



## SYMPOSIUM

# Locomotion and the Cost of Hunting in Large, Stealthy Marine Carnivores

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**Synopsis** Foraging by large (>25 kg), mammalian carnivores often entails cryptic tactics to surreptitiously locate and overcome highly mobile prey. Many forms of intermittent locomotion from stroke-and-glide maneuvers by marine mammals to sneak-and-pounce behaviors by terrestrial canids, ursids, and felids are involved. While affording proximity to vigilant prey, these tactics are also associated with unique energetic costs and benefits to the predator. We examined the energetic consequences of intermittent locomotion in mammalian carnivores and assessed the role of these behaviors in overall foraging efficiency. Behaviorally-linked, three-axis accelerometers were calibrated to provide instantaneous locomotor behaviors and associated energetic costs for wild adult Weddell seals (*Leptonychotes weddellii*) diving beneath the Antarctic ice. The results were compared with previously published values for other marine and terrestrial carnivores. We found that intermittent locomotion in the form of extended glides, burst-and-glide swimming, and rollercoaster maneuvers while hunting silverfish (*Pleuragramma antarcticum*) resulted in a marked energetic savings for the diving seals relative to continuously stroking. The cost of a foraging dive by the seals decreased by 9.2–59.6%, depending on the proportion of time gliding. These energetic savings translated into exceptionally low transport costs during hunting ( $COT_{HUNT}$ ) for diving mammals.  $COT_{HUNT}$  for Weddell seals was nearly six times lower than predicted for large terrestrial carnivores, and demonstrates the importance of turning off the propulsive machinery to facilitate cost-efficient foraging in highly active, air-breathing marine predators.

## Introduction

A defining characteristic of animals, especially predatory animals, is their mobility, and for millennia scientists have been fascinated by the way in which highly mobile animals move. Technological advances in visualizing and recording swinging legs, flapping wings, and sweeping flippers have helped to satisfy this curiosity and driven the science of animal locomotion forward by providing an unprecedented view of predation on land, in air, and in water. As early as the late 1800s, Eadweard Muybridge revealed the nuances of galloping horses, walking lions, hopping kangaroos, and flying eagles through revolutionary stop-motion photography (Muybridge 1987). More recently, techniques such as high speed videos of feeding fish (Mehta and

Wainwright 2007), accelerometer recorders on pouncing felids (Wilson et al. 2013a; Scantlebury et al. 2014; Williams et al. 2014) and lunging blue whales (Goldbogen et al. 2013), digital particle-image velocimetry of hovering hummingbirds (Warrick et al. 2005), swimming dolphins (Fish et al. 2014) and fishes (Lauder and Drucker 2002; Flammang et al. 2013), as well as camera-toting Weddell seals diving 400 m below the Antarctic sea ice (Davis et al. 1999; Williams et al. 2004) have demonstrated how wild animals obtain food. The question that often remains, however, is what energetic costs did the hunter incur for such predatory movements?

The key to efficient foraging, regardless of the environmental media in which it takes place, is an

economy of movement that prevents the cost of moving body parts from overwhelming the energetic benefits of eating mobile prey (Stephens et al. 2007). For aquatic vertebrates the work of Paul Webb and Danny Weihs and their colleagues have provided a remarkable foundation for understanding how form and function in fish support their feeding and their avoidance of being eaten by larger aquatic predators. The generalized conclusions from Webb's and Weihs' collective work are that swimming movements are energetically expensive, and that adaptations in body form and locomotor machinery among aquatic vertebrates provide a myriad of ways that mitigate these costs and facilitate efficiency (see Webb 1975; Webb and Weihs 1983). Often, it is the capability for intermittent swimming that dictates the energetic efficiency leading to successful predation and survival (Webb 2002; Weihs 2002a).

### Building an efficient swimming predator

In 1982, Webb defined the optimum morphologies for steady and unsteady swimmers among actinopterygian fishes, building on the hydrodynamic theories of Lighthill (1971), Alexander (1967, 1968), Weihs (1972, 1973), Wu et al. (1975), and many others (see Webb 1975, 1982). For steady swimmers, a narrow peduncle, a rigid streamlined body, and a tail with a large aspect ratio, as exemplified by tuna, maximized thrust while minimizing drag. In comparison, the five key features of an unsteady swimmer, such as a pike, include a large caudal fin and body area, a flexible body, a deep caudal peduncle, an anterior stabilizing mass, and a large muscle-mass to body-mass ratio to support fast starts and fast turns necessary for overtaking prey. From theoretical and biomechanical tests, these investigators found that the diversity in body form of fishes was based on optimum shapes that reduced the waste of energy during drag and recoil movements as the animals performed routine foraging behaviors; form was elegantly matched to feeding function (Webb 1984a, 1988; Weihs 1989).

