



Rush and grab strategies in foraging marine endotherms: the case for haste in penguins

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The speed at which air-breathing marine predators that forage by diving should swim is likely to depend on a variety of factors that differ substantially from those relevant in animals for which access to oxygen is unlimited. We used loggers attached to free-living penguins to examine the speed at which three species swam during periods searching for prey and compared this to their speeds during actual prey pursuit. All penguin species appeared to travel at similar speeds around 2 m/s during normal commuting between the surface and feeding depths, which accords closely with minimum costs of transport. However, Adélie penguins, *Pygoscelis adeliae*, slowed down to feed, Magellanic penguins, *Spheniscus magellanicus*, speeded up and king penguins, *Aptenodytes patagonicus*, travelled at a variety of speeds, although mean speed did not change from normal commuting. Since energy expenditure, and therefore oxygen usage, in swimming animals increases with the cube of the speed, we hypothesized that prey escape speed (a function of prey size) and prey density would prove critical in determining optimum pursuit speeds in predators. Simple models of this type help explain why it is that some penguin species apparently benefit by increasing speed to capture prey while others benefit by decreasing speed.

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Both terrestrial and aquatic predators have two main strategies for securing prey: sit and wait and active pursuit (e.g. Nagy & Shoemaker 1984; Secor & Diamond 1998). Both entail quite different energetic expenditures with the pursuers tending to expend energy at relatively higher rates but recouping appropriately high energetic gains (e.g. Secor 1995). High rates of energy expenditure (e.g. Suarez 1992, 1996; Hammond & Diamond 1997) can be tenable for extended periods provided that enough oxygen is accessible to maintain aerobic metabolism and there is adequate substrate availability within the body (Jones & Lindstedt 1993; Suarez 1998). The situation is more complex, however, in species that actively pursue to feed but operate in environments where oxygen is not available to them, for example air-breathing marine predators such as cetaceans, pinnipeds and some seabirds (Thompson et al. 1993; Boyd et al. 1995; Butler & Jones 1997).

There are fairly well-defined rules for optimum speeds in animals during normal travel whether this be walking (e.g. Pinshow et al. 1977), flight (see e.g. Pennycuik

1997) or swimming (Culik et al. 1994b; Hind & Gurney 1997; Lovvorn et al. 1999). However, power requirements for swimming increase as a cubed function of the speed (e.g. Bannasch 1995) and because many air-breathing predators exploit multiple prey from a patch underwater during single dives (Wilson 1995) it is not necessarily optimal for such animals to pursue prey at their maximum speed.

We used loggers on three species of free-living penguin to examine their speeds during normal underwater swimming and during prey pursuit, hypothesizing that where inter- and intraspecific differences are observed, they can be explained in terms of birds maximizing foraging efficiency according to the behaviour of the prey. In an attempt to define the effect that prey behaviour might have on pursuit speed we developed a simple model to see whether observed patterns might be explained by (1) prey escape speed (itself a function of prey size) and (2) prey density.

METHODS

We used three types of logger to measure swim speeds.

(1) UWE200PDT (speed, temperature, depth) loggers (102 × 20 mm diameter, 50 g; Little Leonardo, Tokyo, Japan) with a memory of 12 Mb and 12 bit resolution, set

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to record swim speed and dive depth at 1-s intervals. Swim speed was measured as the number of rotations of an anteriorly mounted propeller. We calibrated these units by towing them in a pool at speeds (0–2.5 m/s) determined by an electric reel and ascertained the general validity of the calibrations by plotting rate of change of depth acquired from free-living birds against measured swim speed for all recorded values and assuming that the lowest number of propeller rotations corresponded to the same speed at the maximum rate of change of depth for birds swimming vertically up or down the water column (Fletcher et al. 1996; Crocker et al. 1997; Blackwell et al. 1999).

(2) KS400PDT (speed, temperature, depth) loggers (110 × 25 mm diameter, 81.5 g; Little Leonardo, Tokyo, Japan) with a memory of 12 Mb and 12 bit resolution, set to record swim speed and dive depth at 1-s intervals (see details in Ropert-Coudert et al. 2000). Swim speed was measured as the number of rotations of an anteriorly mounted propeller and this was converted to flow speed (m/s) by the same method as that used for UWE200PDT loggers.

(3) DKLOG 600 (speed, temperature, depth, direction, light intensity) loggers (140 × 58 × 25 mm, 160 g; Driesen & Kern GmbH, Bad Bramstedt, Germany) with a memory of 2 Mb and 16 bit resolution, set to record swim speed at 2- or 4-s intervals. Swim speed was measured by a differential pressure sensor using the Prandtl tube principle. Units were calibrated on a life-sized model of a penguin in a swim canal (21 m long) and run at speeds between 0 and 2 m/s (for Magellanic penguins, *Spheniscus magellanicus*).

The differences in logger mass stem primarily from different hardware configurations of the systems used to study the birds which were developed over a number of years. Despite this, all systems were hydrodynamically shaped according to suggestions in Bannasch et al. (1994) and Culik et al. (1994a) to reduce drag. Not all units were tested to determine their drag but similar units tested on Adélie penguins, *Pygoscelis adeliae*, in a swim canal (see Culik et al. 1994a) increased energy expenditure of birds swimming at 2.2 m/s by 6.1%. This figure is likely to be comparable in Magellanic, which are roughly the same size, and less in king penguins, *Aptenodytes patagonicus*, which are ca. three times heavier than Adélie penguins (Williams 1995).

