quantify the extent to which human disturbance might reduce quality of habitat or resources. Increasing whales' energetic costs or reducing their ability to acquire prey, if the effect is sufficiently strong, can change the demographic parameters that influence effective population size (Anthony and Blumstein, 2000). Similarly, management guidelines that seek to alleviate behavioural responses of wildlife may be insufficiently precautionary, because physiological responses to stimuli may occur at much lower levels of exposure than those required to elicit behavioural reactions (Holmes et al., 2005).

The approach that we outline could serve as a model for integration of physiological information into behavioural studies toward a conservation goal, by modelling data from captive and free-ranging animals. The key requirement is that the energetic cost of a variety of activity states must be known. This integration has been done for wintering great cormorants (Gremillet et al., 2003) and similar behaviour-based modelling has allowed managers to predict how oyster-catcher (*Haematopus ostralegus*) populations would respond to a changing environment (Stillman et al., 2000). The difficulty of acquiring physiological data for cetaceans makes this approach extremely challenging. However, these data are available readily for many pinniped species that come ashore for moulting or breeding. One application might be the northern elephant seal, where metabolic rates have been measured when the animals are resting on land, in warm water and in cold water (Noren, 2002). We see this approach as particularly useful for conducting pilot studies to assess quickly and non-invasively whether the magnitude of a stressor is likely to be large enough to justify investing resources into more sophisticated studies. When a stressor is found to be large enough to be of concern, refuge areas can play a role in conservation and recovery strategies.

Terrie Williams, Arliss Winship and two anonymous reviewers for constructive comments.

R E F E R E N C E S

Allendorf, F.W., Bayles, D., Bottom, D.L., Currens, K.P., Frissell, C.A., Hankin, D., Lichatowich, J.A., Nehlsen, W., Trotter, P.C., Williams, T.H., 1997. Prioritizing Pacific salmon stocks for conservation. Conservation Biology 11, 140–152.

Altmann, J., 1974. Observational study of behaviour: sampling methods. Behaviour 49, 227–267.

Anthony, L.L., Blumstein, D.T., 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N-e. Biological Conservation 95, 303–315.

Ashe, E., Williams, R., 2003. Voluntary compliance with the boundaries of a killer whale sanctuary. In: Abstracts of the 14th Biennial Conference on the Biology of Marine Mammals, Greensboro, NC.

Bain, D.E., Dahlheim, M.E., 1994. Effects of masking noise on detection thresholds of killer whales. In: Loughlin, R.R. (Ed.), Marine Mammals and the Exxon Valdez. Academic Press, San Diego, pp. 243–256.

Baird, R.W., 1994. Foraging behavior and ecology of transient killer whales (Orcinus orca), Unpublished PhD thesis in Zoology, Simon Fraser University, Vancouver, British Columbia, Canada.

Baird, R.W., 2001. Status of Killer Whales, Orcinus orca, in Canada. Canadian Field-Naturalist 115, 676–701.

Baird, R.W., Hanson, M.B., 2004. Diet studies of "southern resident" killer whales: prey sampling and behavioral cues of predation. Report to NOAA, Order No. AB133F-03-SE-1070, p. 12.

Barrett-Lennard, L., Heise, K., Saulitis, E., Ellis, G., Matkin, C., 1995. The Impact of Killer Whale Predation on Steller Sea Lion Populations in British Columbia and Alaska. North Pacific Universities Marine Mammal Research Consortium, Vancouver, British Columbia, Canada.

Barrett-Lennard, L.G., Ford, J.K.B., Heise, K.A., 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. Animal Behaviour 51, 553–565.

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., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flahert, C., in press. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology.

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.

Blumstein, D.T., Fernàndez-Juricic, E., 2004. The emergence of conservation behavior. Conservation Biology 18, 1175–1177.

Boyd, I.L., McCafferty, D.J., Walker, T.R., 1997. Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. Behavioral Ecology and Sociobiology 40, 135–144.

Burger, J., Niles, L., Clark, K.E., 1997. Importance of beach, mudflat and marsh habitats to migrant shorebirds on Delaware Bay. Biological Conservation 79, 283–292.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation, 2nd ed. Sinauer Associates Inc., Sunderland.

Corkeron, P.J., 2004. Whale watching, iconography, and marine conservation. Conservation Biology 18, 847–849.

Duchesne, M., Cote, S.D., Barrette, C., 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. Biological Conservation 96, 311–317.

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.

Felleman, F.L., Heimlich-Boran, J.R., Osborne, R.W., 1991. The feeding ecology of killer whales (Orcinus orca) in the Pacific Northwest. In: Pryor, K., Norris, K.S. (Eds.), Dolphin Societies: Discoveries and Puzzles. University of California Press, Berkeley, pp. 113–147.

Foote, A.D., Osborne, R.W., Hoezel, A.R., 2004. Whale-call response to masking boat noise. Nature 428, 910.

Ford, J.K.B., Ellis, G.M., 2006. Selective foraging by fish-eating killer whales (Orcinus orca) in British Columbia. Marine Ecology Progress Series 316, 185–199.

Ford, J.K.B., Ellis, G.M., Balcomb, K.C., 2000. Killer Whales: The Natural History and Genealogy of Orcinus orca in British Columbia and Washington State, 2nd ed. University of British Columbia Press, Vancouver.

Ford, J.K.B., Ellis, G.M., Barrett-Lennard, L.G., Morton, A.B., Palm, R.S., Balcomb, K.C., 1998. Dietary specialization in two sympatric populations of killer whales (Orcinus orca) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76, 1456–1471.