Importantly, many fish species, particularly those feeding on mobile prey, have been found to rely wholly or in part on unsteady locomotion. A generalized, streamlined (fusiform) body shape with a large caudal propeller is considered the ideal compromise between efficient steady swimming and the need for periods of high-powered, unsteady swimming to catch elusive prey, escape from larger predators, and deal with unpredictable movements of the water (Webb 2002; Weihs 2002b). Consequently, the hunting strategies of fish and their successful predation are

correlated to body shape and style of swimming. Fish such as tuna are built for steady swimming. They optimize rates of encountering prey through high-speed cruising but succeed in only 10–15% of their strikes. Conversely, those species built for unsteady swimming (i.e., pike) show capture rates five to seven times higher. Because of their sit-and-wait predation strategies, these unsteady swimmers sacrifice the rate of encountering prey. The hunting success of swimming generalists represents a compromise between steady and unsteady swimming, and fall between these two extremes (Webb 1984b).

### Evolutionary building blocks as constraints for hunting in marine mammals

Specialization for aquatic hunting by air-breathing vertebrates, including marine mammals and aquatic birds, is far less straightforward than for fishes. This is due to a complicated evolutionary history that involved the transition from land to sea, with accompanying ancestral physiology and morphologies (Williams 1999; Berta et al. 2005). As observed for fish (Romer 1966; Lauder 1980; Webb 1982), internal changes likely accompanied external morphological changes that facilitated locomotor efficiency in mammals living in water. However, for marine mammals the internal building blocks for hunting while diving, involved tolerance or modification of physiological, biochemical, and molecular mechanisms originally adapted for terrestrial activities.

In general, hunting is considered one of the most energetically costly of activities for terrestrial carnivores (Gorman et al. 1998; Scantlebury et al. 2014; Williams et al. 2014), especially those events involving maneuvering and fast transitions between activity states (Wilson et al. 2013a, 2013b). In view of this, one might expect that limited on-board oxygen stores required for supporting aerobic processes would constrain energetically expensive hunting tactics in diving mammals that must locate, chase, and consume prey while holding their breath. Despite this, many species of marine mammal demonstrate exceptional speeds and complex maneuvers during foraging (Aguilar de Soto et al. 2008; Goldbogen et al. 2013). Rather than a simple constraint, the physical separation of two critical resources, air at the water's surface and prey at depth, may have led to a unique selection pressure for locomotor efficiency in pinnipeds, cetaceans, and other mammalian groups that hunt while submerged.

Recently, we have begun to use miniaturized accelerometer recorders to evaluate the impacts of

individual locomotor maneuvers on energetic costs in marine (Williams et al. 2004) and terrestrial (Williams et al. 2014) carnivores. Here we specifically ask, did marine mammals follow the same rules as fish for efficient unsteady swimming and success as an aquatic predator?

## Methods

To address this question we examined the physiological responses, swimming behavior, hunting tactics, stroking mechanics, and energetics of free-ranging Weddell seals (*Leptonychotes Weddellii*) instrumented with a suite of submersible monitors. Since 1997, our instruments have included video-data recorders (Davis et al. 1999), two-axis and three-axis accelerometers with pressure meters incorporated into the instruments, as well as electrocardiographic monitors (ECG-ACC depth recorder; UUB/4-EIAP ECG/IBI/Acceleration/Pressure Recording System, UFI, Morro Bay, CA) deployed separately, or in combination, on adult seals to determine how the animals move and forage throughout their dives (Davis et al. 1999; Fuiman et al. 2002, 2007; Williams et al. 2004, 2015). Combined with open-flow respirometry to measure post-dive oxygen consumption, these instrument have allowed us to precisely match instantaneous physiological responses to encounters with prey, swimming biomechanics, activity level, underwater behaviors, and depth. In addition, we have been able to determine the effect of environmental factors on these energetic costs.

### Animals and instrumentation

Adult male and adult female Weddell seals ( $n = 53$ , body mass = 252–561 kg) were captured in McMurdo Sound near Ross Island, Antarctica, during the winter and austral spring 2009–2010 and austral summer in 1997–1999, 2001–2002, and 2014. Details of capture, attachment, and recovery of animal-borne instruments, as well as calibrations with energetics have been described previously (Davis et al. 1999; Williams et al. 2004, 2015). In general, adult seals were instrumented with a miniaturized video-data acquisition (VDAP) platform and other microprocessors attached to neoprene patches glued onto the fur of the animals. The video camera was placed on the head of the seals to provide an “over-the-nose” view throughout the dive. This placement allowed foraging events, encounters with competing seals, and other behaviors to be monitored continuously. The swaying of the head that occurs as an anterior recoil with each stroke of the hind flippers by the seals was recorded on the videos

and used to test the accuracy of the accelerometers in detecting stroking patterns. The recording unit of the VDAP and the accelerometer were placed on the dorsal side of the seal with the latter towards the tail to capture stroking events. The video camera was encircled by an array of near-infrared LEDs that enabled images to be recorded underwater in complete darkness to a distance of approximately 1 m in front of the seals. Based on maximum visual sensitivity, the near-infrared LED light is invisible to the seals and their prey, thus preventing disruption of normal behaviors (Davis et al. 1999). Instrumented animals were released into a nearby ice hole and were free to dive and forage for approximately 5–21 days, at which point the seals were recaptured and the instrumentation removed for download and analysis of data.