Loggers measuring swim speeds were always deployed on breeding penguins (with chicks) for a minimum of one foraging trip and attached with tape (Wilson et al. 1997) or a system combining glue (Araldite) and plastic cable-ties to the birds' lower backs to reduce drag (Bannasch et al. 1994). The species equipped, the time of deployment and devices used were as follows: Adélie penguins, nine birds at Adélie Land, Antarctica (66°7'S, 140°0'E) equipped with UWE200PDT units between mid-December 1998 and mid-January 1999; king penguins, two birds equipped with KS 400PDT units at Possession Island (46°25'S, 51°45'E) between February and March 1996; and Magellanic penguins, five birds equipped with DKLOG 600 units at Cabo Virgenes (52°24'S, 68°26'W), Argentina in December 1999. Permission for the work to

be carried out was obtained from the Commission of the Terres Antarctiques Australes Françaises (for Adélie and king penguins) and the Guarda Fauna de la Provincia de Santa Cruz (for Magellanic penguins).

All birds were equipped following strict protocol procedures based on recommendations made regarding minimizing stress to birds. At Cabo Virgenes we caught, and recovered, birds on the nest by hand. The researcher used a modified clipboard (with a small indentation cut at one end) brought slowly up to the brooding bird's breast, so that the clipboard presented a flat surface in front of the bird. During this process the sitting birds looked over the flat surface of the clip-board but did not show a fight or flight reaction if the researcher maintained a low profile. The researcher then extended an arm under the board (hidden from the view of the bird by the board) and used a nongloved hand to capture the bird gently round the neck. The bird was then lifted slightly with the board still in place, until the body weight made the beak point slightly upwards so that the board could be slowly removed and the grip round the neck changed so that the inner part of the hand reached over the back of the neck so as not to impair breathing. The free hand was then used to support the body weight while the bird was transferred to the researcher's knees where it could be fitted with the appropriate device using the method described in Wilson (1997), developed to minimize stress during the handling of penguins. At Crozet and Durmont Durville, we caught birds on their departure to sea after exchange with their partner by using a blind net to decrease the stress of capture. After their foraging trip, we preferentially caught birds on the shore or, if the return was missed, at the nest site using the same blind net. In addition, guidelines recommended to minimize device effects (Wilson & Culik 1992) were adopted. This included particular device shapes (Bannasch et al. 1994; Culik et al. 1994a), colours (Wilson & Wilson 1989; Wilson et al. 1991) and positions (Bannasch et al. 1994).

All devices deployed were recovered after a mean wearing time ± SD of 34.6 ± 11.1 h in the Magellanic penguins, 26.0 ± 11.9 h in Adélie penguins and 17 and 25 days in the king penguins. All birds were recovered in good condition and did not appear to have suffered as a result of being equipped. After removal of the devices the birds continued tending chicks. No effects of compromised chick growth rates or unusual mortality were observed although at no site was the fate of the brood followed through to fledgling because of researcher time constraints.

Upon recovery of the birds, we removed the devices and downloaded the data on to computers via interfaces. Swim speed data were considered only for depths in excess of 10 m or 20% of the maximum dive depth, whichever was the deeper. This procedure eliminates high-speed subsurface swimming (Wilson 1995; Yoda et al. 1999) where particular energetic and predator avoidance conditions apply (Hui 1987; Yoda et al. 1999). The resulting speed data were considered in detail, being split into two: (1) bottom phases (where birds remained for extended periods at a particular depth; for definition see Le Boeuf et al. 1988) where depth changed erratically, this

being indicative of feeding behaviour (confirmed during deployment of stomach temperature and oesophageal loggers during previous studies on these three species; cf. Wilson et al. 1995; Ropert-Coudert et al. 2001); and (2) all other times. Therefore, two speed types were defined: the commuting speed, which was the swim speed of birds averaged during the commuting phase of dives, and the hunting speed, which was the swim speed of birds averaged during the hunting phase of dives. After pooling, speed data were used to derive speed frequency distributions.

RESULTS

Consideration of the data recorded at 1- or 2-s intervals indicated that during nonfeeding dives, Adélie, king and Magellanic penguins all executed dives that had an approximately V-shaped dive profile (denoted by a fairly constant descent and ascent and relatively little time spent at the point of maximum depth; Fig. 1) during which swim speed varied little, being of the order of 2 m/s (Fig. 1). However, there were interspecific differences in the way the birds reacted to prey. Although the forms of the descent and ascent phases in the depth profiles were similar to those of nonfeeding dives, there were extended bottom phases where speed changed abruptly, decreasing overall in the case of Adélie penguins, becoming more erratic in the case of king penguins, and increasing in the case of Magellanic penguins, although in this latter case this is less apparent because of systematic increases in speed as the birds surfaced (Fig. 1). Separate determination of the frequency distributions of speeds for commuting and prey pursuit showed that modal speeds for commuting were 2.0 m/s for both Adélie and Magellanic penguins while prey pursuit speeds were 1.8 and 2.1 m/s for Adélie and Magellanic penguins, respectively (Fig. 2). Mean commuting speeds \pm SD were 2.03 ± 0.36 , 1.91 ± 0.18 and 1.77 ± 0.40 m/s for Adélie, king and Magellanic penguins, respectively, while prey capture speeds were 1.70 ± 0.45 , 1.91 ± 0.39 and 2.25 ± 0.49 m/s.

