Inferring activity budgets in wild animals to estimate the consequences of disturbances

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INTRODUCTION

Consumptive interactions with wildlife, involving the direct removal of individuals from their population, have long been the focus of wildlife conservationists (Harwood and Stokes 2003; Loveridge et al. 2007; Milner et al. 2007). However, the effects of nonconsumptive interactions have recently been given increasing attention as a result of growing human populations and resource use, and a rapid expansion of agricultural and urban areas and infrastructures, as well as an increasing exploitation of our oceans (Vitousek et al. 1997; Hildebrand 2009). In addition, intentional human–wildlife interactions, for example, wildlife tourism, are growing rapidly (Duffus and Dearden 1990; Woodroffe et al. 2005; O’Connor et al. 2009). Even if such interactions provide an important economic foundation for wildlife conservation, they can affect the behavioral ecology of the targeted species (Lusseau 2004; Woodroffe et al. 2005; Klaassen et al. 2006; Mallord et al. 2007; Christiansen et al. 2010). Repeated behavioral disruptions can have cumulative negative effects on an animal’s bioenergetic budget, which can lead to long-term negative effects on individual vital rates (survival and reproduction) (Bejder 2005; Fortuna 2006; Lusseau et al. 2006; Currey et al. 2009). If a large portion of the population is exposed to such impacts, the conservation status of the affected population can be jeopardized (Lusseau et al. 2006; Currey et al. 2009). Hence, we need to improve our understanding of the mechanisms through which human disturbances can threaten wildlife conservation (Duffus and Dearden 1990; Bejder and Samuels 2003; Blanc et al. 2006; New et al. 2013).

Whalewatching is an example of a nonlethal human–wildlife interaction that in recent decades have experienced a rapid growth around the world (O’Connor et al. 2009). A large number of studies now exist, both on odontocetes (toothed whales) and mysticetes (baleen whales), showing that whalewatching activities can have short-term behavioral effects on the targeted animals, resulting in changes in activity, swimming speed, movement pattern, diving behavior, group formation, and/or vocalization (Novacek et al. 2001; Van Parijs and Corkeron 2001; Williams et al. 2002; Lusseau 2003a; Bejder et al. 2006; Christiansen et al. 2010; Lundquist et al. 2013). It has further been shown for odontocetes that

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whalewatching activities can lead to long-term negative effects on reproductive success (Bejder 2005; Fortuna 2006) and consequently population growth rates (Lusseau et al. 2006; Currey et al. 2009). For mysticetes, data are currently lacking to assess the potential long-term effects of whalewatching on vital rates, which highlight the need for further research into linking behavioral changes to vital rates.

Perhaps the most straightforward way of linking behavioral changes to vital rates in cetaceans is through a bioenergetics framework. All animals partition their lives into different activities (Nikinmaa 1984) to fulfill daily requirements for survival (e.g., maintaining homeostasis) and reproduction. The resulting activity budgets can provide useful information on the relative importance of various activities in terms of energy intake and expenditure and thus provide a direct link to an animal’s bioenergetic budget (Birtiaux et al. 1989; Boyd 1999; Jodice et al. 2003). Bioenergetics in turn can be directly linked to individual vital rates (survival and reproduction) (Costa 1993; New et al. 2013). Activity budgets, therefore, provide a good measure of human disturbance on wildlife (Degrati et al. 2008).

Inferring activity budgets from animal behavior, however, can be challenging for species that are difficult to observe and require multiple observational variables. For such species, including cetaceans, activity states have to be inferred indirectly from other behavioral variables, such as interbreath intervals (IBIs), movement indices (Bailey and Thompson 2006), group cohesion (Bejder et al. 1999), and presence of behavioral events (Lusseau 2006). Here, we propose to use a stepwise method to quantitatively assign hidden activity states to observed multivariate behavioral time series data. We then infer activity budgets from the time series of estimated activity states.