### Diving behavior and mechanics

Both successful foraging and non-foraging dives (confirmed from capture events on accompanying videos) were evaluated. Maximum depth of individual dives was dependent on location in McMurdo Sound and ranged in this analysis from immediately below the surface ice to 580 m.

Behaviors underwater included foraging tactics and stroking mechanics classified according to mode of swimming (unsteady burst-and-glide, continuous stroking, gliding). Predation events were determined from video recordings and accelerometer signatures resulting from extreme activity of the fore-flippers, head, and neck as occur during the consumption of fish. Accelerometer signatures were developed by correlating peak amplitudes and profiles from each axis of the accelerometer to captures of fish confirmed from the video-data recorder. Each video was screened for encounters with prey items, with fish species identified by size, shape, and pigmentation according to the method of Fuiman et al. (2002). In the present study, only encounters with Antarctic silverfish (*Pleuragramma antarcticum*) are included in the analyses. Due to the position of the camera we are able to view the proximity of the silverfish relative to the muzzle of the seal, but not see the opening of the mouth in all cases. Therefore, we use “encounter” to denote fish in the proximity of the muzzle with capture and ingestion presumed if the proximity is less than approximately 10 cm of the mouth of the seal.

Swimming mechanics were determined from lateral sweeps of the posterior half of the body and hind flippers of the seals (Fish et al. 1988) as recorded from accelerometers placed on the backs of the animals. Sampling rate of the accelerometer

microprocessors ranged from 16 to 100 Hz which was synchronized with depth, time, video images, and heart rate (when recorded) from the other instruments. Stroke frequency during descent, when on the bottom, and during ascent was determined for each dive by visually counting the number of stroking cycles in 10 s intervals, using UFI Biolog software (Morro Bay, CA) that integrated depth with accelerometer data. Swimming mode, relative amplitude of strokes, and duration of glides were similarly determined. Because the video-data recorder includes sensors for speed and depth, accelerometers, and a magnetometer (Davis et al. 1999), we were able to determine the instantaneous direction and distance traveled by the seals for construction of three-dimensional diving paths (Fuiman et al. 2007).

### Energetic costs

Pre-dive and post-dive oxygen consumption from a subset of Weddell seals ( $n=9$ ) diving from an isolated ice hole was used to determine total aerobic costs, the cost per stroke, as well as the cost of transport during hunting. Methods for open-flow respirometry for marine mammals have been described by Williams (2001) and Williams et al. (2004) following the protocols of Castellini et al. (1992) for Weddell seals. Briefly, breathing by instrumented seals before and after dives was restricted to a Lexan dome (2.4 m long  $\times$  1.1 m wide  $\times$  0.4 m high) mounted over the breathing hole in the ice. Air was drawn through the dome at 510–550 l min<sup>-1</sup> using a vacuum pump connected to a flow meter and oxygen analyzer (Sable Systems International, Inc., Henderson, NV). Samples of the air were dried (Drierite, Hammond Drierite Co., Xenia, OH) and scrubbed of carbon dioxide (Sodasorb, Chemtron, St Louis, MO). The percentage oxygen in the expired air was monitored continuously and recorded at 1 Hz on a laptop computer using Sable System Expedata software. Calibration of the system and analyses for rates of oxygen consumption are as presented by Williams et al. (2004).

The total energetic cost for stroking periods during the dives was determined by multiplying the number of strokes by 2.39 J kg<sup>-1</sup> stroke<sup>-1</sup> for adult Weddell seals (Williams et al. 2004). Locomotor cost, which describes the energy expended for propulsion only, was determined by dividing the net recovery oxygen consumed during the post-dive period of aerobic dives by the total number of strokes executed during the entire dive (Equation (1) in Williams et al. 2004). The net cost per stroke was then

calculated from the slope of the relationship between locomotor cost and number of strokes for each dive. The resulting stroke cost, 0.044 ml O<sub>2</sub> kg<sup>-1</sup>, was used to determine foraging costs from Equation (9) in Williams et al. (2004) that takes into account body mass, duration of foraging, stroke cost, and number of strokes for each dive.

### Analysis and statistics

Accelerometer outputs and the depth were recorded continuously for each dive. The number of full cycles for each swimming stroke, based on patterns of acceleration, were manually counted using UFI, Inc. software at 10 s intervals for the entire dive. The seal's position during a dive was computed every 1 s from the depth, compass bearing, and swimming speed recorded by the onboard sensors of the VDAP (Fuiman et al. 2002), and used to determine total distance traveled. Linear regressions for the relationships between stroke frequency and speed, distance swum, and total number of strokes executed on a dive, as well as transport costs in relation to body mass, were determined by least-squares methods using statistical software (SYSTAT 2005). The dives used in this analysis were classified as aerobic based on dive duration, and post-prandial based on the duration of fasting (Williams et al. 2004). Mean values  $\pm 1.0$  SEM are presented unless otherwise indicated.

