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Inferring energy expenditure from respiration rates in minke whales to measure the effects of whale watching boat interactions

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ABSTRACT

Quantifying the energetic costs of human induced behavioral disturbance on wildlife is a crucial step to evaluate the potential long-term effects of disturbance on individual vital rates. Standard methods cannot be used for estimating energetic cost of transport because of the large size of most cetaceans, and instead energetic costs are inferred from respiration rates. We quantified the added energetic costs of avoidance to whale watching boats for minke whales (*Balaenoptera acutorostrata*) in Faxaflói bay, Iceland, by comparing minke whale movement tracks and respiration in the presence (impact) and absence (control) of whale watching boats. Energy expenditure was inferred from respiration rates, using published bioenergetic models for minke whales and mass-specific cost of transport (COT) was estimated for different swimming speeds. The sensitivity of the COT estimate to model assumptions was investigated using resampling methods. ANCOVA was used to investigate the effects of swimming speed and whale watching boats on minke whale respiration rate. Respiration rate increased linearly with swimming speed, while COT decreased nonlinearly with increased speed up to an optimal speed between 2.5 and 7.0 m s^{-1}. Respiration rates were higher during interactions with whale watching boats at any given speed, suggesting that boat presence elicited a stress response in the animals, resulting in a 23.2% increase in estimated energy expenditure. Swimming speed also increased during whale watching interactions from 1.62 to 2.64 m s^{-1}, resulting in an additional 4.4% increase in estimated energy expenditure during whale watching interactions. Thus, whale watching boat interactions resulted in an overall increase in estimated energy expenditure of 27.6%, from 56.54 to 72.16 J kg^{-1} min^{-1}. During interactions with whale watching boats, minke whales swam at speeds that were within the lower range of the optimal COT. This suggests that minke whales employ similar avoidance strategies towards whale watching boats as towards natural predators.

1. Introduction

Whale watching has been growing rapidly during the last decades, and as a result most coastal cetacean populations are now exposed to some form of whale watching (O'Connor et al., 2009). Several studies have shown that interactions with whale watching boats can cause changes in the behavior of the targeted animals (Christiansen et al., 2010; Lusseau, 2004; Schaffar et al., 2009; Williams et al., 2006). When disturbances occur repeatedly they can lead to long-term negative effects on individual vital rates (Bejder, 2005; Currey et al., 2009; Fortuna, 2006; Lusseau et al., 2006).

Given the rapid development of whale watching and other marine industries (e.g. marine renewables) (Gross et al., 2003; Honey and Krantz, 2007; O'Connor et al., 2009), it is important to understand how non-lethal effects of disturbance can lead to long-term effects on individual vital rates (Bejder and Samuels, 2003). Following this intent, considerable work has recently been undertaken to understand and inform the mechanistic links between behavioral disruption and vital rates (NRC, 2005). A crucial step in this framework is to understand the mechanistic link between behavioral change and bioenergetics, i.e. how different behaviors relate to energy expenditure and acquisition. Because organisms are constrained by their energy budgets, energy is one of the most important currencies determining the fitness of an organism (Butler et al., 2004). Therefore, understanding how an organism allocates energy to different activities, and how this is affected by external covariates (i.e. whale watching), is of central importance to understanding the physiological, behavioral and evolutionary ecology

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of organisms (Butler et al., 2004). Knowledge of this linkage therefore makes it possible to put disturbance into the context of the overall energy requirements of an animal, so that behavioral variations can be related to offspring investment and survival.

Existing methods to quantify energy expenditure are of limited use for large cetaceans. Doubly labeled water method is too expensive to be used for larger cetaceans, and requires that the same animal is recaptured for a second sampling event, which is seldom feasible (Butler et al., 2004; Fahlman et al., 2008b). Further, since the method does not provide detailed information about the energetic costs of specific activities, it will not be possible to quantify the energetic costs associated with whale watching interactions. While heart-rate methods data can provide energetic costs over very fine temporal scales, it requires calibration with oxygen consumption values obtained via open-flow respirometry techniques (Butler et al., 2004). This limits its application to large cetaceans, which cannot be contained easily in experimental tanks. Measurement of body acceleration, which can be recorded by attaching data loggers to animals, can also serve as a proxy for energy expenditure in animals during movement (Gleiss et al., 2010; Halsey et al., 2009). While this technique can provide high resolution estimates of relative energy expenditure during different activities, in order to obtain estimates of absolute energy expenditure, it needs to be calibrated using respirometry techniques, which again limits its use in large cetaceans.