We use this approach to measure the effect of whalewatching boat interactions on activity budgets of minke whales (Balaenoptera acutorostrata), a mysticete, on one of the feeding grounds of the North Atlantic population (Faxaflói Bay, Iceland) (Christiansen, Rasmussen, et al. 2013). During the last 20 years, the southeastern part of the Bay has experienced a rapidly growing whalewatching industry, with one of the main target species being minke whales. Previous studies in the area have shown that whalewatching boat interactions disrupt the feeding behavior of minke whales (Christiansen, Rasmussen, et al. 2013). The magnitude of this effect, however, was not measured. This study aims to quantify the effect of whalewatching boat interactions on the activity budget of minke whales, to provide the necessary step for linking behavioral changes to bioenergetics, and ultimately understand whether the growth of this industry is threatening the conservation status of this population (New et al. 2013).

**MATERIALS AND METHODS**

**Modeling approach**

A stepwise modeling approach was developed to estimate the activity budget of minke whales and the effect of whalewatching boat interactions (Figure 1). Using multiple behavioral variables (both continuous and categorical), recorded from visual observations of individual animals in continuous time, the underlying distributions of the observed data were used to quantitatively identify and define behavioral types. Activity states were then assigned to each sampling unit, using a combination of hidden (posterior probability distribution of the mixture models) and observed states (Figure 1).

From the resulting time series of activity states, transition probability matrices were estimated using Markov chains. Monte Carlo simulations were then used to simulate time series of activity states, based on the transition probability matrices, to obtain activity budgets, accounting for heterogeneity in duration of activity states (Figure 1).

The following sections describe each step of the modeling procedure in turn when applied to minke whales in Faxaflói Bay, Iceland. By estimating the transition probability matrices, and consequently the activity budgets, both in the presence (impact) and absence of whalewatching boats (control), it was possible to measure the effect of whalewatching boat interactions on minke whale activity budget.

**Observations**

The behavior of minke whales and whalewatching boats were collected by continuous individual focal follows (Almann 1974) in Faxaflói Bay, Iceland, between June and September 2010 and 2011. The methods are described in Christiansen, Rasmussen, et al. (2013). Focal animals were chosen randomly and if another animal was in close proximity of the focal animal, the follow was terminated to avoid measurement errors from sampling the wrong animal. Minke whales tend to be solitary animals on the feeding grounds and this therefore happened rarely (Pike et al. 2008).

![Figure 1](https://academic.oup.com/beheco/article-abstract/24/6/1415/190248) A conceptual diagram showing the structure of the modeling framework developed for minke whales. Each section is described in the main text under the corresponding subheader. DI = directness index; IBI = interbreath interval; SFE = surface feeding event.
Control data, describing undisturbed behavior, 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 (Figure 2). Impact data were collected from commercial whalewatching boats, operating in the southeastern part of the Bay (Figure 2). During the study period, 4 whalewatching companies were operating in Faxaflói Bay from the harbor of Reykjavik, providing a total of 6 boats that varied in size from 13 to 34 m. During the summer field seasons, each boat conducted on average 3 trips per day, with each trip being 3 h long. When a whalewatching boat encountered a whale, the boat generally tried to remain with the same animal for an extended period of time (>15 min). This made it a suitable platform to conduct individual focal follows from. The researcher did not influence the behavior of the whalewatching boat.

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), whereas photogrammetric techniques (Gordon 2001) together with a digital compass mounted on a laser range finder (LaserAce®300, MDL, Aberdeen, UK) were used to measure positions at sea. Surface feeding events (SFEs), direct observations of minke whales engulfing prey at the surface (Lynas and Sylvestre 1988), were also recorded during focal follows. Potential effects of using different measuring techniques and platforms when collecting the control and impact data were investigated in Christiansen, Rasmussen, et al. (2013), who found no effects on the model output. There are also no differences between the control and impact areas in terms of oceanographic features or other habitat features (McLeish 2012).

To avoid pseudoreplication, when possible, the focal whale was photo identified from the whalewatching boats by another researcher (Dorsey 1990). Although this was not possible from land, capture–recapture studies carried out in Faxaflói Bay show a very low recapture probability of individual minke whales in the Bay through the feeding season (Christiansen 2013). It is, therefore, likely that most follows came from different individuals.

