

ENERGY COST OF VESSEL DISTURBANCE TO KITTLITZ'S MURRELETS *BRACHYRAMPHUS BREVIROSTRIS*

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SUMMARY

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We evaluated the energy cost of vessel disturbance for individual Kittlitz's Murrelets *Brachyramphus brevirostris* in Glacier Bay National Park and Preserve in Alaska, USA. We used Monte Carlo simulations to model the daily energy expense associated with flight from vessels by both breeding and non-breeding birds and evaluated risk based on both the magnitude of costs incurred and the degree to which the costs may be chronic. We used two scenarios of vessel disturbance for average- and peak-vessel traffic. Because they are more likely to fly away from vessels, non-breeding birds had a greater increase in energy expenditure when disturbed (up to 30% increase under the average scenario and >50% increase under the peak scenario) than breeders (up to 10% and 30% increases under the average and peak scenarios, respectively). Likewise, non-breeding birds were more likely to experience chronic increases in energy expense (i.e. a greater percentage of days with an increase in energy expenditure) than breeding birds. Our modeling results indicated that breeding and non-breeding birds were both susceptible to fitness consequences (e.g. reduced reproductive success and survival) resulting from the energy cost.

Key words: vessel disturbance, energetics, Kittlitz's Murrelet, *Brachyramphus brevirostris*, Glacier Bay, Alaska

INTRODUCTION

The energetic cost to animals of human disturbance is often evaluated in order to assess the fitness consequences of disturbance within a management context. Energetic costs of disturbance may lead to physiological changes that reduce individual fitness. Indeed, studies have begun to demonstrate fitness consequences of disturbance for a variety of species (e.g. disturbance is inversely related to measures of reproductive success for Woodland Caribou *Rangifer tarandus caribou*: Harrington & Veitch 1992; Hawaiian Monk Seals *Monachus schauinslandi*: Gerrodette & Gilmartin 1990; Eastern Bluebirds *Sialia sialis*: Knight & Swaddle 2007; and California Sea Lions *Zalophus californianus*: French *et al.* 2011).

By virtue of their status, threatened and endangered species are continually evaluated for the potential impacts or fitness consequences of management actions. In many cases, the reasons for a species' decline or path toward successful recovery are largely unknown. Thus, a common dilemma in the management of threatened and endangered species is evaluating the risk of a biologically significant effect of a particular action in the face of uncertainty (Harwood 2000). Fitness consequences could affect vital rates, impart population effects and ultimately jeopardize the existence

of a threatened or endangered species (i.e. as conceptualized for acoustic disturbance by the Population Consequences of Acoustic Disturbance model; NRC 2005).

The Kittlitz's Murrelet *Brachyramphus brevirostris* is a small member of the auk family and is a candidate species for listing under the US Endangered Species Act of 1973 (16 USC, §§1531-43 [Supp. IV 1974]). The species has undergone declines in parts of its range over the past few decades (e.g. ≥ 85% decline in Glacier Bay, Piatt *et al.* 2011; upwards of 63% decline in Prince William Sound, Kuletz *et al.* 2011a; and 84% decline in Lower Cook Inlet and Kachemak Bay, Kuletz *et al.* 2011b), although declines may have tapered off in recent years. The causes of past decline and potential threats currently facing the species are not well known, but possible limiting factors include predation, reproductive failure, food limitation, climate change, fishing bycatch, oil spills and vessel disturbance (Day *et al.* 1999).

Because Kittlitz's Murrelets tend to associate with remote, glaciated regions of Alaska, vessel disturbance may be a localized problem. For example, tidewater glaciers in Glacier Bay National Park and Preserve (GBNPP) are a draw for tourists, and consequently vessel activity is highest near the glaciers. Tourists reach Glacier

Bay primarily by cruise ships, commercial tour boats and private recreational vessels. Kittlitz's Murrelets also prefer to forage in Glacier Bay near tidewater glaciers and the outflow of glacial streams (Piatt *et al.* 2011). Thus, vessel activity overlaps in space and time with the distribution of Kittlitz's Murrelets during their breeding season.

Previously, we quantified the response of birds to typical vessel traffic within Glacier Bay (Agness *et al.* 2008). This type of vessel disturbance can impose energetic costs that carry fitness consequences for marine wildlife (e.g. waterbirds: Schummer and Eddleman 2003; killer whales: Williams *et al.* 2006, Lusseau *et al.* 2009). Here we model the energy expense associated with flight from vessel disturbance by both breeding and non-breeding Kittlitz's Murrelets in GBNPP, and evaluate the risk of biologically significant consequences based on both the cost incurred and the degree to which the costs are a chronic condition. This study also has broader implications for the general need to identify and quantify the sub-lethal effects of various human disturbances on wildlife (Frid and Dill 2002).

METHODS

Model structure and parameters

We developed two models of Kittlitz's Murrelet energy costs for breeding (in the chick-rearing stage) and non-breeding birds (MATLAB, The MathWorks, Inc.) with parameters collected from observed data and published literature (Table 1, Figure 1, Appendix 1 available the Web site). The observed data were collected at seven sites (mean area 3.44 ± 0.52 km²; Agness *et al.* 2008) in GBNPP during summer months (41 days; 9–11 h • d⁻¹) when Kittlitz's Murrelets were breeding (i.e. actively rearing chicks, as inferred from fish-holder behavior observed at sea). We observed their behavior at sea with area-scan and focal-bird sampling techniques. We recorded vessels traveling through the study sites to estimate disturbance rates and also collected data on the vessel size and

speed as well as the birds' responses to the vessel activity (detailed methods in Agness *et al.* 2008).

Breeding birds were considered separately from non-breeding birds, because chick-rearing has a high energetic cost and because adults holding fish tend to dive rather than fly to avoid oncoming vessels (Agness *et al.* 2008). After successfully catching prey at sea for their offspring, murrelets hold a single fish cross-wise in the bill for later delivery to chicks (Carter & Sealy 1987, Strachan *et al.* 1995). From this behavior, we could determine whether murrelets were rearing chicks, i.e. were breeding birds (Speckman *et al.* 2003, Tranquilla *et al.* 2005). This does not mean we believe that all birds observed without fish were non-breeders, but for modeling purposes we assumed they were.