Oxygen consumption has been shown to be strongly correlated with the respiration rate of captive bottlenose dolphins (*Tursiops truncatus*), making it possible to infer the energetic costs of free-swimming cetaceans from respiration rates (Yazdi et al., 1999). The large tidal volumes and high oxygen extraction of cetaceans, together with infrequent and short exchange of lung gases, lend whales little chance of increasing their respiratory minute volumes by other means than increasing respiration rates (Folkow and Blix, 1992). Changes in oxygen uptake of cetaceans are therefore likely to be reflected in the respiration rates (Folkow and Blix, 1992). Based on this assumption, the cost of swimming has been estimated for a number of free-living large cetaceans, from the observations of respiration rate and swimming speed in combination with theoretical values for oxygen consumption (Folkow and Blix, 1992; Kriete, 1995; Sumich, 1983; Williams and Noren, 2009). These studies show that estimated energy expenditure is largely influenced by the swimming speed of the animal. When evaluating the effects of whale watching on energy expenditure of cetaceans it is therefore crucial to take swimming speed into consideration.

In this study we use respiration rate as a proxy for oxygen consumption, to estimate the energy expenditure of free-swimming minke whale (*B. acutorostrata*) at different swimming speeds in relation to whale watching boats in Faxaflói bay, Iceland. The area constitutes an important feeding ground for minke whales in the north Atlantic (Christiansen et al., 2013c; Horwood, 1990) with minke whales being present every year between mid-April and mid-October (Sigurjónsson and Víkingsson, 1997). Whale watching started in Faxaflói bay in 1994 and has since grown rapidly (O'Connor et al., 2009). During the study period, four whale watching companies were operating in Faxaflói bay from the harbor of Reykjavik, providing a total of six boats which varied in size from 13 to 34 m. During the summer field seasons each boat conducted on average three trips per day, with each trip being 3 h long. Studies looking at the effect of whale watching on minke whales in the area, found changes in the behavior of minke whales during whale watching interactions (Christiansen et al., 2013a, 2013b). Here, we aim to quantify the energetic costs of these effects, focusing specifically on the added energy expenditure resulting from these behavioral changes. The results are discussed in light of the swimming energetics of minke whales.

To provide insight into the avoidance strategy used by minke whales towards whale watching boats, we estimated the speed at which the mass-specific cost of transport (COT) is at its minimum, and compared this to the mean swimming speeds of whales in the presence and absence of whale watching boats. The sensitivity of the COT estimate to model assumptions is evaluated using resampling methods. This is the first study that rigorously attempts to assess the relative influence of uncertainty in model parameters on model output.

2. Methods and materials

2.1. Data collection

Movement tracks of arbitrarily chosen minke whales were recorded by continuous individual focal follows (Altmann, 1974) in Faxaflói bay, Iceland, between June and September 2010 and 2011. Follows were terminated if another animal was in close proximity of the focal animal, to avoid measurement errors from sampling the wrong animal. Since minke whales tend to be solitary animals, this rarely happened. Control data were collected from a 27-m tall lighthouse (64°04′56″N, 22°41′24″W) located in Garður on the northern tip of the Reykjanes peninsula (Fig. 1). In Faxaflói bay, interactions between whale watching boats and cetaceans take place far from land (Fig. 1), which made it impossible to collect impact data from the same research platform. Instead impact data was collected from commercial whale watching boats. Despite this limitation, the control and impact sites were separated by only 20 km, and whales have been observed moving freely between sites within the same day. Further, there were no differences between the two areas in terms of oceanographic features (depth, sea surface temperature, current velocity and bearing) (McLeish, 2012).

The time of every surfacing was recorded together with the position of the whale. From land, positions were measured using a theodolite (Wild T16, Wild Heerbrugg, Heerbrugg, Switzerland), while photogrammetric techniques (Gordon, 2001) together with a digital compass mounted on a laser range finder (LaserAce®300, MDL, Aberdeen, UK) were used to measure the position of the whale at sea. The methods are described by Christiansen et al. (2013a), who added correction factors to the distance estimates to account for measurement biases related to the different research platforms, and showed that the model output were robust to measurement errors. They also tested for potential biases resulting from observer errors (individual variation and experience level) on the probability of missing a surfacing and on measurement accuracy, but found no difference between observers (n = 12) (Christiansen et al., 2013a). Surface conspicuous behavioral events, such as surface feeding were also recorded during focal follows (Lynas and Sylvestre, 1988). Environmental factors, such as sea conditions (Beaufort scale) and tidal height were also recorded.

2.2. Behavioral variables

The mean respiration rate of each track was estimated by dividing the total duration of the track by the number of surfacing. Mean swimming speed was estimated for each track by dividing the total surface distance (the sum of the distances between all surfacing within a track) by the duration of the track. The directness index (DI), or linearity of movement, for each track was calculated by dividing the surface distance between the end-points of the track by the total surface distance (Williams et al. 2002):

$$DI = 100 \left(\frac{D}{\sum_{i=1}^{n} d_i} \right) \tag{1}$$

where D is the surface distance between the end-points of the track and d_i represents the surface distance between two succeeding surfacing in the track. DI values range between 0 (circular movement) and 100 (linear movement).