Two-way ANOVA with replicates, with speed type (commuting or pursuit) as grouping factor and individuals as within factor, showed that the differences were highly significant in both Adélie and Magellanic penguins (Table 1). Although interactions were significant in both species, each individual Adélie penguin had hunting speeds that were slower than the commuting speeds, and each individual Magellanic penguin had commuting speeds that were slower than the hunting speeds (see detailed statistics in Appendix). In the case of king penguins, no significant differences were found between the two speed types (Table 1); however, analysis of the interactions between individuals and speed types revealed that this absence of difference occurred in only one of the two birds considered (see Appendix). A larger sample size for king penguins should help clarify the speed trends adopted during the different phases of dives. The significant interactions found in the three species may have resulted from the large number of dives used for calculations. Detailed consideration of speeds of Adélie

penguins during prey capture indicated considerable interbout variability according to patch: the same individual might swim at speeds of less than 1 m/s to exploit a particular patch and then, a few minutes later, swim in excess of 2 m/s to exploit another patch (cf. Fig. 3).

DISCUSSION

The attachment of external devices to marine animals is known to affect many aspects of foraging behaviour (e.g. Walker & Boveng 1995) and particularly relevant here is that penguin swim speed is reported to be reduced with increasing device size (Wilson et al. 1986). Appropriate device streamlining plays a major role, however, in minimizing such device effects (Bannasch et al. 1994) and for this reason our units were carefully shaped to this effect. Despite this, it is likely that our data underestimate speeds achieved by unequipped birds. We believe, however, that trends in swim speeds are likely to remain unchanged because, given the increase in drag imposed by attached devices, it is unlikely that penguins will swim faster than the lowest cost of transport unless there are very good reasons for so doing (see below).

Underwater swim speeds in many air-breathing marine predators, including penguins, can be grouped into four main categories according to the particular behaviour with which they are associated: porpoising; normal underwater swimming; predator evasion; and prey capture (Hooker & Baird 1999; Skrovan et al. 1999; Otani et al. 2000; Stelle et al. 2000). In our analysis we have attempted to identify and subsequently eliminate porpoising behaviour which has been discussed in some detail by various authors (e.g. Hui 1987; Blake & Smith 1988; Yoda et al. 1999). Furthermore, we do not consider predator evasion, which presumably does not occur very often and is likely to involve maximum speeds. In restricting ourselves to data where birds were diving relatively deeply we have, to a great extent, primarily isolated normal underwater travelling and prey capture speeds. It is generally accepted that the speeds at which penguins travel underwater (for a general discussion see Oehme & Bannasch 1989; Bannasch 1995) accord closely with their minimum cost of transport (COT; defined as the energy required to transport a given mass for a given distance: Tucker 1970; e.g. Culik et al. 1991; Culik & Wilson 1991). This allows predators to travel the maximum distance with minimal energy and is highly relevant for animals that encounter prey that must be located by extensive searching (Wilson 1995) and, more particularly, because these animals cannot breathe during such periods (Wilson et al. 1996). Our results indicate, however, that the speeds used during prey capture are highly variable interspecifically, and that these speeds do not conform either with those relevant for the lowest COT or for absolute maxima. Prey types of the penguin species considered here vary from highly mobile pelagic school fish, for example taken by Magellanic penguins (Scolaro et al. 1999), to less active myctophids (cf. Ropert-Coudert et al. 2000), taken by king penguins (Cherel & Ridoux 1992), and to slow-swimming (Kanda et al. 1982)

