

IN FOCUS

To breathe or not to breathe: optimal strategies for finding prey in a dark, three-dimensional environment



Photo credit: Short-finned pilot whale surfacing with parts of a large squid in the mouth. Photo by Pablo Aspas with permission from the Canary Islands Government.

N. Aguilar de Soto, M.P. Johnson, P.T. Madsen, F. Díaz, I. Domínguez, A. Brito & P. Tyack (2008) Cheetahs of the deep sea: deep foraging sprints in short finned pilot whales off Tenerife (Canary Islands). *Journal of Animal Ecology*, **77**, 936–947. doi: 10.1111/j.1365-2656.2008.01393.x

The use of sophisticated telemetry logging devices has revealed that short-finned pilot whales employ energetic sprints to chase down their deep-dwelling prey. These sprints are costly in terms of energy, and therefore oxygen, which is a valuable resource for an animal that has to hold its breath while hunting. This finding highlights the challenges faced by ecologists when trying to develop foraging models for marine predators because many of the key parameters, such as movements in three dimensions, marine prey fields and metabolic adaptations of diving animals, remain largely unknown.

Quantitative assessment of the interactions between predators and their prey is an important focus of ecology, and is used by disciplines as diverse as fisheries management and biological control. Foraging theory attempts to model how predators search their environment for potential prey, and one off-shoot of this endeavour, optimal foraging theory, predicts that animals will do this optimally (Stephens & Krebs 1986). This theory places search behaviour in an evolutionary

context, assuming that species have evolved optimal strategies for their particular suite of environmental circumstances. A central tenet of this theory is that organisms will maximize their net energy gain with respect to the diverse costs associated with acquiring that energy. Although well-studied in both laboratory and terrestrial systems, quantifying strategies in marine systems have proved more elusive. There are several reasons for this. One is that marine predators inhabit a different world to terrestrial species. They must find prey in a three-dimensional environment and, for air-breathing

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species such as turtles, seabirds and marine mammals, there is the additional constraint of needing to return to the surface regularly to breathe. The other reason is technological – it is generally impossible to watch marine predators hunting, and marine biologists have had to wait until they had the capacity to ‘follow’ free-ranging animals as they searched for food. This task is most commonly achieved nowadays by attaching electronic tags to free-ranging animals; the tags record and transmit data describing diving behaviour and position.

One of the most advanced tags being employed at the moment is the DTag developed by Mark Johnson and Peter Tyack of the Woods Hole Oceanographic Institution (Johnson & Tyack 2003). These tags record a suite of parameters including three-dimensional acceleration, depth and, crucially for the species that they study, sound. These devices therefore enable the three-dimensional reconstruction of an animal’s path through the water column, as well as swim speed and even fluking rate. When these data were coupled with simultaneous recordings of echolocation clicks, they provided a powerful tool for examining the fine-scale foraging behaviour of large, diving animals. In the study of Aguilar *et al.* (2008) the DTags were deployed on short-finned pilot whales *Globicephala macrorhynchus* (Gray), revealing some unexpected results that may require a re-assessment of foraging models developed for marine predators. These models suggest that animals should swim at the minimum cost of transport (Thompson, Hiby & Fedak 1993; Thompson & Fedak 2001), enabling them to balance their rate of oxygen consumption (and hence time submerged at the foraging zone) and the energy returned in the form of prey encounters. However, the whales in that study performed high-speed sprints to catch deep-dwelling prey, and the energetic cost of these sprints was far in excess of the minimum cost of transport. In so doing, this study highlights the three key factors that marine ecologists must measure before their quantitative understanding of foraging strategies will match those of terrestrial ecologists: the animal’s use of the third dimension, prey field distribution (energy input) and the animal’s energetic expenditure (energy output).