We focused on bird-flight energy because flight is energetically costly for *Brachyramphus* Murrelets (Pennycuik 1989, Elliot *et al.* 2004). Kittlitz's Murrelets spend most of their time swimming at or below the sea surface (Agness *et al.* 2008), so we assumed all flight was caused by vessel response.

We considered energy costs to birds explicitly by evaluating the percent of simulations in which the proportional change in energy resulted in increased energy expense, given different threshold levels, vessel scenarios and breeding status (Table 2, Figure 1). We simulated 10000 bird-days for each model using a Monte Carlo approach, where a bird day represented the daily energy expense of an average Kittlitz's Murrelet. Each iteration represented a new day, and we assumed that each day a single bird could be encountered by every vessel passing through the area. For each bird day, the rate of vessel traffic was randomly sampled from a discrete set of observations of the number of vessels per day. This method, also known as bootstrapping (Efron & Tibshirani 1994), does not require fitting a distribution to observations and therefore requires no assumptions about shape parameters. Each vessel was iterated through stochastic assignments to vessel categories and corresponding flight risks to birds. The occurrences of vessel

TABLE 1
Parameters used to develop breeding and non-breeding bird models

Model	Parameter			
	Static parameters ^a	Category	Probability of disturbance characteristic	Probability of flight
Breeding	Vessel speed	Fast / Medium	0.648	0.020
		Slow	0.352	See below "far at slow speed"
	Vessel approach distance	Far at slow speed	0.157	0.132
		Close at slow speed	0.843	0.000
Non-breeding	Vessel size	Cruise ship / Tour boat	0.219	0.656
		Small / Medium / Large recreational vessel	0.781	0.358
	Non-static parameters	Observed variable	Data source	Methods subsection^b
Both models	Vessel rate	Vessel rate	Agness <i>et al.</i> 2008	Vessel traffic scenarios
	Vessel flight energy	Flight time	Agness unpubl. data	Flight energy from vessels
	Daily energy expenditure	Kittlitz's Murrelet mass	Piatt unpubl. data	Daily energy expenditure

^a All static parameters were derived from field study by Agness *et al.* 2008.

^b Additional details about distribution-based parameters are located in the following subsections of Methods.

characteristics and bird-flight responses were modeled using binomial distributions with probabilities calculated from observed data (Table 1, Agness *et al.* 2008). Because flight response varied with vessel factors such as speed, size and approach distance, we included these factors explicitly in the model to predict the probability of flight (Table 1). Note that breeding birds and non-breeding birds exhibited different responses to vessels, and the model incorporates those differences. Breeding birds were much more likely to dive underwater, and vessel speed and distance were the important factors affecting the outcome (Agness *et al.* 2008). Non-breeding birds were much more likely to take flight from approaching vessels, and the overriding factor was vessel size, not distance or speed (Table 1, Figure 1).

Flight energy from vessels

We obtained additional data and made several assumptions in order to calculate flight power. Morphological data for the Kittlitz's Murrelet (J. Piatt unpublished data) and derivation of an allometric ratio from a related species (Elliott *et al.* 2004) were used to estimate wing span and wing area (Agness 2006). Assumptions used to calculate flight power were (1) constant flight altitude (a simplifying assumption in the absence of data), (2) mass increase of 10 g for breeding Kittlitz's Murrelets to account for the additional weight of fish carried (~7g fish weight, based on 100mm length forage fish caught by trawl; Robards *et al.* 2003) and an additional increase in weight (3g) to account for the unknown effects of