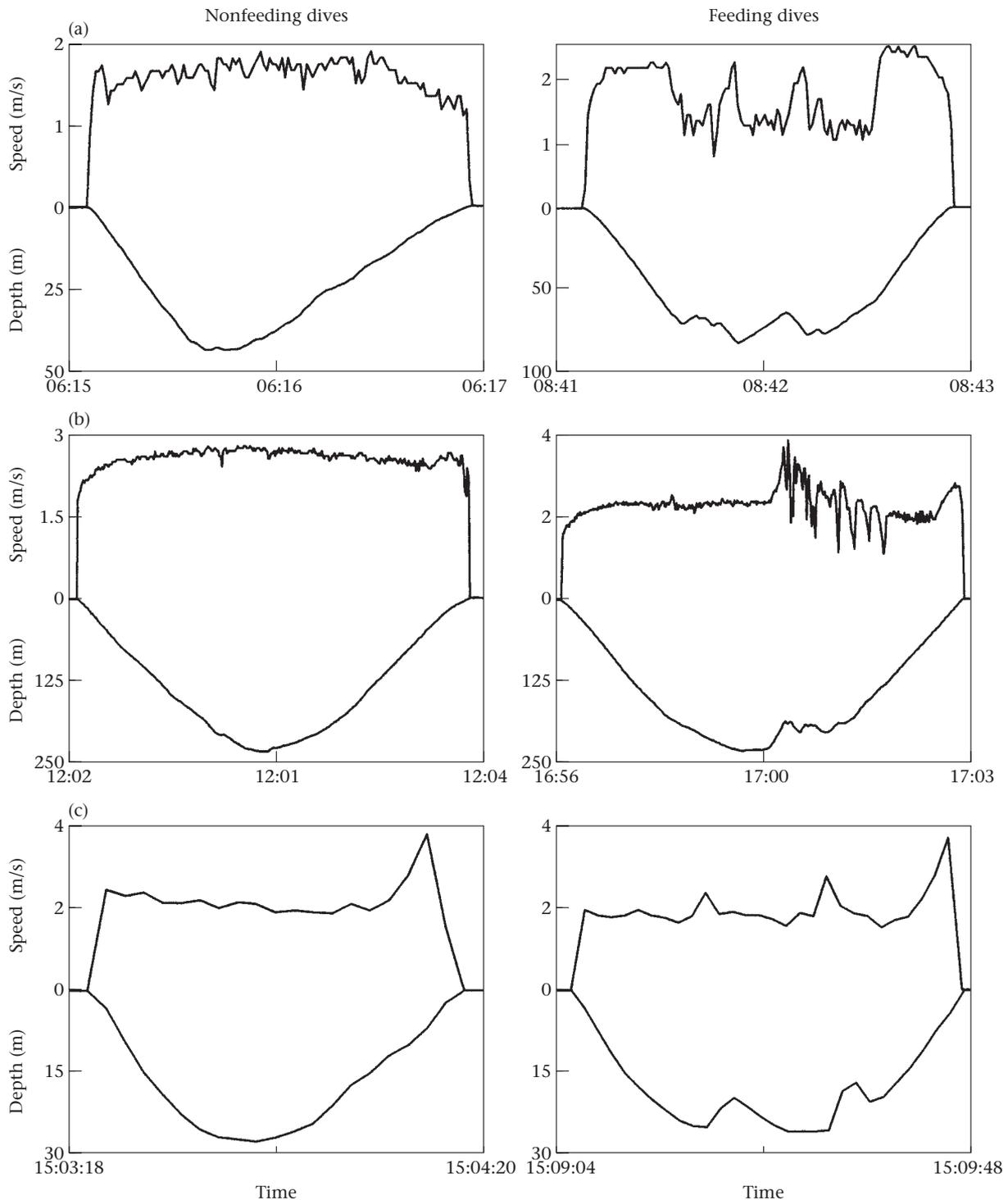


Figure 1. Swimming speed of penguins in relation to dive depth for searching and feeding birds. Examples shown are from (a) an Adélie penguin, (b) a king penguin and (c) a Magellanic penguin. That the Adélie penguins were feeding or not during the dives was ascertained by use of oesophageal temperature sensors (for details see [Ropert-Coudert et al. 2001](#)). See also [Ropert-Coudert et al. \(2000\)](#) for discussion of the characteristics of king penguin feeding dives.

euphausiids, taken primarily by Adélie penguins ([Williams 1995](#)). Unfortunately, direct observations of how penguin prey are caught are rare (e.g. [Zusi 1975](#)). However, the variability in commuting and pursuit speeds suggests that there are energetic advantages in pursuing prey at

different speeds according to prey type and these can be examined by way of a simple model.

Fairly extensive work with air-breathing underwater predators in swim channels or flumes indicates that energy expenditure as a function of time (EE , J/s) rises as

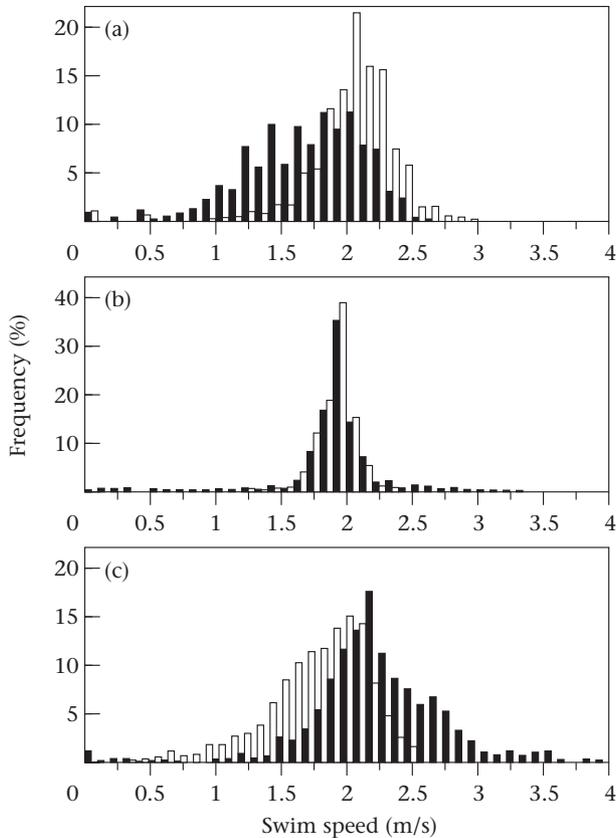


Figure 2. Frequency distributions of speed of (a) Adélie, (b) king and (c) Magellanic penguins during commuting between the surface and feeding depth (\square) and during periods when birds were feeding (\blacksquare). The data presented are derived only for periods when the birds were deeper than 10 m to exclude porpoising behaviour and to reduce the proportion of near-surface travel data.

an approximately cubed function of the swim speed (Boyd et al. 1995; Culik et al. 1996; Bethge et al. 1997) which we formulate as:

$$EE=f(S) \quad (1)$$

where S is swim speed (m/s). We assume that during normal foraging there are three main phases: prey perception, pursuit and capture. These may be typified by a particular distance between predator and prey where the prey is first detected (D , m) and that, having detected prey, the predator swims at a particular speed (S_{pred} , m/s) after the prey, which swims away at a specific speed (S_{prey} , m/s) for a time (t , s) whereupon the prey is normally captured (cf. Schoener 1979). This formulation is simplistic and assumes that the predator swims in a straight line after the prey, which swims away and that neither engages in substantial acceleration and deceleration during the the pursuit which would entail substantial extra costs (see below). A rapidly changing swim trajectory by the prey would lead to a different trajectory adopted by the predator which, if it were not complicated by changes in acceleration, would be analogous, in essence, to the simple straight line pursuit. The total distance covered by the predator during the

pursuit includes the detection distance plus the total distance swum before the prey is captured and is:

$$S_{\text{pred}} \times t = D + (S_{\text{prey}} \times t) \quad (2)$$

so that

$$t = D / (S_{\text{pred}} - S_{\text{prey}}) \quad (3)$$

The energy expended during a chase (E , J) is thus given by

$$E = t \times K \times f(S_{\text{pred}}) = K(D / (S_{\text{pred}} - S_{\text{prey}})) \times f(S_{\text{pred}}) \quad (4)$$