### Behavioral variables

From the surfacing times, minke whale IBIs were calculated as the time elapsed between 2 consecutive surfacing in a follow. If a surfacing time was missed, no IBI was calculated for that interval. In this study, a sampling unit corresponded to one IBI. From the positional data, directness index (DI) was calculated to describe the linearity of movement of each sampling unit in a follow (Williams et al. 2002). Based on previous studies, DI was calculated for every sampling unit based on 3 positions (surfacing) (Christiansen, Rasmussen, et al. 2013):

$$ DI = 100 \left( \frac{D}{d_1 + d_2} \right) $$

where $D$ is the distance between the first and third position, $d_1$ is the distance between the first and second position, corresponding to the net movement of the whale during the preceding IBI, and $d_2$ is the distance between the second and third position, corresponding to the net movement of the whale during the IBI of interest (Christiansen, Rasmussen, et al. 2013). Thus, the DI for each sampling unit corresponds to the linearity of movement from the beginning of the previous IBI to the end of the present IBI. DI ranges between 0, sinuous movement, and 100, linear movement.

The occurrence of SFE was used as a categorical variable, with SFE being either present or absent during a sampling unit.

### Behavioral types

The surfacing pattern of cetaceans is generally a series of shorter dives followed by a longer dive. Although the shorter dives function to optimize the replenishment of oxygen levels, the longer dives allow the animal to maximize the time spent performing

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**Figure 2**

Map of the Faxaflói Bay study area in Iceland, showing the minke whale movement tracks that were used in the analyses. Black and gray tracks correspond to control and impact data, respectively.
certain activities (e.g., searching for or capturing prey). Dives can, therefore, be divided into distinct dive types, based on the distribution of IBIs. We fitted univariate mixture models to the density distribution of IBI, using expectation maximization, to identify different dive types within the IBI data (R 2.14 2011, mixtools package, Benaglia et al. 2009). IBIs for observations ending with a SFE were excluded from analysis because those observations were directly used to classify activity states (see Activity States section). Different number of components (dive types) and distributions were tested, using the default random starting values for the model parameters. The best fitting model was selected using Akaike’s information criterion (AIC), which provides a relative measure of the goodness of fit of statistical models. We restricted the maximum number of components in the mixture model to 4 given the diving biology of this taxa (Croll et al. 2001). Based on the posterior probabilities of the best fitting mixture model, a dive type (component) was assigned to each sampling unit. As for IBI, univariate mixture models were used to identify different movement types (components) from the density distribution of DI, again excluding SFE observations. As before, the best fitting model was selected using AIC and a specific movement type was assigned to each sampling unit, based on the posterior probabilities of the best fitting mixture model. For both variables, a threshold level of $P = 0.5$ was used when assigning components based on the posterior probabilities. The resulting parameter outputs from the 2 mixture models provided the density distribution of the identified components in the model, as well as their relative occurrence, $\lambda$, in the observed data set.