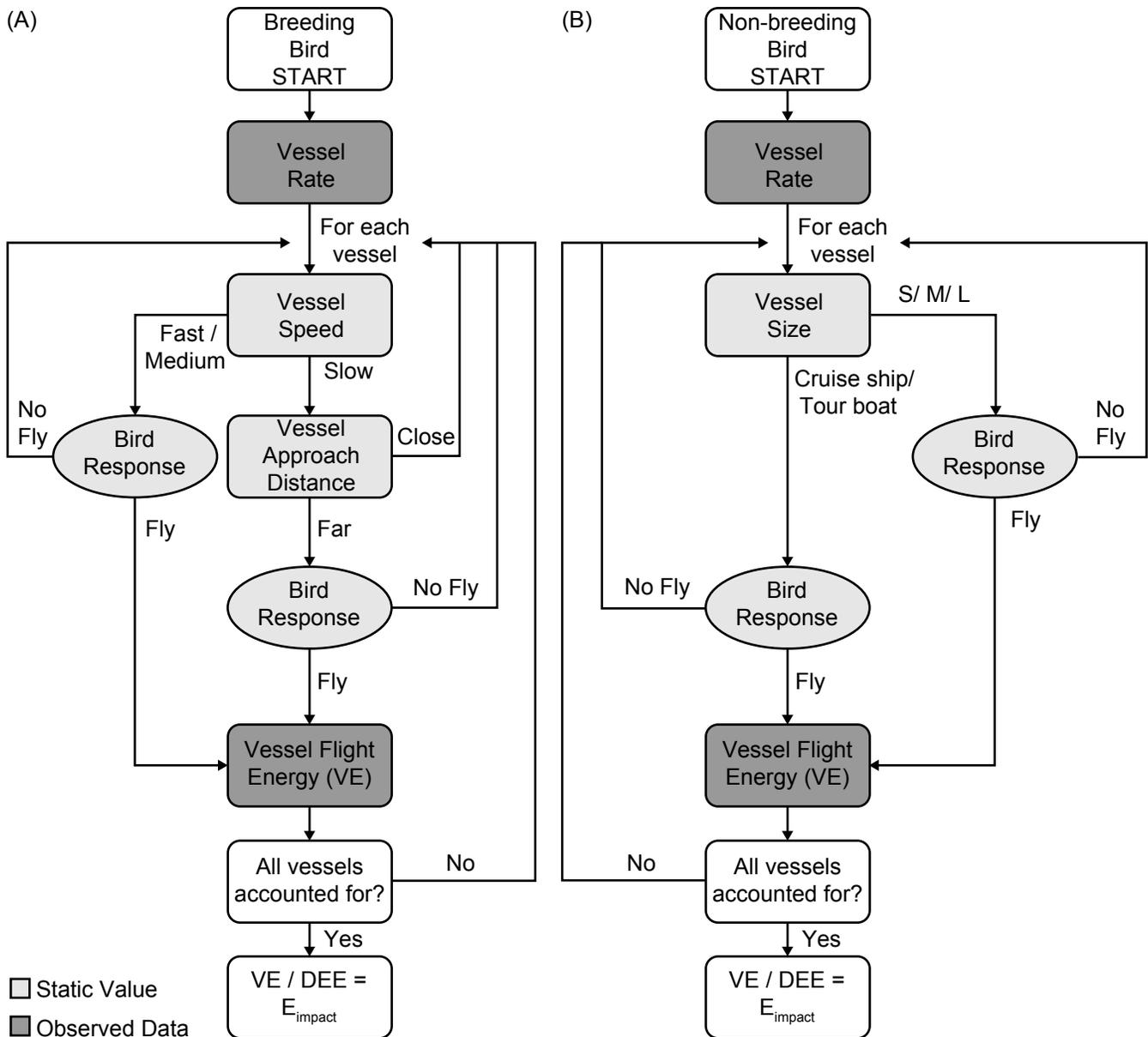


Fig. 1. Schematic diagrams of the model structures for the (A) breeding bird and (B) non-breeding bird simulations.

TABLE 2
Prediction of increased energy costs incurred
by an average Kittlitz's Murrelet

Model	Vessel traffic scenario	Magnitude of energy increase (%); % days (n = 10 000) increases occurred			
		>0%	>10%	>30%	>50%
Non-breeding	Average	85.8	2.1	0.0	0.0
	Peak	100.0	100.0	95.7	15.9
Breeding	Average	25.6	0.0	0.0	0.0
	Peak	98.8	10.2	0.0	0.0

frontal drag caused by the fish held cross-wise in the bill, and (3) flight speed of "maximum range speed" (speed that maximizes the distance travelled per unit of energy expended; Pennycuik 1989, as described in Agness 2006).

We used the aerodynamic flight performance model (Pennycuik 1989, Flight, version 1.15) to calculate the power of Kittlitz's Murrelet flight using two scenarios: breeding murrelets flying at low altitude (5 m, breeders flight from vessels), and non-breeding murrelets flying at low altitude (5 m, non-breeders flight from vessels). The power that corresponded with maximum range speed on power curves was 50.04 kJ/h for breeding murrelets and 47.16 kJ/h for non-breeding murrelets.

