Killer whale evasive tactics vary with boat number

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Abstract

Controlled exposure experiments that measure animal response to vessels can inform relevant wildlife-viewing guidelines and reveal how they make decisions about changes in their environment. Previous experimental studies documented stereotyped avoidance responses by killer whales to boats. Additional observations collected during these studies showed an apparent shift in avoidance behaviour at high traffic levels. Our study tested experimentally whether whales did respond differently to approach by few (1–3) versus many (>3) vessels. Data were collected in summer 2004 in Johnstone Strait, British Columbia, using a theodolite to track the positions of boats and individually identifiable focal whales during control and treatment (few vs. many boats) phases. The responses of 16 adult male killer whales differed significantly between treatment levels (Wilcoxon's test, $P = 0.0148$). Swimming paths became more tortuous when few boats approached whales, but straighter as many boats approached. Pooling treatments would have masked significant responses with high statistical confidence (Wilcoxon's test, $P > 0.999$), falsely suggesting that boat presence had no effect. The division between few and many boats was supported by 140 opportunistic observations on 26 whales from a population of 216. We used generalized additive models to control for the effects of confounding variables, detected a non-linear relationship between number of boats and whales' swimming path directness and confirmed an inflection point at approximately three boats within 1000 m. We urge caution when designing controlled exposure assessments that rely on a simple absence–presence framework, which can mask multivariate or non-linear responses. Experimental design, coupled with analytical techniques incorporating statistical power and appropriateness of treatments and response variables, must be considered when interpreting the biological significance of null findings from impact assessments. Our study provides new information about levels of habitat degradation that this marine apex predator can tolerate.

Introduction

A number of studies have examined the impacts of human activities on behaviour, energetics and reproductive success of a variety of wildlife taxa. These studies demonstrate that there is an observer effect in wildlife viewing, such that our presence may disrupt the activities of the animals we watch. In some cases, these effects are striking, and obvious both to tourists and to researchers and managers aiming to reduce tourism impacts. Birdwatchers know this, and curtail their movements to reduce their influence, but also simply to prevent birds from fleeing. In the coastal environment, an approaching boat can cause hauled-out seals to enter the water (Suryan & Harvey, 1999). Diving seals make for poorer viewing than those ashore, so it is in both the animals' and the tourists' best interests that guidelines reduce the probability of such a startle response. An

extremely subtle example is our disruption of wary predators when we are not physically there. Human-built trails and roads in Alberta, Canada, have increased the 'tortuosity' of paths followed by wolves *Canis lupus* (Whittington, St Clair & Mercer, 2004). Thus, even without posing absolute barriers, trails and roads altered wolf movement across their territories. Such a finding may seem obvious in hindsight, but it provides a useful mechanism for defining good wolf habitat, identifying how to protect it (i.e. complete closure areas) and linking short-term behavioural responses to fitness. In the bird, seal and wolf examples, avoidance responses range from the overt to the subtle, but they are real, and may carry costs. Human activities that make wolves adopt more circuitous routes to reach a destination can cost them energy if increased travel time replaces time budgeted for resting. The effect is exacerbated if the increased travel time comes at the expense of time budgeted

for feeding, as may be the case for grizzly bears (White, Kendall & Picton, 1999).

In the marine environment, whalewatching is a growing industry worldwide (Miller, 1993; Hoyt, 1997) and managers have implemented whalewatching guidelines or regulations in many countries (IWC, 2005). Many recommendations came from whalewatchers themselves, who identified that boats influence whale behaviour, and wanted to minimize that this tendency (e.g. JSKWC, 1996). Anthropogenic activity is a concern for two at-risk killer whale populations in the north-eastern Pacific (Baird, 2001). However, assessing the effects of human presence on cetaceans is difficult. We can expect cetacean avoidance responses to be subtle and difficult to detect, because we observe animals only when they surface to breathe, and because unlike flying birds, whales can rarely move quickly enough to escape people in powerboats. Despite the difficulty in conducting impact assessments on free-ranging cetaceans, studies have quantified the effects of vessel traffic on behaviour (e.g. Williams, Trites & Bain, 2002b; Williams et al., 2002a; Lusseau, 2003; Scheidat et al., 2004), activity and energetic budgets (Lusseau, 2004; Williams, Lusseau & Hammond, 2006) and habitat use and possibly reproductive success (Bejder, 2005). One feature common to these studies is that they report inconspicuous, stereotyped behavioural cues that cetaceans displayed when approached by boats. The responses of cetaceans to boats are generally small, but real.