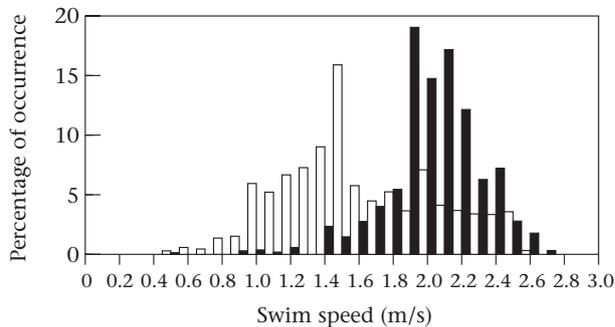
where K is a constant. This formulation for the energy expended does not consider rapid changes in acceleration that might occur during a chase. This can be alluded to using standard derivations for power and work (using values for muscle and flipper efficiency), work and mass, and distance travelled to speed and acceleration (see Culik et al. 1994b). Although the amount of acceleration and deceleration undertaken during prey capture is difficult to assess in many air-breathing marine predators, prey capture by penguins usually occurs within 5 s of the initial increase in speed (Ropert-Coudert et al. 2001) so that extensive changes in these parameters are unlikely. In general, however, the more the animal accelerates and decelerates during a chase, the higher the energy expended will be and the lower the efficiency. If we assume that at the end of the chase the predator catches a single prey item (and that, for simplicity, prey are all homogeneous with respect to size, energy content, etc.), then the gain in relation to the costs (G) can be defined by:

$$G = 1/K(D / (S_{\text{pred}} - S_{\text{prey}})) \times f(S_{\text{pred}}) \quad (5)$$

Were the predator not to capture a prey item at the end of a certain proportion of chases, the cost per prey item overall would rise although this would not change the gain per cost per prey item values in individual cases where the predator was successful. The general solution for this (Fig. 4a) shows that where prey are stationary the optimum swim speed for prey capture accords with the lowest cost of transport, but that as prey escape speed increases, so too does the optimum predator pursuit speed. In this formulation the optimum pursuit speed does not change as a function of perception distance between predator and prey (Fig. 4b). Note that it is relevant, in this treatise, to consider that many predators, including penguins, usually feed on aggregating prey and thus will ingest multiple prey during a single dive (e.g. Boyd et al. 1995; Wilson 1995). The time that an air-breathing predator may spend underwater acquiring prey is dependent on the rate of energy expenditure and oxygen stores; with reducing speed (and dependent on rate of energy expenditure and therefore rate of oxygen expenditure) underwater time can be increased. However, whether we consider that predators underwater optimize energy or oxygen in the acquisition of prey, or whether this is to be considered directly or as subtracted from a particular oxygen (or energy) store which the animal

Table 1. Results of a two-way ANOVA with replicates testing differences in the speed types (commuting versus hunting speeds) in Adélie, king and Magellanic penguins

	<i>df</i>	Sum of squares	<i>F</i>	<i>P</i>
Adélie				
Individual	4	333.159	502.948	<0.0001
Error	25 515	4225.359		
Speed type	1	1578.126	9490.456	<0.0001
Speed type×Individual	4	245.640	369.305	<0.0001
King				
Individual	1	11.290	132.958	<0.0001
Error	2410	204.647		
Speed type	1	0.018	0.202	0.653
Speed type×Individual	1	15.159	165.652	<0.0001
Magellanic				
Individual	4	2.316	2.522	0.040
Error	1325	304.200		
Speed type	1	139.232	591.254	<0.0001
Speed type×Individual	4	2.275	2.415	0.047

**Figure 3.** Frequency distributions of speed of an Adélie penguin in two consecutive prey patches (□: bout 1; ■: bout 2). The patches were separated by an interval of ca. 10 min. Speeds in the two bouts ($X \pm SD = 2.08 \pm 0.28$ and 1.46 ± 0.59 m/s) are significantly different (ANOVA one-way: $F_{1,2854} = 923.7$, $P < 0.0001$).

takes down with it makes no difference to the outcome. The optimum solution remains the same (Fig. 4a).

Many predators should attempt to optimize prey acquisition with respect to time since the time window when prey are available for capture may be limited. For example, many waders can forage only at low tide (e.g. Goss-Custard 1977) while underwater predators that hunt visually can forage only during daylight (e.g. Wilson 1995). In addition, for animals provisioning young, the rate at which the young must be provisioned may be critical, even if it ultimately reduces the absolute energetic efficiency of the foraging adult. To examine time-limited foraging, the gain per unit cost for prey items must simply be divided by the time taken to capture prey (Fig. 4c). This scenario actually pushes the optimum speed higher than if only the gain per cost per prey item is considered (cf. Fig. 4a).

This alone would seem to explain why some penguins increase swim speeds when capturing prey although the increases do not entail that the birds travel at maximum speeds. It does not, however, explain why some penguins,

and some fur seals, reduce swim speeds to capture prey (Boyd et al. 1995; cf. Thompson et al. 1993).

