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Does optimal foraging theory predict the foraging performance of a large air-breathing marine predator?

R. B. Tyson [a, b, *], A. S. Friedlaender [a, c], D. P. Nowacek [a, d]

[a] *Nicholas School of the Environment, Duke University Marine Laboratory, Beaufort, NC, U.S.A.*
[b] *Sarasota Dolphin Research Program, Chicago Zoological Society, Sarasota, FL, U.S.A.*
[c] *Marine Mammal Institute, Department of Fisheries and Wildlife, Oregon State University, Newport, OR, U.S.A.*
[d] *Pratt School of Engineering, Duke University, Durham NC, U.S.A.*

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Optimal foraging theory (OFT) suggests that air-breathing diving animals should minimize costs associated with feeding under water (e.g. travel time, oxygen loss) while simultaneously maximizing benefits gained from doing so (e.g. foraging time, energy gain). Humpback whales, *Megaptera novaeangliae*, foraging along the Western Antarctic Peninsula appear to forage according to OFT, but the direct costs and benefits in terms of their behaviours (e.g. allocation of time) have not been examined. We compared the foraging behaviour of humpback whales in this region inferred from multisensor high-resolution recording tags to their behaviour predicted by OFT time allocation models assuming the following currencies were being maximized: (1) the proportion of time spent foraging, (2) the net rate of energetic gain and/or (3) the ratio of energy gained to energy expended (i.e. efficiency). Model predictions for all three currencies were similar, suggesting any of these OFT models were suitable for comparison with the observed data. However, agreement between observed and optimal behaviours varied widely depending on the physiological and behavioural values used to derive optimal predictions, highlighting the need for an improved understanding of cetacean physiology. Despite this, many of the theoretical OFT predictions were supported: shallow dives (i.e. <100 m), which were short and executed most frequently, yielded the highest proportions of foraging time, and the greatest net rates of energy gain and were the most efficient. In addition, dive and foraging times increased in duration rapidly with increasing maximum dive depths to approximately 100 m and then at lower rates with deeper dives. Our findings offer a thorough examination of the applicability of time allocation OFT models to the behaviours of a large, air-breathing, diving predator and provide insights into the foraging ecology and physiology of humpback whales in the Western Antarctic Peninsula.

Optimal foraging theory (OFT) suggests that animals are adapted to exploit resources as efficiently as possible; natural selection should favour foraging strategies that are efficient in minimizing foraging costs (e.g. travel time, oxygen loss) while simultaneously maximizing benefits (e.g. energy gain) (Macarthur & Pianka, 1966). Mathematical models to predict the foraging behaviours of air-breathing diving animals, such as birds and marine mammals, have been developed under the framework of central-place foraging (Orians, Pearson, Horn, Mitchell, & Stairs, 1979), where the surface acts as the central place to and from which an animal returns between dives (Houston & McNamara, 1985). Time allocation OFT models theorized by Kramer (1988) and derived by Houston and Carbone (1992) are commonly used for this purpose because they predict the optimal foraging and surfacing durations of divers in response to changes in travel time and dive depth assuming that either the proportion of foraging time, the net rates of energetic gain and/or the energy gained versus energy expended (i.e. efficiency) is being maximized. These models are based on the assumption that the time spent travelling to and from a prey patch will increase with increasing prey patch depth (Houston & Carbone, 1992). Consequently, the amount of oxygen used during a dive and the time needed to replenish it between dives will increase with increasing prey patch depth (Kooyman & Ponganis, 1998) and the time available for foraging will decrease (Houston & Carbone, 1992). Because prey acquisition is assumed to increase linearly with foraging duration, air-breathing diving animals should

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* Correspondence and present address: R. B. Tyson, Sarasota Dolphin Research Program, Chicago Zoological Society, c/o Mote Marine Laboratory, 1600 Ken Thompson Pkwy, Sarasota, FL 34236, U.S.A.
E-mail address: rtyson@mote.org (R. B. Tyson).

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maximize these currencies (i.e. foraging time, energy gain, efficiency) by optimizing surface time and thus overall oxygen stores (Houston & Carbone, 1992).

Initial tests of the Houston and Carbone (1992) optimal foraging theory models (hereafter referred to as the OFT models) were limited to experiments with captive animals (e.g. common pochard, *Aythya ferina*: Carbone & Houston, 1994; tufted duck, *Aythya fuligula*: Halsey, Woakes, & Butler, 2003; Brünnich's guillemot, *Uria lomvia*: Elliott, Davoren, & Gaston, 2008), but the advancement of bio-logging tools (e.g. time-depth recorders, accelerometers) has enabled further testing with free-ranging diving animals including common eiders, *Somateria mollissima sedentaria* (Guillemette, Woakes, Henaux, Grandbois, & Butler, 2004; Heath, Gilchrist, & Ydenberg, 2007), harbour seals, *Phoca vitunila concolor* (Heaslip, Bowen, & Iverson, 2014), fin whales, *Balaenoptera physalus* (Acevedo-Gutiérrez, Croll, & Tershy, 2002), and blue whales, *Balaenoptera musculus* (Acevedo-Gutiérrez et al., 2002; Doniol-Valcroze, Lesage, Giard, & Michaud, 2011). Such applications allow for an examination into the extent that an animal's behaviour can be explained in terms of its physiology and/or ecology (Houston, 2011). For example, Acevedo-Gutiérrez et al. (2002) compared observed dive times of foraging blue and fin whales to those predicted by an OFT model. Their results suggest that the foraging strategies of blue and fin whales are energetically expensive and limit the dive time of these large predators.