The detection of avoidance responses by cetaceans will benefit from carefully designed controlled-exposure experiments, especially by land-based observers. In Johnstone Strait, British Columbia (BC), Canada, research and whalewatch communities work together to draft common-sense guidelines, test efficacy experimentally and update them in an iterative process. Commercial whalewatch operators recommended that boaters approach whales slowly, from the side and to parallel the animals' path at distances no closer than 100 m (JSKWC, 1996). Two experimental studies were begun in 1995 to test the relevance of local whalewatching guidelines. The first measured how whales responded to one boat following the guideline by approaching the animal slowly, from the side, and paralleling the whale's path at a 100 m distance (Williams et al., 2002b). The second measured how whales responded to one boat violating local whalewatching guidelines by 'leapfrogging' – a practice in which boaters speed up when close to whales in order to place their boat in a whale's predicted path (Williams et al., 2002a). Both studies revealed that whales, on average, attempted to increase their distance from boats by increasing their path tortuosity, that is, by deviating from the more predictable path that they were following immediately before the experimental approaches. Opportunistic observations revealed that the magnitude of this horizontal avoidance response increased as a boat approached closer than 100 m.

The consistency between these experimental and opportunistic studies suggests that, for northern resident killer whales, summary statistics describing the tortuosity of swimming paths can be considered a suitable response variable to describe an animal's tolerance for various approach distances and activities. Previous experiments, though, measured how whales responded to the activities of a single boat, while killer whales are often approached by more than one boat. In order to test the effects of higher-traffic conditions, hypotheses can be generated from correlations between boat number and whale behaviour measured under opportunistic conditions, and then tested experimentally. One such comparison was reported from opportunistic data by Williams et al. (2002b), who found an inconsistency between whale response to boat number and proximity. Whales in that study showed a decrease in path directness as boats approached more closely, but an increase in path directness as boat number increased. The findings suggested that killer whales responded differently to a few boats than to many, occurring when approximately three boats approached within 1000 m of the whale. The authors hypothesized that:

> An irregular path may be a useful avoidance tactic with a single boat, but ineffective with more than one. In a multiple-vessel scenario, a dive that takes a whale farther from one boat may bring it closer to another.
> . . . This compromise deserves further attention in the form of a multiple-vessel experiment (Williams et al., 2002b).

Here, we report on results from that multiple-vessel experiment. Studies on other species show a shift in dolphin avoidance strategies depending on the number of boats present (Bejder, 2005; Lusseau, 2005), ranging from short-term evasion to long-term area avoidance. The at-risk status of killer whales (Baird, 2001), and the increasing level of boat traffic around them (Foote, Osborne & Hoelzel, 2004) create an urgent need for science to inform management of boat number around killer whales. In the case of the endangered southern resident killer whale population, there are more whalewatching boats than whales to watch (Koski, 2004).

The primary goal of our study was to test whether northern resident killer whales responded differently to an experimental approach by few boats than to many. Our secondary goal was to provide a quantitative description of whale behavioural data collected across a wider range of traffic conditions (boat number) and with a larger sample of individuals than could be obtained practically using experimental approaches. We use these results to generate hypotheses to be tested in future on the adjacent, but endangered southern resident population.

Methods

Field methods

We collected data from a cliff opposite Robson Bight–Michael Bigg Ecological Reserve (Johnstone Strait, BC, Canada, 50°30′N, 126°30′W), from 1 July through 11 September 2004. We used an electronic theodolite to record locations of boats and whales via a laptop computer

equipped with custom software (THEOPROG: see Williams 2002*a,b*).

As whales entered the study area, we selected a focal whale. We identified individual whales by referencing photo-identification catalogues (Ford, Ellis & Balcomb, 2000) and choosing a distinctive focal animal that could be tracked continuously for at least 15 min. Once a focal whale was chosen, we used the theodolite to 'mark', or record, the position of the focal at each surfacing (i.e. the time and position of each breath was recorded). We recorded vessel positions as frequently as possible to plot its trajectory with respect to that of the focal animal. We subsequently refer to each record of at least 20 min of observation of a focal animal as a 'track'. We summarized boat and whale data such that each track was represented only once in the analyses.