Following a marine predator as it moves through its dimensional space has always been something of a holy grail that few studies have achieved (Hindell *et al.* 2002; Watwood *et al.* 2006). In the absence of complete information on animal movement, much analysis of foraging strategies has had to focus on two-dimensional surface tracks. These data are being subjected to increasingly sophisticated analyses that attempt to identify different modes of movement, and in particular to identify foraging and non-foraging behaviours (Hays *et al.* 2006; Tremblay, Roberts & Costa 2007; Patterson *et al.* 2008). This increased analytical rigour has now enabled simple foraging models to be tested and several studies have compared animal paths to Levy flight models (Austin *et al.* 2006b; Bradshaw, Sims & Hays 2007). Nonetheless, these approaches, while well-suited to surface-feeding animals (Pinaud & Weimerskirch 2007), are inadequate for deep-diving species such as phocid seals, toothed-whales, turtles, and many fish species. For these species, marine ecologists either

use the third dimension (depth) in relation to time (time/depth profiles) or they merge depth data with surface location data at varying spatial and temporal scales. Several recent studies have used this approach to describe area restricted search patterns better (Bailleul *et al.* 2008) and even to test the importance of scale on universal foraging strategies (Sims *et al.* 2008). These studies provide insights by aggregating data from many dives and so are not examining behaviour at the finest possible scale. The data supplied by DTags enable ecologists to examine foraging behaviour at the scale of individual dives. However, even with the new and exciting advances in measuring animal behaviour deep below the surface, our interpretation of behaviours is limited by a lack of knowledge of their prey. Are they large and fast, or small and schooling? These basic data are needed (and often assumed) in models of foraging strategies.

A second holy grail of marine ecologists is the ability to measure aspects of the prey field. In Aguilar *et al.* (2008), the highly energetic sprints of the pilot whales can only make sense if they are rewarded with large, energy-dense prey. Almost all other studies of marine predators have also been forced to make assumptions about potential prey in the absence of independent data on prey distribution and abundance. Some of the most intriguing studies have been able to use proxies for prey encounters and captures, and in doing so have been able to provide, albeit indirect, information on prey fields. These proxies range from changes in buoyancy associated with changing fat stores (Biuw *et al.* 2007), the detection of feeding events by oesophageal, stomach and mouth-opening sensors or quantification of behavioural events such as sprints (Myers & Hays 2006; Ropert-Coudert *et al.* 2006; Austin *et al.* 2006a; Horsburgh *et al.* 2008). The challenge for marine ecologists is now to incorporate data on prey fields with foraging behaviour to test and improve existing foraging models (Mori 1998; Mori *et al.* 2002).

Foraging theory attempts to explain a predator’s search strategies in terms of cost–benefit analysis. The potential costs for a foraging animal are many and varied and include exposure to predation, loss of mating opportunities and the energy expended in searching for and capturing prey. Energy expenditure is often the most easily measured and modelled of these costs and is a prominent feature of many foraging models. In models developed for diving animals, energy expenditure (and therefore oxygen consumption) plays a major role in determining how long an animal can remain submerged. Many models therefore emphasize oxygen balance, including the increased time on the surface that results from excessive oxygen consumption, which reduces potential foraging opportunities (Houston & Carbone 1992; Carbone & Houston 1996). Unfortunately, knowing the energetic costs of submerged behaviours is far from straightforward, particularly as marine mammals are thought to have greater control over their metabolic rate than their terrestrial counterparts (Boyd 2002). Air-breathing marine vertebrates are able to vary their metabolic rates at a range of temporal scales, ranging from hypo-metabolism within a single dive, to protracted seasonal changes (Boyd 2002). Marine predators employ a

suite of behavioural and physiological mechanisms when diving that can greatly influence the rates of oxygen consumption, and understanding the complexity of these responses in relation to prey capture is an on-going challenge.

This paper therefore highlights the simplicity of existing foraging models for air-breathing marine predators, most of which focus on the need to maximize time in the prey field and perhaps this emphasis has been misplaced. As the sprinting pilot whales show us, there are a range of strategies that work. These whales behave in a way that is far from optimal from the perspective of energy conservation, making expensive sprints, but this is a strategy that pays off because of the large return. Comparisons with terrestrial systems remain problematic. An obvious contrast to the cheetahs of the title is that large predators such as cheetahs capture prey that are close to their own body mass, representing a rich source of energy, and the successful hunter doesn't need to hunt again for a relatively long time. In the case of the pilot whales, the prey are relatively small, and so successful hunters cannot rest on their laurels, but need to hunt again almost immediately. The other obvious difference is that cheetahs don't have to sprint while holding their breath!

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