### Results and discussion

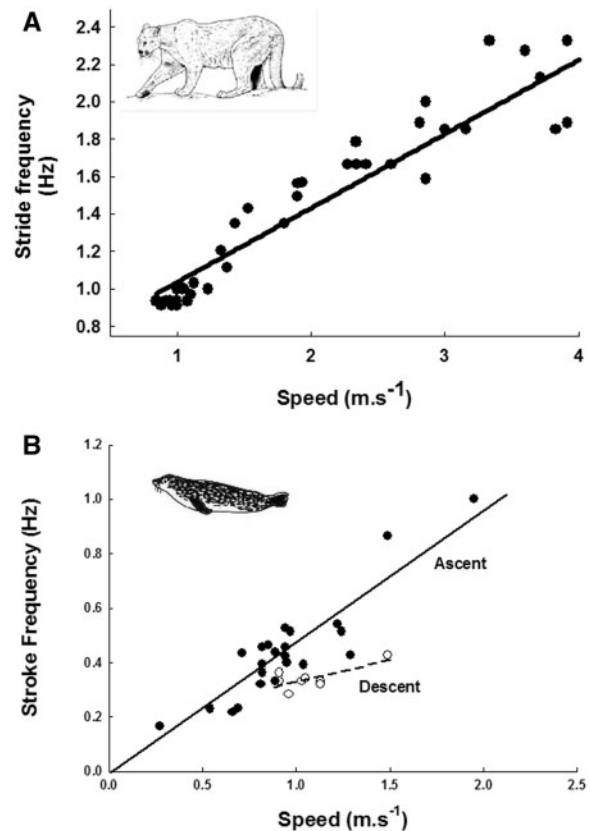
From external appearances it is apparent that marine mammals have followed many of the same morphological and hydrodynamic rules that promote cost efficient swimming by fishes. These include, (1) a streamlined body shape for low-drag swimming, (2) lift-based propulsion throughout the stroking cycle, (3) preferred speeds that avoid high drag, and (4) use of cost-efficient swimming gaits. Thus, across six of seven major mammalian lineages leading to marine-adapted mammals (Reeves et al. 2002), the morphology of the body approaches the optimum shape for minimization of drag and for efficient movement through water (Fish 1993). The fineness ratio, a metric of streamlining based on the ratio of total length to maximum diameter of the body, of most marine mammals remains within 30% of the theoretical optimum of 4.5 for a body of rotation and is typically within 10% of the associated minimum drag.

Similarly, the swimming style of marine mammals follows many of the form-function patterns of performance proposed for fishes by Webb (1975, 1984a)

and Weihs (2002a, 2002b). As pursuit predators foraging on highly mobile prey, cetaceans and pinnipeds have evolved from the drag-based paddle style of swimming characteristic of their terrestrial ancestors to the lift-based propulsion with hydrofoils typical of fishes (Fish 1993). Only the polar bear has retained the energetically inefficient stroke-recovery dog paddle. The lift-based swimming mode of highly derived marine mammals allows for efficient, rapid, high-powered propulsion. However, there are notable limits in performance compared with fishes. Preferred speeds of marine mammals are comparatively narrow ( $1.1\text{--}1.8\text{ m s}^{-1}$ ) across body masses ranging from 50-kg porpoises to 30,000-kg sperm whales (Sato et al. 2007). In addition, extreme morphological specialization in the form of marked narrow-necking of the caudal peduncle, as seen in high-speed tuna is rare among extant marine mammals. Such specialization reduces the magnitude of energy-wasting side forces that contribute to lateral recoil of the swimmer's anterior (head wag), a condition that was evident in the videos of the Weddell seals.

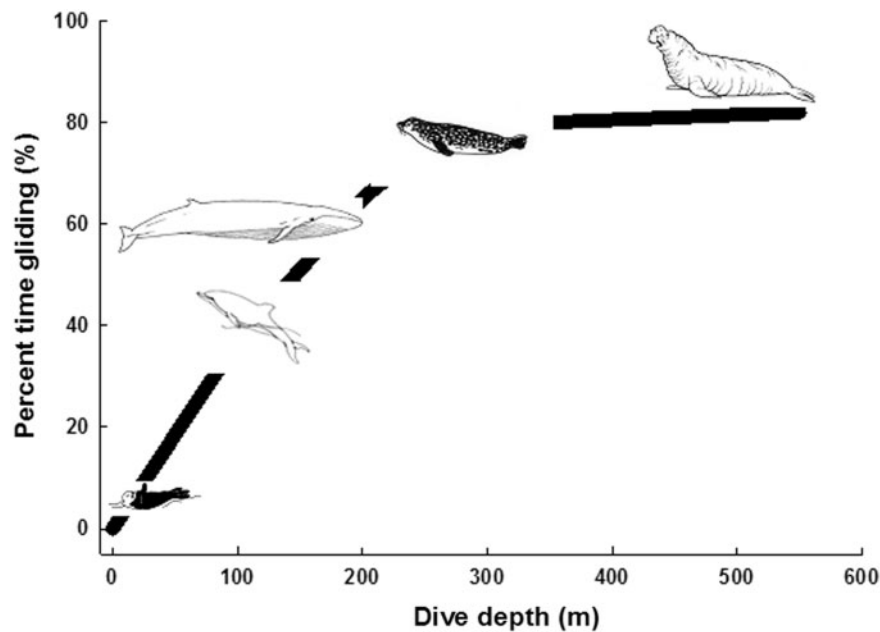
As noted above, the selection pressures on internal physiological processes differ markedly between fishes and marine-adapted mammals due to the necessity to surface to breathe by the latter. With oxygen stores serving as a critical limiting resource, we find that the success of a foraging marine mammal in capturing prey is comparatively high once prey are located. Thus, the capture success of seals approaches the 70–80% level of unsteady swimmers such as pike rather than the 10–15% success rate of cruising tuna (Webb 1982). Furthermore, Weddell seals incorporate a variety of swimming modes including extended glides, burst-and-glide swimming, and a rollercoaster pattern of movements that vary in the duration of pauses in active stroking, and contribute to overall foraging efficiency while hunting silverfish (*P. antarcticum*).