Experimental trials versus opportunistic observations

The local whalewatchers had agreed to participate in experiments before the beginning of our study. At the outset of each experimental trial, we requested whalewatchers' cooperation in creating an experimental control phase by remaining farther than 1000 m from the focal whale for *c*. 20 min, and an experimental treatment phase by approaching the focal for a typical whalewatching session for an additional 20 min. The control section referred to the data collected over a continuous 20-min period during which no boat approached the focal whale within 1000 m. The treatment section referred to the 20-min minimum period immediately following this control period in which at least one experimental vessel approached within 1000 m of the same focal animal. Each animal served as its own control, and the control phase always preceded the treatment.

We summarized boat traffic variables for every experimental trial for *post-hoc* categorization into one of two treatment levels based on the number of boats that approached the whale during the experimental section: approach by *few* (1–3) versus *many* (> 3) boats (based on the hypothesis generated in Williams *et al.*, 2002*b*).

On most occasions, however, conditions prevented us from manipulating traffic around the focal animal, so-called opportunistic observations. On these occasions, we selected focal animals and measured whale behaviour and boat activity in the same way as described for the experimental trials.

Analysis methods

For each track, we interpolated the number of boats within 100, 400 and 1000 m of the focal whale at the time of each surfacing. Then, we recorded the maximum, inclusive count for each of these radii for each track (called MAX100, MAX400 and MAX1000). Similarly, we recorded the minimum distance ever observed between the focal whale and any boat, referred to subsequently as the point of closest approach (PCA).

We calculated the response variable, the *directness index*, using the methods described in earlier experimental studies published on this population (Williams *et al.*, 2002*a,b*). The directness index measures path predictability, and is generated by dividing the distance between end-points of a path by the cumulative surface distance covered during all dives and multiplying by 100. The directness index is a ratio of the diameter of a circuitous path to its perimeter, and ranges from zero (a circular path, where the whale ends up exactly where it started) to 100 (a straight line).

We analysed our data in three ways:
1. *Categorical analysis of experimental data with two treatment levels: few versus many boats:* We used paired, non-parametric tests to assess the significance of behavioural responses of whales to our experimental treatments. For each trial, we calculated the whale's response to the experimental approach. The response data were then placed in two categories: a sample of responses of whales exposed to approach by few (1–3) boats, and a second sample of responses of whales to many (> 3) boats approaching. We used the Mann–Whitney *U*-test (Zar, 1996) to assess whether the treatment variable influenced the ranking of each observation of whale behavioural response.
2. *Analysis of experimental trials with one treatment level: boat presence:* We then reran the analyses ignoring the boat number grouping variable, thereby pooling data in an absence–presence framework. We used the Wilcoxon matched-pairs signed-ranks test.
3. *Descriptive analysis of opportunistic data:* We used generalized additive models (GAMs) to describe variation in whale swimming path directness as linear or non-linear functions of both traffic-related and non-traffic-related candidate predictor variables, using a set of objective criteria for adding or dropping terms. GAMs use splines for interpolating between observed data by placing 'knots' automatically at observed data. We used package mgcv for *R* to determine the shape of the relationships between predictors and response using thin-plate regression splines (Wood, 2001). The optimal degree of flexibility that can be justified by the data is estimated in a maximum likelihood framework, while penalizing the model for overparameterization or oversmoothing (Wood, 2001). The higher the estimated degrees of freedom (edf) given to any term in the model, the more flexible that relationship was estimated to be.

We considered the following potential explanatory variables for inclusion in the model: month, time, age, sex, PCA, MAX100, MAX400 and MAX1000. Factor variables were entered as linear or grouping terms. Continuous variables were entered as candidates for smoothing [*s*(*x*)] by mgcv.

The following summarizes our backward stepwise model specification procedure, which followed the framework proposed by Wood (2001):
1. We fitted a fully saturated model to the data: {DI∼month + time + *s*(age) + sex + *s*(PCA) + *s*(MAX100)-*s*(MAX400) + *s*(MAX1000)} with the default degree of smoothing (10 knots, 9 edf).
2. We assessed model fit in mgcv, to show coefficients, GCV score, explanatory power (deviance explained) and fit

(residual plots). Term-wise *P*-values for each coefficient presuppose that the other terms are in the model.

