



## Testing optimal foraging theory models on benthic divers



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Empirical testing of optimal foraging models on diving air-breathing animals is limited due to difficulties in quantifying the prey field through direct observations. Here we used accelerometers to detect rapid head movements during prey encounter events (PEE) of free-ranging benthic-divers, Australian fur seals, *Arctocephalus pusillus doriferus*. PEE signals from accelerometer data were validated by simultaneous video data. We then used PEEs as a measure of patch quality to test several optimal foraging model predictions. Seals had longer bottom durations in unfruitful dives (no PEE) than those with some foraging success ( $PEE \geq 1$ ). However, when examined in greater detail, seals had longer bottom durations in dives with more PEEs, but shorter bottom durations in bouts (sequences of dives) with more PEEs. Our results suggest that seals were generally maximizing bottom durations in all foraging dives, characteristic of benthic divers. However, successful foraging dives might be more energetically costly (e.g. digestive costs), thus resulting in shorter bottom durations at the larger scale of bouts. Our study provides a case study of how the foraging behaviour of a central place forager foraging in a fairly homogeneous environment, with relatively high travel costs, may deviate from current foraging models under different situations. Future foraging models should aim to integrate other aspects (e.g. diet) of the foraging process for more accurate predictions.

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The ability to acquire resources is crucial for the survival and fitness of animals. Optimal foraging theory (OFT) is a widely used conceptual framework for explaining and predicting foraging behaviours of animals. It attempts to predict how an animal makes foraging decisions to maximize the net rate of energy intake (also known as the 'currency' that is being optimized) by minimizing energy costs while maximizing energy gain under relevant constraints in a particular situation (Pyke, Pulliam, & Charnov, 1977; Stephens & Krebs, 1986). Thus, OFT provides testable predictions that can improve our understanding of how animals make foraging decisions to cope in heterogeneous environments where food availability fluctuates spatially and temporally.

For air-breathing diving aquatic animals (hereafter divers), including turtles, marine mammals and seabirds that forage in a three-dimensional environment, OFT is also known as optimal diving theory. Optimal diving theory attempts to model how divers modify their time allocation within a dive. A dive is typically broken

into four phases: descent, bottom (time assumed to be spent foraging), ascent and a postdive surface interval (SI), when the animal stays on the surface to replenish its oxygen stores before its next dive (Heerah, Hindell, Guinet, & Charrassin, 2014). Bestley, Jonsen, Hindell, Harcourt, and Gales (2014) broadly classified optimal diving models as either physiological or ecological models. Although this dichotomy has limitations, as the optimal diving models already integrate physiological and ecological constraints to some extent, this categorization is useful as it simply considers one type of constraint to be more dominant than the other. We therefore used this dichotomy in a very general sense, while recognizing that it does not affect the fundamental notion of foraging currency in OFT, which in this case is energy for all foraging models mentioned in this paper.

Physiological models place emphasis on oxygen depletion of divers (Houston & Carbone, 1992; Kramer, 1988) because, unlike terrestrial animals, divers are ultimately limited by oxygen when they dive. Thus, physiological models assume that within a dive cycle, divers should maximize their bottom duration (i.e. when divers can gain net energy), while minimizing travel duration (i.e. when divers incur a net cost; predictions 1, 2 in Table 1) and/or

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**Table 1**  
Predictions of optimal diving models and optimal foraging models that were tested on Australian fur seals, including the response variable and covariates used for statistical analysis (for each prediction or model)

Prediction	Type	Response variable	Covariates(s)	Source
1 For relatively long travel durations, foraging time decreases with travel duration	Physiological	Bottom duration	Travel duration	Houston and Carbone 1992
2 Proportion of time spent in the foraging area decreases with travel duration	Physiological	Percentage bottom duration (=bottom duration/dive duration)	Travel duration	Houston and Carbone 1992
3 Dive duration increases with dive depth and/or travel duration	Physiological	Dive duration	Dive depth and travel duration	Kramer, 1988, Houston and Carbone 1992, Mori et al. 2002 Kramer, 1988
4 Resource gain (no. of prey encountered) increases linearly with search time spent at depth	Physiological	Prey encountered	Bottom duration	Kramer, 1988
5 Postdive surface interval increases as dive duration increases	Ecological	Postdive surface interval	Dive duration	Thompson and Fedak 2001
6 Optimal stay-time should be greater in more productive patches than in less productive patches (dive scale patch quality); however, optimal stay time should be shorter where the environment (bout-scale habitat quality) as a whole is more profitable	Ecological	Bottom duration	Dive scale patch quality, bout scale patch quality and dive depth (control)	Charnov, 1976
7 For deep dives, bottom duration should be largely invariant, no matter the prey density/patch quality	Ecological	Bottom duration	Prey presence or absence (controlled for travel duration and depth), and the dive scale prey encounter or prey encounter rate	Thompson and Fedak 2001
8 Ascent and descent rates should increase with patch quality if seals are reducing transit time	Ecological	Ascent and descent rates	Patch quality represented by prey encounters or prey encounter rate	Thompson and Fedak 2001

extend their dive duration when travel duration increases (prediction 3 in Table 1). Therefore, patch quality should be less important to divers primarily constrained by their physiology (Thompson & Fedak, 2001).

