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The Long-term Consequences of Short-term Responses to Disturbance Experiences from Whalewatching Impact Assessment

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Studies often use behavioral responses to detect the impact of given disturbances on animals. However, the observation of these short-term responses can often lead to contradicting results. Here we describe studies focusing on the impacts of whalewatching to show how the biological relevance of short-term responses can be inferred from contextual information. They showed that short-term behavioral responses could have long-term consequences for individuals and their populations using information about variation in response magnitude with exposure levels, long-term population biology data, and multiple response variables. They showed that the added energetic constraints of the responses can impair life functions and lead to influences on vital rates with the potential to affect population viability. Individuals will manage disturbances as another ecological variable and will assess its costs in relation to other energetic trade-offs associated with the occupancy of the habitat in which the disturbance takes place. This can lead to rapid shift in tactics to cope with the disturbance, such as shift from short-term avoidance tactics to long-term habitat abandonment. When individuals cannot elude proximity to the disturbance, their fitness is reduced as observed through reduced reproductive success. These studies provide mechanisms to inform the US National Research Councils' Population Consequences of Acoustic Disturbance framework in which the influence of noise impact of on marine mammal conservation can be studied.

Many studies are now highlighting that what we perceive as short-term responses to disturbances can have unforeseen consequences for the life history of individuals exposed to those disturbances and the dynamics of their populations (Coltman et al., 2003; Cooke & Schramm, 2007; Lusseau, Lusseau, Bejder & Williams, 2006a; Proaktor, Coulson, & Milner-Gulland, 2007). These consequences can occur at an ecological scale with for example added energetic constraints from the responses influencing the homeostasis of individuals. They can also occur at an evolutionary scale. For example, selective harvesting can influence the genetic make-up of populations by selectively removing individuals with similar traits that are highly heritable (Coltman et al., 2003). These impacts influence the viability of populations, either by decreasing their fitness or by decoupling the populations from the environment in which they evolve because disturbances become a driving force for the life history of individuals at either of the temporal scales.

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In excess of 700 to 1000 cetacean populations routinely interact with tour boats (Hoyt, 2001). The potential impact of interactions between cetaceans and tourist vessels has been studied for more than 20 years (Baker & Herman, 1989; Corkeron, 2004). Over this period a wide variety of short-term effects has been detected on many species (Au & Green, 2000; Bejder, Dawson, & Harraway, 1999; Blane & Jaakson, 1995; Hastie, Wilson, Tufft & Thompson, 2003; Lusseau, 2006; Nowacek, Wells, & Solow, 2001; Williams, Trites, & Bain, 2002). These include changes in respiration patterns, variation in path directedness and other short-term behavioral alterations resulting from apparent horizontal and vertical avoidance tactics (Frid & Dill, 2002). However, it has been difficult to move from the description of short-term changes, which sometime appeared contradictory, to a more comprehensive understanding of the biological relevance of these impacts (Corkeron, 2004). Indeed interpreting behavioral responses outside the biological and ecological context in which they are studied has been shown to be uninformative (Beale & Monaghan, 2004; Bejder, Samuels, Whitehead & Gales, 2006a; Gill, Norris, & Sutherland, 2001).

Recent studies show that these short-term avoidance tactics can lead to biologically significant effects which can have long-term consequences for individuals and their populations (Bejder, 2005; Bejder et al., 2006a; Bejder et al., 2006b; Foote, Osborne, & Hoelzel, 2004; Lusseau, 2005; Lusseau, Slooten, & Currey, 2006b; Williams, Lusseau, & Hammond, 2006). These latter studies have taken a multi-contextual approach to elucidate the mechanisms linking short-term avoidance tactics to long-term impacts. Using comparisons between control and impact sites and long-term life history data they have revealed how whalewatching disturbance, a chronic intermittent stressor, had short-term effects on the lives of cetaceans which lead to long-term consequences for the viability and fitness of individuals and their populations. Whalewatching refers here to interactions between vessels and both dolphins and whales. Here we use three examples to highlight these mechanisms. We argue that this work is paving our understanding of principles governing the impacts of human activities on cetaceans. In particular, research in the effects of whalewatching can contribute significantly to a better understanding of the transfer functions in the Population Consequences of Acoustic Disturbance (PCAD) model (National Research Council, 2005).