3. For each linear term, we examined whether the parameter coefficient (slope) was near 0 and the significance term near 1. If so, we removed the term to see whether the GCV score decreased and the explanatory power of the model increased. If so, we dropped the term from the model. If no marked improvement was detected by removing the term (or if dropping a term led to a worse fit), then we retained the term in the model.

4. For each smooth model term, we examined whether the estimated number of degrees of freedom was near 1. We evaluated whether the 95% confidence intervals for that term included zero across the range of observations. If so, we dropped the term temporarily, to see whether the GCV score dropped and the explanatory power of the model increased.

5. We dropped a term from the final model if it satisfied all three of the conditions in step 4. If the first criterion was met (edf $\approx$ 1) without satisfying the other two, then we replaced the smooth term with a linear one. If replacing the smooth term with a linear one reduced the model's explanatory power, then we retained it as a smooth term with edf $\approx$ 1.

Finally, we looked at the relationship between the animals' path directness and the number of boats. We conditioned on the selected model describing variation in path directness index, but placed knots manually along the *x*-axis describing variation in boat number. This allowed us to assess objectively where the curve changed shape, by using Akaike information criterion (AIC) to determine objectively where a node ought to be placed.

Results

Effort and sample size

We collected data on 72 of the 73 days between 1 July and 11 September 2004, representing 792 h of search effort. Whales were present for at least part of the day on 60 of these 73 days. In total, our study represents 73.8 h of continuous observation (i.e. of tracks > 20 min in length) of focal animals using the theodolite. We conducted a total of 16 experimental trials. Despite good cooperation from whalewatchers, non-whale-oriented traffic (particularly during a 10-day commercial fishing opening) disrupted dozens of otherwise-suitable control data collection periods. Opportunities to conduct experimental approaches became rare enough that we decided to restrict our trials to males, and excluded one experimental approach of a female from the analyses. We collected a total of 140 opportunistic tracks on 26 focal whales. Of the 16 experimental trials, focal animals were approached (within 1000 m) on eight occasions by 1–3 boats, and by 4–17 boats on the remaining eight occasions.

Responses of whales to experimental approach by few versus many boats

Figure 1 shows the distribution of the response variable during the experimental trials; however, our statistical
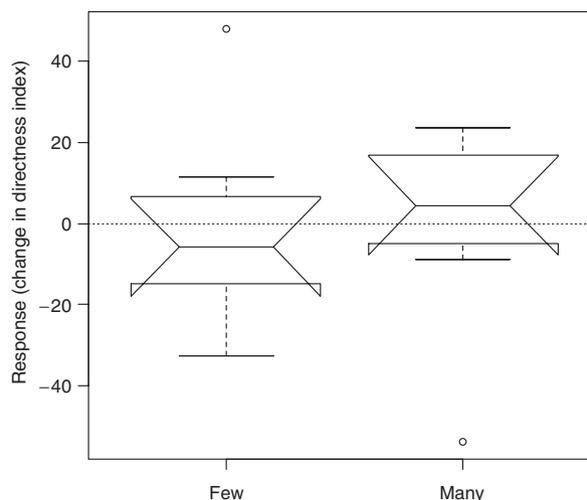

Figure 1 Response (difference in path directness index between the treatment and control phase) by focal male killer whales to experimental approach by few (1–3) versus many (4–17) boats within 1000 m.

analyses used non-parametric tests based on ranks, rather than raw data. Whales approached within 1000 m by few (1–3) boats decreased their index of path directness by 14.0 points relative to that observed during preceding, control conditions (from a mean of 82 to a mean of 67.9). Those approached within 1000 m by many (4–17) boats actually increased the directness of their paths on average by 12.9 points than during control conditions (from a mean of 70.9 to a mean of 83.8). These responses differed significantly between treatment levels (Mann–Whitney *U* test, two-tailed *P* = 0.0148).

We used these data and rearranged the formula for calculating directness index to estimate the distance a whale would have to travel along a circuitous route to cover 100 m of a straight-line distance. In the absence of boats (i.e. a whale displaying a path directness index of 82), a whale would have to swim 122 m (i.e. 100/0.82) along a circuitous path to cover the straight-line distance of 100 m. The same whale, adopting a mean swimming path directness index of 67.9, would have to swim 147 m along a circuitous path to cover the 100 m straight-line distance. The total distance a whale would have to travel in the presence of 1–3 boats represents a 20.7% increase over the total distance it would swim to cover the same ground in the absence of boats. Whales approached by 4–17 boats would actually increase the efficiency of their paths: from 141 m (control) to 119 m (treatment) required to make 100 m of headway.