Each swimming stroke by diving marine mammals represents a debt to be paid from on-board stores of oxygen sequestered in the tissues. Like fishes, both terrestrial and marine mammals show linear increases in the frequency of limb movements as forward speed increases (Fig. 1). However, there is an important caveat for free-ranging seals. In contrast to the ascent phase of dives, stroke frequency during descent is decoupled from speed in Weddell seals. This is due primarily to the incorporation of prolonged (>12 s) periods of gliding during descent, which is characteristic for a wide variety of marine mammals (Fig. 2; Williams et al. 2000). For dives exceeding 80 m in depth, over 78% of the Weddell seal's descent may



**Fig. 1** Stride mechanics of running mountain lions (A) compared with stroke mechanics of diving Weddell seals (B). Stride frequency and stroke frequency for aerobic performance are plotted in relation to speed for lions running on a level outdoor course, and for seals diving below the Antarctic sea ice. Each point represents a single exercise trial or dive. Solid lines show the least squares linear relationships through the data points as described by, stride frequency =  $0.64 + 0.40$  speed ( $n = 40$ ,  $r^2 = 0.88$ ,  $P < 0.0001$ ) and stroke frequency<sub>ascent</sub> =  $0.50$  speed ( $n = 24$ ,  $r^2 = 0.82$ ,  $P < 0.0001$ ). Note the change in the relationship during descent (open symbols) where stroke frequency<sub>descent</sub> =  $0.17 + 0.16$  speed ( $n = 8$ ,  $r^2 = 0.52$ ,  $P < 0.0450$ ). Data are from Williams et al. (2014) for lions and the present study for seals.

be spent gliding rather than actively stroking. This ability to “turn the motor off” has been attributed to changes in buoyancy with compression of the lungs at depth and allows the seals to maintain average swimming speeds during descent of  $1.1\text{ m s}^{-1}$  without actively stroking. Variations in this strategy among marine mammals include gliding on ascent by exceptionally buoyant species such as right whales (Nowacek et al. 2001), and changes in the speed of gliding due to seasonal fluctuations in stored body fat (Biuw et al. 2003; Mitani et al. 2010). Incorporating this intermittent mode of swimming affords an energetic advantage, with Weddell seals realizing a 9.2–59.6% reduction in the energetic costs of diving relative to



**Fig. 2** Percentage of the time spent gliding during descent in relation to depth of the dive for five species of marine mammal (sea otter, bottlenose dolphin, blue whale, Weddell seal, elephant seal). Except for the dolphins, the range in depth was determined by the free-ranging behavior of the animals. Data include values from the present study (Weddell seals), unpublished data (sea otters, T.M. Williams), and from Williams et al. (2000).

continuous stroking, depending on depth (Williams et al. 2000). This saving of energy translates into increased duration of aerobic dives, and hence of foraging time, despite limited availability of oxygen when submerged.

Rather than a single style, the swimming modes of Weddell seals varied considerably throughout a dive, and corresponded to changes in energetic costs. Swimming modes alternated between gliding on descent, burst-and-glide swimming on ascent, and continuous stroking on initial ascent and during capture of prey (Fig. 3). Such variability and use of interrupted modes of swimming are typical of aquatic vertebrates from sharks to pinnipeds, and have been shown to provide an energetic advantage over continuous locomotion (Williams et al. 2000; Gleiss et al. 2011). Interestingly, large-scale migrations both of birds and of mammals (Davis and Weihs 2007; Gleiss et al. 2011; Bishop et al. 2015) and the intra-dive foraging periods of pinnipeds (Fig. 4) often incorporate a rollercoaster series of powered and non-powered phases which can result in enhanced performance, and in energetic benefits (Fig. 5), depending on the context.