Methods

We undertook studies on bottlenose dolphins (*Tursiops* sp.) at two sites: Shark Bay, Australia (Bejder et al., 2006a) and Fiordland, New Zealand (Lusseau, 2004). We will also present work carried out in collaboration with other authors on killer whales (*Orcinus orca*) off Vancouver Island, Canada (Williams et al., 2006). In Shark Bay, immediate responses to controlled vessel approaches were evaluated at both control and impact sites, depending on whether whalewatching occurred at those sites or not. Observed effects were related to long-term dolphin photo-identification records, reproductive rates and cumulative exposure measures to vessels (Bejder, 2005; Bejder et al., 2006a; Bejder et al., 2006b). In a similar fashion, we measured immediate behavioral responses of individuals and schools of bottlenose dolphins to boat interactions in Fiordland in two populations that were exposed to different levels of boat interactions. These two populations, one residing in Doubtful Sound and another whose home range centers on Milford Sound, are exposed to similar ecological conditions but are distinct. We then related these responses to long-term habitat use and reproductive success in relation with the rate of exposure to these disturbances (Lusseau, 2003a; Lusseau, 2003b; Lusseau, 2004, 2005; Lusseau et al., 2006a; Lusseau et al., 2006b). The Fiordland study also benefited from a natural experiment in that we made predictions regarding the consequences of increased tourism

levels in Doubtful Sound following the results of the study (2000-2002) that were tested after tourism intensity did increase in subsequent years (2003-2007).

Results

Shark Bay, Australia

In Shark Bay, dolphin abundance was compared within adjacent tourism and control sites, over three consecutive 4.5-year periods wherein tourism levels increased from zero (1988-1993), to one (1993-1998), to two (1998-2003) dolphin-watching operators. As the number of tour operators increased from one to two, there was a significant average decline in dolphin abundance (14.9%; 95% CI = -20.8 to -8.23), approximating a decline of one per seven individuals in the tourism site. In contrast, abundance in the adjacent control site, which was not used by tour boats, did not change significantly (Bejder et al., 2006b).

Additionally, the behavioral response of dolphins to experimentally controlled boat interactions was quantified at two sites: the impact site mentioned above, and another control site, located 17km away from the impact site, that had similar ecological features. The movement of dolphins became more erratic during interactions and dolphin schools tightened. However, the effect size was smaller at the impact site (Bejder et al., 2006a), which traditionally would have been explained as a sign of “habituation”. However, in the light of the abundance study, it is more parsimonious to infer that individuals left at the impact site could afford to respond as much as others at the control site, because of reduced fitness. Indeed, the reproductive success of females in this area was linked to their cumulative exposure to boat interactions (Bejder, 2005).

Fiordland, New Zealand

The Milford Sound population was exposed to approximately seven times more tourism traffic than the Doubtful Sound population (Lusseau, 2004). Interactions affected behavioral budget in a similar fashion in both fiords leading to significant increased time spent travelling and decreased time spent resting (Lusseau, 2003a, 2004). They also increased the duration of travelling bouts, leading to added energetic challenges for individuals with less relative energetic stores (i.e., females and especially females with calves or pregnant). These added costs were apparent in that females tended to have different avoidance strategies than males, undergoing vertical avoidance strategies only when the boat interaction intrusiveness was such that it was highly likely to lead to injuries to non-avoiding individuals (Lusseau, 2003b).

While tourism exposure was much higher in Milford Sound than Doubtful Sound, the time spent interacting with boats in both fiords was similar (Lusseau 2004). This was linked to an avoidance of Milford Sound by dolphins during seasons with high tourism traffic (boat traffic was the only oceanographic predictor of residency pattern: $r = -0.814$, $p = 0.021$, Lusseau, 2005). In addition, when dolphins visited the fiord they avoided location with high boat traffic at peak traffic hours ($r = -0.888$, $p = 0.0018$, Lusseau, 2005). There was a linear relationship between boat traffic and dolphin-boat interaction pattern until the average time elapsed between two interactions reached 68 minutes (Lusseau, 2004; Lusseau et al., 2006b). Beyond this point,