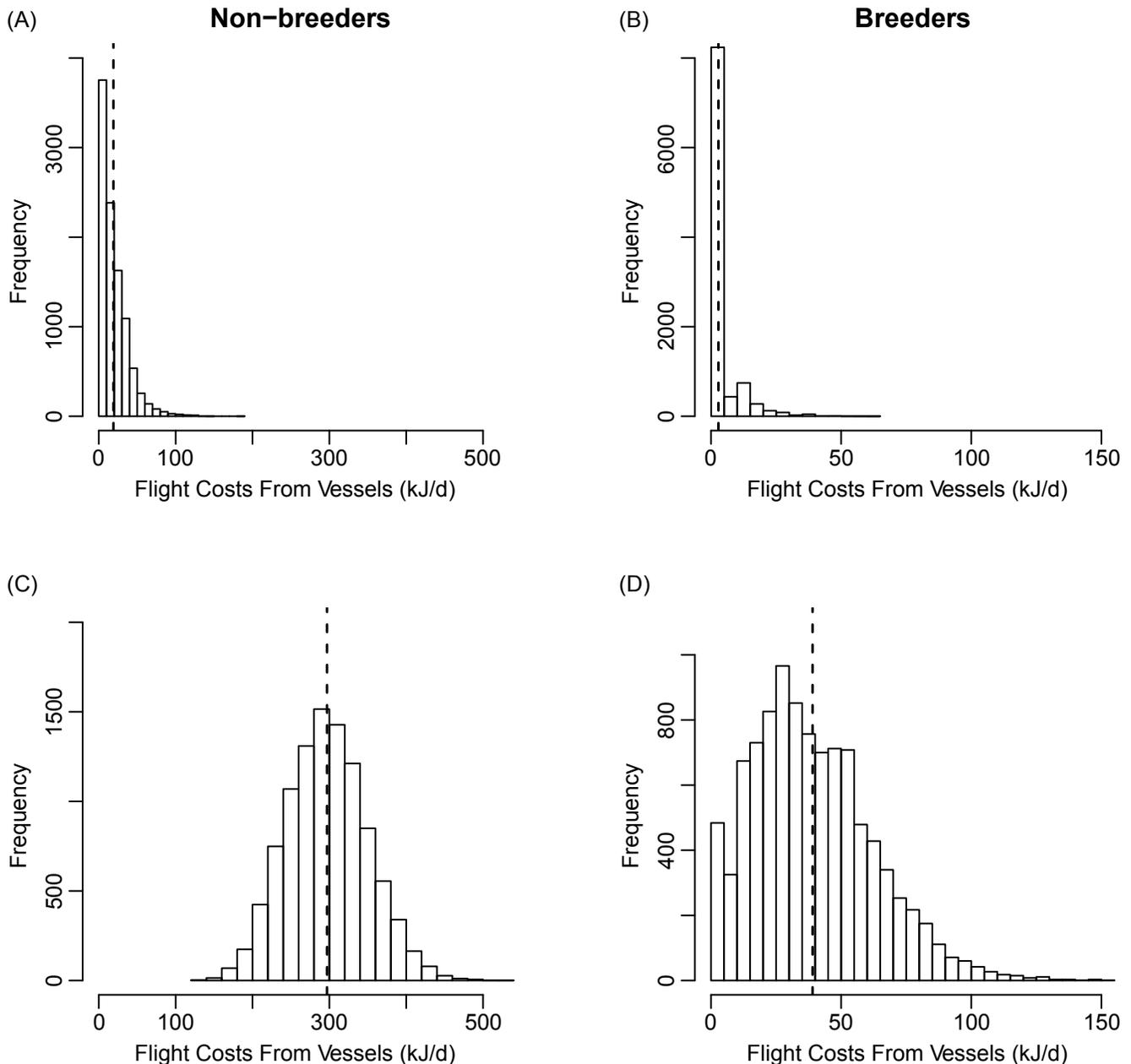


Fig. 2. Model simulations of energy costs of flight from vessels for (A) non-breeding birds under average vessel traffic; (B) breeding birds under average vessel traffic; (C) non-breeding birds under peak vessel traffic; and (D) breeding birds under peak vessel traffic.

We calculated the energy costs for birds disturbed by vessels by sampling with replacement from direct observations ($n = 101$ of flight times for individual Kittlitz's Murrelets). Mean flight time was $67 \pm \text{SE } 4 \text{ s}$ (A. Agness unpublished data). These observations were conducted from land-based viewing stations and are underestimates of flight time, because flight could only be recorded while the bird in flight remained within the observer's field of view, and most of the observations were not complete (i.e. birds kept flying beyond the observer's field of view for an unknown period of time). The set of observations represent opportunistic focal sampling of randomly selected birds during vessel events. When flight from a vessel occurred in our simulations, the randomly sampled flight time was multiplied by the respective energy value to estimate energy consumed such that:

$$E_{fv} = t_f P_i$$

where E_{fv} is the energy cost of the flight, t_f is the length of the flight in hours and P_i is the power required for that flight depending on whether the bird is breeding.

Daily energy expenditure

We used the following equations to estimate basal metabolic rate (BMR) and field metabolic rate (FMR) of Kittlitz's Murrelets (for details, see Appendix 2 available on the Web site):

$$\text{BMR} = (2.3 \cdot M^{0.774} \pm 26.0) \cdot 1.18 \text{ (Bryant \& Furness 1995)}$$

$$\text{FMR} = 3.78 \cdot \text{BMR} \text{ (Birt-Friesen et al. 1989)}$$

Vessel traffic scenarios

We developed two scenarios to evaluate the energy expense of a Kittlitz's Murrelet for days with average and peak vessel traffic. The scenarios were evaluated for the energy expense of breeding and non-breeding birds using a Monte Carlo approach. We randomly sampled with replacement from the set of observations of vessel traffic rate per day ($n = 42 \text{ d}$; Agness *et al.* 2008) and randomly sampled from this distribution to assign a representative vessel rate for the day. We then generated each vessel's characteristics (size, speed or approach distance) using binomial distributions with probabilities observed from field data (Agness *et al.* 2008). We simulated peak vessel traffic based on 2004 vessel quotas established by GBNPP management, in which up to 36 vessels (two cruise ships, nine large tour boats and 25 private recreational motor vessels) were permitted to enter the waters of GBNPP each day during the summer season. We assumed all 36 vessels could potentially disturb a Kittlitz's Murrelet twice (72 disturbances) by traveling into and out of glaciated fjords frequented by Kittlitz's Murrelets in Glacier Bay (Piatt *et al.* 2010).

Evaluating biological significance

We compared the mean energy costs of each scenario using two sample t -tests. We also qualitatively evaluated the biological significance of the increase in energy expense using two parameters: (1) the magnitude of increase in energy expense under the two vessel scenarios and (2) the degree to which increased energy expense was a chronic condition for individuals. We evaluated these parameters by calculating the percentage of bird days (out of 10000 simulated days) that resulted in energy increases of a range of magnitudes

(from $>0\%$ to $>50\%$ increase in daily energy expenditure). We also translated the magnitude of increase in energy expense into a biologically meaningful currency of the birds' prey consumption, i.e. numbers of forage fish.

Sensitivity analysis

In order to test the sensitivity of our model to our chosen parameters, we performed two forms of sensitivity analyses (Hamby 1994). For static parameters, an individual parameter perturbation analysis was completed. We ran simulations with a 10% increase in each parameter value singly and calculated the difference in the mean energy expenditure, given each parameter value (Kitchell *et al.* 1977). Sensitivity was then calculated as follows:

$$\text{Sensitivity} = \frac{F(x + 0.1x) \cdot F(x)}{0.1 \cdot F(x)}$$

where $F(x)$ is the mean energy used under the original parameter estimate x and $F(x + 0.1x)$ is the result under a 10% increase in the parameter value. Sensitivity values of 1 indicated a one-to-one relationship with the parameter and mean energy expenditure. Therefore, values either much less than or much greater than 1 indicated low or high sensitivity, respectively.

We used bootstrapping to explore the sensitivity of the models to vessel rate and flight duration. For each model, we iterated through all possible vessel rates (1 to 72) and all possible flight times (1 to 253) 10000 times to generate a distribution of flight costs possible for each vessel rate and flight time. We then regressed these values against vessel rate or flight time, fixing the intercept at 0, to obtain a regression coefficient that we interpreted similarly to the sensitivity values from individual parameter perturbation.