Activity states

We defined activity states from the 3 behavioral variables (IBI, DI, and SFE) for each sampling unit in our follows. Follows needed to be of a minimum length of 2 activity states to constitute a time series. The activities of animals can broadly be divided into feeding and nonfeeding (NF) activities. For minke whales, feeding activity can either be directly observed at the surface or take place deeper down in the water column, hidden from the observer (Lynas and Sylvestre 1988; Christiansen, Rasmussen, et al. 2013). We will refer to these 2 forms of feeding as surface feeding (SF) and foraging, respectively. SF activity was directly observed as the occurrence of SFE at the surface. Foraging activity on the other hand was a hidden state and indirectly inferred from the relationship between IBI and DI. mysticetes generally have longer IBI during foraging activity compared with NF activity, as they attempt to maximize the time spent under water (Würsig et al. 1986; Croll et al. 2001; Acevedo-Gutiérrez et al. 2002). This suggests that IBI could be a useful indicator of feeding activity (Würsig et al. 1986). However, because Faxafloi Bay is a relative shallow bay (mean depth <40 m) with prey often being present close to the surface, IBI alone might not be sufficient to infer foraging activity. Minke whales in Faxafloi Bay feed predominantly on sandeels Ammodytes sp. (Vikingson and Elvassor 2010), which has a patchy distribution and are relatively stationary in movement (Wright et al. 2000). This suggests that once a whale is in a suitable prey patch, the surface movement during foraging activity should be defined by sinuous movement (low DI), describing an animal maneuvering to return to the same location (Barraquand and Benhamou 2008). Minke whale foraging activity was, therefore, defined as long dive types occurring during sinuous movement, representing an animal making prolonged dives while staying within the same foraging patch (Bailey and Thompson 2006; Stelle et al. 2008). This was supported by previous studies on minke whales in the area (Christiansen, Rasmussen, et al. 2013). All other combinations of movement and dive type were defined as NF activity. NF activity, therefore, includes not only linear NF activity (including both shorter and longer IBI), often referred to as traveling in other studies (Stelle et al. 2008), but also short sinuous dives, which could be preparatory dives occurring just before a foraging or SF dive. Although we acknowledge that preparatory dives surely serve another purpose than the ordinary NF dives, there is no difference in terms of bioenergetics. Because minke whales are capital breeders (Christiansen, Vikingsson, et al. 2013), no reproduction, and therefore socializing activity (Stelle et al. 2008), occurs on the feeding grounds.

Transition probability matrices

We estimated the transition probability between activity states, the proportion of time a succeeding activity state was observed following a preceding activity state (Lusseau 2003b; Christiansen et al. 2010). Markov chains quantify the dependence of a succeeding event on preceding events (Guttorm 1995; Caswell 2001). Diagnostic plots for temporal autocorrelation and partial autocorrelation function revealed a temporal autocorrelation of lag 1 for the IBI data. A first-order Markov chains were therefore used, where the succeeding event is only dependent on the immediately preceding event. Because this dependence can be affected by any extrinsic factor taking place between events, it is possible to calculate the probability that a minke whale will change from one activity state to another when whalewatching boats are either present (impact) or absent (control) (Lusseau 2003b; Christiansen et al. 2010). This effect can then be quantified and tested for by comparing these 2 probabilities. The time series data of activity states, one for each follow (i.e., individual whale), were first compiled into 2-way contingency tables of preceding activity state versus succeeding activity state, one for control and one for impact situations (Lusseau 2003b; Christiansen et al. 2010). Transition probabilities from proceeding to succeeding activity states were then calculated for both control and impact situations (Lusseau 2003b):

$$P_{ij} = \frac{a_{ij}}{\sum_{i=1}^{n} a_{ij}} \quad \sum_{j=1}^{n} P_{ij} = 1$$

where $i$ is the preceding activity state, $j$ is the succeeding activity state, $n$ is the total number of activity states (i.e., 3), $a_{ij}$ is the number of transitions observed from activity state $i$ to $j$, and $P_{ij}$ is the transition probability from $i$ to $j$ in the Markov chain.

We estimated 2 transition probability matrices, one for control and one for impact situations. The effect of whalewatching boats interactions were statistically tested by comparing the impact (observed frequency) and control contingency tables (expected frequency) using a goodness-of-fit test in R. Each control transition was also compared with its corresponding impact transition using a 2-tailed $\chi^2$-test for proportions (Fleiss 1981). The magnitude of the effect was equal to the difference between the 2 transition probability matrices, $P_{ij}^{\text{impact}} - P_{ij}^{\text{control}}$.

Activity budgets

To estimate the activity budget of the minke whales, Monte Carlo methods were used to simulate individual time series (follows) of activity states based on the transition probability matrices obtained from the Markov model. One thousand simulations were run for both control and impact situations. First, an empty vector of activity states were created in R, with each empty value representing a...
sampling unit to which an activity state, as well as duration, was randomly assigned. The initial activity state was arbitrary assigned as NF activity. The next state was then randomly chosen from the transition probability matrix obtained from the Markov chain model, with the preceding state being the previous activity state in the simulated time series. This procedure ensured that if the activity state changed from one time step to the next, this would also change the transition probability to the following time step because the preceding activity state for that time step would be different. This procedure was repeated for the entire vector.