Galicia, E., Baldassarre, G.A., 1997. Effects of motorized tour boats on the behavior of nonbreeding American flamingos in Yucatan, Mexico. Conservation Biology 11, 1159–1165.

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.

Gremillet, D., Wright, G., Lauder, A., Carss, D.N., Wanless, S., 2003. Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. Journal of Applied Ecology 40, 266–277.

Guinet, C., Barrett-Lennard, L.G., Loyer, B., 2000. Coordinated attack behaviour and prey sharing by killer whales at Crozet Archipelago: strategies for feeding on negatively-buoyant prey. Marine Mammal Science 16, 829–834.

Hoelzel, A.R., 1993. Foraging Behavior and Social Group-Dynamics in Puget-Sound Killer Whales. Animal Behaviour 45, 581–591.

Holmes, N., Giese, M., Kriwoken, L.K., 2005. Testing the minimum approach distance guidelines for incubating Royal penguins Eudyptes schlegeli. Biological Conservation 126, 339–350.

Inglis, G.J., Gust, N., 2003. Potential indirect effects of shellfish culture on the reproductive success of benthic predators. Journal of Applied Ecology 40 (6), 1077–1089.

International Whaling Commission, 1994. Forty-fourth Report of the International Whaling Commission, Cambridge.

Johnstone Strait Killer Whale Committee (cited as JSKWC), 1991. Background report. BC Min. of Environment, Land and Parks and Dept. of Fisheries and Oceans.

Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B., Hornocker, N.G., 2002. Effects of roads and human disturbance on Amur tigers. Conservation Biology 16, 97–108.

Kleiber, M., 1975. The fire of life: an introduction to animal energetics. R.E. Kreiger Publishing, Huntington, New York, USA.

Kriete, B., 1995. Bioenergetics in the killer whale, *Orcinus orca*, Unpublished PhD thesis in Zoology. University of British Columbia, Vancouver, BC, Canada.

Kruse, S., 1991. The interactions between killer whales and boats in Johnstone Strait, B.C. In: Norris, K.S., Pryor, K. (Eds.), Dolphin Societies: Discoveries and Puzzles, University of California Press, California.

Lopez, J.C., Lopez, D., 1985. Killer whales (*Orcinus orca*) of Patagonia and their behavior of intentional stranding while hunting nearshore. Journal of Mammalogy 66, 181–183.

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

Lusseau, D., 2003b. 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.

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.

Lusseau, D., Williams, R., Wilson, B., Grellier, K., Barton, T., Hammond, P.S., Thompson, P.M., 2004. Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic dolphins. Ecology Letters 7, 1068–1076.

Miller, P.J.O., 2002. Mixed-directionality of killer whale stereotyped calls: a direction of movement cue. Behavioral Ecology and Sociobiology 52, 262–270.

Morton, A.B., Symonds, H.K., 2002. Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. ICES Journal of Marine Science 59, 71–80.

Nichol, L.M., Shackleton, D.M., 1996. Seasonal movements and foraging behaviour of northern resident killer whales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus* spp.) in British Columbia. Canadian Journal of Zoology 74, 983–991.

Noren, D.P., 2002. Thermoregulation of weaned northern elephant seal (*Mirounga angustirostris*) pups in air and water. Physiological and Biochemical Zoology 75 (5), 513–523.

Ormerod, S.J., 2002. Applied issues with predators and predation: editor's introduction. Journal of Applied Ecology 39, 181–188.

Ronconi, R.A., St Clair, C.C., 2002. Management options to reduce boat disturbance on foraging black guillemots (*Cepphus grylle*) in the Bay of Fundy. Biological Conservation 108, 265–271.

Ross, P.S., Ellis, G.M., Ikonomou, M.G., Barrett-Lennard, L.G., Addison, R.F., 2000. High PCB concentrations in free-ranging Pacific killer whales, *Orcinus orca*: effects of age, sex and dietary preference. Marine Pollution Bulletin 40, 504–515.

Slooten, E., Fletcher, D., Taylor, B.L., 2000. Accounting for uncertainty in risk assessment: case study of Hector's dolphin mortality due to gillnet entanglement. Conservation Biology 14, 1264–1270.

Stillman, R.A., Goss-Custard, J.D., West, A.D., Le V. Dit Durrell, S.E.A., Caldow, R.W.G., McGrorty, S., Clarke, R.T., 2000. Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. Journal of Applied Ecology 37, 564–588.

Stockwell, C.A., 1991. Behavioral reactions of desert bighorn sheep to avian scavengers. Journal of Zoology 225, 563–566.

Sutherland, W.J., 1998. The importance of behavioural studies in conservation biology. Animal Behaviour 56, 801–809.

White, D., Kendall, K.C., Picton, H.D., 1999. Potential energetic effects of mountain climbers on foraging grizzly bears. Wildlife Society Bulletin 27, 146–151.

Williams, R. 2003. Cetacean studies using platforms of opportunity. Unpublished PhD thesis in Biology. University of St Andrews, St Andrews, Scotland, UK.

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

Williams, R., Bain, D.E., Ford, J.K.B., Trites, A.W., 2002b. Behavioural responses of male killer whales (*Orcinus orca*) to a 'leapfrogging' vessel. Journal of Cetacean Research and Management 4 (3), 305–310.

Williams, T.M., Estes, J.A., Doak, D.F., Springer, A.M., 2004. Killer appetites: assessing the role of predators in ecological communities. Ecology 85, 3373–3384.

Wilson, B., Dill, L.M., 2002. Pacific herring respond to simulated odontocete echolocation sounds. Canadian Journal of Fisheries and Aquatic Sciences 59, 542–553.