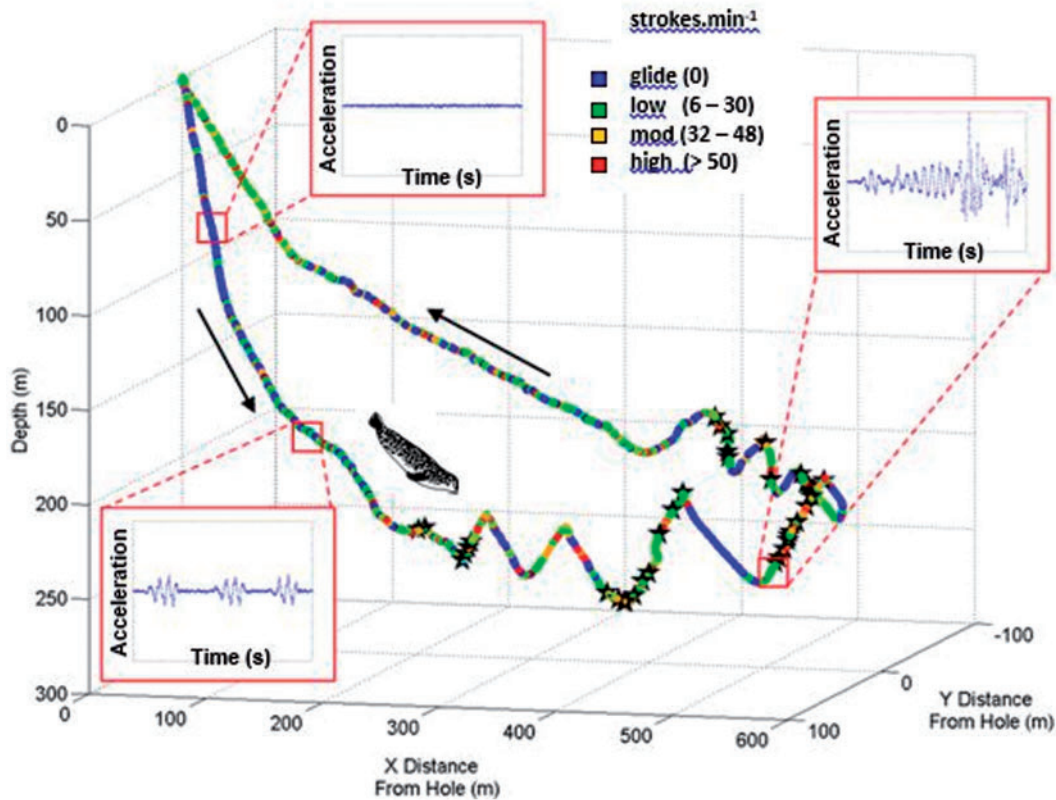
For the foraging seals, each rollercoaster dip and rise was associated with a low-frequency ( $7.2 \pm 0.7$  strokes  $\text{min}^{-1}$ ,  $n=489$ ) stroking descent followed by a moderate stroke frequency ( $28.5 \pm 0.8$  strokes  $\text{min}^{-1}$ ,  $n=790$ ) ascent and encounters with fish (Figs. 4 and 5; Williams et al. 2015). Only rarely

did the seals feed on descent. Currently, we cannot distinguish between energetic and tactical advantages provided by these maneuvers. During periods of high ambient light in McMurdo Sound, Weddell seals attacked silverfish from below 81% of the time. It is unclear whether the seals were using backlighting to enhance visual contrast, minimizing its own visual contrast, or simply positioning itself out of the fish's visual field to enhance capture success. Regardless of whether or not the rollercoaster movements allow the seals to surreptitiously strike prey from below, the use of intermittent stroking clearly provides an instantaneous energetic benefit. Average instantaneous costs alternated between  $17.2 \pm 1.6$  J  $\text{kg}^{-1} \text{min}^{-1}$  ( $n=489$ ) and  $68.2 \pm 2.0$  J  $\text{kg}^{-1} \text{min}^{-1}$  ( $n=790$ ) on each dip and rise of the foraging period, respectively (Fig. 5). Overall, the energy expended performing this rollercoaster series of movements constituted a major cost to foraging seals compared with the energy expended for descending or ascending (Fig. 4 inset). This was due both to the relative duration of each period as well as to the number of strokes taken.

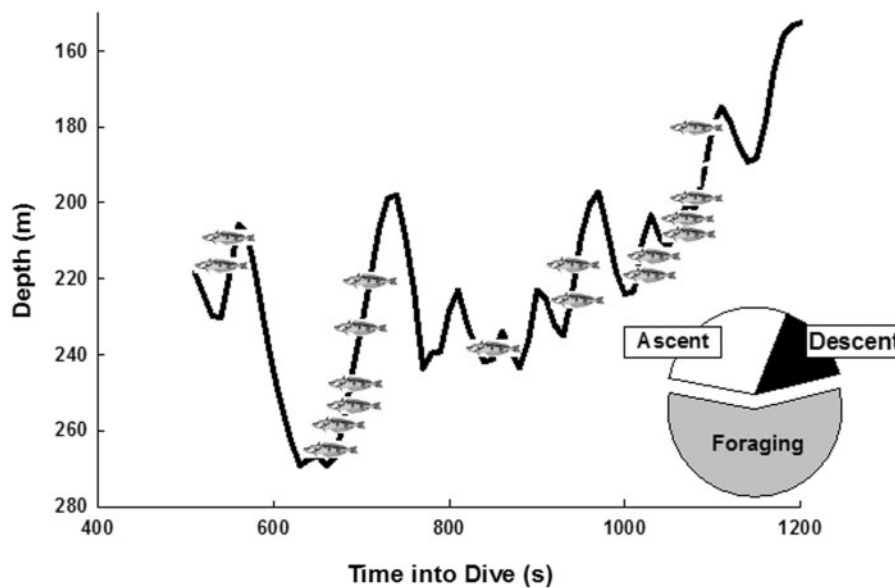
As might be expected, the distance swum by Weddell seals depended on the total number of strokes taken, according to the relationship,