To account for the heterogeneity in duration of stay in each activity state (i.e., the variation in IBI), a duration was assigned to each state, based on the distribution of the mixture model for IBI (see Behavioral types). For each state assigned as foraging activity, a random value was taken from the density distribution of the long dive type from the IBI mixture model because this was the only dive type occurring during foraging activity. Because NF activity comprised several dive types (two or more depending on the output from the IBI mixture model), it was necessary to first assign a dive type to each state classified as NF activity. This was done randomly using the lambda values obtained from the mixture model for IBI, which represented the relative occurrence of a specific dive type in the observed data. To discount for the proportion of long dives belonging to foraging activity, new lambda values were obtained from a Gaussian mixture model applied only to the IBI data for NF activity. Once a dive type had been randomly selected, a random IBI value was taken from the selected density distribution. For states assigned as SF activity, a random value for IBI was taken from a Gaussian density distribution estimated from the SF dives alone.

After allocating activity states, and durations of states, the first 100 states in the time series were removed as a burn-in period so that each simulation begun with a randomly chosen activity state. The time series was then cut at an upper limit of 1 h, estimated from the state durations. One hour was chosen because it represented the longest recorded interaction time between a whale-watching boat and a single animal. The activity budget was then estimated by calculating the sums of the durations for the different activity states and dividing them by the total duration of the time series (i.e., 1 h). Doing this for every simulation resulted in a density distribution of the relative proportion for each activity state in the activity budgets, both for control and impact situations.

**Sensitivity analysis**

The activity budgets in this study resulted from Monte Carlo simulations based on transition probability matrices between activity states. These matrices in turn resulted from the assignment of activity states to the observed behavioral variables in a follow, based on a set probability threshold of $P = 0.5$ for the posterior probabilities of the 2 univariate mixture models for IBI and DI. We assessed the sensitivity of the model output (activity budget) to potential misclassifications of activity states from the mixture models by altering this threshold level. The threshold level used when assigning foraging activity was increased at steps of 0.1 (10% units) from $P = 0.5$ to $P = 0.8$. All data points falling below this threshold value were classified as NF activity. The full modeling approach was then applied to each of these data sets, and the resulting activity budgets were compared visually.

**RESULTS**

Minke whale behavioral data were collected on 118 days during 2 field seasons between June and September 2010 and 2011, giving a total of 164 h of minke whale observations. A total of 5386 estimates (1579 control and 3807 impact) of IBI, DI, and SFE were obtained, belonging to 648 follows (211 control and 437 impact; a set probability threshold of $P = 0.5$ for the posterior probabilities of the 2 univariate mixture models for IBI and DI). We assessed the sensitivity of the model output (activity budget) to potential misclassifications of activity states from the mixture models by altering this threshold level. The threshold level used when assigning foraging activity was increased at steps of 0.1 (10% units) from $P = 0.5$ to $P = 0.8$. All data points falling below this threshold value were classified as NF activity. The full modeling approach was then applied to each of these data sets, and the resulting activity budgets were compared visually.

**Behavioral types**

Visual inspection of the density distribution of IBI and logged IBI of minke whales revealed a number of distinct dive types (components) for minke whales in Faxaflói Bay (Figure 3a). Using a univariate Gaussian mixture model on the log-transformed data, 3 dive

**Figure 3**

Density distribution of (a) logged IBI and (b) inverse DI for minke whales in Faxaflói Bay, Iceland, showing the density distributions of the identified dive and movement types (components), respectively. (a) The 3 dive types: short (solid line), medium (dashed line), and long dives (dotted line) were identified using a univariate Gaussian mixture model. (b) The 2 movement types: linear (dashed line) and sinuous movement (solid line) were identified by a univariate gamma mixture model. $n = 5254$. 

types were identified, which were referred to as short (mean = 2.70, SD = 0.28), medium (mean = 3.29, SD = 0.59), and long dives (mean = 4.64, SD = 0.55). The relative occurrence of the 3 dive types in the data set, estimated from the $2\lambda$ parameters, was 0.36, 0.34, and 0.30 for short, medium, and long dives, respectively. The 3-component mixture model provided a better fit to the observed data ($AIC = 12616.71$) than the 2-component ($AIC = 12655.65$) and 4-component mixture models ($AIC = 12619.71$).