Blue and fin whales, like other balaenopterids (e.g. humpback whales, *Megaptera novaeangliae*; minke whales, *Balaenoptera bonaerensis*), feed via a process known as lunge feeding, which involves accelerating with a burst of energetic fluking towards and engulfing a mass of prey-laden water that may be greater than the whale's body mass (Goldbogen, Potvin, & Shadwick, 2010), filtering the prey through keratinized plates of baleen and swallowing the captured prey. Simulations based on hydrodynamic models that coupled balaenopterid structure and function, fluid dynamics and krill evasion behaviours have revealed that this process can be up to 3.7 times the active metabolic rate for a 27 m blue whale, but varies widely with whale size (Potvin, Goldbogen, & Shadwick, 2012). This high energetic cost associated with lunging (i.e. the amount of oxygen consumed) may contribute to the dive durations of these large marine predators being shorter than predicted for their body size (Acevedo-Gutiérrez et al., 2002; Goldbogen et al., 2008; Goldbogen et al., 2006; Goldbogen, Pyenson, & Shadwick, 2007).

While the energetic cost of lunging may contribute to foraging dives being shorter than expected in balaenopterids, foraging dives may also be short because it is optimal for them to be so (Doniol-Valcroze et al., 2011; Houston & Carbone, 1992; Kramer, 1988). Because oxygen is acquired at the surface with diminishing returns, the lengthening of dives increases the amount of time required on the surface for replenishing oxygen stores (Kooyman & Ponganis, 1998), decreasing the time available for foraging under water (Kramer, 1988). Thus, while air-breathing diving animals could theoretically perform long dives at shallow depths, short dives allow for shorter recovery times and more time spent underwater foraging (Kramer, 1988). In support of this prediction, Doniol-Valcroze et al. (2011) found that shallow dives of blue whales (i.e. <150 m) were short and resulted in the highest feeding rates. Similarly, Ware, Friedlaender, and Nowacek (2011) reported that humpback whales executed only one or two lunges during shallow dives (i.e. <25 m). While Ware et al. (2011) did not discuss the duration of these shallow dives, these whales are physiologically capable of executing several lunges per dive but only do so at greater depths (Friedlaender, Tyson, Stimpert, Read, & Nowacek, 2013).

There is evidence that humpbacks along the Western Antarctic Peninsula feed according to the general principles of OFT (Macarthur & Pianka, 1966). For example, humpbacks in this region adjust their foraging behaviours according to the depth and density of their primary prey, Antarctic krill, *Euphausia superba* (Friedlaender, Johnston, Tyson, Kaltenberg, et al., 2016). These whales forage almost exclusively at night, when krill are near the surface, and they rest or travel near the surface during the day, when krill are at depth (Friedlaender et al., 2013). In addition, these whales modulate their feeding depth with respect to their prey, targeting denser prey patches on deeper dives (Friedlaender et al., 2016). These behavioural choices suggest that whales are altering their behaviours to maximize their benefits while foraging.

In the present study, we compared the diving and foraging behaviours of humpbacks along the Western Antarctic Peninsula inferred from multisensor high-resolution recording tags to behaviours predicted by OFT models. We hypothesized that humpbacks would allocate their time during foraging dives to maximize at least one of the following currencies: (1) the proportion of time available for foraging, (2) the net rate of energetic gain and/or (3) the ratio of energy gained to energy expended (i.e. energetic efficiency). We addressed this hypothesis by assessing agreement between observed and predicted behaviours and examining variation in model fit and adherence to model assumptions. Our findings provide insights into the foraging ecology and physiology of humpback whales and offer a thorough examination of the OFT model's applicability to large, free-ranging, air-breathing diving predators.

METHODS

Observed Whale Behaviour

We used multisensor archival digital acoustic recording tags (DTAGs, Johnson & Tyack, 2003) to infer the diving and foraging behaviours of humpback whales ($N = 13$ adults) in the near-shore waters of the Western Antarctic Peninsula during 2009 and 2010 (Table 1). DTAGs (hereafter referred to as tags) are small data loggers commonly used with marine mammals that incorporate triaxial accelerometers and magnetometers to record animal orientation (50 Hz), a pressure sensor to record depth and a hydrophone (96 kHz). We approached whales for tagging from oblique angles at idle or low speeds with a Zodiac Mark V rigid-hulled inflatable boat with a four-stroke outboard motor both to minimize behavioural disturbance to the whale and to maximize personal safety. We deployed tags on whales using a 6 m hand-held carbon-fibre pole via four silicon suction cups. Whale behaviour was not visibly affected by tagging (other than immediate startle responses by some) and preliminary examinations of the tag data suggested a return to pretagging behaviour within a few dives, consistent with other tagging studies (e.g. Hazen et al., 2009; Nowacek, Johnson, & Tyack, 2004). A corrodible active release was programmed to release the tag's suction cups from the whales after ~24 h, after which tags were recovered and data downloaded for analysis. These research activities were permissible under National Marine Fisheries Service Permit 808-1735, Antarctic Conservation Act Permit 2009-014 and Institutional Animal Care and Use Committee of Duke University (IACUC A049-112-02).

We used an automatic lunge detector in the software program TrackPlot (Ware, Arsenault, & Plumlee, 2006) to identify putative feeding lunges executed by the whales from the tag data (see Friedlaender et al., 2013; Tyson, Friedlaender, Stimpert, Ware, & Nowacek, 2012; Ware et al., 2011). The detector locates distinct fluctuations in the flow noise (speed) recorded by the tag's hydrophone that are characteristic of the rapid accelerations and