dolphins switched from a short-term behavioral avoidance strategy to long-term avoidance strategy (habitat displacement) because the former strategy was no longer beneficial (Lusseau, 2004). Tourism activities affect only a portion of the home range of the Milford Sound population. Therefore, habitat displacement is a possible tactics for the individuals to manage the impacts. In contrast, tourism activities are pervasive throughout the home range of the Doubtful Sound population. We predicted that if boat interactions were to intensify and pass the 68-minute threshold, the population could only cope by decreasing its reproductive success (Lusseau et al., 2006b). Once boat traffic increased beyond the 68-minute threshold, the population suffered a dramatic decline in abundance (Currey, Dawson, & Slooten, in press; Lusseau et al., 2006b), passing from 67 to 56 individuals in a very short period. There was also a drastic significant decline in reproductive success with an increase in neonatal/stillbirth deaths (1994-1999: stillbirth presence: 2/5 years, stillbirth rate: 0.13 stillbirth/year; 2000-2007: 6/7 years, 0.34 stillbirth/year; randomization tests respectively: $p=0.044$ and $p=0.043$ (Lusseau et al., 2006b) and overall calf survival rate (Currey et al., submitted). This decline in calf survival could explain solely the population decline (Currey et al., submitted).

Vancouver Island, Canada

This study showed that boat traffic was also significantly affecting the behavioral budget of northern resident killer whales (Williams et al., 2006). They reduced foraging opportunities and increased travelling time. However, a simple bioenergetic model showed that while the behavioral effect size was greater for travelling than for foraging, the loss in foraging opportunity was leading to a greater energetic cost, by decreasing energy intake by 18%. In contrast, the added energetic cost of increased activities was only leading to a 3 to 4% increase in energy output for individuals (Williams et al., 2006). This showed that the biologically significant impact of boat interactions principally focused on food intake for this population. Such studies can help us prioritize management actions to minimize the biological significance of the impact. In this example, preventing boat interactions while whales are foraging will have a disproportionately greater influence on the overall impact of whalewatching than other restrictions would. Therefore establishing no-boat zones around foraging hotspots would be an ecologically and economically sensible measure (Lusseau & Higham, 2004).

Discussion

Results presented here indicate biologically significant impacts of an apparently benign human activity, i.e., watching whales and dolphins. The success of detecting population level effects was based on long-term population monitoring and the availability of information on the variation in vessel exposure between individuals, sites, and populations. The influence of these impacts on population viability can be inferred using the dose response relationships these studies describe. Early individual-based models show that these impacts are highly likely to endanger the viability of small populations which have restricted immigration/emigration because of the increased cumulative exposure they incur (Lusseau et al., 2006a).

The consequences of energetic challenges

The published studies we present here show that increased energetic challenges, either as added travelling costs or reduced foraging opportunities, can lead to reduced fitness for individuals. If such challenges occur too often, individuals shift into long-term avoidance strategies when possible by avoiding the degraded areas. However, such long-term decisions have to be balanced with other costs and benefits to leave a habitat degraded by whalewatching or leave a school exposed to whalewatching. These trade-offs lead to non-linear relationships with a rapid shift into long-term strategies when short-term tactics are no longer beneficial. This highlights that these behavioral systems, like other complex systems, can be shifted from one basin of attraction to another quite rapidly (van Nes & Scheffer, 2007). Individuals that cannot leave degraded habitat have reduced fitness leading to, at least, reduced reproductive success. This shows that at the population-level these shifts in basin of attraction may not always lead to evolutionary stable solutions.

Modeling population-level consequences

This described link between whalewatching disturbance exposure and reproductive success and survival probability can be used in agent-based simulations to define the likelihood that these effects can endanger the viability of exposed cetacean populations (Lusseau et al., 2006a). More importantly, the uncertainty surrounding the estimated dose-response curves can be incorporated in these models, so that its influence on the likelihood populations will remain viable can be accounted (Lusseau et al., 2006a). Agent-based simulations provide a tool to disturb artificial individuals in a population in a realistic manner because the rules of interactions (timing, duration, number of interactions, temporal variation) can be informed by empirical data. Unsurprisingly, these models illustrate how small populations, with restricted immigration and/or emigration, are less likely to survive even low levels of whalewatching exposure (Lusseau et al., 2006a). That is because such features increase the cumulative exposure to disturbance per capita. In addition, once the population starts to decline, restricted immigration means that exposure per individual intensifies, precipitating the population in an extinction vortex (Lusseau et al., 2006a).