$$\text{Distance swum} = 218.4 + 2.58(\text{stroke number}) \quad (1)$$

$$(n = 143 \text{ dives}, r^2 = 0.91, P < 0.0001),$$



**Fig. 3** Representative foraging dive for a Weddell seal feeding on Antarctic silverfish. The three-dimensional dive plot shows depth in relation to distance from a breathing hole and is color-coded for stroke frequency. Black stars show encounters and captures of silverfish by the seals during the rollercoaster segment. Corresponding acceleration versus time traces illustrating the three primary swimming modes: gliding (blue), stroke-and-glide (intermittent blue and green), and constant, high-amplitude stroking prior to, and during, the capture of fishes and initial ascent (green to orange-red) are presented in the insets. Each dot represents 1 s. (Redrawn from Williams et al. 2015).



**Fig. 4** Detailed illustration of depth in relation to time into the dive for a Weddell seal feeding on Antarctic silverfish. Fish symbols denote the point of encounter and capture. Seals alternate gliding periods during descent phases with powered ascents and captures of fish when performing this rollercoaster foraging tactic. The inset chart shows the relative energetic costs for foraging during this period (gray), compared with ascent (white) and descent (black) phases of the dive.

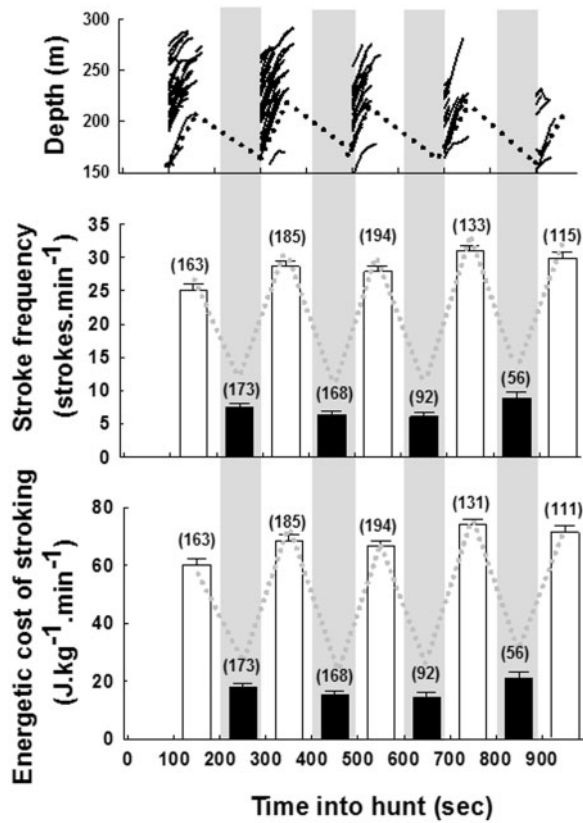


Fig. 5 Sequential changes in depth of the dive (top), stroke frequency (middle), and energetic cost of stroking (bottom) in relation to time during descent (black bars, gray column) and ascent (white bars) of the rollercoaster segment of foraging dives of Weddell seals ( $n=41$  dives). Black lines in the top panel illustrate the change in depth during powered ascents and captures of fish. The dotted black line represents a schematic of the general rollercoaster pattern for all seals. Bars and whiskers in the middle and bottom panels are mean  $\pm 1$  SEM. Numbers in parentheses represent the number of data points for all dives.

where distance is in total meters swum along the dive path calculated at 1 s intervals as described by Williams et al. (2004) and stroke number represents the total stroke cycles executed during the dive (Fig. 6). Using this relationship and the instantaneous costs determined from stroking patterns during the foraging period, we were able to calculate the energetic costs of transport during hunting ( $COT_{HUNT}$ ) from

$$COT_{HUNT} = \frac{\text{energetic cost}}{\text{distance traveled}}. \quad (2)$$

Here, energetic cost is represented by post-dive recovery costs in  $\text{mlO}_2 \text{ kg}^{-1}$  determined from Equation (9) in Williams et al. (2004) and the distance traveled is in  $m$  from Equation (1). These hunting costs are distinguished from minimum transport costs ( $COT_{MIN}$ ) by taking into account the complexities and intermittent locomotion required for moving across wild