The situation described above essentially refers to an animal hunting fairly mobile prey that are at an appreciable distance from the predator. However, as D tends to zero and prey escape speeds become a negligible fraction of predator swim speed the model breaks down. In such instances, the rate at which the predator is able to process prey becomes an important consideration. In the case of penguins, all birds, including those that feed on swarming crustaceans, seize prey individually, there being no recorded cases of penguins filter feeding (Zusi 1975). Although we could not measure prey density in our studies, it is known that krill occur in swarms at high densities (O'Brien 1987). One option would be to consider that predators consuming crustaceans in dense swarms have an essentially bell-shaped curve of prey-processing rate as a function of predator speed (e.g. Stephens & Krebs 1986). This may be the case (cf. Goss-Custard 1977) but this option has inherent in it the concept that higher prey densities make animals less efficient at gathering, perhaps because of some confusion effect (e.g. Cushing & Harding-Jones 1968). Another option, and one that we consider here, is that at particularly high speeds or high prey densities, predators eventually reach their prey-processing maximum so that further increases in either speed, or density, do not lead to a change (either increase or decrease in prey-processing speeds). However, irrespective of which of the two options we take, the general output is the same, as can be seen below. Prey encounter rate (de/dt) and penguin speed (S_{pred}) are not independent. A penguin swimming through a swarm of crustaceans of a particular density will encounter linearly more animals per unit time if it swims faster so that:

$$de/dt = C \times S_{\text{pred}} \quad (6)$$

where C is a constant dependent on absolute prey density. Since, however, the predator will potentially be able

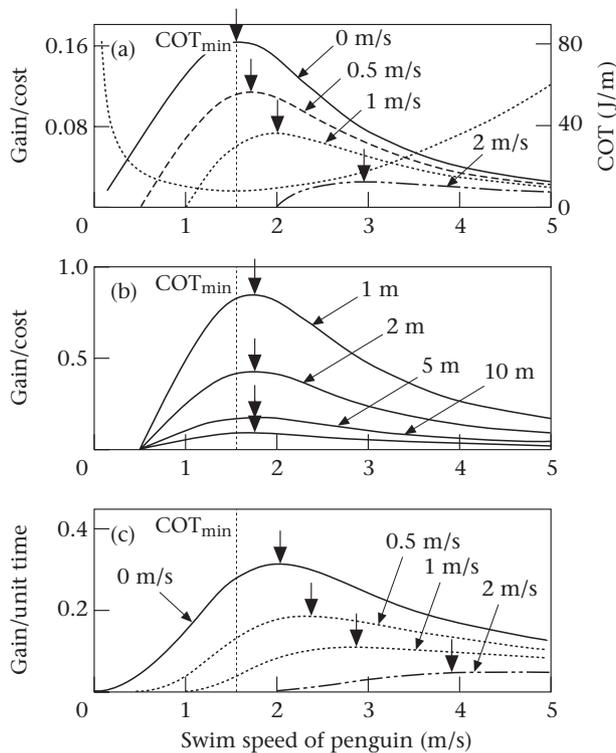


Figure 4. (a) Energetic gain in relation to cost per prey item as a function of penguin pursuit speed for birds chasing single prey attempting to escape at different speeds (0–2 m/s). Maxima are shown by arrows. In all cases it is assumed that the prey were detected at a distance of 1 m. The general formula for energy expenditure (EE , J/s) as a function of speed (S , m/s) (documented in the text as $EE=f(S)$) is taken from [Culik et al. \(1994b\)](#) (for Adélie penguins) and is $EE=S^3 \times 2.9 - S^2 \times 6.3 + S \times 5.8 + 5.9$. The cost of transport is shown for comparison (dotted line) and the speed at which the cost of transport (COT) is minimized is denoted by the vertical dotted line. (b) Energetic gain in relation to cost per prey item as a function of penguin pursuit speed for birds chasing prey attempting to escape at 0.5 m/s but initially detected at different distances from the penguin (1–10 m). Conditions otherwise as in (a). (c) Energetic gain in relation to cost per unit time as a function of penguin pursuit speed for birds chasing prey attempting to escape at different speeds (0–2 m/s). Conditions otherwise as in (a).

to process prey within a specific radius of its swim path, C can be taken to be the number of prey encountered within that radius per linear unit distance swum (cf. [Thompson et al. 1993](#)). If we assume that up to a specific speed predators can process a specific proportion ($C1$) of all prey encountered then the rate at which prey are processed (prey-processing speed) is:

$$(dp/dt) = C1 \times C \times S_{pred} \quad (7)$$

up to a maximum $(dp/dt)_{max}$. Thus, by travelling faster, or by swimming in denser swarms, predators can increase the rate at which they encounter prey although the speed at which the predators reach $(dp/dt)_{max}$ is lower in denser swarms ([Fig. 5a](#)). Note that even if the predator has a changing ability to process prey with increasing speed this will not change the fundamental nature of the dp/dt versus S_{pred} relationship.