RESULTS

Both breeding and non-breeding Kittlitz's Murrelets increased energy expenditure in response to vessel scenarios. Both breeding and non-breeding Kittlitz's Murrelets exerted more energy under peak-traffic scenarios (mean energy expended $39.0 \pm \text{SE } 0.23 \text{ kJ/d}$ for breeding birds and $297 \pm \text{SE } 0.52 \text{ kJ/d}$ for non-breeding birds) than under average vessel traffic (mean expended $2.8 \pm \text{SE } 0.1 \text{ kJ/d}$, $t = 150.2$, $P < 0.001$ for breeding birds and $19.1 \pm \text{SE } 0.19 \text{ kJ/d}$, $t = 497.7$, $P < 0.001$ for non-breeding birds; Fig. 2). Non-breeders exerted more energy than breeders in response to vessels for both scenarios ($t = -83.0$, $P < 0.001$ and $t = 448.26$, $P < 0.001$).

The magnitude of energy increase and the degree to which that increase was chronic varied by vessel scenario and whether birds were breeders or non-breeders (Table 2). The increase in energy expenditure was greater for non-breeders (up to 30% increase under the average scenario and $\geq 50\%$ increase under the peak scenario) than for breeders (up to 10% and up to 30% under the average and peak scenarios, respectively) under both vessel scenarios. Likewise, non-breeding birds were subject to more chronic increases in energy expense (i.e. a greater percentage of days in which the energy increase is likely to occur) than breeding birds, with both the most chronic and highest magnitude increases incurred by non-breeding birds under the peak-traffic scenario.

Magnitude of energy increase translated into a range of additional prey requirements for individual birds. On average, one forage fish weighs $\sim 7 \text{ g}$ (Robards *et al.* 2003, from mid-water trawls in Glacier

Bay) and has an energy density of 5.2 kJ/g wet mass (Pacific Sandlance *Ammodytes hexapterus*, Anthony *et al.* 2000). One Pacific Sandlance represents 27.67 kJ, assuming an assimilation efficiency of 76% (used in other studies of Marbled Murrelets *Brachyramphus marmoratus* and Cassin's Auklets *Ptychoramphus aleuticus*, i.e. Hull *et al.* 2001, Montevicchi & Piatt 1984, Hodum *et al.* 1998). Therefore, one sandlance represents 4% of a Kittlitz's Murrelet's daily energy expense ($27.67/700.0 \text{ kJ} = 0.04$), and the percentage increase in energy requirement (0, 10, 30 and 50) translates directly to the currency of forage fish (approximately 0, 3, 8 and 13 fish, respectively).

Sensitivity analysis of static parameters in our models revealed some sensitivity to parameters associated with vessel characteristics, and less sensitivity to the probability of flight in response to vessels (Table 3). Total flight costs from vessels and flight cost per hour exhibited a one-to-one relationship in the non-breeding bird model. Vessel rate was most influential in this model; a one-vessel increase in vessel rate was associated with an average increase in total energy costs of 3.99 kJ (Table 4). In the breeding bird model, outputs were most sensitive to the probability of a slow vessel with a close approach distance. This was an inverse relationship, with higher probability leading to lower total vessel flight costs. Flight time from vessel disturbances had greater impact in the non-breeding bird model than in the model for breeders.

DISCUSSION

We have demonstrated that breeding birds incur small increases in energy expense (<10%) under average vessel conditions, but, nonetheless, these small incremental increases in energy could have significant biological consequences. Chick-rearing has been documented as an energetically expensive life stage for birds in general, and birds may perform at or near maximum levels possible (i.e. Drent & Daan 1980). Additional energy demands above the usual demands for breeding birds could cause energetic stress or energy requirements beyond their capacity to replace (Golet *et al.* 2004, Daan *et al.* 1996). Chick-rearing for Kittlitz's Murrelets takes approximately 25 days (Agness 2006), and additional energy expense incurred during this period could be significant for individuals near the limits of their work capacity (Wikelski & Cook 2006). We believe that among all the fish-eating Alcidae, Kittlitz's Murrelets are likely to have a relatively small capacity to buffer extra energy demands because their small size and high mass-specific metabolic demand may place them "on the edge" of their physiological capacity.

To put these costs in perspective, our analysis suggests that, without vessel disturbance, Kittlitz's Murrelets need to eat about 76% of their body mass in sandlance daily (or 25 fish). This is probably

TABLE 4
Sensitivity values for non-static parameters

Model	Variable	Regression coefficient	P value
Non-breeding	Vessel rate	4.02	<0.001
	Flight time	0.01	<0.001
Breeding	Vessel rate	0.60	<0.001
	Flight time	0.29	<0.001

the highest mass-specific demand of any fish-eating alcid. By comparison, the Common Murre needs to consume only about 45%–55% of its body mass in sandlance daily. Breeding Kittlitz's Murrelets experiencing average vessel disturbance need to consume up to 83% of their body mass (or 28 fish), while non-breeding birds under the peak disturbance scenario need to acquire an average of 107% of their body mass in fish daily (or 36 fish).

Acquisition of these extra fish has its own cost associated with it for searching, diving, capture and digestion (although these costs are likely minor by comparison to flight costs). The additional time and energy spent foraging for those fish could reduce time available for traveling to the nest and therefore potentially compromise chick success (i.e. growth and survival). In addition, breeders that usually dive to avoid oncoming vessels (Agness *et al.* 2008) may experience negative consequences. Sometimes diving birds eat the fish they have been holding (to avoid loss), or they accidentally drop it during the diving escape (Speckman *et al.* 2004). Either way, if diving results in a lost chick meal it could affect the growth or survival of the chick or impair survival of the adult bird who must again expend energy to catch another fish.