The density distribution for DI was heavy tailed, so a univariate gamma mixture model was used to identify and describe the components in the observed data. To better conform to the gamma distribution, the mixture model was applied to the inverse of DI ($\text{abs}(\text{DI} - 100)$), which transformed the distribution from being negatively skewed to being positively skewed. Because DI was bounded between 0 and 100, this transformation did not affect the order of the observations in the density distribution, apart from reversing them. The gamma mixture model identified 2 distinct movement types (components) (Figure 3b), which we referred to as linear (shape = 0.51 and scale = 21.45) and sinuous movement (shape = 10.05 and scale = 6.05). The $\lambda$ parameter for the 2 movement types gave a relative distribution of 0.87 and 0.13 for linear and sinuous movement, respectively. The 2-component mixture model provided a better fit to the observed data ($AIC = 37832.91$) than the 3-component ($AIC = 38033.98$) and 4-component mixture models ($AIC = 37832.91$).

Activity states

Foraging and NF activity were defined and classified quantitatively based on the relationship between dive type and movement type, with long sinuous dives (a sampling unit classified as long dive type and sinuous movement type) corresponding to foraging activity, whereas all other combinations of dive type and movement type were defined as NF activity (Figure 4). SF activity was based solely on the observation of SFE occurring at the end of a dive interval, irrespective of dive type and movement type (Figure 4).

Transition probability matrices

The Markov chain analysis showed that interactions with whalewatching boats affected the transition probability between activity states for minke whale (goodness-of-fit test, $\chi^2 = 73.64$, df = 4, $P < 0.0001$) (Figure 5). Minke whales engaged in NF activity were more likely to remain in the same state ($\zeta$-test, $\zeta = 5.02$, $P < 0.0001$) than to change to foraging ($\zeta$-test, $\zeta = -3.17$, $P = 0.0015$) or SF activity ($\zeta$-test, $\zeta = -3.95$, $P = 0.0001$) during interactions with whalewatching boats. The magnitude of these differences was a 4.3% increase in the likelihood of remaining in a NF state (NF $\rightarrow$ NF: 91.5–95.4%), whereas the probability of changing to foraging or SF activity decreased with 40.2% (NF $\rightarrow$ For: 4.9–2.9%) and 54.2% (NF $\rightarrow$ SF: 3.6–1.7%), respectively (Figure 5). Also, the probability of changing from foraging to NF activity ($\zeta$-test, $\zeta = 2.20$, $P = 0.0276$) increased with 13.1% (For $\rightarrow$ NF: 81.9–92.7%) during whalewatching interactions.

Activity budgets

In the absence of whalewatching boats, minke whales spent about 11.5% (SD = 0.069) of their time foraging and 3.8% (SD = 0.033) SF, whereas the remaining 84.7% (SD = 0.076) of their time
was spent NF (Figure 6). During interactions with whalewatching boats, NF activity increased with 6.4% units (SD = 0.095) in relative proportion, whereas foraging decreased with about 4.3% units (SD = 0.086) and SF decreased with 2.1% units (SD = 0.041). In the presence of whalewatching boats, whales spent 7.2% (SD = 0.052) of their time foraging, 1.6% (SD = 0.023) SF, and 91.2% (SD = 0.058) in NF activity (Figure 6). In terms of bioenergetics, the cumulative time spent feeding (the sum of foraging and SF activities) decreased with 6.4% units, from 15.3% (SD = 0.076) to 8.8% (SD = 0.058), during interactions with whalewatching boats. This represented a 42% decrease in the proportion of time spent engaged in energy acquiring activities.