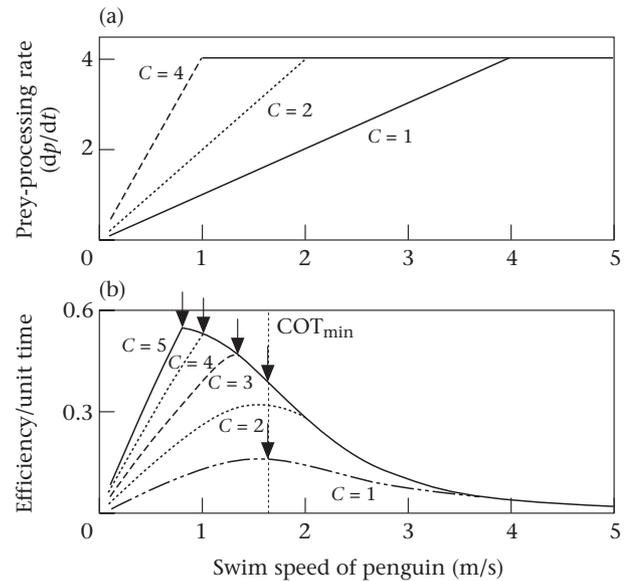


Figure 5. (a) Proposed relationship between the rate at which penguins can harvest prey (dp/dt) and penguin speed for three different prey densities. The densities (C terms) are given as the number of prey in a volume of water defined by a specific radius around the swim trajectory of the penguin per m length. It is assumed that the birds can harvest all prey encountered up to encounter rates of 4. (b) Rate of prey ingestion/rate of energy loss of a penguin feeding on slow-moving, dense prey as a function of speed for various prey densities. The prey densities used are 1, 2, 3, 4 and 5 prey per unit volume of water searched (see above).

This formulation can now be subject to efficiency calculations of the type described (equation 5) above, to see the effect that the cubed increase in energy expenditure with increasing predator swim speeds has for animals per unit time underwater ([Fig. 5b](#)). In this it can be seen that predators should generally swim slower when exploiting prey in denser swarms but the degree to which the swim speed should be less than the COT depends entirely on the density of the prey and the maximum rate at which the predator can exploit it. Note that, were there to be no limitation on the rate at which the predator could process prey, then all efficiency optima would occur at the lowest COT (cf. [Fig. 4a, b](#)). Thus, if prey densities are so low that, virtually irrespective of swim speed, predators do not have a prey encounter rate that leads to a saturation in processing abilities, then these predators should always swim at their lowest COT (cases for $C=1$ and $C=2$ in [Fig. 5b](#)). This was not observed in penguins in the wild and, since our data from Adélie penguins show a decrease in swim speed during prey exploitation, it indicates that these birds have reduced speed to accord with and optimize their maximum prey-processing capacity. Similarly, swim speed should vary according to the particular prey swarm being exploited (assuming some natural variability in density, [O'Brien 1987](#)) and this was indeed observed ([Fig. 3](#)).

In addition to the assumptions discussed above we also assume in our model that the probability of prey capture, at the moment the predator strikes, is independent of predator speed and we have no data to examine the

validity of this. However, given that the probability of prey capture might conceivably rise or fall with predator speed, this could potentially reverse the outcome of the model. It is perhaps relevant, however, that during a strike penguins rapidly extend the neck to secure the prey (see Falla 1937, cited in Zusi 1975), so that the probability of capture success during this final phase may indeed be independent of actual swim speed.

The formulation that we have above is a general case, illustrated in the figures with the specific case of the Adélie penguin (Figs 4, 5), but can be applied to any specific case with appropriate values. Actual values for energetic gain and loss will depend on the species in question and on prey type so that a comprehensive treatment of efficiency should include consideration of the time lost in commuting between the surface and foraging depth as well as recovery time at the surface between dives (see Ydenberg & Clark 1989; Boyd et al. 1995). None the less, it is interesting, and probably relevant, that Adélie penguins, which show decreased speeds during prey pursuit, feed primarily on krill, whereas the other species are fish feeders (Williams 1995). Maximum swim speed underwater is dependent on body size, with larger animals being able to swim faster (Peters 1983). Krill is a small animal (generally less than 60 mm long), known to aggregate into large swarms (Nicol & de la Mare 1993) with densities of 1–100 individuals/m³ (O'Brien 1987), and maximum prey escape speeds of the order of 0.14 m/s (Kanda et al. 1982). Thus, these crustaceans will tend to meet the conditions that will lead to a slowing down of swim speed to optimize efficiency (Fig. 5b). Magellanic penguins consume large quantities of pelagic schooling fish such as anchovy (Engraulidae) and sardine (Clupeidae) where fish length frequently exceeds 100 mm (Scolaro et al. 1999). Such fish may travel up to ca. 2.8 m/s (e.g. Hunter & Zweifel 1971; Wardle 1975; Beamish 1978) so a proper pursuit phase is clearly appropriate here with a corresponding increase in penguin swim speed (Fig. 4). King penguins feed primarily on lanternfish (Myctophidae) ranging from 20 to 90 mm long (Cherel & Ridoux 1992). At this size, these fish should be capable of appreciable burst swimming speeds (Wardle 1975; Peters 1983) to escape predators which would suggest pursuit speeds above the COT for king penguins, which is clearly not the case. However, Barham (1966) reported that during the day, at the depths at which king penguins feed, these lanternfish appear to be torpid, showing little sign of rapid movement (cf. Ropert-Coudert et al. 2000). Perhaps, despite their size, these fish accord more closely with the krill situation than with that of shoaling epipelagic fish.