Furthermore, the nesting strategy of Kittlitz's Murrelets and their flight commute costs to and from the nest are almost certain to be more energy-intensive than the flight costs of seabird species that informed our estimate of FMR (i.e. seabirds in Table 1 of Birt-Friesen *et al.* 1989 generally nest along the shore or on islands at sea). As such, daily energy costs to breeding Kittlitz's Murrelets are likely even higher than we estimated here. By demonstration, we estimate that Kittlitz's Murrelets spend 0.003–0.80 h in flight during one-way trips to inland nests, with a flight speed of 94 km/h and distance traveled inland from shore of nests ranging from 0.3–75 km, mean $18.28 \pm 4.89 \text{ SE km}$ ($n = 14$ nests; Day

TABLE 3
Sensitivity values for static parameters

Model	Variable	Sensitivity ^a
Non-breeding	Probability of cruise ship or tour boat	0.21
	Probability of flight from cruise ship or tour boat	0.11
	Probability of flight from small, medium or large vessel	0.66
	Flight cost per hour, from vessels	1.01
Breeding	Probability of medium or fast vessel	-0.41
	Probability of flight from fast or medium vessel	0.13
	Probability of a slow vessel with close approach distance	-4.89
	Probability of a flight from a slow vessel with far approach distance	0.62
	Flight cost per hour, from vessels	0.78

^a Value of 1 indicates a one-to-one relationship between the parameter and mean flight cost from vessels, and values much less than or much greater than 1 indicate low or high sensitivity, respectively.

et al. 1983, Day 1995, Day *et al.* 1999). Given that Kittlitz's Murrelets provision the chick four to six times daily and both adults share this task equally (Naslund *et al.* 1994, Day *et al.* 1999), a bird could spend close to 5 h in flight each day commuting to and from their nest during chick rearing ($0.8 \text{ h} \cdot 2 = 1.6 \text{ h}$ per round trip and $1.6 \text{ h} \cdot 3 \text{ round trips} = 4.8 \text{ h}$). These high costs support the idea that Kittlitz's Murrelets may be "on the edge" with respect to their physiological capacity.

Non-breeding birds, on the other hand, have more flexibility in their activity budgets than breeders (e.g. based on the considerable time spent loafing on the water, Agness *et al.* 2008). Under average vessel conditions, we found that non-breeders incurred small (<10%) increases in energy most of the time and rarely incurred larger (>30%) increases. They can likely compensate for such increases occasionally (i.e. capturing up to three additional fish with little loss to fitness). However, it is questionable and unknown whether they can cope with small additional costs if a chronic (almost daily) condition prevails, as was predicted under both average- (86%) and peak-traffic (100%) scenarios.

Sensitivity analyses indicated that our model outputs were most influenced by vessel rates and, for breeding birds only, by the proportion of slow vessels that led to bird responses at far distances (400–1000 m). Other vessel characteristics or flight probabilities did not severely impact vessel flight costs to birds. Therefore, our models should be robust even if additional parameter uncertainty exists. Our conclusions about energetic impacts to birds depend on the vessel rates and characteristics observed during our field study. If these characteristics or vessel rates no longer represented average conditions, our model results would need to be updated. Additional monitoring of vessel traffic throughout Glacier Bay would increase sampling to support vessel-rate estimates and ensure that our average-traffic scenario was realistic.

Our Monte Carlo method incorporated uncertainty through stochasticity in parameters and bird behavioral responses, but we concede that model-structure uncertainty may exist. We may have overlooked important components of bird-energy expenditure. For example, excluding the cost of diving in response to vessel disturbance may underestimate the energy expense. Although only a few measurements of the diving patterns of small alcids have been made and estimates of the energy costs of diving were restricted to biomechanical models (Watanuki *et al.* 2006, Harding *et al.* 2009, Lovvorn 2010), flight is almost certainly the most costly activity for murrelets at sea (i.e. Lovvorn & Jones 1994).

Direct measurements of metrics underlying our estimate of daily energy expenditure would improve the accuracy of our impact assessment. For example, an estimate would be improved by incorporating natural variation in daily energy expenditure, such as variation in energy efficiency or feeding rates (fish per day). Similarly, additional mass measurements for Kittlitz's Murrelets would increase the sample distribution supporting estimates of BMR.

Our peak vessel-traffic scenario represents an extreme case of Kittlitz's Murrelet exposure to vessel traffic, given the daily quota for GBNPP. The scenario for an average day of vessel traffic provides a more realistic picture of the daily conditions in localized areas of GBNPP. However, the peak-traffic scenario does provide a measure of the increased impact of high levels of traffic on Kittlitz's

Murrelets (i.e. chronic energy increases >13 additional fish for non-breeders and >3 additional fish for breeders), which may help to guide future vessel-management decisions. Certainly, if vessel quotas are increased substantially, there is greater likelihood that average-traffic conditions would more closely resemble peak-traffic conditions represented in this study.

More research on Kittlitz's Murrelets and their interactions with vessels would help evaluate the possible effects of additional vessel management. For example, a study addressing movement of radio-tagged Kittlitz's Murrelets could better characterize their duration of flight response from vessel disturbances. Values for flight times used in our study represented minimum estimates, because observations ceased when a bird flew out of the direct view of the observer. Evaluating time budgets of birds could improve our understanding of the potential flexibility in energy expenditure (e.g. Ronconi and Burger 2008), build on the model framework used here and allow for more comprehensive energetic modeling.

In many cases, human disturbance is not seen to directly affect species fitness (e.g. direct mortality or reproductive failure) but may still cause fitness consequences indirectly. As our study suggests, increasing vessel disturbance means that birds need to locate and capture additional prey, and this could compromise their energy budgets, potentially leading to effects on reproduction, growth or survival. These outcomes need to be considered in the light of possible interactions with natural environmental variation (e.g. weather). Determining the connection between chronic stressors and the fitness of bird populations is necessary to increase the effectiveness of conservation and management strategies.

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REFERENCES

- AGNESS, A.M. 2006. Effects and impacts of vessel activity on the Kittlitz's Murrelet (*Brachyramphus brevirostris*) in Glacier Bay, Alaska. Master's Thesis University of Washington, Seattle, WA, USA. p. 135.
- AGNESS, A.M., PIATT, J.F., HA, J.C. & VANBLARICOM, G.R. 2008. Effects of vessel activity on the near-shore ecology of Kittlitz's Murrelets (*Brachyramphus brevirostris*) in Glacier Bay, Alaska. *Auk* 125: 346–353.
- ANTHONY, J.A., ROBY, D.D. & TURCO, K.R. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology* 248: 53–78.