Simple physiological diving models assume that divers encounter prey at a constant rate in the prey patch, so the number of prey encounters in a dive should increase linearly with bottom duration (prediction 4 in Table 1; Kramer, 1988). Consequently, longer dive durations, longer bottom durations and/or higher dive rates have been used as proxies for increased foraging success and energy gain (Austin, Bowen, McMillan, & Iverson, 2006) even though this may not necessarily be true (Thums, Bradshaw, Sumner, Horsburgh, & Hindell, 2013; Watanabe, Ito, & Takahashi, 2014). For many species, longer dive durations require a longer time on the surface to reoxygenate (prediction 5 in Table 1; Zimmer et al., 2010) reducing the proportion of time spent diving relative to overall time spent at sea (Elliott, Davoren, & Gaston, 2008a).

Ecological models consider ecological factors such as prey density, quality and distribution, which are attributed to ‘patch quality’ (Charnov, 1976; Mori, 1998; Mori & Boyd, 2004; Thompson & Fedak, 2001), as primary constraints in foraging. The marginal value theorem (MVT), a classic and influential concept in OFT, is often used to model how an optimal forager allocates its time within a hierarchical patchy environment (however, see Shepard, Lambertucci, Vallmitjana, & Wilson, 2011 who used it to model physiological currencies), whereby smaller-scale, short-term patches of varying patch quality are nested within larger-scale, long-term habitats. The MVT assumes that an animal foraging in small-scale patches will experience patch depletion effects and therefore predicts that a forager should leave all patches, regardless of their profitability, when the instantaneous extraction rate (i.e. ‘marginal value’) reaches the average overall extraction rate for the habitat as a whole (Charnov, 1976). This leads to two opposing predictions: the patch residence time of a forager should be longer in a higher productivity, small-scale patch, but shorter in a higher productivity, large-scale habitat (prediction 6 in Table 1; see Figure 1 in Watanabe et al., 2014).

The MVT can be applied to divers, for which individual dives can be considered a small-scale patch, and a series of dives with

relatively short surface intervals between them (bouts) can be considered large-scale habitat. Most studies have shown support for either the short-term (Austin et al., 2006; Sparling, Georges, Gallon, Fedak, & Thompson, 2007) or long-term (Mori & Boyd, 2004; Thums et al., 2013) predictions of the MVT on captive and wild marine predators, while one has recently shown support for both small- and large-scale predictions for Adélie penguins, *Pygoscelis adeliae* (Watanabe et al., 2014).

The model developed by Thompson and Fedak (2001) uses a simple ‘give-up’ rule based on the diver’s ability to assess patch quality, while still emphasizing the importance of maximizing bottom duration in a high-quality patch; their model predicts that shallow divers should terminate a dive early in a poor-quality patch, as travel costs are relatively inexpensive. Conversely, deep divers should maximize bottom duration, regardless of patch quality (prediction 7 in Table 1). In addition, Thompson and Fedak (2001) also predicted that divers should increase ascent and descent rates as patch quality increases (prediction 8 in Table 1).

Empirical tests of these model predictions are rare due to the lack of data on prey fields, and therefore patch and habitat quality. Measuring the foraging success of free-ranging divers has largely been limited to using proxies such as dive or bottom duration, body condition (Thums et al., 2013) or animal track-based methods (Dragon, Bar-Hen, Monestiez, & Guinet, 2012a, 2012b), in the absence of evidence of actual prey feeding events.

Animal-borne video cameras are one of the few practical methods for directly measuring the prey field. However, they are costly, can be difficult to deploy and have limited recording capacity (Biuw, McConnell, Bradshaw, Burton, & Fedak, 2003; Thums, Bradshaw, & Hindell, 2011). Studies that used them have relatively small sample sizes and short-term records (Heaslip, Bowen, & Iverson, 2014) preventing the testing of foraging theory predictions at larger timescales. Alternatively, accelerometers can measure characteristic head and jaw movements of an animal during prey encounter or captures, and also provide longer data records (Hochscheid, Maffucci, Bentivegna, & Wilson, 2005). When used in combination, short-term video evidence of a diver’s foraging behaviour can be used to quantitatively validate the prey encounter events (PEE) of free-ranging predators detected by

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