Because the simulated time series were limited to 1 h in duration, the resulting density distributions for both the control and impact...
data were quite spread (Figure 6), sometimes resulting in single activity states being completely dominant in the activity budget (proportion = 1). For this reason, the effect of whalewatching boats was not always unidirectional, with the density distributions of the differences in relative proportions overlapping with zero for all 3 activity states (Figure 7). Thus, there was considerable variation in the effect of whalewatching boats on the activity budget of minke whales when looking at a time period of only 1 h. By increasing the duration of the simulations, the spread of the density distributions became narrower, resulting in a more uniform effect of whalewatching boat interactions on the activity budget (Supplementary Figure S1).

Sensitivity analysis
The effect of whalewatching boats on the activity budget of minke whales was similar when using different probability threshold levels, ranging from $P = 0.5$ to $P = 0.8$, when assigning foraging activity to sampling units (Figure 7). This shows that the results of the modeling approach were robust to potential errors when assigning activity states from the posterior probabilities of the 2 univariate mixture models (Figure 3).

DISCUSSION
Activity budgets
Undisturbed minke whales engaged in feeding-related activities (foraging and SF) for about 15% of their time. Because our definition of feeding activity relates directly to the time whales are engaged in foraging or SF dives, this excluding other types of dives associated with feeding activity (e.g., preparatory dives), it can be linked easier to energy acquisition and therefore prey intake. The average field metabolic rate of an average-sized (7.5 m, 4800 kg) adult minke whale in Iceland is 0.057 kJ/kg/min (standard error [SE] = 0.003) (Christiansen 2013). On top of this, it deposits on average about 72,000 kJ/day (95% CI = 35,000–109,000) of energy into its blubber layer during the summer feeding season (Christiansen, Vikkingsson, et al. 2013). This together adds up to a total daily energy requirement of about 460,000 kJ/day (95% CI = 390,000–540,000). If we, for simplicity, assume that our control activity budget is representative also of night time activities (data were only collection between 6 AM and 6 PM), the average rate of energy intake would equal about 2100 kJ (95% CI = 1800–2400) per minute active feeding. With minke whales in Faxaflói Bay feeding primarily on sandeels (Vikkingsson and Elvarsson 2010), this would equal a prey intake of about 370 g (95% CI = 310–430) of sandeel biomass per minute active feeding or 92 fish (95% CI = 77–107) per minute (based on an average energy density of 6.0 kJ/g wet mass and an average body mass of 4.0 g, Nordøy et al. 1995; van Deurs et al. 2011), assuming that a minke whale absorbs about 92% of the energetic content of the ingested prey (Nordøy et al. 1995). Although these estimates are greatly simplified, they provide a valuable step forward in linking behavior to bioenergetics in minke whales.

Effects of whalewatching
This study shows that interactions with whalewatching boats affect the activity budget of minke whales, causing a decrease in both foraging and SF activity. Although similar effects have been observed in odontocetes (Lusseau 2003b; Williams et al. 2006; Christiansen et al. 2010), this is the first study showing an effect of whalewatching boat interactions on the activity budget of a mysticete species. The results furthers the findings of Christiansen, Rasmussen, et al. (2013), who found that whalewatching boats disrupted the feeding behavior of minke whales but did not quantify the magnitude of this effect. This study shows that whalewatching boat interactions resulted in a 42% decrease in overall feeding activity of minke whales. If we, for simplicity, assume a linear relationship between feeding activity and energy acquisition, a 1 h whalewatching boat interaction would result in a 8100 kJ (95% CI = 6800–9400) decrease in energy acquisition. Further, it has been shown that NF minke whales increase their swimming speed, and consequently energy expenditure with about 28% during interactions with whalewatching boats, resulting in a field metabolic rate of 0.072 kJ/kg/min (SE = 0.003) (Christiansen 2013). This would result in an overall net energy loss of about 12000 kJ (95% CI = 8000–16000), or 63.4% (95% CI = 49.5–73.3), during 1 h of whalewatching interactions.