Responses of whales to experimental approach by any number of boats (i.e. contrasting whale behaviour during absence and presence of boats)

For illustrative purposes, we contrasted behaviour in a simple presence–absence framework by pooling the two

experimental treatment levels. In the absence of boats, the mean path directness index of focal whales was 76.4. When approached by boats (from 1 to 17 boats), the mean directness index was 75.8. This difference was not statistically significant (Wilcoxon's matched-pairs signed-ranks test, two-tailed $P > 0.9999$).

Results of GAM fitting

The model described variability in whale behaviour best as a function of two boat traffic-related (MAX400 and MAX1000) and two traffic-unrelated (month and age) variables (Table 1). The explanatory power of the selected model was good: the model explained 67.7% of the deviance (i.e. residual sums of squares, Wood, 2001). In general, paths became more direct as the season progressed, and as the number of boats within 400 m increased. Age and number of boats within 1000 m entered the selected model as smooth terms, and Fig. 2 shows how directness index related to the smoothed components of these two variables.

The P-values listed are approximate, and should be interpreted with caution (Wood, 2001), because they are conditional on all other terms being in the model, the accuracy of the smoothing parameters and any scale parameter estimate. As a result, some model terms were retained even though their P-values were > 0.05, for the reasons outlined in 'Methods'. Note that a poor model fit was found (as evidenced by patterns in residual plots) when specifying a quasi or gamma distribution in path directness data on a 0–100 scale. This was addressed by standardizing the data – expressing them as a proportion by dividing by 100, so that 0 represented a circular path and 1 a straight line. The response was then modelled in a quasibinomial (maximum likelihood) framework with a logit (1/0) link, which alleviated the patterns that were previously evident in the residual plots.

Table 1 Summary of the selected generalized additive model describing variation in directness index

Family: quasibinomial
Link function: logit
Formula: DI~month + s(age) + MAX400 + s(MAX1000) − 1

	Parametric coefficients			
	Estimate	SE	t ratio	Pr($>|t|$)
Month	0.15381	0.01857	8.281	1.1382e–13
MAX400	0.084724	0.09028	0.9384	0.34972
	Approximate significance of smooth terms			
	edf	χ^2	P-value	
s(age)	2.04	3.0592	0.22666	
s(MAX1000)	2.784	5.1208	0.14729	
Deviance explained =67.7%			n=140	

The terms dropped from the model included sex, time, PCA and MAX100, as well as the intercept.
edf, estimated degrees of freedom.

Using B splines to verify the node between 'few' and 'many' boats

We conditioned on the selected model describing variation in path directness index, but manually placed knots at every observed value of MAX1000. A plot of AIC of the model describing path directness index against the knot position is shown (Fig. 3). AIC was the lowest when the knot was placed at MAX1000 = 3. This provides an objective identification of the optimal placement of the node separating few from many boats.

Discussion

Our study demonstrates a non-linear relationship between the number of boats and the tortuosity of killer whale swimming paths, and confirms an inflection point at approximately three boats approaching a whale within 1000 m. We interpret this as evidence that the whales have identified a way to evade few boats, but abandon that tactic when crowded by multiple boats. These results make sense in the context of turning gambits used by prey to evade faster predators; whales followed the stereotyped evasive tactics around boats that prey species use under predation risk when space is unrestricted, and in which there is nowhere to hide (see Frid & Dill, 2002; Williams *et al.*, 2002b). Carefully designed studies are needed to measure how whales interact with their environment, and to quantify the effects of habitat degradation on their viability. Our study offers guidance for design of appropriate vessel impact assessments for southern resident killer whales, for example, and provides, for the first time, an estimate of the number of boats at which northern resident whales shifted avoidance strategies. Here, we show that this effect starts at a relatively low level of traffic – only three boats within 1000 m.