Since maximum speed depends on body length, penguins feeding on larger prey will tend to increase speed during feeding whereas those feeding on smaller prey will tend to slow down. Penguins may be divided into two major groups depending on prey type: those feeding primarily on small swarming crustaceans (essentially birds within the genera *Pygoscelis* and *Eudyptes*) and those feeding on larger fish and squid (genera *Aptenodytes*, *Eudyptula*, *Megadytes*, *Spheniscus*; reviewed in Williams 1995). If the general dichotomy in prey types between the

various penguin genera is reflected in a dichotomy in prey exploitation speeds, we might expect other inter-generic differences in foraging behaviour to stem from this. For example, since fast swimming uses more energy and therefore oxygen stores faster, we might expect fish-feeders to have much shorter dives than crustacean feeders when prey are being exploited (after correcting for allometric effects, see Peters 1983). There may be knock-on consequences, for example for how long the birds can remain in a patch, the likelihood that they will exceed their aerobic dive limit based on this, and how difficult they find relocating a patch.

Finally, the overall success of a particular pursuit strategy in a particular area will be a complex interplay of various factors. Since the escape speed of the prey is related to its body length the predator's energy expenditure in pursuit is related to prey body length and consequently so is the time that the predator can spend exploiting the patch (larger prey can be exploited only for a short time). Conversely, the energy recouped by the predator is related to prey body length so that the benefits of feeding on larger prey may more than compensate for the shorter exploitation time and higher energy expenditure. The optimum strategy for prey exploitation will be dependent on the abundance of prey, the size of patches, the depth at which they are located, and the chance that an exploited patch may be relocated after a predator has returned to the surface to breathe. Despite the complex nature of this scenario, advances in remote-sensing systems, including onboard logging of the behaviour of free-living air-breathing predators make it conceivable that we will resolve many of these aspects in the near future.

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Appendix

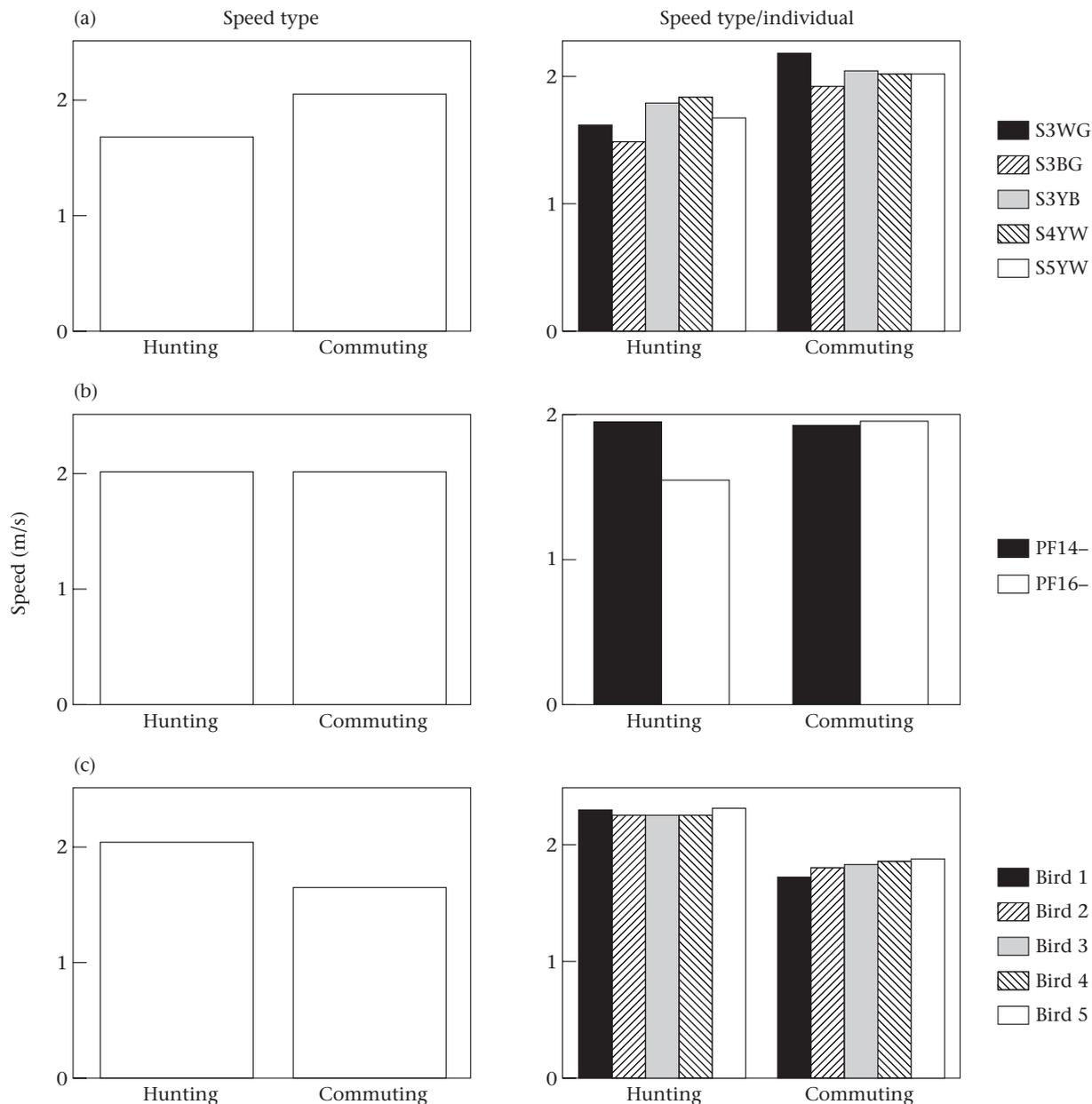


Figure A1. The statistical results obtained in a two-way ANOVA with replicates for (a) Adélie penguins, (b) Magellanic penguins and (c) king penguins. Interaction bar plots are given for speed according to type (hunting or commuting) for hunting or commuting speeds for the different individuals studied.