![Figure 7](https://academic.oup.com/beheco/article-abstract/24/6/1415/190248)

Figure 7
Conditional density plots (hdcde package, Hyndman et al. 1996) showing the difference in relative proportion (effect size) of minke whale activity states in the presence and absence of whalewatching boats, as a function of different probability threshold values used when assigning foraging activity (Figure 4). Observe that the distributions for all 3 activity states overlapped with zero.
Modeling approach

The proposed modeling approach was able to deal with autocorrelated multivariate behavioral information coming from different families of distributions. The model included a combination of both hidden and observed states and was able to account for heterogeneity in bout durations. By using this quantitative modeling approach, our model was not subject to the limitations and potential biases associated with visual classification of activity states (Marsh and Hanlon 2004), which allowed us to handle continuous time series data, which added realism to the model. A quantitative approach also makes comparative analysis between study areas and populations easier, by providing a consistent and objective way of defining and classifying activity states. Biological knowledge was still incorporated in the modeling approach, by playing an integral part when defining activity states, and thus informing the model. This way, the modeling approach was closely guided by biological relevance rather than being a pure statistical/mathematical approach.

Our modeling approach is in many ways similar to a hidden Markov model (Patterson et al. 2009; Langrock et al. 2012); however, because of the many complex attributes of the data, a stepwise approach was easier to implement. Patterson et al. (2009) highlights 2 major problems when using stepwise modeling approaches, where activity states are first classified before being related to covariates in a separate analysis. First, this approach does not take into consideration uncertainty in the activity state classification. We address this problem in the sensitivity analysis of this study, which demonstrates that altering the probability threshold values used when assigning foraging activity had little effect on the resulting activity budgets. Secondly, covariates in stepwise modeling approach are only able to affect the transition probability between activity states (the behavioral process) and not the classification of states per se (the behavioral expression) (Patterson et al. 2009). Although this study clearly shows that whalewatching boats can affect the behavioral process of minke whales, disturbance can also affect the expression of activity states (i.e., the density distribution of IBI), as shown in other studies (Lesage et al. 1999; Williams and Ashe 2007; Wirsing et al. 2007). To test this, we repeated our modeling framework, but instead of using a single mixture model for all the IBI data, separate mixture models were used for the control and impact data to classify dive types and consequently activity states. The resulting activity budgets showed no apparent difference from the original model (Supplementary Figure S2), thus providing support for the effect of whalewatching boat interactions on minke whales being on the behavioral process rather than the expression of behavior.

CONCLUSIONS

Methods that inform the links between short-term behavioral changes and long-term effects on individual vital rates in animals are urgently needed to help resolve the rapidly growing issue of nonconsumptive effects of human–wildlife interactions (Duftus and Dearden 1990; Bejder and Samuels 2003; Blanc et al. 2006; New et al. 2013). This study presents a novel modeling approach to quantitatively infer activity budgets from animal behavior, to inform the first necessary link between behavior and bioenergetics. Using this approach, we showed that interactions between whalewatching boats and minke whales affected the whales’ activity budgets. Our results show that whalewatching boat interactions reduced the amount of time minke whales spend feeding, potentially leading to a 42% decrease in energy intake during 1 h of interactions. This is the first time that the biological relevance of whalewatching behavioral disruptions has been shown for a mysticete species. However, these findings alone are not a cause for concern, as the effect must be seen in light of the overall exposure of individual minke whales to whalewatching boats through the feeding season. We now need to estimate individual exposure rates to whalewatching boats (Lusseau et al. 2012), to quantify the seasonal effect on activity budgets and link these changes to potential vital rate effects (New et al. 2013). This would provide a mechanism to understand how wildlife tourism can influence the conservation status of whales. Further, the impact data in this study comprise interactions of different durations (Bejder et al. 1999), distances to the whale (Richardson et al. 1985), number of whalewatching boats (Williams and Ashe 2007), and potentially varying boat behaviors (Williams et al. 2011). With all these factors having the propensity to influence the behavioral response of the targeted animals, future studies should aim to identify which of these factors are the main drivers behind the behavioral changes and focus management actions toward minimizing these effects. Finally, it would be worthwhile, although challenging, to also add the socioeconomic aspects of whalewatching into the picture and make a more comprehensive cost–benefit analysis of whalewatching effects on whale conservation.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.behavco.oxfordjournals.org/