We hypothesize that the behaviour of southern resident killer whales under extremely high traffic conditions will appear similar to that under no-boat conditions, because increasing path tortuosity will cease to be an effective evasive manoeuvre beyond some traffic saturation point. Assessing the role of boat traffic on southern residents directly is problematic, primarily because there are too many boats to allow experimental control over studies. Even if an experiment on southern residents were possible, a variety of factors could lead to a null finding. When we contrasted the path directness under no-boat conditions with those under all boat-present conditions (i.e. conducting a binary analysis by pooling treatment levels), the average response did not differ significantly from zero (Wilcoxon's matched-pairs signed-ranks test, two-tailed $P > 0.9999$). Ignoring the complexity of responses might have led to a false conclusion that boats do not alter the behaviour of killer whales, when in fact, boats altered behaviour in at least two opposing ways. Unfortunately, the complexity and subtlety of demonstrated avoidance responses may require researchers to collect large (and logistically and financially challenging) sample sizes to detect those real effects. Collecting a large sample size on free-ranging cetaceans will be
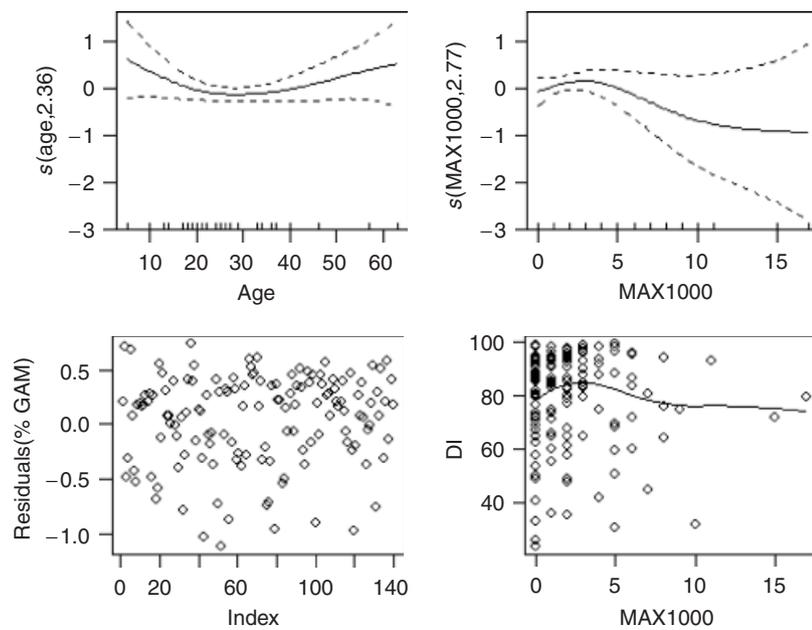
Figure 2 Smooth terms in the selected generalized additive model (GAM; top), residuals (lower left) and the raw data for boat number and directness index (lower right).
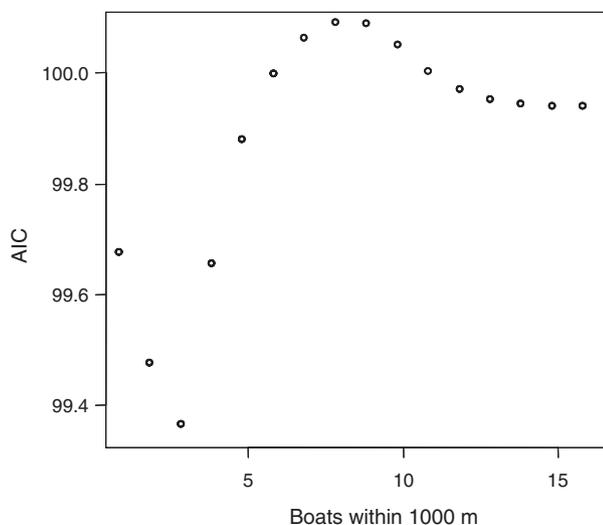

Figure 3 The x-axis represents the point at which a knot was placed manually, when fitting a B spline through the opportunistic data, conditional on the selected model (Table 1 and Fig. 2). The y-axis represents the Akaike information criterion (AIC) value of that model. AIC was the lowest when a knot was placed manually at MAX1000 = 3.

difficult, so we encourage complementing small experimental datasets with larger opportunistic ones using appropriate statistical modelling methods to control for confounding effects.