Insights for the PCAD model

These studies provide templates to inform the PCAD model (Figure 1). The highlighted studies bring valuable insight into the three transition functions of the PCAD model. They show that repetitive short-term behavioral change can influence life functions by imposing additional costs to the energetic budget of individuals. The resulting impact on individuals will vary with the life history of the targeted species. In some instances, decreased energy intakes will predominantly drive the impact of the responses, while in others it may be the added energetic cost of transport.

Impacts on life functions can affect vital rates. These studies show that the influence of these changes on vital rates is non-linear, their impact shifting abruptly around a threshold. At this stage, whalewatching studies only provide a mechanistic function in an energetic framework. Other life functions may be

impaired, such as socializing, and those impacts can also have influences on vital rates, such as reproduction rate. Much work is needed to understand the principles governing these mechanisms that will be highly species-specific.

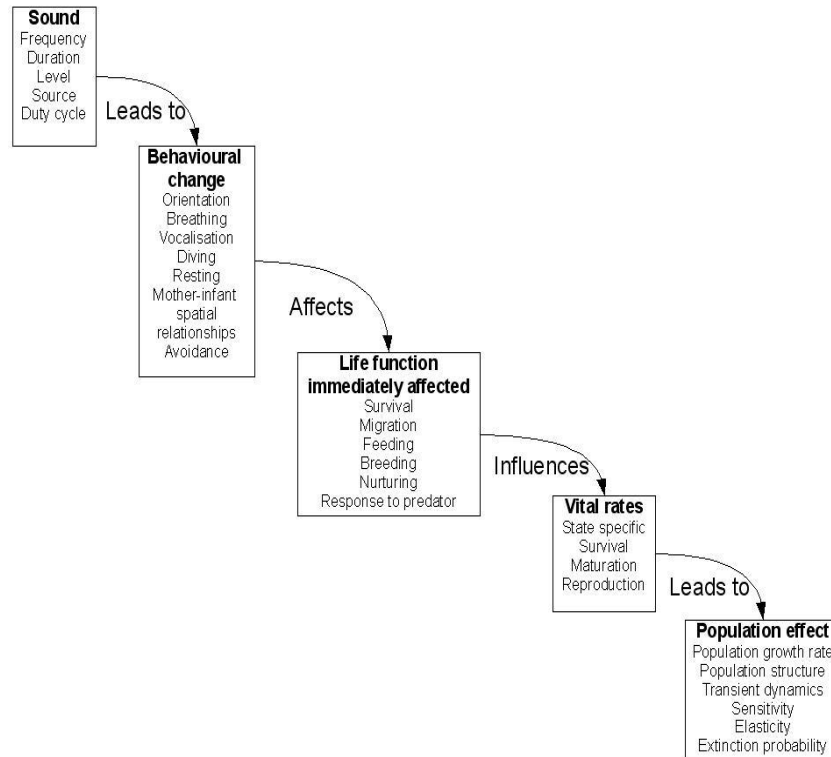


Figure 1. Modeling population-level consequences. Printed as modified from the Population Consequences of Acoustic Disturbance model developed by the US National Research Councils (National Research Council, 2005) with permission from the National Academies Press, Copyright 2005, National Academy of Sciences.

Finally, as it has been shown in the case of other anthropogenic impacts (Slooten, Fletcher, & Taylor, 2000), the alteration of vital rates can lead to influences on the viability of populations. This will depend on the resilience of the population's carrying capacity and therefore small, closed population are highly likely to be more prone to extinction under these scenarios.

Conclusion

We have shown here that there is high propensity for individuals to have context-specific responses to disturbances. It is also expected that human activities will have disproportionate influences on different individuals depending on their current fitness and life history strategy (Lusseau, 2003b; Munch & Conover, 2003; Perez-Tris, Diaz, & Telleria, 2004). If the impacts of these activities are significant enough to select against sensitive individuals, these disturbances may also influence the evolutionary dynamics of populations since the predisposition for risk-taking behavior may be heritable

in many species (Brick & Jakobsson, 2002; van Oers, Drent, de Goede, & van Noordwijk, 2004). This population-level adaptation could result in lower observed effect size of disturbance. Such variation can be interpreted as the population “habituating” to the disturbance when in fact the population is reacting to this disturbance in several dimensions. This conclusion highlights the need for contextual information to define the biological relevance of observed short-term effects and the danger of interpreting these effects out of context.

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