- BIRT-FRIESEN, V.L., MONTEVECCHI, W.A., CAIRNS, D.K. & MACKO, S.A. 1989. Activity specific metabolic rates of free-living Northern Gannets and other seabirds. *Ecology* 70: 357–367.
- BRYANT, D.M. & FURNESS, R.W. 1995. Basal metabolic rates of North Atlantic seabirds. *Ibis* 137: 219–226.
- CAIRNS, D. K., MONTEVECCHI, W.A., BIRT-FRIESEN, V.L. & MACKO, S.A. 1989. Energy expenditures, activity budgets, and prey harvest of breeding Common Murres. *Studies in Avian Biology* 14: 84–92.
- CARTER, H.R. & SEALY, S.G. 1987. Fish-holding behavior of Marbled Murrelets. *Wilson Bulletin* 99: 289–291.
- COULSON, T., BENTON, T.G., LUNDBURG, P., DALL, S.R.X., KENDALL, B.E. & GAILLARD, J.M. 2006. Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 273: 547–555.
- DAAN, S., DEERENBERG, C. & DIJKSTRA, C. 1996. Increased daily work precipitates natural death in the Kestrel. *Journal of Animal Ecology* 65: 539–544.
- DAY, R.H., KULETZ, K.J. & NIGRO, D.A. 1999. Kittlitz's Murrelet (*Brachyramphus brevirostris*). In Poole, A. and Gill, F. (Eds). *The Birds of North America*, No. 435. Philadelphia: The Birds of North America, Inc.
- DAY, R.H., PRICHARD, A.K. & NIGRO, D.A. 2003. Ecological specialization and overlap of *Brachyramphus* murrelets in Prince William Sound, Alaska. *Auk* 120: 680–699.
- DAY, R.H., OAKLEY, K.L. & DARNARD, D.R. 1983. Nest sites and eggs of Kittlitz's and Marbled Murrelets. *Condor* 85: 265–273.
- DAY, R.H. 1995. New information on Kittlitz's Murrelet nests. *Condor* 97: 271–273.
- DAY, R.H. 2011. Evaluating population trends of Kittlitz's Murrelets in Alaska. Juneau, AK: Alaska Biological Research, Inc., for the Alaska Department of Fish and Game.
- DRENT, R.H. & DANN, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225–252.
- EFRON, B. & TIBSHIRANI, R.J. 1994. Introduction to the Bootstrap (Monographs on Statistics & Applied Probability, vol 57). Chapman and Hall.
- ELLIOT, K.H., HEWETT, M., KAISER, G.W. & BLAKE, R.W. 2004. Flight energetics of the Marbled Murrelet, *Brachyramphus marmoratus*. *Canadian Journal of Zoology* 82: 644–652.
- ELLIOTT, K.H. & GASTON, A.J. 2005. Flight speeds of two seabirds: a test of Norberg's Hypothesis. *Ibis* 147: 783–789.
- FRENCH, S.S., GONZÁLEZ-SUÁREZ, M., YOUNG, J.K., DURHAM, S. & GERBER, L.R. 2011. Human disturbance influences reproductive success and growth rate in California Sea Lions (*Zalophus californianus*). *PLoS ONE* 6: e17686. doi:10.1371/journal.pone.0017686
- FRID, A. & DILL, L. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6: 11.
- GABRIELSEN, G.W., MEHLUM, F. & NAGY, K.A. 1987. Daily energy expenditure and energy utilization of free-ranging black-legged kittiwakes. *Condor* 89: 126–132.
- GABRIELSEN, G.W. 1994. Energy expenditure in Arctic seabirds. Ph.D. Thesis, University of Tromsø, Norway.
- GABRIELSEN, G.W. 1996. Energy expenditure of breeding common murres. *Occasional Papers of the Canadian Wildlife Service* 91: 49–58.
- GERRODETTE, T. & GILMARTIN, W.G. 1990. Demographic consequences of changed pupping and hauling sites of the Hawaiian Monk Seal. *Conservation Biology* 4: 423–430.
- GOLET, G.H., SCHMUTZ, J.A., IRONS, D.B. & ESTES, J.A. 2004. Determinants of reproductive costs in the long-lived Black-Legged Kittiwake: A multiyear experiment. *Ecological Monographs* 74: 353–372.
- HAMBY, D.M. 1994. A review of techniques for parameter sensitivity analysis of environmental models. *Environmental Monitoring and Assessment* 32: 135–154.
- HARDING, A.M.H., EGEVANG, C., WALKUSZ, W., MERKEL, F., BLANC, S. & GREMILLET, D. 2009. Estimating prey capture rates of a planktivorous seabird, the Little Auk (*Alle alle*), using diet, diving behaviour, and energy consumption. *Polar Biology* 32: 785–796.
- HARRINGTON, F.H. & VEITCH, A.M. 1992. Calving success of woodland caribou exposed to low-level jet fighter overflights. *Arctic* 45: 213–218.
- HARWOOD, J. 2000. Risk assessment and decision analysis in conservation. *Biological Conservation* 95: 219–226.
- HULL, C.L., KAISER, G.W., LOUGHEED, C., LOUGHEED, L., BOYD, S. & COOKE, F. 2001. Intraspecific variation in commuting distance of Marbled Murrelet (*Brachyramphus brevirostris*): Ecological and energetic consequences of nesting further inland. *Auk* 118: 1036–1046.
- HODUM, P.J., SYDEMAN, W.J., HENKVISSER, G. & WEATHERS, W.W. 1998. Energy expenditure and food requirement of Cassin's Auklet provisioning nestlings. *Condor* 100: 546–550.
- KISSLING, M.L., LUKACS, P.M., LEWIS, S.B., GENDE, S.M., KULETZ, K.J., HATCH, N.R., SCHOEN, S.K. & OEHLERS, S. 2011. Distribution and abundance of the Kittlitz's Murrelet in selected areas of southeastern Alaska. *Marine Ornithology* 39: 3–11.
- KITCHELL, J.F., STEWART, D.J. & WEININGER, D. 1977. Applications of a Bioenergetics Model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* 34: 1910–1921.
- KIGHT, C.R. & SWADDLE, J.P. 2007. Associations of anthropogenic activity and disturbance with fitness metrics of eastern bluebirds (*Sialia sialis*). *Biological Conservation* 138: 189–197.
- KULETZ, K.J., NATIONS, C.S., MANLY, B., ALLYN, A., IRONS, D.B. & MCKNIGHT, A. 2011. Distribution, abundance, and population trends of the Kittlitz's Murrelet *Brachyramphus brevirostris* in Prince William Sound, Alaska. *Marine Ornithology* 39: 97–109.
- KULETZ, K.J., SPECKMAN, S.G., PIATT, J.F. & LABUNSKI, E.A. 2011. Distribution, population status and trends of Kittlitz's Murrelet *Brachyramphus brevirostris* in Lower Cook Inlet and Kachemak Bay, Alaska. *Marine Ornithology* 39: 85–95.
- LINNELL, J.D., SWENSON, C.J.E., ANDERSEN, R. & BARNES, B. 2000. How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin* 28: 400–413.
- LOVVORN, J.R. & JONES, D.R. 1994. Biomechanical conflicts between diving and aerial flight in estuarine birds. *Estuaries* 17: 62–75.
- LOVVORN, J. R. 2010. Modeling profitability for the smallest marine endotherms: auklets foraging within pelagic prey patches. *Aquatic Biology* 8: 203–219.
- LUSSEAU, D., D.E. BAIN, R. WILLIAMS J.C. SMITH. 2009. Vessel traffic disrupts the foraging behavior of southern resident killer whales (*Orcinus orca*). *Endangered Species Research* 6: 211–221.
- MEHLUM, F., GABRIELSEN, G.W. & NAGY, K.A. 1993. Energy expenditure by black guillemots (*Cepphus grylle*) during chick-rearing. *Colonial Waterbirds* 16: 45–52.