Our results also have implications for mitigating the impact of habitat degradation on valued marine predators. One way to alleviate effects is to identify areas of demonstrated importance to the whales, and to close these areas to boats altogether (Lusseau & Higham, 2004). In addition, one will need sensible guidelines for managing whalewatching outside protected areas, and our results suggest that those guidelines should also aim to reduce crowding. In future, we may be able to combine recommendations on approach distance and boat number in the same guideline. Beale & Monaghan (2004) present a model in which cliff-nesting birds perceive people as 'predation-free predators', whereby the perception of predation risk is a function of both the number and proximity of observers. The authors suggest that setting one approach distance is insufficient when the number of visitors is variable. They recommend that large groups of people be kept farther from nesting areas of vulnerable species than small groups, or that approach distances be determined for the largest group of people who are likely to visit the site. Studies on terrestrial mammals have also shown that predator group size may be a good predictor of the behaviour of prey species. The flight initiation distance of Thomson's gazelle was related to the number of predators approaching: gazelles were likely to flee from packs of hyenas at a much larger distance than they did from a solitary predator (Walther, 1969). In the killer whale case, one might design whalewatching guidelines to have different approach distances for different numbers of boats, or to set the overarching set-back distance to the one we would wish all boaters to keep when 120 boats are trying to approach a whale at once.

The risk of predation, whether perceived or actual, strongly influences prey behaviour. These behaviourally mediated, non-lethal or predation-risk effects can form a so-called 'ecology of fear' (Brown, Laundre & Gurung, 1999; Ripple & Beschta, 2004). In the marine environment,

boats may be thought of as introducing artificial habitat structures (albeit temporary, ephemeral ones) into killer whale habitat that may impede locomotion, or increase perceived risk associated with locomotion by making whales more conspicuous to human, predation-free predators. The resulting behaviour becomes a balancing act between what the animals want to do (e.g. evade boats, minimize received noise level from outboard motors; Williams *et al.*, 2002*a*) and what they need to do in this important habitat (e.g. mate or feed; Ford *et al.*, 2000; Williams *et al.*, 2006). Understanding how foraging animals make decisions about their movement patterns will assist us in assessing the consequences of habitat degradation or fragmentation.

Often, when predators and prey are both relatively mobile and there is no spatial refuge for the prey, no clear pattern of relative spatial distribution of predators to prey will result overall (Formanowicz & Bobka, 1989). However, interruptions to the activities of individual animals in terms of increased vigilance can carry costs. Flexible movement patterns can provide animals with adaptive predator responses. For example, small rodents adopted straighter paths in the presence of predators than in their absence (Lagos *et al.*, 1995); subsequent simulations suggested that the information that these animals had about predation risk and the availability of alternative habitat would influence their movement patterns, overall abundance and distribution (Russell, Swihart & Feng, 2003). While individual animals may have options in terms of behavioural plasticity, the decisions that they make about locomotion will affect their fitness. Consequently, summary statistics about swimming paths of killer whales can be informative insofar as they tell us something about how whales cope with disturbance while maximizing their fitness. Recent analyses suggest that these vessel-avoidance activities of killer whales may carry energetic costs (Williams *et al.*, 2006). When exposed to much higher levels of anthropogenic habitat degradation in the form of acoustic harassment devices, resident killer whales abandoned a part of their historic range altogether (Morton & Symonds, 2002). The present study reminds us that habitat degradation is a continuum. Animals make decisions along the way between dealing with small consequences of repeated disturbance (in terms of disrupting prey acquisition in a well-known foraging area, e.g.), to abandoning preferred habitat. Measuring reference points between individual-level disturbance and displacement will help to ensure that population-level effects are mitigated before they occur.

Acknowledgements

References

Baird, R.W. (2001). Status of killer whales in Canada. *Can. Field Nat.* **115**, 676–701.

Beale, C.M. & Monaghan, P. (2004). Human disturbance: people as predation-free predators? *J. Appl. Ecol.* **41**, 335–343.

Bejder, L. (2005). *Linking short and long-term effects of nature-based tourism on cetaceans*. PhD thesis, Dalhousie University, Halifax, NS, Canada.

Brown, J.S., Laundre, J.W. & Gurung, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* **80**, 385–399.

Foote, A.D., Osborne, R.W. & Hoelzel, A.R. (2004). Whale-call response to masking boat noise. *Nature* **428**, 910.

Ford, J.K.B., Ellis, G.M. & Balcomb, K.C. (2000). *Killer whales*. 2nd edn. Vancouver: UBC Press.