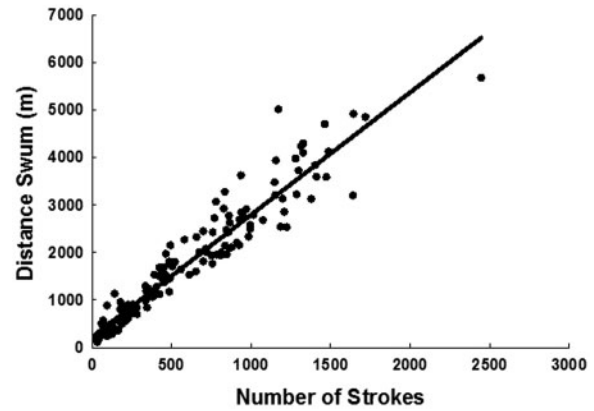


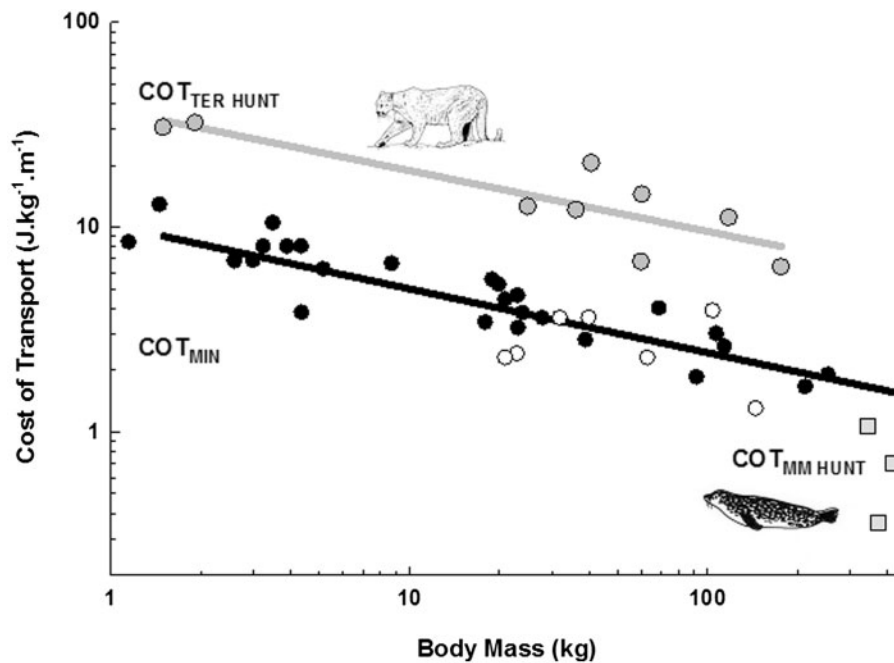
Fig. 6 Total distance swum in relation to number of strokes taken during a dive for free-ranging Weddell seals ( $n=143$  dives from eight seals). Each point represents an individual dive. The solid line shows the least squares linear relationship through the data points as described in the text. Note that only aerobic dives, as determined from Williams et al. (2004), are used in this analysis.

landscapes and seascapes. In contrast,  $COT_{MIN}$  is typically determined from linear, level running on a treadmill or from constant swimming in a flume.

We have previously reported that the energetic demands for predatory movements by large terrestrial mammals average 3.8 times the predicted  $COT_{MIN}$  (Williams et al. 2014). These exceptional costs have been attributed to the energetic expenditures associated with intermittent locomotion, turning maneuvers, and kinematic changes due to uneven or variable substrates (Kramer and McLaughlin 2001; Bidder et al. 2012; Wilson et al. 2013b). In the present study, we find that intermittent locomotion in the form of extended glides, burst-and-glide swimming, and a rollercoaster pattern of movements results in the opposite pattern for wild Weddell seals (Fig. 7). For these swimmers, intermittent swimming promotes energetic efficiency such that  $COT_{HUNT}$  is 2.2 times lower than the predicted  $COT_{MIN}$ .

Overall, this study demonstrates that Weddell seals dive conservatively, using a variety of swimming modes to minimize the number of swimming strokes performed during a dive. Benefits include the parsimonious use of limited stores of oxygen, which maximizes the time spent submerged while foraging, and promotes a high rate of prey-capture relative to many species of fish (Webb 1984a). Furthermore, because constant stroking at depth has been associated with cardiac instability both in pinnipeds and in cetaceans (Williams et al. 2015), intermittent swimming may also promote physiological constancy for this group of swimmers that once evolved from terrestrial mammals.





**Fig. 7** Energetic transport costs in relation to body mass for marine and terrestrial mammals. Minimum costs of transport ( $COT_{MIN}$ ) for terrestrial mammals on treadmills (black circles) and marine mammals swimming in flumes (open circles) are described by a single regression (black line) as presented in Williams (1999). Transport costs during hunting by free-ranging carnivorous mammals differ from this minimum, with the costs to wild terrestrial mammals ( $COT_{TER\ HUNT}$ ; gray circles, and line presented in Williams et al. 2014) and marine mammals ( $COT_{MM\ HUNT}$ ; gray squares representing three Weddell seals in the present study) showing higher and lower energetic costs, respectively.

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