- MONTEVECCHI, W.A. & PIATT, J.F. 1984. Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. *Comparative Biochemical Physiology A* 78: 15–20.
- NASLUND, N.L., PIATT, J.F. & VAN PELT, T. 1994. Breeding behavior and nest site fidelity of Kittlitz's Murrelet. Abstracts of Pacific Seabird Group meeting, 26–29 January 1994, Sacramento, CA. pp. 33–34
- NRC (NATIONAL RESEARCH COUNCIL). 2005. Marine mammal populations and ocean noise: determining when noise causes biologically significant effects. Washington, DC: The National Academies Press. p. 145.
- PENNYCUICK, C.J. 1989. Bird flight performance: A practical calculation manual. New York: Oxford University Press.
- PIATT, J.F., ARIMITSU, M., DREW, G., MADISON, E.N., BODKIN, J. & ROMANO, M.D. 2011. Status and trend of the Kittlitz's Murrelet *Brachyramphus brevirostris* in Glacier Bay, Alaska. *Marine Ornithology* 39: 65–75.
- ROBARDS, M., DREW, G., PIATT, J., ANSON, J., ABOOKIRE, A., BODKIN, J., HOOGIE, P. & SPECKMAN, S. 2003. Ecology of selected marine communities in Glacier Bay: Zooplankton, forage fish, seabirds and marine mammals. Anchorage, AK: USGS Alaska Science Center, Biological Science Office.
- ROGERS, D.L., PIERSMA, T. & C.J. HASSELL. 2006. Roost availability may constrain shorebird distribution: Exploring the energetic costs of roosting and disturbance around a tropical bay. *Biological Conservation* 133: 225–235.
- RONCONI, R.A. & BURGER, A.E.. 2008. Limited foraging flexibility: increased foraging effort by a marine predator does not buffer against scarce prey. *Marine Ecology Progress Series* 366: 245–258.
- SPECKMAN, S.G., PIATT, J.F. & SPRINGER, A.M. 2003. Deciphering the social structure of marbled murrelets from behavioral observations at sea. *Waterbirds* 26: 266–274.
- SCHUMMER, M.L. & EDDLEMAN, W.R. 2003. Effects of disturbance on activity and energy budgets of migrating waterbirds in south-central Oklahoma. *Journal of Wildlife Management* 67: 789–795.
- STRACHAN, G., MCALLISTER, M. & RALPH, C.J. 1995. Marbled Murrelet at-sea and foraging behavior. In: Ralph, C.J., Hunt, Jr., G.L., Raphael, M.G. & Piatt, J.F. (Eds.) Ecology and conservation of the Marbled Murrelet. General Technical Report PSW-152. Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station. pp. 247–253.
- TRANQUILLA, L.M., PARKER, N.R., BRADLEY, R.W., LANK, D.B., KREBS, E.A., LOUGHEED, L. & LOUGHEED, C. 2005. Breeding chronology of Marbled Murrelets varies between coastal and inshore sites in southern British Columbia. *Journal of Field Ornithology* 76: 357–367.
- WATANUKI, Y., WANLESS, S., HARRIS, M., MIYAZAKI, M., LOVVORN, J.R., TANAKA, H. & SATO, K. 2006. Regulation of stroke patterns in wing-propelled divers: a comparison among alcids and a penguin. *Journal of Experimental Biology* 209: 1217–1230.
- WHITE, JR., D., KENDALL, K.C. & PICTON, H.D. 1999. Potential energetic effects of mountain climbers on foraging grizzly bears. *Wildlife Society Bulletin* 27: 146–151.
- WIKELSKI, M. & COOK, S.J. 2006. Conservation physiology. *Trends in Ecology and Evolution* 21: 38–46.
- WILLIAMS, R., LUSSEAU, D. & HAMMOND, P.S. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation* 133: 301–311.