Formanowicz, D.R. & Bobka, M.S. (1989). Predation risk and microhabitat preference: an experimental study of the behavioral responses of prey and predator. *Am. Midl. Nat.* **121**, 379–386.

Frid, A. & Dill, L.M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* **6**, 11 [online: http://www.consecol.org/vol6/iss_1/art11].

Hoyt, E. (1997). *The potential of whale watching in Europe*. Bath: Whale and Dolphin Conservation Society.

International Whaling Commission (cited as IWC). (2005). Report of the Scientific Committee. *J. Cetacean Res. Mgmt.* **7** (Suppl.), 1–391.

Johnstone Strait Killer Whale Committee (cited as JSKWC). (1996). *Johnstone strait whale watching guide*. British Columbia: BC Ministry of Environment, Land and Parks and Department of Fisheries and Oceans.

Koski, K. (2004). *The soundwatch boater education program: trends in vessel traffic with southern resident killer whales*. Washington: The Whale Museum, Friday Harbor.

Lagos, V.O., Contreras, L.C., Meserve, P.L., Gutiérrez, J.R. & Jaksic, F.M. (1995). Effects of predation risk on space by small mammals: a field experiment with a Neotropical rodent. *Oikos* **74**, 259–264.

Lusseau, D. (2003). Male and female bottlenose dolphins *Tursiops* sp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Mar. Ecol.-Progress Series* **257**, 267–274.

Lusseau, D. (2004). The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. *Ecol. Soc.* **9**, 2.

Lusseau, D. (2005). The residency pattern of bottlenose dolphins (*Tursiops* spp.) in Milford Sound, New Zealand, is related to boat traffic. *Mar. Ecol. Prog. Ser.* **295**, 265–272.

Lusseau, D. & Higham, J.E.S. (2004). Managing the impacts of dolphin-based tourism through the definition of critical habitats: the case of bottlenose dolphins (*Tursiops* spp.) in Doubtful Sound, New Zealand. *Tourism Mgmt*. **25**, 657–667.

Miller, M.L. (1993). The rise of coastal and marine tourism. *Ocean Coastal Mgmt*. **20**, 181–199.

Morton, A.B. & Symonds, H.K. (2002). Displacement of *Orcinus orca* by high amplitude sound in British Columbia, Canada. *ICES J. Mar. Sci.* **59**, 71–80.

Ripple, W.J. & Beschta, R.L. (2004). Wolves and the ecology of fear: can predation risk structure ecosystems. *Bioscience* **54**, 755–766.

Russell, R.E., Swihart, R.K. & Feng, Z. (2003). Population consequences of movement decisions in a patchy landscape. *Oikos* **103**, 142–152.

Scheidat, M., Castro, C., Gonzales, J. & Williams, R. (2004). Behavioral responses of humpback whales (*Megaptera novaeangliae*) to whalewatching boats near Isla de la Plata, Machalilla National Park, Ecuador. *J. Cetacean Res. Mgmt*. **6**, 63–68.

Suryan, R.M. & Harvey, J.T. (1999). Variability in reactions of Pacific harbor seals, *Phoca vitulina richardsi*, to disturbance. *Fish. Bull.* **97**, 332–339.

Walther, F.R. (1969). Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni*: Guenther 1884). *Behaviour* **34**, 184–221.

White, D., Kendall, K.C. & Picton, H.D. (1999). Potential energetic effects of mountain climbers on foraging grizzly bears. *Wildl. Soc. Bull.* **27**, 146–151.

Whittington, J., St Clair, C.C. & Mercer, G. (2004). Path tortuosity and the permeability of roads and trails to wolf movement. *Ecol. Soc.* **9**, 4 [online http://www.ecologyand society.org/vol9/iss1].

Williams, R., Bain, D.E., Ford, J.K.B. & Trites, A.W. (2002*a*). Behavioral responses of male killer whales to a 'leapfrogging' vessel. *J. Cetacean Res. Mgmt*. **4**, 305–310.

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

Williams, R., Trites, A.W. & Bain, D.E. (2002*b*). Behavioral responses of killer whales to whale-watching traffic: opportunistic observations and experimental approaches. *J. Zool. (Lond.)* **256**, 255–270.

Wood, S.N. (2001). mgcv: GAMs and generalized ridge regression for R. *R News* **1**, 20–25.

Zar, J.H. (1996). *Biostatistical analysis*. New Jersey: Prentice-Hall.